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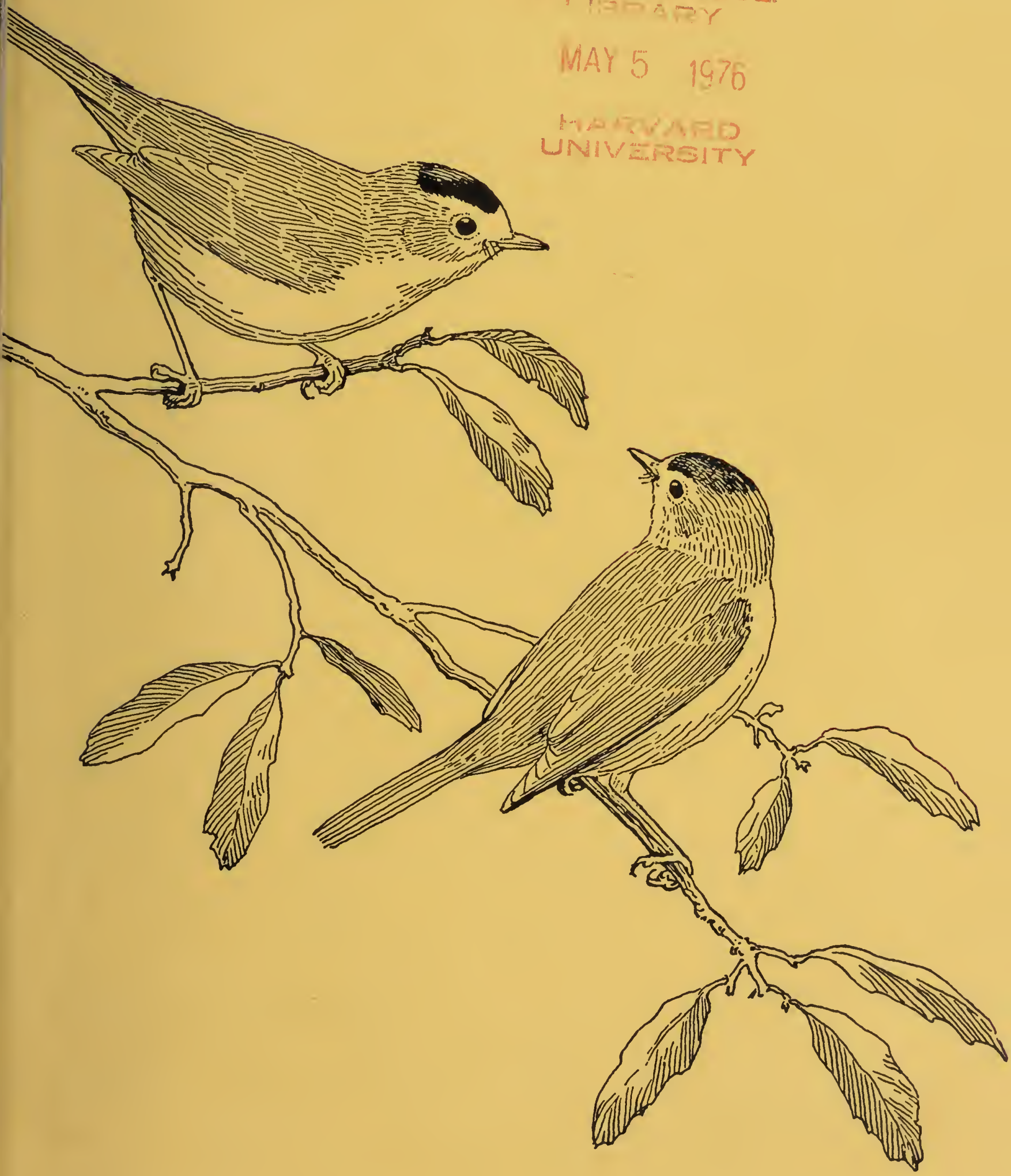

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One-day-old Mute cygnets *(Cygnus olor):* left, recessive "white" female; right, heterozygous "gray" male. Scale: one-half life size.

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THE COLOR PHASES OF DOWNY MUTE SWANS

Colleen Helgeson Nelson

The terms "gray" and "white" have traditionally been used to describe the 2 color phases of the downy Mute Swan (*Cygnus olor*). While the terms are satisfactory for field and laboratory use, they give no indication of any brighter colors that might be present in the plumage or unfeathered parts. When I examined 3 live, newly-hatched cygnets from Rhode Island in 1967 and 3 from Michigan in 1970, I found that not only were there traces of color present in both phases, but also that these traces could be measured. Accordingly, color measurements were taken using Ridgway's *Color Standards and Color Nomenclature* (by the author, Wash., D.C., 1912) and the *Atlas de los Colores* (Villalobos, El Ateneo, Buenos Aires, 1947); these were subsequently equated with glossy samples from the Munsell *Book of Color* (Munsell Color Co., Baltimore, 1966). I made color and line sketches, took black and white photographs, and prepared a chart, part of which is shown in Table 1.

The mechanism behind the occurrence of color phases in the Mute Swan is now known to be a single sex-linked recessive gene (Munro et al., Auk 85: 504–505). The Michigan cygnets (1 gray ♂, 2 white ♀♀) were the offspring of a "Polish" (= white) cob and a Royal (= gray) pen. Charles Willey reported (pers. comm.) that the Rhode Island cygnets (2 gray, 1 white, all ♀♀), shipped as star-pipped eggs, had a "dominant" female parent and a male parent of "questionable" dominance, which turned out to have been heterozygous. All 3 of the gray cygnets examined had only one gene for gray color: the Michigan male was heterozygous for white; the 2 Rhode Island females were monozygous. Sex of the cygnets was determined by cloacal examination.

One might expect the cygnets of homozygous Royal parents to be grayer, with darker bills and feet, than cygnets of mixed parentage. Although I have not had the opportunity to examine such cygnets in the hand, 2 other observations

TABLE 1

COLOR ANALYSIS OF PLUMAGE AND UNFEATHERED PARTS OF MUTE CYGNETS

Color Authority	Underparts	Upper back	Upper mandibles	Tarsi
		Gray phase		
Villalobos	N–19	0–13–2°	N–7	00S–9–1°
Munsell	N 9/	10 YR 6/1.5	N 4/	10 YR 4/0.5
Ridgway*	± White	XLVI Smoke Gray	LI Iron Gray/LI Dark Olive-Gray	LI Dark Olive-Gray/LI Deep Olive-Gray
		White phase		
Villalobos	N–19	00S–17–4°	0–9–1°	00S–(11–13)–5°
Munsell	N 9/	10 YR 8/2	10 YR 5/1.5	7.5 YR 6/4–6.5/4
Ridgway*	± White	XL Tilleul Buff	XLVI Dark Grayish-Olive/LI Deep Olive-Gray	XL Wood Brown/XL Avellaneous

* Plate number and named color only. The diagonal (/) is a regular part of the Munsell notation; used elsewhere, it denotes a shade *between* those given on either side of it.

suggest that the expectation is reasonable. A brood of extremely dark-billed, dark-footed cygnets that I saw in 1969 in Shubenacadie, N. S., had "no known recessive ancestry" (Eldon Pace, pers. comm.), and the bill and feet of an unsexed, newly-hatched captive Royal cygnet were described in 1964 as "charcoal gray" by the bird's owner, Carroll Smith (letter with color slide). Certainly, if heterozygous cygnets are lighter in color than are homozygous gray cygnets, a good color standard would be useful in assessing the amount of variation between them.

The so-called white cygnet is not lacking in *color* (see frontispiece), but only in the larger amount of neutral darker pigment that is present in cygnets of the gray phase. Actually, the "true colors" of the Mute cygnet are revealed most clearly in the white phase. This phenomenon is seen nowhere better than in the colors of the upper back and feet (see Table 1). In both cases, the colors of these parts in white phase cygnets are discernibly lighter (higher in *value*) and brighter (greater degree of *chroma*) than are the colors of corresponding areas on gray-phase cygnets. Thus, the gray and white phases of the Mute cygnet seem not to be a case of "either/or" but of "more or less," a condition that suggests 2 pairs of alleles (unpaired in ♀♀), one for *more* gray (= gray cygnet) and one for much *less* (= white cygnet), with still another pair of alleles to provide a more or less constant amount of pale, delicate *chromatic* pigment (hue) for both phases.

ACKNOWLEDGMENTS

I thank the Rhode Island and Michigan Departments of Natural Resources for providing live cygnets for my research, and I thank the Canada Council for financial support of my work in 1969 and 1975. I am grateful to Kenneth C. Parkes for a critical reading of the manuscript.

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NEW LIFE MEMBER

Martha Hatch Balph has recently become a life member of the Wilson Ornithological Society. Dr. Balph is an Adjunct Assistant Professor in the Department of Wildlife Science, Utah State University, Logan. Her primary interest in ornithology is behavior. She has published several papers in professional journals based upon her research in passerine ontogeny and social behavior. She belongs to the AOU, COS, Animal Behaviour Society, Ecological Society of America, and several other scientific associations. In addition to her professional interests, Dr. Balph enjoys hiking, skiing, and zoological illustrating. She is married to Dr. David F. Balph, who is also a behaviorist on the faculty of the Department of Wildlife Science at USU; they have two sons.

A KEY TO DOWNY CYGNETS WITH ANALYSIS OF PLUMAGE CHARACTERS[1]

COLLEEN HELGESON NELSON

Boyd (in Scott et al. 1972), noting the difficulty in identifying newly-hatched cygnets, provided color descriptions, based on live specimens, of the natal plumage and unfeathered parts of the true swan species and the Coscoroba (*Coscoroba coscoroba*). Having examined study skins of young cygnets of all species, except the Coscoroba, and having studied live cygnets of the 3 North American species, I found that the various downies could also be distinguished by means of bill and down characters. To assist field and laboratory ornithologists, I present here an illustrated key (Figs. 1–28) based on these characters and describe the plumage colors and patterns that further characterize the cygnets. Specimens examined are listed in the Appendix.

The classification used in the key departs from the congeneric concept put forth by Delacour and Mayr (1945) and uses instead the genera *Cygnus* and *Olor*, proposed by Wetmore (1951) for the white swans, supported by osteological evidence presented by Howard (1946) and Woolfenden (1961). This is the generic classification adopted in the *A.O.U. Check-list of North American Birds*, 5th edition (1957). The classification of species within the genus *Olor* is that of Parkes (1958); species of *Cygnus* are classified according to Delacour and Mayr (1945).

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[1] I dedicate this paper to Dr. Alexander Wetmore, on the occasion of his 90th birthday.

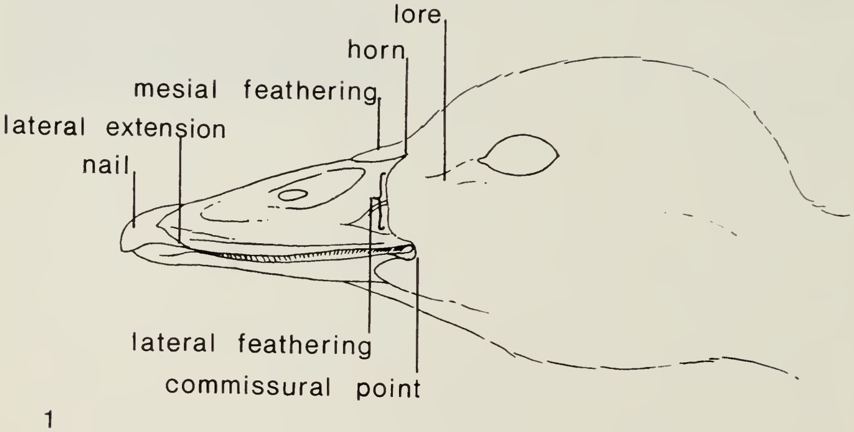
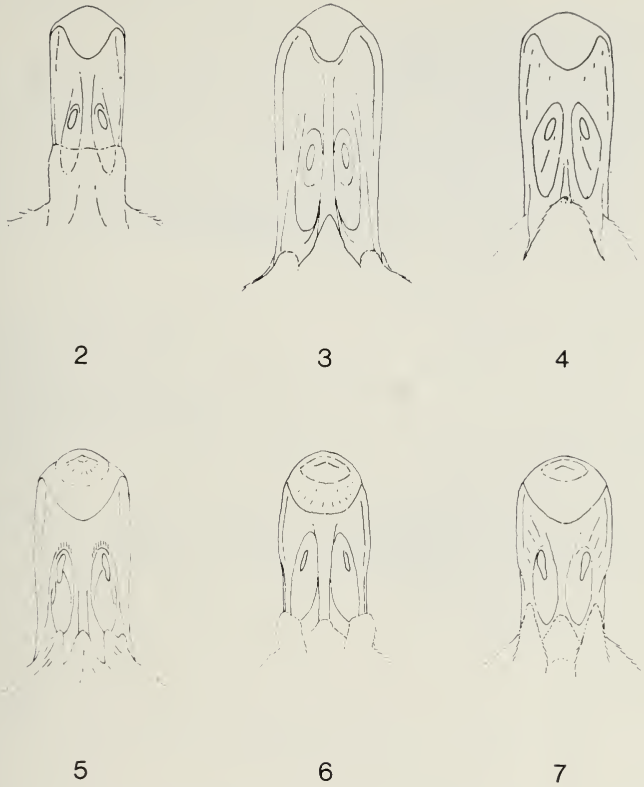


FIG. 1. Glossary of terms.



Figs. 2–4. Bills of *Cygnus* species. Figs. 5–7. Bills of *Olor* species.

A Key to the Downy Cygnets of the World

1a. Compared to size of bill, nail small and/or narrow, especially toward posterior border (Figs. 2 and 3); lateral extensions of nail prominent in dorsal view (Fig. 4); bill dark-colored, nail *markedly lighter.* Genus *Cygnus.* Go to 2.

Caution: in very young *live* cygnets, nail appears colorful because it is translucent and color of blood shows through.

1b. Compared to size of bill, nail large and wide, *slightly* narrower near posterior border (Figs. 5 and 6); lateral extensions of nail *not* prominent in dorsal view (Fig. 7); bill light-colored, nail more or less *same color.* Genus *Olor.* Go to 4.

2a. Lateral feathering extends along edges and over top of upper mandibles nearly to nostrils. Black-necked Swan, *Cygnus melanocoryphus.* Figs. 8–10.

2b. Lateral feathering extends only slightly (2–4 mm.) beyond commissural point. Go to 3.

3a. Lateral feathering curves back toward eyes from commissural point; lores *unfeathered.* Black Swan, *Cygnus atratus.* Figs. 11–13.

3b. Lateral feathering extends upward in nearly straight line from commissural point; lores *feathered.* Mute Swan, *Cygnus olor.* Figs. 14–16.

4a. Lateral feathering extends forward in *single long point well beyond* mesial feathering, often nearly to nostrils. Whooper Swan, *Olor cygnus.* Figs. 17–19.

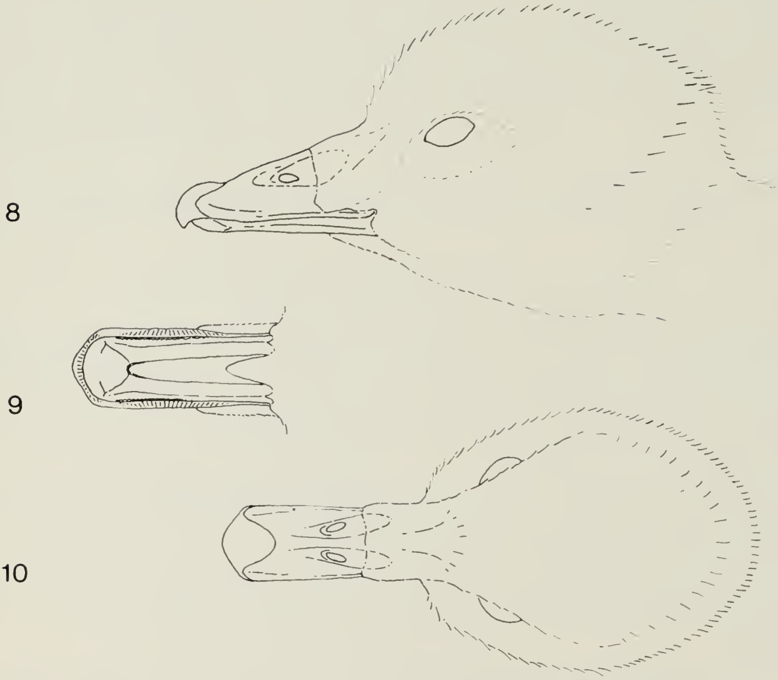
4b. Lateral feathering extends forward more or less *equally* with mesial feathering, *never* in single long point, *never* nearly to nostrils. Go to 5.

5a. Lateral feathering markedly "sculptured," horns of bill *never* feathered; nail more or less *triangular* posteriorly; down on face and around bill short and velvety, more or less smoothly appressed to head. Trumpeter Swan, *Olor buccinator.* Figs. 20–22. See also photographs in Banko (1960:118–119) and in Scott et al. (1972: plate 26).

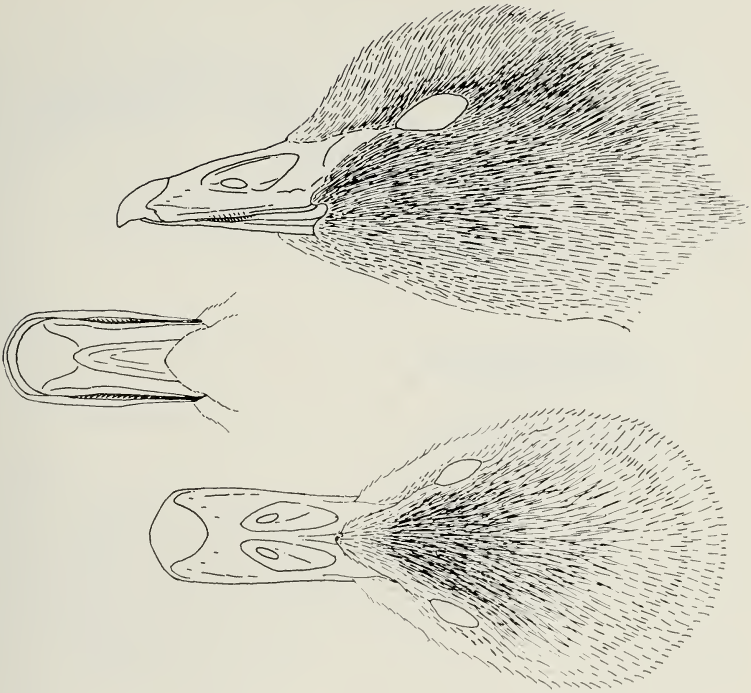
Caution: in museum specimens prepared from *unhatched* cygnets, down of all species may appear short and rumpled.

5b. Lateral feathering "sculptured" but edges frequently obscured by down (Fig. 23), horns of bill *frequently* feathered; nail usually more or less *rounded* posteriorly; down on face and around bill relatively long and fluffy, often standing out markedly from head. Whistling Swan, *Olor c. columbianus*, Figs. 23–25, and Bewick's Swan, *Olor c. bewickii*, Figs. 26–28. See also photographs in Bailey (1948:150) and in Scott et al. (1972: plate 32).

Caution: a few *O. c. bewickii* may have nails somewhat triangular posteriorly, but the down characters will serve to separate these from *O. buccinator.*



Figs. 8–10. Black-necked Swan, *C. melanocoryphus.* BM(NH)97.11.14.184.

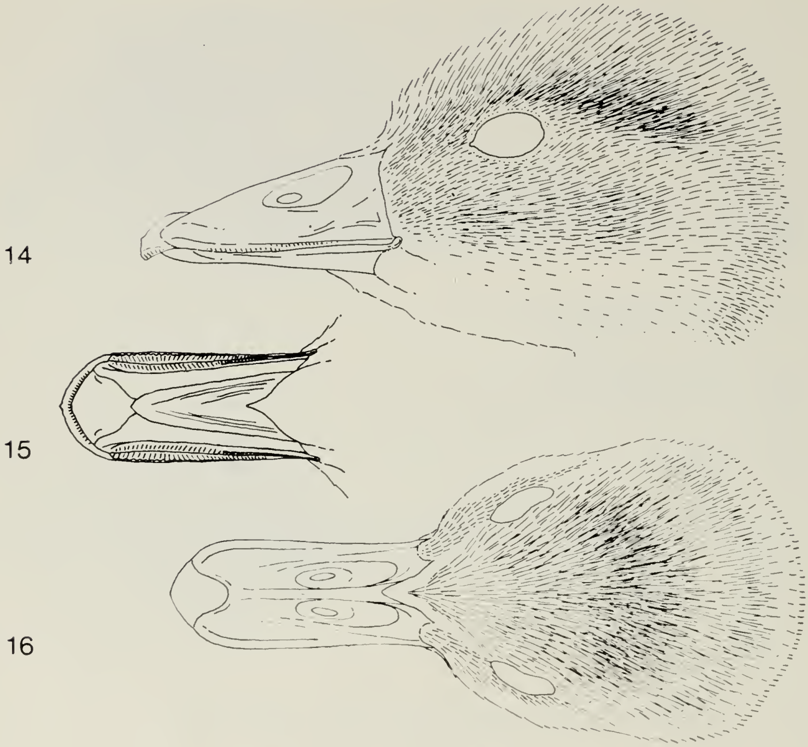


FIGS. 11–13. Black Swan, *C. atratus.* UND uncat. ♀.

CYGNET COLOR COMPARISONS

Other characters that separate the cygnets into 2 distinct groups are the pattern of the dorsum and the hues of the plumage. Both of these characters are best seen in live, newly-hatched cygnets or in clean, well-prepared skins. The *Olor* cygnets have 2 large white shoulder spots and narrow white wing-patches, while the *Cygnus* downies are without dorsal spots. Two Black-necked cygnets were checked at the base of the dorsal down for evidence of spots; there was none. Only the Mute and Black cygnets have narrow, inconspicuous, pale grayish wing-patches; the Black-necked cygnet appears almost completely white.

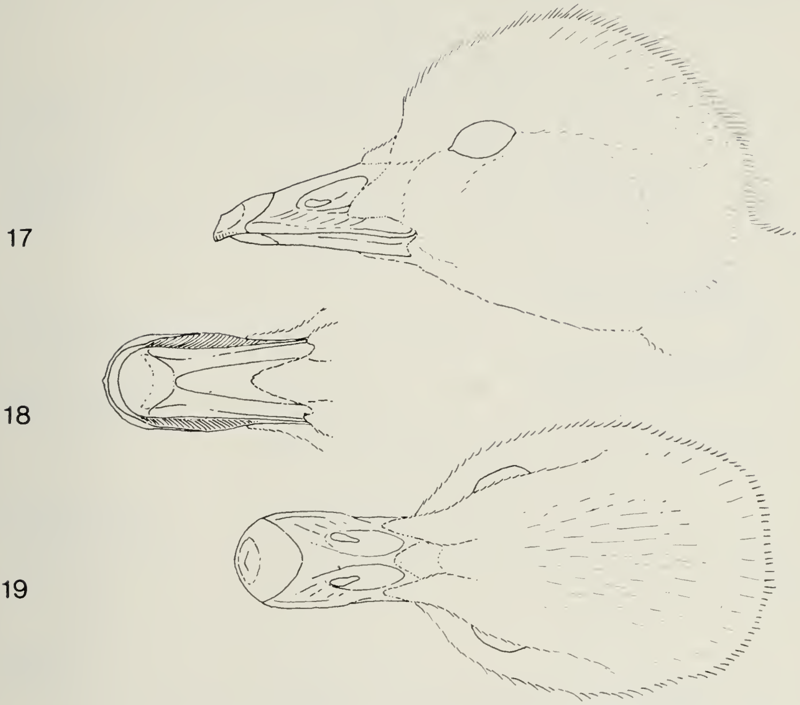
While Delacour's statement (1954) that downy cygnets are "pale grey and white, without any distinct markings" is basically true, the grays of the two groups are discernibly different in both hue and value. Using terms suggested by Palmer (1962), the basic hue of the *Cygnus* group on the Villalobos scale is scarlet-orange; that of the *Olor* cygnets, orange-scarlet. The scarlet-orange appears as a brownish or yellowish gray, the orange-



Figs. 14–16. Mute Swan, *C. olor*. BM(NH) 81.5.1.6056.

scarlet as a warm, yet rather "bluish" gray (Table 1). *Cygnus* downies are also measurably darker than those of *Olor*. This is true even of the downy Black-necked Swan, outwardly the whitest of all the cygnets, but darker than any other species at the *base* of the dorsal down. The contrast in value between down tip and down base is startling.

I determined the colors present in the plumage of the cygnets by matching certain areas on clean, well-prepared specimens to each of 3 commonly used color standards. Areas measured were the superciliary area, the cheeks, crown, hindneck, upper back, rump, and underparts. The cygnets were viewed on a light-colored wood table, with north daylight at the left, very pale-colored walls at the right, and fluorescent light on an off-white ceiling. A white paper was placed beneath each bird being measured and appropriate masks were used in comparing samples. The sample areas were matched first to the Villalobos *Atlas de los Colores* (1947), then to the Munsell *Book of Color* (1929). The nearest Ridgway (1912)

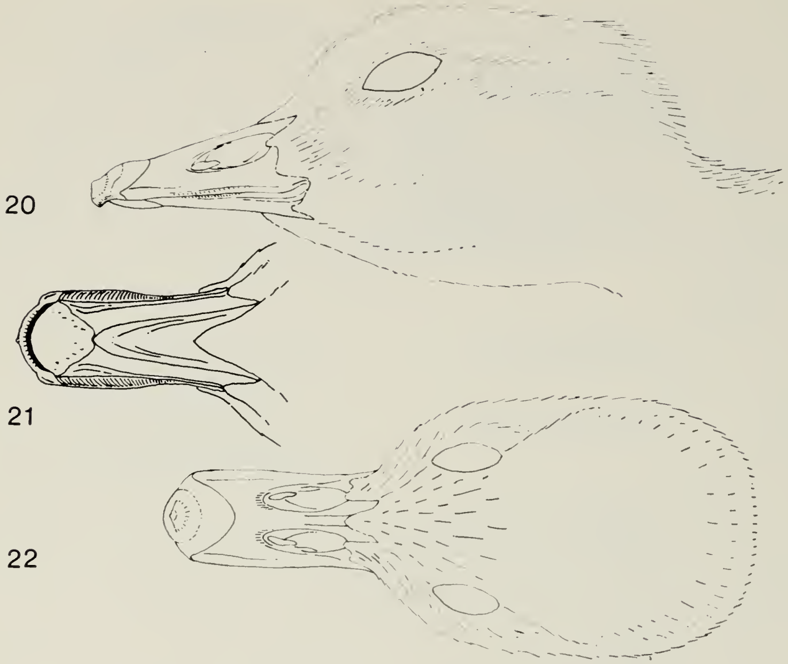


Figs. 17–19. Whooper Swan, *O. cygnus.* WTS 3244 ♂.

equivalents were determined first by correlating the Villalobos samples to a reverse index prepared from the Conversion Tables appended to the *Atlas* and then checking the Ridgway equivalents thus obtained against the specimen, using color chips from a good copy of the latter work. For the sake of brevity, only the lightest and near-darkest colors are listed in Table 1. These are, respectively, the colors of the underparts and of the upper back, the latter being, in nearly all cases, of a lower value than those of the crown and hindneck, but higher than that of the rump, which is usually the darkest part of the bird.

Precise comparisons between my correlations and those of Hamly (1949) and Smithe (1974) proved unfeasible because of dissimilar viewing conditions and the use of different copies of Ridgway's work, many of which vary slightly from one to another.

The Ridgway verbal color notation is well-known to biologists, but a short resumé of the less frequently used Villalobos and Munsell systems would be useful here. In both systems, the *hues*, composed of basic colors,



Figs. 20–22. Trumpeter Swan, *O. buccinator.* UND uncat. ♀.

such as reds, yellows, greens, purples, and combinations thereof, are identified by *letter* symbols. The Munsell system has, in addition, a numeral preceding the letter or letters to designate the proportions of basic colors present in the hue. In both systems, the *first* numerals following the letters indicate the lightness or *value* of the hue (Villalobos scale = 0 to 20; Munsell scale = 1 to 10); the *second* numerals describe its brightness or *chroma* (Villalobos scale = 1° to 12°; Munsell scale = 1 to 20). Saturated (= brilliant) hues used in the 2 systems are not always equivalent, nor can all values and chromas of a single hue in one system be matched entirely within a single hue in the other. This latter is especially true of dull colors that are either very pale or very dark. Similar variations exist between the Ridgway notation and both the Munsell and Villalobos notations. These and other color systems have been discussed by Palmer and Reilly (1956) and more recently by Smithe (1974).

SUMMARY

Differences in bill and down characters, as well as those of pattern and basic hue, will separate the downy young of all swan species. On the

TABLE 1

COLOR ANALYSIS OF DOWNY CYGNET PLUMAGE[1]

Species	Underparts	Upper back
C. olor		
Gray phase BM(NH) 1925.5.17.1	N/OOS–19–1°[2] 10 YR 9/0.25 ± White	OOS–13–2° 10 YR 6.5/1 ± XLVI Drab-Gray/ XLVI Light Drab
White phase (Prepared newly-hatched specimen not available).		
C. atratus UND uncat. ♀	OOS–18–2°[3] 10 YR 8.5/0.5 White/LI Pale Olive-Gray	OOS–11–2° 10 YR 5.5/1.5 ± LI Deep Olive-Gray/ XLVI Drab
C. melanocoryphus BM(NH) 1935.4.1.2	N/OOS–19–1° 10 YR 9/0.25 ± White	N/OOS–17–1°[4] 10 YR 8/0.5 ± White/XLVI Pale Smoke Gray
O. cygnus WTS 3244 ♂	N–19/20 5 YR 9.5/0.25 ± White	SSO–13–1° 5 YR 6.5/0.5 ± XLVII Light Mineral Gray
O. buccinator UND uncat. ♀	N–19/20 5 YR 9.5/0.25 ± White	N/SSO–14–1° 5 YR 7/0.25 ± XLVII Light Mineral Gray
O. c. columbianus MMMN 2323	N/SSO–19–1° 5 YR 9/0.25 ± White	SSO–14–2° 5 YR 7/0.75 ± XLVII Light Mineral Gray
O. c. bewickii WTS 681 ♀	N–19/20 5 YR 9.5/0.25 ± White	SSO–15–1° 5 YR 7.5/0.5 ± XLVII Light Mineral Gray/LI Pallid Mouse Gray

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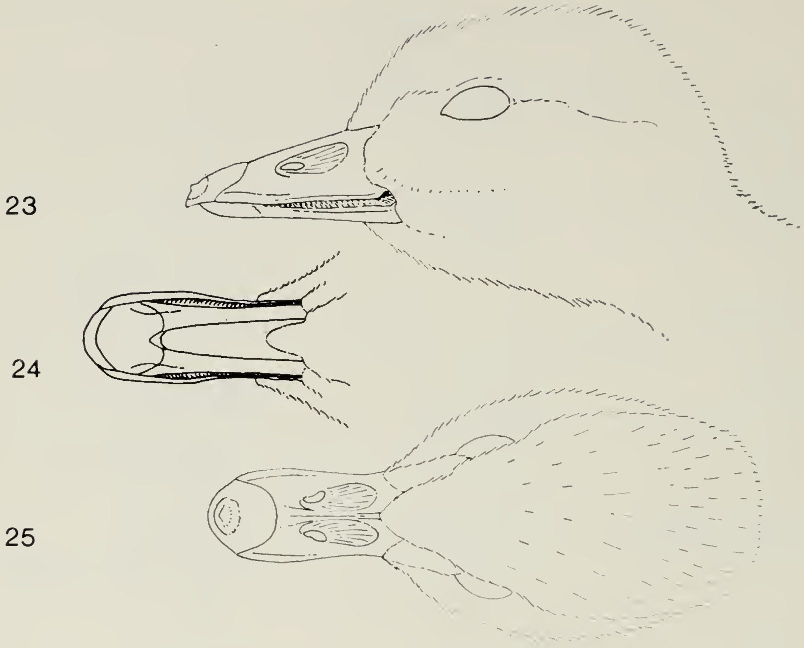
[1] Order of listings: Villalobos, Munsell, Ridgway (plate number and named color only). The diagonal (/) is a regular part of the Munsell notation; used elsewhere, it denotes a shade *between* those given on either side of it.

[2] Chin was a bit darker: N–17; 10 YR 8/0.25; ± White/LI Pale Olive-Gray.

[3] Chin was noticeably darker and a bit duller: OOS–14–1°; 10 YR 6.5/0.5; ± XLVI Pale Smoke Gray/XLVI Drab-Gray.

[4] Base of dorsal down: OOS–7–2°; 10 YR 4/1.5; Broccoli Brown/XLVI Chaetura Drab. I was unable to obtain a sample of Broccoli Brown to check.

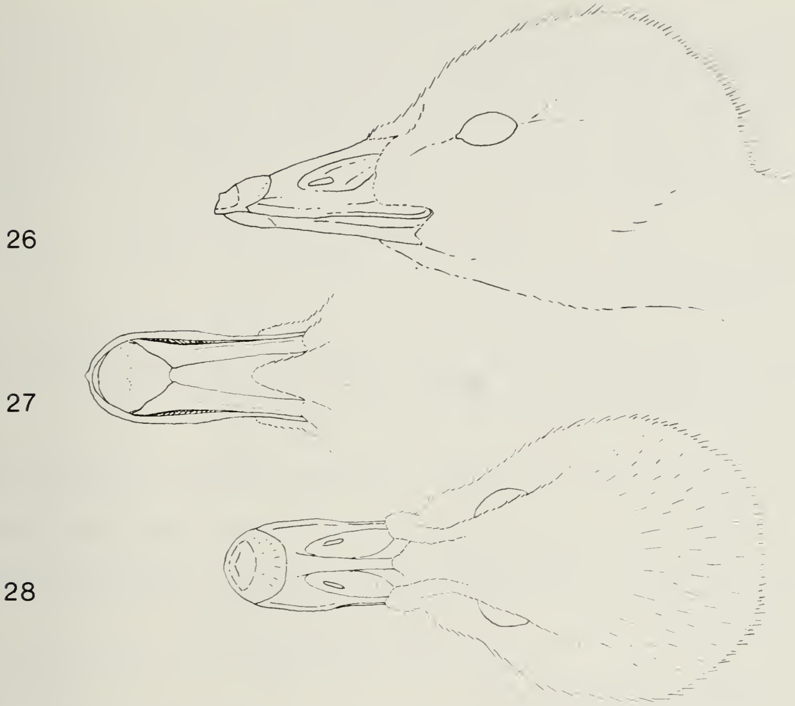


FIGS. 23–25. Whistling Swan, *O. c. columbianus.* FMNH 13566.

basis of these characters, cygnets fall into 2 groups, the same 2 groups into which their adult counterparts can be placed according to osteological evidence put forth by Howard (1946) and Woolfenden (1961) as well as to anatomical and plumage characters described by Wetmore (1951). The plumage and bill character differences among *Olor* cygnets support the species allocation proposed for this genus by Parkes (1958) on the basis of anatomical and behavioral characters. Two genera, *Cygnus* and *Olor*, and 6 species are recognized.

ACKNOWLEDGMENTS

Live specimens were provided by the Rhode Island and Michigan Departments of Natural Resources, the Round Lake Waterfowl Station, the Delta Waterfowl Research Station, and the Wildfowl Trust; study skins were loaned by the British Museum (Natural History), the American Museum of Natural History, the U. S. National Museum, the Field Museum of Natural History, the Royal Ontario Museum, the University of North Dakota, and the Wildfowl Trust. Permission to import eggs and young



FIGS. 26–28. Bewick's Swan, *O. c. bewickii.* BM(NH) 1938.12.14.177.

of Mute Swans was granted by the Canadian Wildlife Service; rearing pens were loaned by Delta Waterfowl Research Station and Canada Cement Company, Ltd. Research facilities were used at the Delta Waterfowl Research Station, the Round Lake Waterfowl Station, the Wildfowl Trust, the Shubenacadie Provincial Wildlife Park, the Manitoba Museum of Man and Nature, the Carnegie Museum, and the National Museum of Canada. I acknowledge gratefully the assistance of these institutions. Research for the project of which this paper is a part was assisted in 1963 by a grant from the Chapman Fund of the American Museum of Natural History and by a Grant-in-Aid-of-Research from the Society of the Sigma Xi—RESA, in 1969 by a short-term artist's grant with travel allowance from the Canada Council, and in 1975 by a grant from the Explorations Program of the Canada Council. In addition, Carnegie Museum provided *per diem* expenses during a short visit in 1967. I thank these agencies for their generous support. Finally, I wish to thank Kenneth C. Parkes for a critical reading of the manuscript.

LITERATURE CITED

American Ornithologists' Union. 1957. Check-list of North American birds, 5th ed. Am. Ornithol. Union, Baltimore.

Bailey, A. M. 1948. Birds of Arctic Alaska. Popular series no. 8. Colorado Mus. Nat. Hist., Denver.

Banko, W. E. 1960. The trumpeter swan. Its history, habits and population in the United States. North Am. Fauna no. 63.

Delacour, J. 1954. The waterfowl of the world. v. 1. Country Life Ltd., London.

——— and E. Mayr. 1945. The family Anatidae. Wilson Bull. 57:1–55.

Hamly, D. H. 1949. The Ridgway color standards with a Munsell notation key. J. Opt. Soc. Am. 39:592–599.

Howard, H. 1946. A review of the Pleistocene birds of Fossil Lake, Oregon. Carnegie Inst. Washington Publ. 551:141–195.

Munsell Color Company. 1929. Munsell book of color. 2 parts. Munsell Color Co., Inc., Baltimore. (Matte samples).

Palmer, R. S. 1962. Handbook of North American birds. v. 1. Yale Univ. Press, New Haven.

——— and E. M. Reilly, Jr. 1956. A concise color standard. A.O.U. Handbook Fund. 1–8.

Parkes, K. C. 1958. Systematic notes on North American birds. 2, The waterfowl (Anatidae). Ann. Carnegie Mus. 35:117–125.

Ridgway, R. 1912. Color standards and color nomenclature. By the author, Washington, D.C.

Scott, P. and the Wildfowl Trust. 1972. The swans. Michael Joseph, London.

Smithe, F. B. 1974. Naturalist's color guide and Naturalist's color guide supplement. Am. Mus. Nat. Hist., New York.

Villalobos-Dominguez, C. and J. Villalobos. 1947. Atlas de los colores. El Ateneo, Buenos Aires.

Wetmore, A. 1951. Observations on the genera of the swans. J. Wash. Acad. Sci. 41:338–340.

Woolfenden, G. E. 1961. Post-cranial osteology of the waterfowl. Bull. Fla. State Mus. Biol. Ser. 6(1):1–129.

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APPENDIX

Institutional abbreviations are used as follows: American Museum of Natural History = AMNH, British Museum (Natural History) = BM (NH), Delta Waterfowl Research Station = DWRS, Field Museum of Natural History = FMNH, Manitoba Museum of Man and Nature = MMMN, National Museum of Canada = NMC, Royal Ontario Museum = ROM, Round Lake Waterfowl Station = RLWS, U.S. National Museum = USNM, University of North Dakota = UND, The Wildfowl Trust, Slimbridge = WTS.

Live cygnets examined: all 1–2 days old

C. olor	Michigan: Grand Traverse Co., ¼ mi. N Traverse Cy. on East Bay (1 gray ♂, 2 white ♀♀); Rhode Island: Newport Co., Little Compton (3 ♀♀; 2 gray, 1 white).
O. buccinator	British Columbia: 21 mi. SE Atnarko, Lonesome Lk. (2 n.s.), in coll. WTS; Montana: Beaverhead Co., Red Rock Lakes Migratory Waterfowl Refuge (1 ♀, 1 n.s.), in coll. DWRS. *No leucistic cygnets seen.*
O. c. columbianus	Alaska: between Bethel and Hazen Bay—the "flats" (8 n.s.), in coll. RLWS.

C. atratus, C. melanocoryphus, O. cygnus, O. c. bewickii: no live cygnets seen.

Prepared specimens examined: mostly very young; ages given are from tag data

C. olor	England: Thames, BM(NH) 81.5.1.6056, and Thames at Sunbury, BM(NH) 1925.5.17.1, both gray; Ontario: York Co., Stouffville, ROM 10096 ♂, white, captive.
C. atratus	New York: Nassau Co., NYC, Central Pk., AMNH 35201, captive; Oklahoma: Cleveland Co., Norman, Lemmon's Farm, UND uncat. ♀, captive, c. 2½ wks.
C. melanocoryphus	Argentina: Entre Rios, Santa Elena, BM(NH) 97.11.14.184; no loc., BM(NH) 1935.4.1.2 ♀, captive, 14 da.
O. cygnus	England: Menagerie, BM(NH) J.42, captive; no loc.: "Ex Coll. Baker," BM(NH) unreg'd.; orig. loc.? WTS 3244 ♂, captive, 1 da.
O. buccinator	Alberta: Grande Prairie region, Airport Slough, Hermit Lk., Wolf Lk., NMC uncat. ♂♂ (3), and Buffalo Lakes nr. Sexsmith, Clairmont Lk., Saskatoon Lk. nr. Wembley, NMC uncat. ♂♂ (4), n.s. (2), 4 taken from shell, others newly-hatched except Wolf Lk. specimen c. 2 da.; Montana: Beaverhead Co., Red Rock Lakes Migratory Waterfowl Refuge, UND uncat. ♀, captive, 3 da. *No leucistic specimens examined.*
O. c. columbianus	Alaska: Pt. Barrow, Chipp R., FMNH 13566; NW Territories: Dist. Keewatin, Southampton I., MMMN 2323, 1 week; Adelaide Penin., nr. E side Sherman Basin, NMC 46317, 46319—20 ♂♂, 46318; Dist. Mackenzie, Mackenzie Delta, Kendall I., 135° 18′ W long., 69° 26′ N lat., USNM 46926, c. 2 da.
O. c. bewickii	Siberia: Yenisei, BM(NH) 1938.12.14—176 and 177; orig. loc.? parents wild-caught in Holland and England, WTS 681 ♀, captive.

THE EFFECTS OF ORCHARD PESTICIDE APPLICATIONS ON BREEDING ROBINS

Eric V. Johnson, Guilford L. Mack, and Daniel Q. Thompson

In June 1965, the senior author visited a commercial fruit farm in New York's Hudson River Valley and discovered that American Robins (*Turdus migratorius*) were nesting in the orchards despite the fact that DDT and other toxic chemicals were applied regularly to the apple trees as part of a pest control program. At that time most DDT-robin studies had dealt with Dutch elm disease control programs on university campuses (e.g., Wallace 1962) or in residential communities (e.g., Wurster et al. 1965); no studies had concerned DDT-songbird relationships in agricultural areas with a long history of heavy organochlorine insecticide applications.

The results reported here are the culmination of a 3-year field and laboratory investigation of robin-pesticide ecology on this farm. The objectives were to examine robin productivity and behavior patterns in the orchards, as well as organochlorine insecticide content of the birds and their food items.

STUDY AREA AND METHODS

Study area.—This study was conducted on a commercial apple, cherry, and peach farm located near the village of New Paltz in New York's central Hudson Valley. The farm (Fig. 1) comprised a total of about 138 ha, with 97 ha in mature fruit trees on a northwest-facing slope. The orchards were bordered on the northwest, south, and northeast by woodlots of 36.4, 26.3, and 10.1 ha respectively; in addition a brushy edge of 26.3 ha formed the eastern boundary. The ground cover beneath mature apple and cherry trees, along the spray paths, and around the irrigation ponds was poison ivy (*Rhus toxicodendron*) and orchard grass (*Dactylis glomerata*), as well as many "volunteer" perennial grasses and legumes (including red clover, *Trifolium pratense*, and vetch, *Vicia americana*). Orchards of peach trees and newly planted apple trees were customarily cultivated throughout the growing season with a rotary disc.

The woodlots were fairly mature second-growth mixed hardwoods composed of elm (*Ulmus americana*), hickory (*Carya* sp.), beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), red maple (*Acer rubrum*), and hemlock (*Tsuga canadensis*), with hornbeam (*Carpinus caroliniana*) and yellow birch (*Betula lutea*) the major understory species, and with little ground cover. Other unplanted areas were all poorly drained marginal habitat with a scrubby growth of forbs and shrubs (*Cornus* sp. and *Salix* sp.).

The major reason for working on this study area was the long history of pesticide application. The land had been planted in fruit trees since the mid-1920's, and had received DDT since 1947. Application rates of DDT in the late 1940's were 45 kg or more of pure compound per ha/year; organophosphates were replacing most organochlorines while this study was in progress.

Spray schedules followed very closely the general recommendations for fruit crops issued by the New York State College of Agriculture and Life Sciences at Cornell Uni-

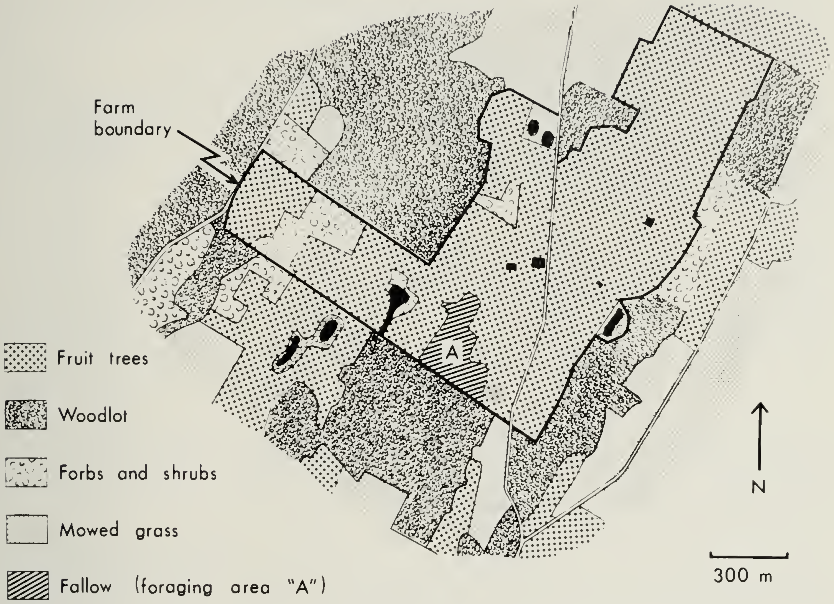

Fig. 1. The New Paltz, New York, study area.

versity. A detailed account of all sprays applied to the farm would be extremely complex, since each orchard was individually treated according to apple variety and insect damage. A summary of the major insecticides applied to the apple trees during this investigation, and the application rates, are listed in Table 1. The grower was generally careful to avoid spraying during windy periods, but sometimes this was unavoidable. Under windy conditions (velocities of 25 to 40 km/hr) the spray could be seen to drift at least 30 m downwind.

Methods.—During each of the 3 summers of field work, the entire farm (29 orchards) was systematically searched at least twice, once in early May and again in mid-June, to locate robin nests. Subsequent searches in early winter, after the leaves had fallen, were made to obtain estimates of the number of nests not located each summer. Nearly all robin fledglings produced in the orchards were banded with U.S. Fish and Wildlife Service bands and, in addition, with colored bands to facilitate sight identification of individuals after they had left the nest.

Movement patterns of robins to and from their foraging areas were followed by a 2-man team using walkie-talkies. Despite the fact that individual adults were not marked, we are certain that birds so followed were correctly identified as to nest occupancy. The time, if any, between loss of sight of a bird by one observer and acquisition by the other was usually less than 10 sec. Furthermore the birds were distributed rather sparsely throughout the orchards so that it was highly probable that a bird seen carrying food into a particular orchard was returning to the nest known to be active in that area.

Food item determinations were made from gizzard contents of all robins collected for residue analysis. The sample consisted of 20 adults shot in April and 10 shot in June

TABLE 1

MAJOR INSECTICIDES APPLIED TO THE STUDY ORCHARDS

Compound	% active ingredient	Kg actual per ha per application	No. of applications each year
DDT	50	5.61	2
Dieldrin	50	1.40	2
Guthion	25	1.40	7 to 10 in various combinations
and			
Carbaryl	50	5.61	
Lead arsenate	98	22.45	2 or 3

and July, in both 1966 and 1967 (a total of 60 birds), as well as 33 nestlings (1 to 14 days old) removed from nests in 1967. Additional birds were obtained in 1968. Food items brought to nestlings by adults were identified as completely as possible by watching nests with binoculars and a 30× telescope.

An indoor experiment was conducted during the winter of 1967–68 to determine if earthworms could survive in the orchard soil. As controls, five 0.028-m^3 boxes were filled with soil from unsprayed areas of the farm where worms were living in good numbers. Twenty 0.028-m^3 boxes were divided into 4 sub-groups. Each sub-group received soil from one apple orchard on the farm where robins nested successfully each year. Soil was taken in October when, it was thought, it would contain a maximum load of chemicals. Efforts were made to take all soil in such a manner that the resulting hole measured 0.3 m × 0.3 m × 0.3 m; that is, soil was taken down to the 0.3 m level rather than scraped from the surface where most chemicals are likely to be concentrated (Chisholm et al. 1950). All soil was examined prior to the introduction of worms. Worms present in the control soil were removed; none were found in orchard samples. Into each box we put 25 worms collected from an unsprayed area of soil type similar to that of orchard soil. *Lumbricus terrestris*, *L. rubellus*, and *Octolasium lacteum* were the worm species represented, and individuals were randomly assigned to the boxes. Boxes were kept moist and sod was maintained. Worms were periodically removed by hand from all boxes, weighed, counted, and returned. The experiment was terminated at the end of 90 days.

From April to June, 1968, 45 traps for invertebrates were placed in the apple orchard of highest robin nesting density, and 45 in an adjacent, heavily used foraging area of approximately equal size. The traps were empty, unused paint cans, 10.2 cm deep and 8.6 cm in diameter, with an overhanging lip; they were sunk into the ground so their tops were flush with the ground surface. All traps were opened for 2-day periods, then emptied, contents counted and identified, and traps closed until the next sampling period. There were 7 such sampling periods, covering the time from mid-April until mid-June, roughly the peak of robin breeding activity.

No sampling of caterpillars was conducted, nor were there any experiments concerning them, since, unlike ground beetles and worms, they were "target organisms" of the spray program and were extremely scarce on orchard trees.

Soils throughout the study area were sampled for DDT and dieldrin analyses in April, 1966, before spraying of chlorinated hydrocarbons began, and again in early October after all such spraying had ceased. Five cores 4.13 cm in diameter and 7.62 cm deep were collected from under the "drip zone" of each of 10 trees in 4 separate orchards. Fifty cores were also collected from each of 2 areas of non-orchard habitat where robins foraged.

Invertebrates, principally earthworms (Lumbricidae) and caterpillars (mostly Tortricidae), were collected by hand both before and during the robin breeding season from the major foraging areas. Commercial cherries were analyzed as a composite sample of ripe fruit removed at random from 20 trees. Wild cherries (*Prunus serotina*) were likewise analyzed as one sample of fruit removed from bushes at 2 different locations on the farm periphery.

Each year, in late April, 10 robins were collected from the orchards, and 10 were obtained at the same time from adjacent unsprayed areas within 300 m of the sprayed orchards. Ten additional robins were collected from the orchards each year in the period from late May to mid-July.

Our original intention was to collect 10 unincubated eggs for analysis in 1967. Only 3 fresh eggs were obtained because of the difficulty in locating nests while the clutches were incomplete.

Seventeen live and apparently healthy nestlings of known age were collected in 1967 from 10 orchard nests, and 15 additional nestlings from 9 nests were collected when discovered dead in or near their nests. Two additional robins raised on the study area were captured as independent juveniles in the cherry orchard in 1967, and these were also collected for analysis.

Extraction procedure for robin tissue analysis was essentially that of Hamence et al. (1965), involving extraction with acetone and hexane, with an acetonitrile cleanup. Birds were plucked rather than skinned, and brain, liver, and muscular tissue ("remainders") of the adult birds were analyzed separately. Eggs were extracted according to a method provided by W. L. Reichel, Patuxent Wildlife Research Center, which involved drying the sample with sodium sulfate and extracting with petroleum ether or acetone for 15 hr. All extracts were eluted through a florisil column (Mills et al. 1963) to separate DDE and dieldrin; the column was standardized according to the lauric acid method of Mills (1968).

All analyses were conducted by gas chromatography using an electron affinity detector. Temperature at injection port was 225°C; temperature of the column and detector was 195°C. The carrier gas was nitrogen. Six different columns were used, either 0.92 m × 0.32 cm or 1.78 m × 0.32 cm, packed with varying combinations of Dow 11, QF-1, DC 200, and XE-60 on Gas-chrom Q 60/80 mesh, Gas-chrom Q 80/100 mesh, or Chromsorb W 60/80 mesh. Certain identifications were confirmed by thin-layer chromatography.

RESULTS

Nesting activity.—To construct nesting-activity curves (Fig. 2), we back-dated nests found active during the breeding season by allowing 1 day for each egg, 12 days for incubation (including the day the last egg was laid), and 14 days for fledging. As determined from these nest-activity curves, there were at least 22, 22, and 13 breeding pairs of robins present in 1966, 1967, and 1968 respectively.

The nesting season began each year about 20 April, and extended at least until 10 July, with the peak of nesting occurring between 25 May and 1 June

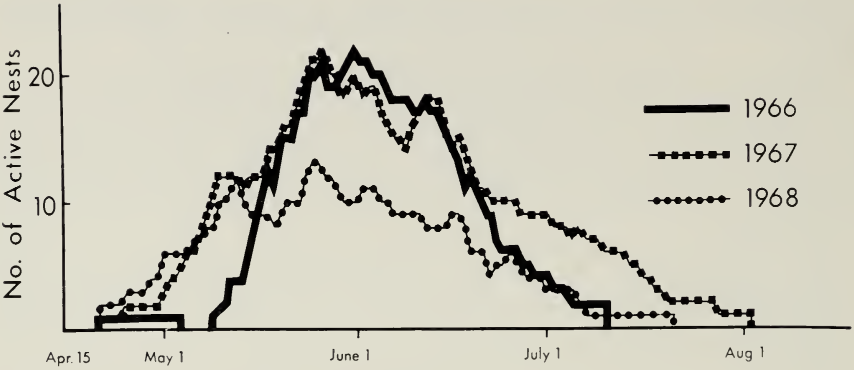

FIG. 2. Robin nesting activity in the study area for 3 years. The peak of each curve denotes the minimum number of breeding pairs present for that year.

(Fig. 2). This period of breeding activity agrees closely with that reported by several authors for this latitude (Howell 1942, Eaton 1914, Young 1955). While the length of the nesting season allows time for at least 2 successful broods per female, the unimodal shape of the nesting-activity curves are probably the result of late successful first nestings of birds whose first attempts failed.

Clutch size.—Frequencies of clutch sizes in this study were compared by chi-square analysis with pooled data obtained in 3 other robin studies (Table 2). Results indicated a highly significant difference, $p < .005$, with a higher frequency of 1-egg clutches and a lower frequency of 4-egg clutches in the present study.

Egg and nestling mortality.—A mortality curve for 294 eggs (Fig. 3) shows that mortality was fairly evenly distributed over the first 20 days, from day of laying until nestlings were 7 days old. Beyond that point nestling mortality was negligible. All eggs were assumed present on the first day of laying to avoid masking mortality during clutch completion. In many cases, the exact day of death or predation was known. In instances where eggs or chicks were alive at one visit but dead on the next, we have taken the median day as the date of death. The sharp decline between day 1 and 2 of the nestling period is an artifact of the way we have chosen to treat unhatched eggs. In this period, we counted as dead all eggs which failed to hatch, regardless of whether they were infertile or contained dead embryos.

Causes of mortality were diverse. Predation was generally attributable to House Wrens (*Troglodytes aedon*), Blue Jays (*Cyanocitta cristata*), or Common Grackles (*Quiscalus quiscula*), though red and gray squirrels (*Tami-*

TABLE 2

COMPARISON OF FREQUENCIES OF ROBIN CLUTCH SIZES FROM NEW PALTZ STUDY AREA WITH POOLED FREQUENCIES OF 3 EARLIER ROBIN STUDIES[1]

No. of eggs	Other studies		This study	
	No.	Percent	No.	Percent
1	3	0.3	2	2.5
2	64	5.4	7	8.6
3	520	44.0	43	53.1
4	576	48.8	29	35.8
5	18	1.5	0	0.0

[1] Howell 1942, Young 1955, Howard (For Mass. and N.Y.) 1967.

asciurus hudsonicus and *Sciurus carolinensis*) also occurred in the area. We have no adequate data on post-fledging mortality, but house cats (*Felis domestica*) were present and caught some poorly flying young robins.

Inclement weather was also a mortality factor, possibly involved in the death of embryos and certainly in that of young nestlings. In 1967, 6 nestlings

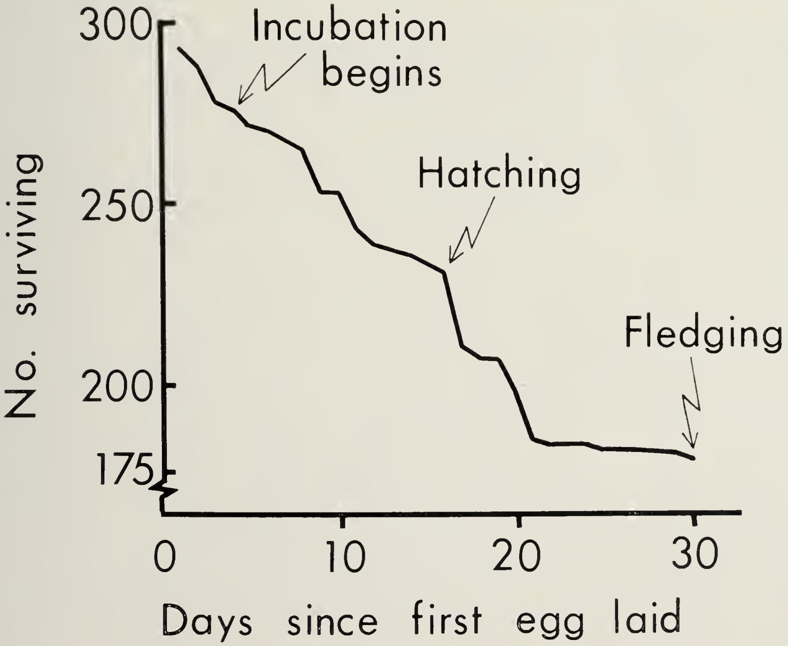

FIG. 3. Robin egg and nestling mortality pooled for 1966, 1967, and 1968.

Table 3

Robin Reproductive Success

	1966		1967		1968	
	Orchards	Northeast[1]	Orchards	Northeast	Orchards	Northeast
Mean clutch size (n)	3.4 ± 0.1[2] (30)	3.7(271)	3.0 ± 0.1(34)	3.5(116)	3.3 ± 0.1(20)	3.4(92)
% hatching success (n)	70(111)	no data	74(108)	no data	68(76)	no data
% egg-to-fledgling success (n)	64(111)	53(829)	59(108)	52(400)	51(76)	59(278)
Mean no. young produced per successful nest (n)	3.1 ± 0.2(23)	3.3(135)	2.2 ± 0.2(29)	3.0(68)	2.4 ± 0.2(18)	3.0(55)
Mean no. young produced per active nest (n)	1.9 ± 0.3(37)	2.0(222)	1.6 ± 0.2(39)	1.3(115)	1.5 ± 0.3(26)	1.8(83)
% nest success based on active nests (n)	62(37)	64(222)	74(39)	59(115)	62(26)	66(83)

[1] From North American Nest Record Cards for New York, New Jersey, Pennsylvania, Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut.

[2] Standard error.

TABLE 4

COMPARATIVE REPRODUCTIVE DATA

	This study (1966–68)	Howard (1967)	Young (1955)	Howell (1942)	Nolan (1963)	Nice (1957)
Species	Robin	Robin	Robin	Robin	Several[1]	Several[2]
Mean clutch size	3.2	3.5	3.4	3.4	–	–
% hatching success	71.2	–	58	–	38.6	59.8
% egg-to-fledgling success	60.9	–	45	–	17.6	45.9
Mean number of young produced per successful nest	2.6	–	2.9	2.4	–	–
% nest success[3]	66.7	–	49	65.0 and 49.3	21	49.3

[1] Birds with elevated open nests in scrub habitat.

[2] Altricial birds with open nests.

[3] Based on all nests with at least one egg; a successful nest produced at least one successful fledgling.

(2 different nests) were found dead following 2 days of constant rain; in 1968, 4 nestlings in one nest were discovered dead after an 11 cm rainfall. Presumably the female left the nest to forage, thus exposing the young to the elements. Male robins sometimes sat on the nest rim, but we never saw one incubate or brood.

Nesting success.—Robin reproductive data obtained in this study were compared with similar data from 9 northeastern states collected through the North American Nest Record Card Program (Table 3). Only those cards based on several visits to the nest and with incubation and nestling periods agreeing with those reported in other studies were included. Certain other qualifications were also applied to make the data as nearly comparable as possible.

Despite a lack of statistical treatment, certain trends are clear. Orchard robins in this study consistently produced fewer eggs per clutch, though differences were not extreme. They also produced fewer fledglings per successful nest than nests reported on the nest record cards, a reflection of the reduced clutch size. Hatchability and egg-to-fledging success were in close agreement, with orchard birds faring better in many instances.

Table 4 compares the robin reproductive data obtained in this study with similar information presented in 3 other major robin studies. as well as with reproductive information presented in 2 studies of birds which build open nests and have altricial young. Again, orchard robins fared as well as or better than the birds reported in these investigations in all categories except clutch size.

Nest searches in late November, after the leaves had fallen, allowed a

TABLE 5

SPRING NEST-FINDING SUCCESS AND ESTIMATES OF ROBIN PRODUCTIVITY

Year	% of robin nests found in spring	Estimate of total no. of robin nests built in study orchards	Estimate of total robin fledglings produced
1966	51	90	135
1967	82	78	66
1968	83	47	43

measure of the efficiency of nest-finding during the breeding season and estimation of total robin productivity in the orchards. They also provided a basis for estimating the total number of nests on the study area by the application of the formula:

$$\text{Total nests} = \frac{\text{number of nests found in spring} \times \text{number of nests found in fall}}{\text{number of spring nests found in fall}}$$

Furthermore, we could determine whether nests not found until fall had contained at least one successful fledgling on the basis of the presence of feather sheath fragments (Johnson 1967). Spring nest-finding success rates and estimates of total numbers of young robins produced in the orchards are presented in Table 5. We attribute the low rate of spring nest discovery in 1966 to the fact that EVJ was not living on the study area that season, whereas he was present during the entire breeding seasons of 1967 and 1968.

Fledgling survival.—Young robins disappeared from the vicinity of their nests within 2 days of fledging, and were subsequently difficult to identify by means of color bands because they remained high in trees. Mist-netting was carried out from the last week in June to 10 July each year in a cherry orchard where large numbers of birds were attracted by ripening fruit. The aim of this effort was to determine post-fledging survival of robins and to detect the presence of birds banded as nestlings in previous years.

In 1966, we recaptured 17 of 61 birds previously banded the same season as nestlings in orchard nests. The mean age of these birds was 35 days, or 21 days post-fledging. They all had full tails, and were apparently independent. Our relative recapture efficiency was estimated at 28%. In 1967, only 2 banded orchard-reared robins (6%) were recaptured as independent juveniles; in 1968, no banded orchard-reared juveniles were recaptured.

We attribute the yearly differences in recapture rates to differences among seasons and cherry crops. The year 1966 was dry, and the crop (with irrigation) was excellent. In 1967, a cold spring significantly reduced the crop

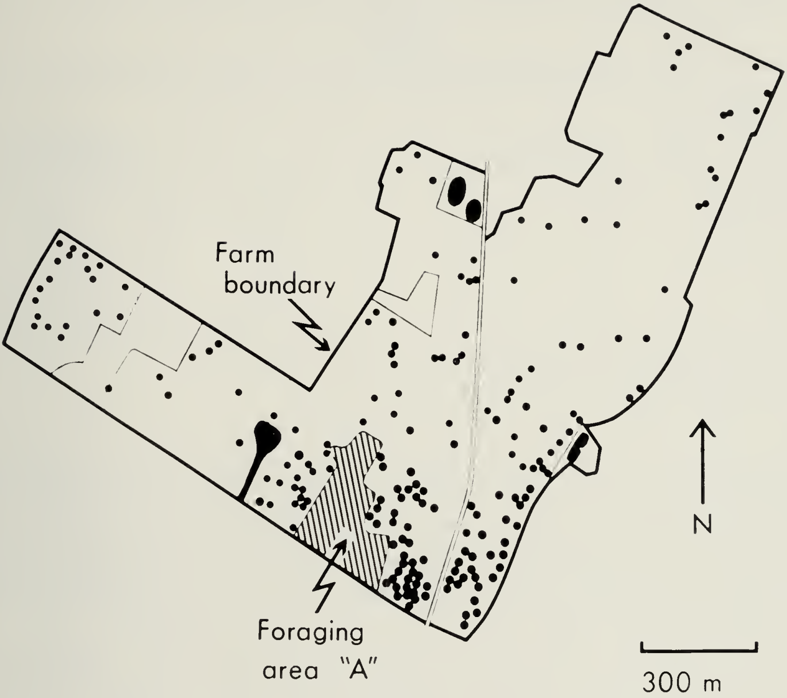

FIG. 4. Robin nest distribution on the farm for the years 1966, 1967, and 1968.

compared with 1966, and consequently there were fewer birds (Austin-Smith, pers. comm.). The crop was good in 1968 but extensive rains during picking-time ruined about 80% of the cherries. In addition, this rain made mist-netting virtually impossible throughout most of the period of peak bird abundance.

In 1966 the results of netting indicated that post-fledging survival of young robins raised in orchard nests was good. There was apparently no drastic mortality when young were between the ages of 14 and 35 days. We suspect that this was also the case in 1967 and 1968, but low bird numbers and poor netting conditions adversely affected our captures. In 1967 and 1968, we did not recapture any birds banded as orchard nestlings in previous years. This is perhaps not surprising in view of the overall 50% mortality rate for robins suggested by Farner (1945), and the very low return (4 of 250) of banded nestling robins to a Massachusetts suburb in the following year (Howard, pers. comm.).

Adult mortality.—In 2 cases, the male partner of a pair disappeared while their nest was active. The female successfully raised the young to fledging in

TABLE 6

RESULTS OF FORCING EARTHWORMS (LUMBRICIDAE) TO LIVE IN SPRAYED ORCHARD SOIL FOR 90 DAYS[1]

Group	No. Worms[2]		Wt. Loss(%)	DDT Plus Degradation Products (ppm, wet wt.)
	Begin	End		
Control	125	221[3]	31.0[3]	3.0
I	125	28	85.5	47.3
II	125	58	77.5	21.8
III	125	42	82.6	22.1
IV	125	68	71.5	11.9

[1] Totals of 5 replications in each group.
[2] Groups I through IV were in sprayed soil from mature apple orchards.
[3] Significantly different from all other groups, $p < .025$.

both instances. Two females incapable of flight were discovered near nests containing young. One had mechanical injuries but the other was "in tremors." In the latter case, the young were dead and were collected along with the female for residue analyses. We can find no published information on the frequency of disappearance of one member of a pair of nesting robins, but 4 individuals lost in 3 years from 57 pairs does not seem excessive.

Nest distribution and density.—Robin nest density in the orchards was never high. The mean distances between active nests (including only those simultaneously active on the day or days of maximum nest activity) were 102, 159, and 232 m in 1966, 1967, and 1968 respectively. Nests tended to be clumped about the major foraging area of recently cleared land (Fig. 4). Of the estimated total number of nests built in the study orchards each season, at least 30, 26, and 38% (1966, 1967, and 1968) were constructed within 153 m of this area. Other nests were scattered over the rest of the farm, often with over 300 m separating neighbors.

Foraging areas.—In all years of the study, robins were seen foraging under orchard trees in early April. These birds were in migrating flocks composed principally of males. From late April until July, there were very few observations of robins on the ground under orchard trees, despite the fact that observers on foot were present in the study area up to 10 hours a day. Following preliminary observations in 1966, observers equipped with walkie-talkies followed birds from 29 nests in 161 foraging trips in 1967; in no case were birds observed foraging directly under sprayed orchard trees. Instead, they used woodlots, marginal areas, and especially the large section (5.1 ha) of recently cleared land adjacent to the south woodlot ("A" in Fig. 1). The same was true in 1968. Mean distance from nests to foraging areas was 122 m in 1967 (29 nests), and 103 m in 1968 (19 nests), with extremes of 30 and 300 m.

TABLE 7

PESTICIDE RESIDUE LEVELS IN SOILS OF THE STUDY AREA IN 1966

Source of Soil	DDT + DDE Range of Levels (ppm, wet wt.)
Young apple orchard	90 – 150
Semi-abandoned apple orchard	106 – 180
Mature apple orchard	127 – 391
Mature apple orchard	427 – 441
Robin foraging area ("A")	2 – 11
Northwest edge of study area	<1 – <1

Food items.—Observations made in late March and early April showed that migrating flocks fed extensively on rotten apples left on the ground from the previous autumn's crop. The gizzard contents of 5 birds collected during this period were 97% apple by volume. At commencement of the breeding season, earthworms were the most important item, followed by lepidopterous larvae and beetles. By late June, however, the adult birds' diets consisted of 70% fruit, principally commercial varieties of sweet cherries which were grown on the study area. Worms and caterpillars assumed a secondary importance. Gizzards of nestlings contained, in order of importance: earthworms, lepidopterous larvae (chiefly Tortricidae: *Archips argyrospila*), and cherries. These results agree generally with those of Beal (1915).

Invertebrate populations.—Trapping by pitfall trap-cans in 1968 resulted in a good representation of the animal component of robins' diets: worms, carabid beetles, spiders, snails, and some lepidopterous larvae. Under orchard trees, nearly 30,000 trap-hours resulted in 0.7 captures per 100 trap-hours, with 11% of 315 traps making captures. In the foraging area, the same number of trap-hours produced 4.5 captures per 100 trap-hours, involving 57% of 315 traps. Ground-dwelling invertebrates were apparently 5 or 6 times more abundant in the unsprayed area than in the orchard. This factor may actually be even larger since most of the items captured in the orchard were trapped under trees adjacent to unsprayed areas.

The earthworms forced to live in orchard soil had high mortality and weight loss compared with those living in unsprayed control soil. Pooled totals of the 5 replicates in each group are shown in Table 6. A Kruskal-Wallis rank test (Steel and Torrie 1960) showed that, at the end of 90 days, experimentals had significantly fewer numbers of worms and significantly more overall weight loss than controls ($p < .025$). The presence of more than the original number of worms in the control group at the end of 90 days was

TABLE 8

INVERTEBRATE PESTICIDE RESIDUE LEVELS

Source of Sample	Composition of Sample	Date	DDT and Related Compounds	Dieldrin
Foraging Area "A"				
	Worms	4/19	0.8[1]	0[1]
	Worms	4/25	0.6	0
	Composite[2]	5/23	0.2	0
	Worms	6/1	2.1	0.2
	Worms	7/21	1.4	0.1
New Orchard Planting				
	Worms	4/13	3.7	trace
	Worms	7/21	7.7	0.5
Brushy Edge				
	Worms	4/19	0.6	0
Woodlot				
	Worms	6/1	2.9	0.2
	Caterpillars[3]	6/20	1.0	0.6
	Worms	7/25	1.4	0.2
Mature Orchard				
	Composite[2]	5/23	0.6	0

[1] All values ppm, fresh weight basis.
[2] Worms + beetles (Carabidae) + caterpillars.
[3] Principally *Archips argyrospila.*

probably due to overlooked eggs in the soil at the beginning of the experiment, and/or reproduction by the control worms.

Pesticide levels.—Soils within the study area exhibited a wide range of pesticide levels. Results of analyses of soil samples are shown in Table 7. It should be understood that the values of Table 7 are maximal because the cores were taken directly under the crown periphery (drip zone) where highest residue levels in soil are expected. Dieldrin was detected in measurable amounts only in fall samples and did not exceed 2.6 ppm.

While residue levels would be expected to be higher in the fall, immediately following spraying, than in the spring, this was not always the case. Sampling error may be partially responsible for this apparent inconsistency, but other factors such as runoff of residues, delayed decomposition of vegetation containing residues, and protection of the soil by leaves may have been important. Most levels in orchard soils agree with those reported by Chisholm et al. (1950). The values in excess of 300 ppm are higher than any published data, but the study area has a 20-year history of DDT application. In addition, samples in this investigation were taken only from the drip zone; other studies

Table 9

Mean Pesticide Residue Levels in Adult Robins[1]

	1966			1967		
	Spring orchard	Spring reference	Summer orchard	Spring orchard	Spring reference	Summer orchard
Brain						
DDE	0.9(0.30)[2]	1.2(0.31)	2.6*(0.62)	0.9(0.33)	0.8(0.19)	2.2**(0.39)
DDT	2.1(0.22)	2.1(0.21)	1.0(0.39)	1.1(0.13)	1.1(0.33)	1.8(0.46)
Dieldrin				0.2(0.09)	0.2(0.05)	0.6*(0.15)
Liver						
DDE	1.5(0.32)	2.9(1.08)	10.1**(2.69)	1.3(0.36)	1.4(0.35)	3.8**(0.74)
Dieldrin				0.7(0.27)	0.4(0.11)	1.0(0.16)
Remainder						
DDE	3.1(0.55)	2.8(0.67)	6.5*(0.98)	3.0(0.76)	3.8(1.58)	8.6**(1.61)
DDE-fat basis				84.9(66.46)	113.2(52.10)	169.0*(17.03)
DDT	9.8(2.03)	7.1(1.99)	6.7(2.35)	6.7(4.50)	2.9(1.32)	7.3(1.68)
DDT-fat basis				191.2(131.00)	79.9(34.25)	139.0(32.19)

[1] All values ppm, wet weight basis, unless otherwise indicated. Sample sizes range from 8 to 11. All tests were Kruskal-Wallis rank.

[2] Standard error.

* Significantly different from other 2 categories in group, $p < .05$.

** Significantly different from other 2 categories in group, $p < .01$.

report that samples were taken from under trees, but do not specify any particular site. DDT is one of the most persistent of the chlorinated hydrocarbons and has been shown to last longest in heavy clay soils with high organic content (Edwards 1966). The study area soil matched this description well. It is difficult to explain the absence of dieldrin in spring soil samples since this compound is also highly persistent (Edwards 1966). It was sprayed at far lower rates than DDT, however, and had not been used for as many years.

Results of pesticide residue determinations for invertebrates were based on pooled extractions (up to 25 g) of several individuals of different species (Table 8). Data from a single mature orchard indicated that total residue levels were low; however, a seasonal trend was apparent in that residue levels in invertebrates peaked at about 1 June, shortly after DDT and dieldrin application, and dieldrin was not detected in any sample collected before that season's dieldrin application. Analysis of live worms raised for 90 days in pesticide-treated and untreated soil showed that the treated worms had much higher DDT residue levels than either the controls or field-collected samples (Table 6).

Commercial cherries from the study area showed no measurable residues; wild cherries from woodlot margins contained less than 0.2 ppm total residues.

The results of the analyses of adult robins are presented in Table 9. All DDT values are for the p-p′ isomer; no o-p′ isomer was encountered though it occurs as about 20% of commercial DDT preparations. Each year there was a seasonal increase in DDE levels in all tissues examined with no corresponding increase or decrease in DDT. In 1967, the fat content of "remainders" was determined, and the expression of ppm on a fat basis shows that the increase was not simply a reflection of an increase in fat. We have not included DDD in the table because of its highly irregular occurrence. When present, it was usually in the livers where it is probably formed (Wurster et al. 1965). Dieldrin values are shown only for 1967 birds; analytical problems in 1966 led us to exclude that year's data. Remainders were not extracted for this compound unless there was evidence of its presence in excess of 1 ppm.

The one adult female found in tremors in 1967 contained 15 ppm DDT plus degradation products (wet weight basis) as well as 2.6 ppm dieldrin in the brain, and 7.4 ppm dieldrin in the liver. These are the highest levels found in any adults examined and suggest pesticide poisoning. Jefferies and Davis (1968), in their study of Song Thrushes (*Turdus ericetorum*), suggest that these dieldrin levels should at least be considered dangerous.

The 3 fresh eggs examined contained an average of 12.2 μg of DDT and related compounds per ml of egg, while 7 eggs that did not hatch averaged 13.4 μg per ml. A 2-sample rank test leads to acceptance of the null hypothesis of no difference between samples. Levels are not expressed as ppm since an egg loses weight during development and thus ppm of pesticides would appear to increase with age of the egg. The maximum level encountered was 35.2 μ g/ml in an unhatched egg. Interpretation of these data is difficult. There is no guarantee that the fresh eggs would have hatched; thus, one cannot say for certain that they were "normal." Many factors can result in an egg's failure to hatch. From these data, and from the high rate of hatching success (Table 4), it seems probable that pesticides did not play a significant role in reducing hatchability of robin eggs in the study orchards.

Nestlings were analyzed on a whole-bird basis. Four live birds aged 1 to 5 days averaged 4.7 ppm DDT and related compounds (wet weight basis); 7 live birds aged 6 to 10 days, 4.2 ppm; and 6 live birds aged 11 to 15 days, 6.1 ppm. Six young found dead (3 each from 2 nests) aged 2 and 4 days averaged 16.9 ppm; 5 nestlings found dead, aged 6, 7, and 9 days, averaged 3.0 ppm; and 2 young found dead, aged 11 and 14 days, averaged 4.4 ppm. Two juveniles which were recaptured in the cherry orchard at the ages of 34 and 45 days contained residue levels which agreed closely with those found in summer orchard adults. In all young examined, dieldrin levels (whole bird) never exceeded 2 ppm.

DISCUSSION

The most important observation explaining good robin reproductive success in this polluted environment was that birds did not forage in areas which received direct spray. The reasons for this are readily apparent. We noted previously that worms were not present in sprayed soil and, in fact, showed high mortality when forced to live in it (Table 6). It is not possible at this time to pinpoint any one chemical or combination of chemicals responsible for this. There is published information, however, which suggests that at least 4 chemicals applied to the study orchards may be deleterious to worm survival. Baker (1946) reported that earthworm populations decreased markedly after an elm grove was sprayed heavily with DDT. Slater (undated) reported that lead arsenate is effective as a vermicide when applied at the rate of 2.27 kg per 93 m^2. Orchard applications did not approach these levels, but the compound had been applied continually for 20 years in many sections. Slater also mentioned that DDT will kill earthworms. Edwards (1969) reported that carbaryl "seriously decreased populations of earthworms" (p 92), and in addition stated that, in poor orchard soil, "earthworms . . . were killed by copper residues from spraying" (p 91). Copper was not sprayed in our study area during the years of this investigation, but Bordeaux mixture (copper sulfate) was used extensively before the advent of modern organic insecticides. Thus it seems likely that worms had been absent from the study orchards for over 20 years and will probably not reappear until spraying of such compounds ceases and residues degrade. These observations do not agree with those of Menhinick (1962), who compared soil and litter invertebrate populations in sprayed orchards with those in an unsprayed habitat. He found good numbers of lumbricids in both sprayed and unsprayed areas. However, lead arsenate was applied to his sprayed area at the rate of only 6.7 kg/ha/yr (compared with 45 kg/ha/yr in this study); he did not mention the use of carbaryl.

Our reason for sampling orchard soil for residue analysis was to examine pesticide levels in the robins' food chain from the source (presumably orchard soil) to the birds. When it became evident that orchard soil residues played only a prohibitive role, if any, in regard to invertebrates, the soils pertinent to our original purpose were those of the unsprayed foraging areas. The last 2 values in Table 7 are for soils from such areas, and are quite low. These results indicate that pesticide application by speed sprayer was remarkably efficient in confining the pesticides to the intended target area. Soil collected at foraging area "A" contained less than 1⁄10 the residues of adjacent sprayed orchards bordering it on 3 sides. Soil from a site about 60 m from the nearest sprayed orchard contained less than 1 ppm total DDT residues.

Invertebrates living in these soils contained residue levels (Table 8) which reflected soil levels. Values are very similar to those reported by Davis and Harrison (1966) for worms, beetles, and slugs living in soils containing low levels of chlorinated hydrocarbons (0.03 to 0.7 ppm). Wheatley and Hardman (1968) found little concentration of dieldrin and DDT-complex compounds in *Lumbricus terrestris* when soil levels were below 1 ppm for each compound; DDE and dieldrin were concentrated 2.9 and 2.5 times respectively. When these observations are applied to the data of Tables 7 and 8, it is evident that the same was probably true for the worms of robin foraging areas in this study. There was no detectable "biological magnification," and residue levels in food items which the birds actually used were low.

Robin eggs contained levels of DDT and DDE which probably reflect the lipophilic nature of the compounds. Results of other studies on possible effects of various pesticides on hatchability are somewhat contradictory. Genelly and Rudd (1956) found no decrease in hatchability of pheasant eggs containing more than 150 ppm DDT, but more recent work suggests that DDT or one of its metabolites is responsible for a decrease in eggshell thickness in some raptorial and piscivorous birds (Ratcliffe 1967, Hickey and Anderson 1968, Porter and Wiemeyer 1969). No cracking of eggshells was observed in the present study, and egg breakage was extremely uncommon.

Low concentrations of pesticides in adults were consistent with the levels in the food items. Small but significant increases through the season were predictable since the diet was somewhat contaminated. If robins carried low "background" concentrations of pesticides when they arrived in the spring, these levels could be expected to show an increase through the season. Of the DDT-complex compounds, only the metabolite DDE showed a detectable increase in robin tissues. There was no increase in DDT as such. In addition, the presence of DDE in a robin is not necessarily proof of DDT ingestion; DDE may be ingested as such. Dieldrin showed a slight increase in brains, but not livers (Table 9), and this is consistent with the increases noted in the soils and invertebrates.

No adult robins examined in this study contained brain residue levels in excess of 30 ppm DDT plus DDD, a minimum value suggested by Stickel et al. (1966) to indicate pesticide poisoning. Wurster et al. (1965) considered 50 ppm total brain residues as indicative of pesticide poisoning in robins. The one adult in tremors discovered in the study area perhaps died from dieldrin poisoning, but no deaths can be directly attributed to DDT. An additional point for consideration is the fact that the cherries which comprised nearly 70% of the diets of robins in late June and July contained little or no pesticides. Harvey (1967) has shown that surviving Starlings (*Sturnus vulgaris*) placed on a clean diet after receiving high doses of DDT were able to excrete more than 90% of the amount ingested within 10 days after poison in the diet was eliminated. If the same is true for robins, then the high percentage of clean fruit in the orchard robins' diets in summer may have provided them with an opportunity to excrete excess pesticides.

In conclusion, there was no undue mortality of robins in the study area nor would any be anticipated in light of what is known of the birds' foraging habits and the pesticide content of their foods. The conditions which favored the presence of robins on the farm were probably the park-like nature of the orchards in spring and the abundance of suitable nest sites. The birds' ability to forage in areas quite far removed from their nests was perhaps the major factor contributing to their success. The situation was in large measure a fortuitous one, in that future changes in spray program, mulch, or cover management practices might increase the numbers or availability of invertebrates under orchard trees. A situation comparable with what has occurred on college campuses and in residential communities would then exist with the very real possibility of direct mortality from poison ingested with the robins' food and/or reduced natality through disturbance to reproductive physiology.

SUMMARY

From 1966 through 1968, robins reproduced successfully in commercial apple orchards which were periodically sprayed with DDT, dieldrin, and other pesticides. Observations by a 2-man team using walkie-talkies revealed that breeding robins obtained essentially all food for themselves and nestlings from unsprayed areas adjacent to the orchards. Invertebrate trapping in sprayed and unsprayed areas showed that these food items were 5 or 6 times more abundant in unsprayed habitat. Worms forced to live in sprayed orchard soil displayed significantly greater mortality than controls. Mean robin clutch sizes in the study orchards were lower than those reported for robins in other studies, perhaps because of food shortage and/or increased foraging distances. Levels of DDT and its analogs in food items from robin foraging areas did not exceed 8 ppm wet weight basis. From late April to July, adult robins showed small but significant increases in DDE levels in all tissues examined, as well as an increase in dieldrin in brains. Pesticides sprayed on the farm had no direct demonstrable adverse effects on the robins; productivity was high and adult mortality low. The situation was in large measure fortuitous, since any changes in orchard management practices which resulted in the presence or availability of invertebrates under orchard trees would be expected to result in robin mortality and/or reduced breeding success.

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LITERATURE CITED

Baker, W. L. 1946. DDT and earthworm populations. J. Econ. Entomol. 39:404–405.

Beal, F. E. L. 1915. Food of the robins and bluebirds of the United States. U.S. Dept. Agr. Bull. 171.

Chisholm, R. D., L. Koblitsky, J. E. Fahey, and W. E. Westlake. 1950. DDT residues in soil. J. Econ. Entomol. 43:941–942.

Davis, B. N. K. and R. B. Harrison. 1966. Organochlorine insecticide residues in soil invertebrates. Nature 211:1424–1425.

Eaton, E. H. 1914. Birds of New York. Part 2. Univ. of the State of New York, Albany.

Edwards, C. A. 1966. Insecticide residues in soils. Residue Rev. 13:83–132.

———. 1969. Soil pollutants and soil animals. Sci. Am. 220:88–99.

Farner, D. S. 1945. Age groups and longevity in the American Robin. Wilson Bull. 57:56–74.

Genelly, R. E. and R. L. Rudd. 1956. Effects of DDT, toxaphene, and dieldrin on pheasant reproduction. Auk 73:529–539.

Hamence, J. H., P. S. Hall, and D. J. Caverly. 1965. The identification and determination of chlorinated pesticides residues. Analyst 90:649–656.

Harvey, J. M. 1967. Excretion of DDT by migratory birds. Can. J. Zool. 45:629–633.

Hickey, J. J. and D. W. Anderson. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science 162:271–273.

Howard, D. V. 1967. Variation in the breeding season and clutch size of the robin in the northeastern United States and the Maritime Provinces of Canada. Wilson Bull. 79:432–440.

Howell, J. C. 1942. Notes on the nesting habits of the American Robin. Am. Midl. Nat. 28:529–603.

Jefferies, D. J. and B. N. K. Davis. 1968. Dynamics of dieldrin in soil, earthworms, and song thrushes. J. Wildl. Manage. 32:441–456.

Johnson, E. V. 1967. The robin nestling's fate. Mass. Audubon 52:12–14.

Menhinick, E. F. 1962. Comparison of invertebrate populations of soil and litter of mowed grasslands in areas treated and untreated with pesticides. Ecology 43:556–561.

Mills, P. A. 1968. Variation of florisil activity: simple method for measuring adsorbent capacity and its use in standardizing florisil columns. J. Assoc. Off. Anal. Chem. 51:29–32.

———, J. H. Onley, and R. A. Gaither. 1963. Rapid method for chlorinated pesticide residues on non-fatty foods. J. Assoc. Off. Anal. Chem. 46:186–191.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

Nolan, V., Jr. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44:305–313.

Porter, R. D. and S. N. Wiemeyer. 1969. Dieldrin and DDT: Effects on Sparrow Hawk eggshells and reproduction. Science 165:199–200.

Ratcliffe, D. A. 1967. Decrease in eggshell weight in certain birds of prey. Nature 215:208–210.

Slater, C. S. Undated. Earthworms in relation to agriculture. U.S. Dep. of Agric. publication of Agric. Res. Serv. 12 p.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York.

Stickel, L. F., W. H. Stickel, and R. Christensen. 1966. Residues of DDT in brains and bodies of birds that died on dosage and in survivors. Science 151:1549–1551.

Wallace, G. J. 1962. The seventh spring die-off of robins at East Lansing, Michigan. Jack-pine Warbler 40:26–32.

Wheatley, G. A. and J. A. Hardman. 1968. Organochlorine insecticide residues in earthworms from arable soils. J. Sci. Food Agric. 19:219–225.

Wurster, D. H., C. F. Wurster, Jr., and W. N. Strickland. 1965. Bird mortality following DDT spray for Dutch elm disease. Ecology 46:488–499.

Young, H. 1955. Breeding behavior and nesting of the eastern robin. Am. Midl. Nat. 53:329–352.

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REQUESTS FOR ASSISTANCE

Great Gray Owl.—A study is currently in progress to determine the historical and present status of the Great Gray Owl (*Strix nebulosa*) in North America. Any information regarding sight records or possible breeding occurrences of the Great Gray Owl is needed. Your cooperation will be gratefully acknowledged. Send information to: M. Collins, Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2.

Red-cockaded Woodpecker.—The Red-cockaded Woodpecker Endangered Species Recovery Team is trying to develop a recovery plan for this species. In order to quantify its present and recent past status I am cataloging active or recently active Red-cockaded Woodpecker colonies. Please send as much of the following information as possible on known active colonies: (1) specific location—a map if possible, (2) dates and numbers of birds seen, (3) records of active nests, (4) land ownership if known. For colonies that are known to have become inactive in recent years, please send as much of the above information as possible and indicate specific or probable cause of the colony loss. Any documentation would be of great help. Send information to: Jerome A. Jackson, Leader, Red-cockaded Woodpecker Endangered Species Recovery Team, P. O. Box Z, Mississippi State, MS 39762.

WINTER ACTIVITY PATTERNS OF BLACK-CAPPED CHICKADEES IN INTERIOR ALASKA

Brina Kessel

The Black-capped Chickadee (*Parus atricapillus*) is a year-round resident of the mixed deciduous/spruce woodland association of the taiga forests of interior Alaska and thus has proved its ability, in spite of its small size (10–14 g), to withstand the environmental extremes occurring in that region. To learn something of its adaptability, I studied the winter activity patterns of the chickadee near Fairbanks, Alaska. Observations were based primarily on the feeding activity of wild birds about an artificial feeder, and data have been examined in relation to daylength, light intensity, ambient temperature, sky cover, solar radiation, precipitation (which fell as snow during the periods of the study), and wind velocity.

STUDY AREA AND METHODS

The site of the feeding station was in deciduous woods (primarily paper birch, *Betula papyrifera*; quaking aspen, *Populus tremuloides*, and several species of willow, *Salix*, shrubs) at about 230 m elevation on a south-facing slope at 64°53′ N. Lat. and 147°49′ W. Long., about 8 km northwest of Fairbanks and overlooking the broad, flat Tanana Valley.

Some of the environmental factors of the region can indeed be extreme. With Fairbanks only 190 km south of the Arctic Circle, sunlight duration (sunrise to sunset) varies from 22 hr 02 min on the 21st of June to 3 hr 38 min on the 21st of December and changes as rapidly as 7 min per day during part of the year.

Data from the U.S. Department of Commerce (1973) show that temperature extremes have ranged from +36°C in June 1969 to −52°C in January 1969; the mean temperature during July, however, is 14°C and during January is −24°C. At any time from late October through March, temperatures below −34°C may occur, as may above-freezing temperatures. It is not infrequent for temperature shifts of over 27°C to occur within a 24-hour period. During periods of cold weather, there is often a conspicuous vertical stratification of temperatures; the dense, cold air settles into the valley where the typical absence of wind during these cold periods allows stratification to occur. Temperatures at the feeding station, for instance, average about 5°C warmer during the winter than those at the National Weather Service station at Fairbanks International Airport, some 95 m lower in elevation; and, in the early days of a cold snap (before the valley fills with cold), temperatures may be more than 10°C warmer than in the valley bottom.

Precipitation in the Fairbanks area averages only 29.2 cm annually; 9.9 cm fall from October through March, mostly as snow. The mean annual snowfall is 168.5 cm, and the ground is usually snow-covered from about 10 October until the last week of April.

From November 1960 through February 1967 I monitored, with varying degrees of regularity and intensity, the daily activity patterns in winter of Black-capped Chickadees at several feeders located in a birch tree about 3 m outside a large window of my home. Food consisted primarily of sunflower seeds (*Helianthus anuus*), suet, and peanut butter and was available at all times. Observations were entirely visual until 17 February

1964—I sat beside the window and tabulated the number of birds present at the feeding station at a given time. In the morning I was present in time to record the first arrival, and then, depending on the time available, remained to record subsequent arrivals until at least 5 to 10 birds had arrived. In the evening I began observations while substantial numbers were still feeding and recorded numbers remaining as individuals left for their roost sites, finally recording the departure of the last bird.

On 17 February 1964 the peanut butter feeder was automated so that chickadee visits to the peanut butter (the favored food) were recorded on an Esterline-Angus Model AW Graphic Ammeter recorder located inside the house. The 29-cm-high peanut butter feeder was hung inside a wood-mesh cage with a mesh size that excluded all birds but the Black-capped Chickadee. The feeder had 6 feeding loci, 3 arranged in a vertical row on each side. Under each locus, functioning as a perch, was a microswitch sensitive enough that the weight of a chickadee would close it, activating the pen on the recorder. The closing of each additional microswitch increased the amperage reaching the pen, causing it to scribe a longer line on the chart, so it was possible to determine the feeding times of 1 to 6 chickadees by examining the charts. Charts were run at the rate of 30.5 cm per hour.

The feeder loci were only 9 cm apart, so aggressive behavior among the birds usually limited the number simultaneously at the feeder to 2 or 3. Aggressive behavior was suppressed during extreme cold, however, and then all perches were sometimes used. Use of the recorder provided information on the time of first and last feeding each day and a relative picture of the intensity of feeding throughout the day. Lost in comparison to visual methods, however, was information on any differences in timing of arrival vs feeding, on actual numbers of birds present at the feeding station (as opposed to numbers at the peanut butter feeder loci), and the actual light intensity at the times of morning arrivals and evening departures. Between February 1964 and the end of the study, many of the data were gathered via the automated feeder, but from time to time these recordings were supplemented with visual observations.

Because I was working with a wild, free-ranging population of chickadees, knowledge of the population under study was not as good as would have been desirable. Four times during the study, each time in early spring, I trapped and banded all chickadees using the feeders; numbers in different years varied from 25 to 48 birds. As is typical of Black-capped Chickadees, however, the population was composed of small flocks which ranged over a fairly large area, and not all birds visited the feeding station every day. Especially in later years, too, when neighbors constructed other feeding stations, flocks traveled from one station in the neighborhood to another for feeding. A fluid population of varying size, however, should not significantly affect data on first arrival and last departure times or the length of the activity day as recorded at the feeder, but individual variation undoubtedly plays a minor role. Some individuals consistently arrived earlier or later than the main population, perhaps because of closer roosting sites, perhaps because of a somewhat different synchronization (phase angle) of endogenous rhythms to the light cycle, sexual differences, different physiological states, etc. Even with marked birds, however, it was impossible to read color combinations during twilight periods and hence to identify individuals.

Simultaneously with making observations on the activity patterns of the chickadees, environmental data were gathered. Maximum and minimum daily temperatures were recorded at the feeding station throughout the study. Temperature and sky cover at the time of each set of observations were tabulated, and the occurrence of wind or precipitation was noted. Whenever possible, a series of light intensity readings was made, corresponding to times of morning arrivals and evening departures.

For light intensities, a photo cell (a light-dependent resistor), set about 3 cm back into a 2.2 cm diameter tube, was permanently mounted on the top of the inside of a window frame; the opening of the tube was directed at an angle of about 50° toward the ground outside. The light readings were read from an ohmmeter with an expanded scale calibrated to that of a Gossen Lunasix light meter. All readings were taken against a snow surface, and hence the relative light intensities recorded were of light reflected at a constant angle from a white surface. Comparative readings were obtained for reflected and incident light, so I can convert my readings to either luces or foot candles; the lux readings are used in this paper.

Statistical analyses have been employed in an attempt to determine the relative importance of various environmental factors on the chickadee's activity patterns. These factors are so interrelated that it would be impossible otherwise to determine their individual effects. Light intensity, for instance, is related to the daily light cycle, in that it is basically determined by the position of the sun in relation to the horizon; and it is further affected by variability in sky cover, with overcast days being darker at any given time. Temperature is also affected by sky cover, with overcast days in winter tending to be warmer than clear days. And solar radiation has interrelationships with the daily light cycle, light intensity, sky cover, and temperature.

The Biomedical Computer Program "BMDO2R—Stepwise Regression" (Dixon 1973) was used for most of the analyses. In addition to computing stepwise multiple linear regressions, this program provides a matrix of correlations, and I have used results from both types of analyses. In the regression analyses, I used every possible ordering of the independent variables for each dependent variable. The various environmental factors included as independent variables accounted for 93% of the variation in my data for the length of the activity day, 86% for the time of first activity relative to the beginning of morning Civil Twilight (sun 6° below horizon), 85% for the time of last activity relative to the end of evening Civil Twilight, and 79% for feeding intensity. These relatively high percentages lend credence to the results of the analyses.

Some preliminary stepwise regression analyses were made to determine which events in the daily activity cycle to use as "first" and "last" activity (when heard? when arrived? when they fed?), which temperatures to use (temperature at time of beginning and end of activity? yesterday's mean temperature? today's mean temperature?), which sky cover data (mine? National Weather Service data on average daily sky cover? on total opaque sky at the time of first and last activity?), and which solar radiation data (National Weather Service data on total daily solar radiation for yesterday? for today?).

In choosing the event to mark the first and last activity of the day, I decided to lump all types of observed activity in order to obtain as many data points as possible. My data were insufficient for separate analyses of all the individual activities, and 317 lumped observations made between 24 October and 2 March showed little more variability (SD = 7.25 min) than 251 "first arrived" observations made during the same period (SD = 6.92 min). Therefore, first and last activity as used in this paper refer to the time the first or last bird, respectively, was seen at the feeder site, was recorded at the mechanized feeder, or was heard.

Temperature measurements showed considerable interdependency (today's mean temperature showed an 84% correlation with yesterday's mean temperature and a 95% correlation with the temperature at last activity; temperature at first activity showed an 76% correlation with yesterday's mean temperature); based on regression analyses, however, temperatures at the time of first and last activity were selected, although the mean temperatures for the preceding 24-hour period also exerted a significant effect ($P < .001$). My sky cover readings, rating cloud cover from 1 to 5, appeared most influential (see discussion under *Effect of Sky Cover*), as did yesterday's total solar radiation in relation to first activity and today's total solar radiation in relation to last activity.

Data on intensity of feeding are from 69 days for which full-day recordings were obtained after the feeder was automated in 1964. Feeding intensity was determined by calculating the total number of bird-minutes per unit time (either per day or per minute) spent by chickadees at the feeder. These data, of course, are measures of feeding in a free-ranging population, so data given below are all relative and represent only a portion (hopefully a representative sample) of the population's feeding activity. Because of varying numbers of birds using the feeder in different years, direct comparison of even relative feeding intensities between years is not possible, although comparison of general daily activity patterns is feasible.

Several sets of data have been used in the analyses of this study so as to maximize the data base, since information on all factors was not obtained every day. For example, the early discussion on length of activity day is based solely on 161 days where data for both morning and evening were available, whereas later discussions are based on all days where either morning or evening data were available.

RESULTS AND DISCUSSION

Much has been learned about the daily activity patterns of birds since Palmgren's (1935), Paatela's (1938), Franz's (1943, 1949), Wagner's (1958), and Hoffmann's (1959) early observations of birds at northern latitudes. We now know that endogenous rhythms are major controlling factors in the daily and annual cycles of birds and that these rhythms are synchronized with environmental rhythms (primarily the daily light cycle) through entrainment to a Zeitgeber (Aschoff 1967). Studies using specific measurements of a number of environmental factors affecting avian activities under natural conditions have been undertaken (e.g., Leopold and Eynon 1961, Morton 1967a and b, Davis and Lussenhop 1970, and Krantz and Gauthreaux 1975), as have controlled experimental studies of these factors (see Aschoff 1965, Menaker 1971, and others cited below). The reaction mechanism of organisms to environmental factors cannot readily be determined under natural conditions, but the daily and seasonal activity patterns of the Black-capped Chickadee in this study compare so well to the oscillator model theory of endogenous rhythms that there is little doubt that the major environmental factors of light and temperature are influencing activity through their effect on endogenous rhythms.

General Seasonal Pattern of Diurnal Activity Cycle

Fig. 1 shows the times of first and last activity on days for which data were obtained from 1960 through 1967 as well as the beginning of morning Civil Twilight and the end of evening Civil Twilight. During the summer and early

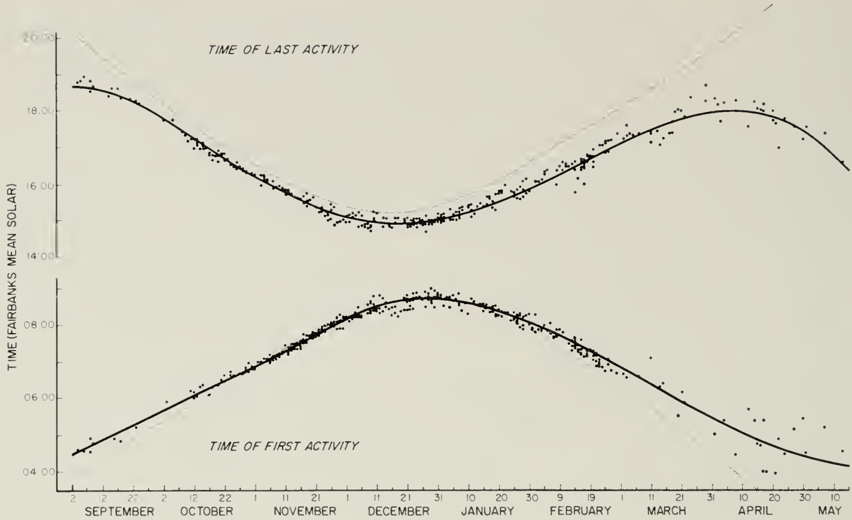

Fig. 1. Times of first and last activity of chickadees recorded from 1960 through 1967. Times have been adjusted for longitude and are true solar times. The dotted lines represent the times of the beginning of morning Civil Twilight and ending of evening Civil Twilight, respectively; the solid lines are best-fit polynomial curves, adjusted somewhat by eye.

autumn, morning activity began after the beginning of Civil Twilight. Within a few days of 1 November, first activity began to occur prior to the beginning of Civil Twilight; and, except during occasional periods of cold stress (see below), chickadees generally continued to become active before the beginning of Civil Twilight until sometime during the first few days of January, after which they again usually remained at roost until after the beginning of Civil Twilight. (During the unusual winter of 1960–61, when temperatures were relatively warm and cloud cover relatively low, chickadees continued to become active before the beginning of Civil Twilight until the third week of January.) Activity ceased prior to the end of Civil Twilight throughout the year, and it ceased even before sunset from sometime during the first half of February until mid-September.

Regression analyses showed that the daily light cycle (= time of beginning and ending of Civil Twilight) is by far the dominant environmental factor affecting the chickadee's activity cycle ($P < 0.001$). The time of 249 first activity observations made between September and May showed a 93.1% correlation with the time of the beginning of morning Civil Twilight and a 96.0% correlation of 193 last activity observations over the same period with the ending of evening Civil Twilight.

The seasonal shifts in the time of first and last activity in relation to changing daylengths, defined as extending from the beginning of morning Civil Twilight to the end of evening Civil Twilight, appear to be adaptational responses to mean annual environmental stresses. In general, as seen in Fig. 1, as daylengths get shorter during the fall and early winter, the activity day gets proportionately longer in relation to the length of day. Not only did chickadees begin activity earliest in relation to morning Civil Twilight at and just prior to the winter solstice, but they had a longer activity day relative to daylength during November, which may be an adaptation for increased feeding and caching activity prior to the most stressful days of winter. (These longer days are apparent in Fig. 1 for the last third of November, in spite of the consistently cold temperatures that occurred during that period during all years of the study—lower temperatures which acted to shorten the activity day.) After the winter solstice, almost as soon as daylengths begin increasing, the activity day decreases relative to daylengths, in spite of the fact that environmental conditions are still severe during January and February. At least 2 influences may be operating here: the autumnal drive toward increased feeding and caching should no longer be operative, and the bird's physiology is beginning to shift toward breeding. (In some years, birds began singing as early as 16–18 December, and in most years they were singing regularly by 1 January.)

Length of Activity Day

Regression analyses of 161 days where both morning and evening data were available showed that daylength was the most important factor determining the length of the activity day ($P < 0.001$), with 53% of the variability in the length of the activity day explained by this factor alone. Other factors which proved significant, after adjusting for all other independent variables, were temperature and day of the year. The activity day is shorter at cold temperatures than at warmer temperatures and vice versa ($P < 0.01$). The significance of the day of the year ($P < 0.001$), after the effects of daylength and temperature have been accounted for, is apparently due in part to the longer activity days observed during late fall and early winter and in part to the shorter activity days relative to daylength that occur progressively after early January as compared to those before the winter solstice.

Average daily sky cover (cloudiness) did not prove statistically significant in its effect on the length of the activity day in the analyses of these 161 days; but, as discussed below, light intensity and sky cover, after adjusting for all other independent variables, affect the times of first and last activity and hence, to some extent, the length of the activity day.

For these 161 days, today's total solar radiation showed a 70% positive correlation with the length of the activity day (the greater the total radiation the longer the activity day), but after the effects of daylength and the day of the year had been accounted for, the additional effect of solar radiation became insignificant. What at first appeared to be an effect of solar radiation was really the result of (1) longer days allowing greater time for accumulation of total solar radiation and (2) the longer days being in the spring and fall when the sun is higher in the sky.

Effect of light intensity.—After the daily light cycle per se (accounted for in my analyses by using activity relative to Civil Twilight as a dependent variable), light intensity exerts the greatest influence on the time of beginning and ending of daily activity of the chickadee ($P < 0.001$). On dark days, activity begins later and ends earlier than on bright days. Delays of up to 5 or 10 min in the commencement of morning activity due to darkness are not unusual. On 23 December 1962, when it took 20 min longer than on the preceding day to reach "threshold" light intensities, first activity also occurred 20 min later; similarly, a 12-min difference between the time of first activity on 27 and 28 December 1960 is ascribable to a parallel delay in light intensities reaching comparable levels.

The sensitivity of chickadees to light intensities appears to change during the year; and, as one would expect, these changes show a direct relationship to the seasonal shifts in the interrelationships of the daily light cycle and the daily activity cycle. Many avian studies have shown seasonal shifts in the time of beginning and ending of various activities relative to the sun's position; and, recently, Pohl (1972) has demonstrated a seasonal change in the sensitivity of the circadian system to light in Redpolls (*Acanthis flammea*). Fig. 2 shows the light intensity at first and last activity for chickadees on all days for which data are available from 1960–1967. As with other species that have been studied (Aschoff and Wever 1962. Leopold and Eynon 1961 and references therein), light intensities in the morning at first activity are considerably lower than in the evening when activity ceases. The range of light intensities relative to activity times is quite great (due in large part to temperature influences), but the best-fit polynomial lines for both morning and evening show a clear trend and the trend lines for morning and evening are similar. In general, the chickadees begin and end their daily activities at lowest light intensities during the last half of November and the first half of December (perhaps until 21 December)—again during the period of decreasing daylengths prior to the winter solstice and during the period of food caching. Dunnett and Hinde (1953), with captive Great Tits (*Parus major*) in England, also found that dawn emergence times were slightly earlier in late November and December relative to sunrise than in October and subsequently. During this period, the Fairbanks chickadees begin their activity in the morning at

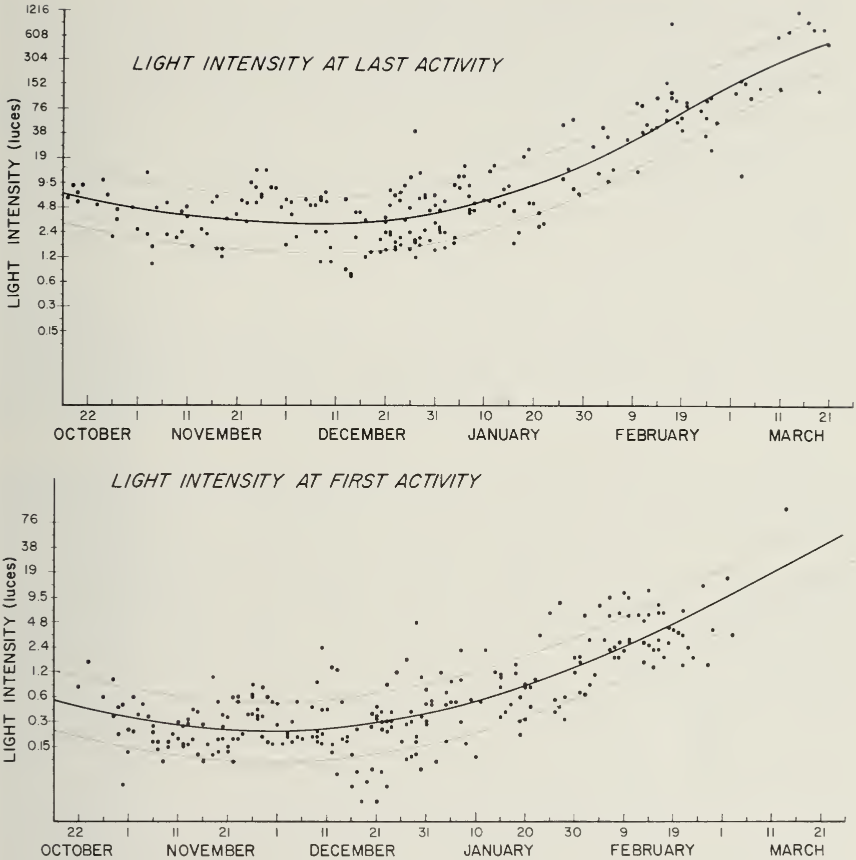

FIG. 2. Light intensity at the time of first and last activity, 1960–1967. The center lines are the best-fit polynomial curves for first and last activity, and the lines on either side are the distance of one standard deviation from the best-fit lines.

light intensities that seem marginal for vision—most commonly at 0.15–0.23 lux, and the end of their activity day is in the 2.4–4.8-lux range. At these light intensities, chickadees sometimes appear to "stumble" about the tree branches, as if it were too dark to see—in spite of the fact that this behavior sometimes occurs in the evening at light intensities far brighter than those at which they functioned adequately in the morning or at another season. After late December, the birds begin and end their activity day at steadily increasing light intensities (see Fig. 2).

The lower light intensities at which the chickadees begin and end their daily activities at a given time of year appear to represent a threshold for activity, a threshold that differs in level morning and evening, at various times of year, and perhaps with temperature. As indicated above, on dark mornings, activity begins correspondingly later, and vice versa in the evenings. The fact that chickadees began activities at the lowest light intensities observed during the study during the unusually warm, cloud-free December of 1960 suggests a possible relationship between environmental temperatures and the shifting threshold of the bird's sensitivity to various levels of light intensity.

Effect of temperature.—On cold days, first activity occurs later relative to the beginning of morning Civil Twilight and the last activity earlier relative to the end of evening Civil Twilight than on warm days, and vice versa. This effect of temperature appears to be a more or less graduated one, with weeks or months of colder mean temperatures showing correspondingly shorter activity days than equivalent warmer periods, although there is some evidence that temperature is more influential, even critical, during extreme cold.

The influence of temperature on the activity period is difficult to demonstrate, largely because light, which is such a dominant factor, interrelates in several ways with temperature. In winter at Fairbanks, meteorological conditions are such that days are either dark (overcast) and relatively warm or are bright (clear) and cold, and these sets of conditions act in opposition to each other in relation to the length of the activity day. Also, when cold temperatures delay the beginning of activity in the morning, the brighter light at first activity is a function of lateness due to temperature rather than a response of the bird to light intensities: the reverse is true when birds roost earlier, and hence at brighter light intensities, on cold days than on warm days. When light was not included in the analyses, temperature showed a significance at the $P < 0.001$ level in its effect on the time of beginning and ending of daily activity relative to Civil Twilight. Also, as indicated above, other statistical analyses relative to the total length of 161 activity days showed temperature significant at the $P < 0.01$ level. Regression analyses of mid-winter data (20 Nov. to 10 Jan.), when environmental stresses are most severe, showed temperature to have almost 2.5 times the influence on the timing of first activity that it had during early and late winter, although temperature was significant at the $P < 0.001$ level during both periods.

In Fig. 1, the times of first activity for 364 observations and last activity for 332 observations made throughout the study are plotted by the day of the year, and best-fit curves, fitted in part mathematically and in part by eye, have been drawn through the points. A rough, overall indication of the effect of temperature can be obtained by averaging the temperatures at the time of first or last activity, respectively, for those days in which activity began or ended later than the mean time, as indicated by the best-fit curve, and comparing these mean temperatures with those days on which activity began or ended earlier than

TABLE 1

MEAN TEMPERATURES (± SD) AT TIME OF FIRST ACTIVITY*

First activity relative to mean time	November	December	January
Later than mean time	−19.1°C ± 9.8 (n = 52)	−22.2°C ± 14.3 (n = 34)	−18.6°C ± 10.3 (n = 35)
	$P < 0.2$	$P < 0.01$	$P < 0.2$
Earlier than mean time	−12.7°C ± 6.0 (n = 34)	−13.3°C ± 8.8 (n = 49)	−14.8°C ± 9.7 (n = 22)

* Using t-test for unpaired observations, unequal variances, and small, unequal sample sizes to test means of adjacent groups (Cochran and Cox 1957). P = probability of getting sample means as different as those observed if temperature was not an influence.

the mean time. The results (Tables 1 and 2) suggest that timing of the first and last activity are, indeed, related to temperature, with data showing greater statistical significance during December, the coldest month.

A further refinement, accounting for the effect of light intensity, can be made by analyzing first and last activity in relation to light intensity and temperature. (Other things being equal, the later the time of first activity—or the earlier the time of last activity—the greater the light intensity.) Using the best-fit polynomial lines in Fig. 2 as the mean light intensity at first or last activity, respectively, mean temperatures above (brighter) and below (darker) this line were calculated. Additional lines were drawn the distance of one standard deviation (= 1.18 lux at first activity, 1.09 lux at last activity) on either side of the best-fit line, and mean temperatures at first and last activity, respectively, were calculated for these further subdivisions. In spite of the great variability

TABLE 2

MEAN TEMPERATURES (± SD) AT TIME OF LAST ACTIVITY*

Last activity relative to mean time	November	December	January
Later than mean time	−13.1°C ± 7.7 (n = 28)	−13.1°C ± 6.5 (n = 32)	−16.0°C ± 9.9 (n = 34)
	$P < 0.01$	$P < 0.001$	$P < 0.01$
Earlier than mean time	−23.6°C ± 9.7 (n = 17)	−24.5°C ± 12.7 (n = 42)	−23.9°C ± 6.7 (n = 17)

* Data analyzed as in Table 1.

TABLE 3

MEAN TEMPERATURES ($\pm$ SD) IN RELATION TO LIGHT INTENSITY AT TIME OF FIRST ACTIVITY*

	November	December	January
More than 1 SD brighter (later) than mean	$-27.0^{\circ}\mathrm{C} \pm 3.7\ (n = 10)$	$-41.1^{\circ}\mathrm{C} \pm 5.9\ (n = 9)$	$-25.6^{\circ}\mathrm{C} \pm 9.1\ (n = 6)$
	$P < 0.001$	$P < 0.001$	$P < 0.2$
1 SD brighter (later) than mean	$-19.2^{\circ}\mathrm{C} \pm 7.9\ (n = 27)$	$-15.5^{\circ}\mathrm{C} \pm 6.2\ (n = 18)$	$-17.7^{\circ}\mathrm{C} \pm 10.4\ (n = 18)$
	$P < 0.01$	$P > 0.3$	$P < 0.3$
MEAN LIGHT INTENSITY			
1 SD darker (earlier) than mean	$-13.6^{\circ}\mathrm{C} \pm 7.2\ (n = 32)$	$-14.5^{\circ}\mathrm{C} \pm 9.1\ (n = 31)$	$-13.3^{\circ}\mathrm{C} \pm 9.0\ (n = 15)$
		$P < 0.02$	$P < 0.1$
More than 1 SD darker (earlier) than mean	$(n = 0)$	$-9.2^{\circ}\mathrm{C} \pm 4.6\ (n = 14)$	$-12.6^{\circ}\mathrm{C} \pm 9.2\ (n = 9)$

* Data analyzed as in Table 1.

in the data, the trends shown in Tables 3 and 4 illustrate the influence of temperature on the timing of the first and last daily activity in chickadees.

Under natural conditions, periods of extreme or widely fluctuating conditions best illustrate relationships. Specific examples of the effect of temperature on chickadee behavior are presented in Fig. 3, where changes of the time of first activity during abrupt and severe shifts in environmental temperatures are shown for brief periods in December 1961 and December 1964. Here, again, it shows that cold temperatures in the morning delay the beginning of the daily activities when compared to warmer temperatures.

Aside from causing shorter activity days, severe cold snaps appeared to affect chickadees in other ways. On mornings preceded by precipitous temperature drops, first activity times were not only later, but were more irregular than usual; instead of taking 5 to 8 min for a substantial number of chickadees to arrive at the feeder site, it would take 10 to 15 min. Another effect was that fewer birds used the feeding station, and, the more severe and longer the cold snap, the more this effect was evident. Either the birds were less active and fed less or their feeding radius was so reduced that few reached the feeder.

TABLE 4

MEAN TEMPERATURES (± SD) IN RELATION TO LIGHT INTENSITY AT TIME OF LAST ACTIVITY*

	November	December	January
More than 1 SD brighter (earlier) than mean	−26.5°C ± 7.9 ($n = 8$)	−42.8°C ± 6.7 ($n = 8$)	−24.5°C ± 6.5 ($n = 9$)
	$P < 0.1$	$P < 0.001$	$P < 0.4$
1 SD brighter (earlier) than mean	−20.1°C ± 6.9 ($n = 13$)	−25.7°C ± 8.9 ($n = 22$)	−21.2°C ± 9.7 ($n = 12$)
	$P < 0.02$	$P < 0.001$	$P < 0.2$
MEAN LIGHT INTENSITY			
1 SD darker (later) than mean	−9.8°C ± 6.9 ($n = 8$)	−12.5°C ± 4.9 ($n = 26$)	−15.6°C ± 8.2 ($n = 14$)
	$P < 0.3$	$P < 0.2$	$P < 0.1$
More than 1 SD darker (later) than mean	−5.6°C ± 5.2 ($n = 6$)	−10.1°C ± 5.2 ($n = 13$)	−10.2°C ± 7.4 ($n = 15$)

* Data analyzed as in Table 1.

Johnson (1957) commented that Fairbanks Black-capped Chickadees were quiet, inconspicuous, and flew less during cold snaps. At my feeder site in late December 1961, when temperatures between 26 and 29 December remained in the −46° to −51°C range (−49° to −53°C in the valley bottoms, Fairbanks International Airport readings), birds using the feeder were so few that I feared a die-off. However, when temperatures bounced back to −28°C on the morning of 30 December, the birds returned and my notes recorded that they were "*much* more lively."

Several things, here, suggest that environmental temperatures may be influencing the chickadee's behavior by acting on an endogenous rhythm. Recently, limited experimental data with House Finches (*Carpodacus mexicanus*) (Enright 1966), Chaffinches (*Fringilla coelebs*) (Pohl 1968a and b), and House Sparrows (*Passer domesticus*) (Eskin 1971) have shown that environmental temperatures affect the endogenous circadian rhythms of homeotherms; and the shorter activity days in the present study caused by colder temperatures are in the direction predicted by the oscillator model theory of endogenous rhythms (Aschoff 1965), as is the apparent reduction of activity on

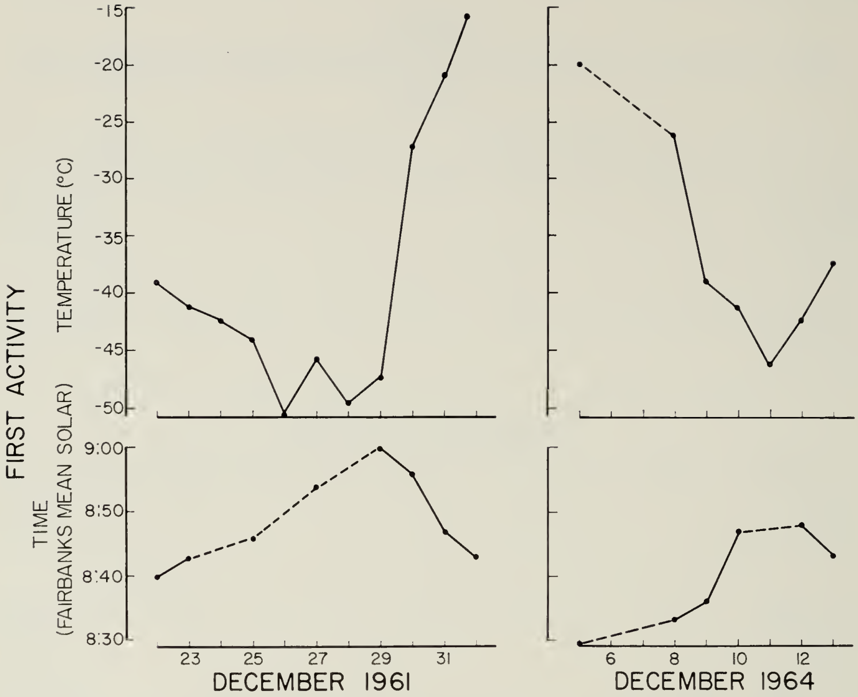

FIG. 3. Times of first activity relative to temperature during abrupt and severe changes of temperature in December 1961 and December 1964. Cold temperatures delayed the beginning of activity compared to warmer temperatures. Dotted lines have been used where intermediate data points are lacking.

cold days. Also, the irregularity of commencement of first activity with sudden changes of temperature is suggestive of phase-shifting of endogenous rhythms.

Regardless of the underlying response mechanism, all of these temperature effects on the activity pattern of the chickadee make it appear that, during periods of extreme cold stress, energy levels are better maintained under conditions of reduced activity rather than traveling distances for food or extending feeding periods. Recently, Chaplin (1974) in New York and Grossman (1975) at Fairbanks have even reported hypothermia in Black-capped Chickadees. Behaviorally on these cold days at Fairbanks, the chickadees fluff their feathers, until they resemble little balls, and withdraw their legs until they are entirely enveloped by the fluffed feathers. Hoar frost frequently develops about their heads from their breath, and excreta "steams" as it drops through the cold air to the ground.

Lawrence (1958) found that Black-capped Chickadees in central Ontario (46°N) also emerged later in the morning and roosted earlier on very cold days. She also noted that on mornings when temperatures were below −29°C, instead of feeding intensely early in the morning as on milder days, the chickadees sought sites sheltered from wind and exposed to the rays of the sun, apparently improving their energy balance behaviorally.

Markgren (1963) found that Bean Geese (*Anser fabalis*) spent much of their time in an inactive, sleeping position during inclement winter weather in Sweden, and Raveling et al. (1972) observed that Canada Geese (*Branta canadensis*) reduced their activity at low winter temperatures in southern Illinois. Raveling et al. (op. cit.) noted that larger-sized subspecies began inactivity at lower temperatures than the smaller ones and suggested that "inactivity is the most adaptive response to severe cold and functions to conserve energy."

Effect of sky cover.—Sky cover, after adjusting for the effects of light intensity, exerts a significant effect ($P < 0.001$) on the time of first activity relative to morning Civil Twilight, the chickadees beginning their activity earlier on clear mornings than on cloudy ones. Sky cover may have some influence on the time of last activity relative to evening Civil Twilight (later on clear afternoons) ($P < 0.10$), but much less so than in the morning.

In examining the effect of sky cover, I worked with several sets of data. I used my own observations made at the feeding station; because the station was on a south-facing, wooded slope and because my observation window faced southward, my sky cover observations were essentially of the southern half of the sky. The other sets I used were from the National Weather Service: total opaque sky at the time of first and last activity and, for last activity, the average daily sky cover from sunrise to sunset. Average daily sky cover appeared to have no effect on the timing of last activity, and total opaque sky cover showed less influence, both morning and evening, than the southern sky from which I recorded my data. It appears, then, that the birds were responding to the part of the sky that they could see, i.e., the southern sky seen from their vantage point on a south-facing slope.

There are 2 possibilities for the differing effect of sky cover in the morning and the evening. The first is that the sky cover may have more of an effect in the morning than in the evening. The other possibility is that, while the sun rises in the southeast and south during the winter in Fairbanks—in the portion of the sky most visible to the chickadees using the feeder site—it sets in the southwest or west, behind a hill and in a part of the sky less completely visible to the birds. If the birds are responding to the effects of a brighter sky or some other effect caused by the sun in addition to cloud cover per se, then responses might differ between the morning and evening.

Leopold and Eynon (1961) noted that early in the year in Wisconsin some birds appeared to require more light for daybreak song on cloudy mornings. They failed to recognize, however, that cloud cover, over and above its effect on light intensity, could affect activity and that the increased light at daybreak song was the result of lateness caused by sky cover.

Effect of solar radiation.—Solar radiation appears to influence the chickadee's activity period at Fairbanks, although not strongly, perhaps because there is so little of it during the portion of the year included in this study. Average total daily solar radiation, in langleys, at Fairbanks in October is around 80; in November, 25–35; in December, about 5; in January, 15–20; in February, 80–95; and in March, over 200.

The effect of today's total solar radiation on the length of 161 activity days analyzed did not prove statistically significant after the effect of daylength and the day of the year had been considered. On the other hand, analyses of today's total solar radiation (after adjusting for all other factors) in relation to last activity relative to Civil Twilight for 90 days between 10 October and 2 March showed a small but significant effect ($P < 0.05$), with roosting occurring earlier when total solar radiation for the day had been greater. While not statistically significant ($P > 0.10$), the same trend showed in data for 228 mornings, i.e., when yesterday's total solar radiation was greater, first activity relative to Civil Twilight occurred later. In other words, over the period of 10 October through 2 March, increased total solar radiation tended to shorten the day.

When I repeated these latter analyses, but restricted the period to 20 November through 10 January, the severest part of the winter, the effect of solar radiation was reversed. That is, the chickadees tended to begin activity earlier and roost later relative to Civil Twilight (= longer days) with increased solar radiation. Again, the effect was statistically significant in my evening data ($P < 0.025$), but not in the morning ($P > 0.10$). (The difference in the significance of solar radiation between morning and evening data is undoubtedly related, at least in part, to the time difference between the time the solar radiation was received and the time activity began or ended. Roosting birds are under the immediate influence of today's total solar radiation, whereas there is a lapse of 12–18 hours between receipt of yesterday's total solar radiation and the first activity of the day.)

Thus, during the relatively longer and warmer days of early and late winter, activity days are shorter when there is more solar radiation; but, during the short, cold days of mid-winter, the length of the activity day is increased slightly when more solar radiation is received. Since the energy balance in very cold weather may be best maintained by inactivity (see *Effect of temperature*), it appears that increased solar radiation, little as it is at this stressful time of year, may improve the energy balance enough to allow slightly longer foraging days.

I cannot provide specific illustrations of the effect of solar radiation from my study, only the statistical evidence cited above. The apparent importance to Black-capped Chickadees of solar radiation in extreme cold temperatures was observed by Lawrence (1958) in central Ontario, however, where she watched fluffed birds perched facing the sun, even on cloudy days, and birds basking high in trees on sunny days.

Krantz and Gauthreaux (1975) found a close correlation in the day-to-day variation in the time of arrival at the roost of Brown-headed Cowbirds (*Molothrus ater*) in South Carolina with the daily amount of solar radiation, later arrival being associated with greater solar radiation. Morton (1967b) found that White-crowned Sparrows (*Zonotrichia leucophrys*) in Washington reduced their feeding activity under conditions of direct insolation (or under artificial short-wave infrared radiation) and concluded that the radiant energy received alleviated the energy costs of thermoregulation in cool situations.

Effect of precipitation.—Snow falling at the time of first and last activity appears to exert a slight effect on the timing of these activities, snow causing first activity to begin later and last activity to end earlier relative to Civil Twilight.

Specific examples of the effect of snow are hard to isolate because of the dominant influence of light and sky cover; conditions are almost always dark and cloudy when it is snowing, and each of these factors contributes individually to later first activity times relative to Civil Twilight. First activity times on the mornings of 28, 29, and 30 December 1960, however, provide a good illustration of the effect of falling snow. The morning of 28 December was dark, overcast, and 0°C, and the first chickadees arrived at the feeder just after 8:32 at 0.10 lux; the next 3 birds arrived within 2.5 min. Snow fell on the morning of 29 December, but, in spite of the snow, light reached intensities equivalent to those on the 28th 8 min earlier; skies were overcast and the temperature was −3°C. Except for the quick visit of a single bird at 8:25 (0.10 lux), there was no activity at the feeder until 8:34 (0.42 lux), and it took another 5 min before the fourth bird had arrived. In my notes, I wrote, "8 min brighter than yesterday, in spite of snow, but chickadees *very* slow in arriving. Late, irregular, extended arrival period, and some never showed up at the feeder." The morning of 30 December was overcast, −8°C, but without snow, and light intensities were similar to those on the 29th. The first bird arrived at 8:20 (0.02 lux) and the fourth bird had arrived by 8:34, reconfirming that falling snow was apparently a delaying factor on the morning of 29 December.

Another example of delay in morning activity apparently due to snow shows up in observations from 13 and 14 December 1960. Both mornings were overcast and light intensities were almost identical; temperatures were −3°C on 13 December and 8°C on 14 December. It was snowing on the morning of 14 December, and chickadees arrived at the feeder 6 min later (0.22 lux brighter) than on the preceding day.

Statistically, the effect of snow can be isolated a bit better from the other influencing environmental factors. However, snow fell during only 28 of my morning and only 24 of my evening observation periods, and the influence is so slight (less than 0.4% of the variability in my data attributable solely to falling snow) that, while definite trends are visible, data are insufficient for statistical significance. The effect on the timing of first activity during the longer days of early and late winter (114 mornings, 24 October–19 November and 11 January–1 March) may have been significant ($P < 0.10$), although data for mid-winter were not ($P > 0.10$). Evening data lacked statistical significance ($P > 0.10$), but the data showed a consistent trend in the direction of falling snow causing earlier roosting.

Kluijver (1950) reported that in the Netherlands rain and snow delayed emergence of Great Tits (*Parus major*) in the morning and that rain often caused earlier retirement in the evening. Odum (1942) reported earlier roosting in Black-capped Chickadees in New York on snowy days. Williams (1941) found a tendency for Chestnut-backed Chickadees (*Parus rufescens*) in California to come to roost at somewhat higher light intensities (= earlier) on rainy days.

Effect of wind.—Wind at the time of first activity tends to delay the beginning of morning activity relative to Civil Twilight. The effect is so slight (less than 0.15% of the variability in my morning data attributable solely to wind) and observations so few (only 22 mornings had wind) that my data are not significant, statistically. All the statistical results, however, show the same delaying trend in the morning due to wind. A specific illustration of this delaying effect is provided by a comparison of conditions on the mornings of 1 and 2 November 1962. It was overcast and −1°C on 1 November; the first bird arrived at the feeder at 6:40 and 3 birds were present by 6:45. It was overcast and −2°C on 2 November, with gusty surface winds. It took 4 min longer on 2 November for light intensities to reach levels equivalent to 1 November, but the first bird did not arrive until 11 min later, at 6:51; 4 birds were present by 6:53.

I am unable to make anything out of my data (20 observations) regarding the influence of wind on the timing of last activity relative to Civil Twilight.

During periods of actual observation, the only consistent pattern I was able to discern relative to wind was that the birds had less tendency to move

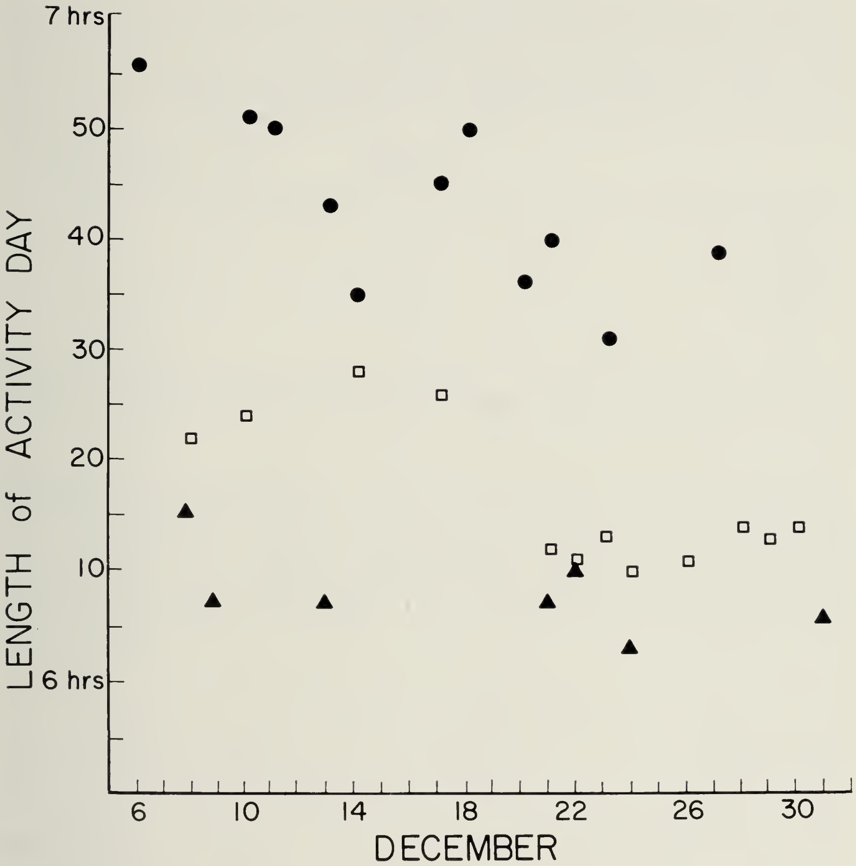

Fig. 4. Length of activity days during December of 1960 [●], 1963 [□], and 1964 [▲]. The longest activity days occurred during the relatively warm, cloud-free December of 1960, and the shortest during the relatively cold, cloudy December of 1964 (cf. Table 5).

about in relatively windy weather than on calmer days and that during periods of gusts the birds either remained tightly perched or temporarily disappeared from the scene, presumably seeking shelter. The morning of 10 January 1961, for example, was a windy, gusty day of −27°C, and I noted that the birds "seem directly affected by wind gusts; they disappear with every strong gust."

Leopold (1949) noted that Black-capped Chickadees in Wisconsin avoided windy situations; and Kluijver (1950) found that the first morning appearance of the Great Tit in the Netherlands was delayed by strong winds, and, at least in March, that such winds had a tendency to cause early retirement.

TABLE 5

COMPARISON OF THE AVERAGE MONTHLY TEMPERATURES AND AVERAGE PERCENT SKY COVER FOR THE VARIOUS DECEMBERS OF THE STUDY*

	Av. Monthly Temperatures (°C)	Av. Percent Monthly Cloud Cover
Dec. 1964	−29.7	72
1961	−29.3	57
1966	−24.9	69
1962	−18.9	65
1963	−12.8	75
1960	−11.7	62

* The shortest activity days occurred in 1964 and the longest in 1960, with activity days being intermediate in length in the other years.

Interrelationships of environmental factors.—All these main environmental influences act on the birds simultaneously, and when individual factors are additive (e.g., possibly low light intensities, complete sky cover, and cold temperatures), the response of the bird is greater than if some of these factors occur in opposition, tending to dampen the individual effects. Some of these interrelationships can be demonstrated in relation to the differing lengths of mid-winter activity days in different years. The shortest mid-winter days were in 1964–65, the longest in 1960–61, and the other years clumped between these extremes (Fig. 4). Unfortunately, I lack complete, pertinent environmental data from my own observations, but much of the annual variation seems explainable even with the more generalized weather data from the National Weather Service. From this source, in Table 5, are listed the average monthly temperatures and the average percent cloud cover for December of the various years. Average cloud cover can be used here as a rough measure of light intensity and sky cover, which are additive in their effects. December 1964 was the coldest and the cloud cover almost the greatest, whereas December 1960 was the warmest and the cloud cover almost the least; the additive effects in each instance apparently resulted in the shortest and longest activity days, respectively.

The relative influence of several of the environmental factors on the chickadee's activity period appears to change during the winter. This shift is most evident from my morning data. Light intensity is by far the most important factor influencing the time of first activity relative to Civil Twilight throughout the winter, but it accounts for more of the variability in early and late winter than in mid-winter (62% vs 52%). Sky cover is the second most influential factor in early and late winter, but drops to third in mid-winter.

Temperature is the second most influential factor during the short, cold days of mid-winter. In the evening, light appears to have more influence on the time of last activity in mid-winter than during early and late winter, and the same is true of the influence on last activity of the time of first activity relative to Civil Twilight.

In comparing statistically the influence of the various environmental factors on the time of beginning and ending of activity relative to Civil Twilight, it became evident that each factor exerts less influence in the evening than in the morning, although light intensity and temperature are still highly significant. This difference again suggests the involvement of an endogenous rhythm, a rhythm that is "set" in the morning and then largely runs its course until activity ceases in the evening. A comparison of the effects of morning environmental factors and evening environmental factors on the time of last activity relative to the end of evening Civil Twilight shows that the light intensity at the time of last activity is the most important factor ($P < 0.001$), accounting for over 30% of the variability after all other factors have been taken into account. The apparent influence on last activity of the time of first activity relative to the beginning of morning Civil Twilight is also highly significant ($P < 0.001$), but accounted for only about 3% of the variation.

Feeding Intensity

Amount of feeding per activity day.—Temperature is the most significant factor affecting feeding intensity ($P < 0.001$); 77% of the variability in daily feeding intensity was attributable solely to temperature, with today's mean temperature being far more influential than yesterday's mean temperature. Feeding intensity showed a 41% negative correlation with daylength ($P < 0.001$), but, after the effect of temperature had been accounted for, daylength was not significant (mid-winter days are cold as well as short). The same situation existed with average sky cover, i.e., average sky cover showed an 11% negative correlation with feeding intensity (the less cloud cover the greater the feeding intensity) ($P < 0.001$), but when temperature was taken into account (colder on clear days), sky cover was no longer significant.

Solar radiation, whether today's or yesterday's total solar radiation, showed a 20% negative correlation with feeding intensity (less radiation, greater feeding intensity) ($P < 0.001$), but after temperature and day of year were considered (cold days are clear with greater solar radiation; mid-winter days are cold and short), solar radiation per se did not show a statistically significant effect on feeding intensity.

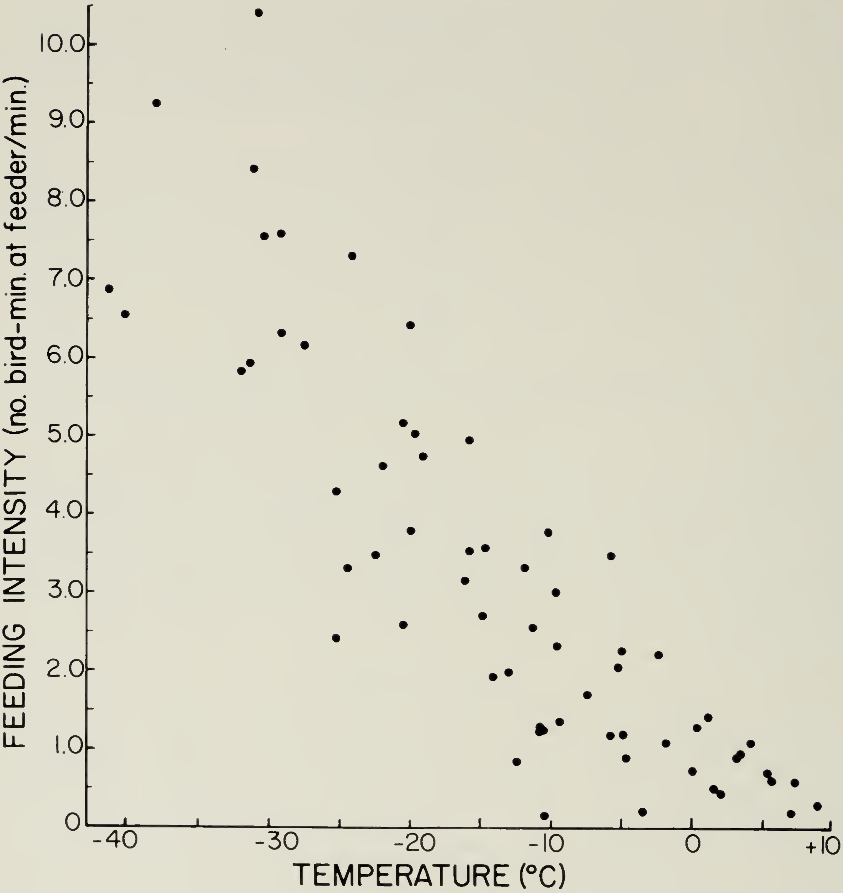

FIG. 5. Feeding intensity relative to daily mean temperatures, 1964–1967. Feeding intensity was derived by dividing the total bird-minutes spent at the feeder per day by the total number of minutes in that activity day.

Figure 5 illustrates the general relationship between environmental temperatures and feeding intensity. Shown clearly is the negative correlation between feeding intensity and temperature. This figure includes data from all years after the feeder was mechanized, and a considerable amount of the vertical scatter is due to the differing size of the population in different years, i.e., a smaller population will spend fewer total bird-minutes per activity day at the feeder than a larger population at any given temperature.

Daily pattern of feeding intensity.—The pattern of 2 daily activity peaks, described by many authors, including Lawrence (1958) for Black-capped

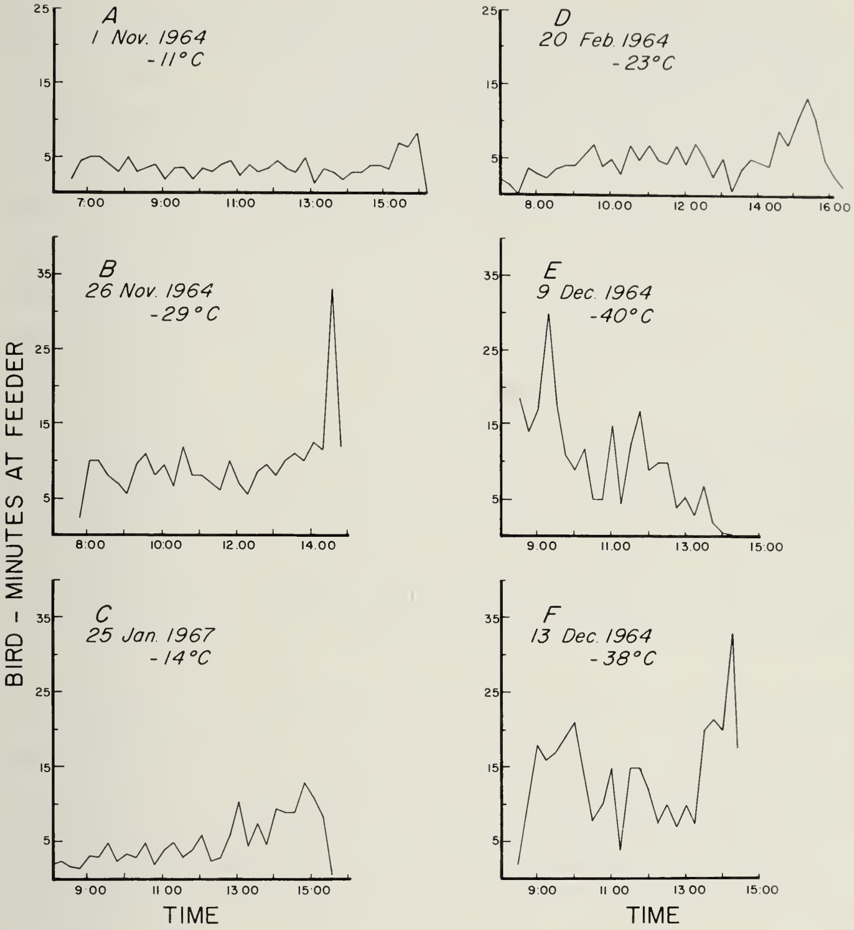

Fig. 6. Typical daily patterns of feeding intensity in chickadees at Fairbanks, Alaska. The total number of bird-minutes spent at the feeder is summed for each 15-min period during the activity day.

Chickadees in Ontario, was not apparent in most of the recordings made of the Fairbanks chickadee population. In fact, the only consistent pattern shown in the recordings was a tendency from mid-October to the end of February for a period of increased feeding activity to occur just before the birds went to roost (Fig. 6 A–D); 37 of the 50 recordings made during this time of year showed this tendency. The intensity peak was most conspicuous during the last 20 to 30 min before roosting, but on many days a gradual increase began as early as noon.

Before mid-October and after the end of February, when the feeder was not used as heavily as during the intervening months, no pattern of feeding intensity was discernible from the recordings.

On the 3 severest days for which I obtained full-day recordings, 2 distinct patterns were exhibited. On 2 days, 9 and 31 December 1964, with mean daily temperatures of −40°C and −41°C, respectively, a period of high intensity feeding occurred in the morning; and, thereafter, intensity decreased throughout the remainder of the day (Fig. 6 E). On the other day, 13 December 1964, there was both a morning and an evening peak (Fig. 6 F); the mean daily temperature of −38°C was a substantial warm-up from the −42°C of the several preceding days. The morning peak of all 3 days can undoubtedly be explained by the need for food (energy) after the chickadees had been roosting for some 18 hours at these extremely low environmental temperatures. The reason for the lack of an evening peak on 9 and 31 December is less clear, however, but appears temperature related. Perhaps the birds obtained sufficient food early in the day, allowing them to conserve energy later in the day by inactivity (see above discussion regarding shorter activity days at cold temperatures). The resumption of the evening peak on 13 December may have been the result of the relative amelioration of environmental temperatures.

CONCLUSIONS

Several apparently adaptive responses of the Black-capped Chickadee to the environmental conditions of interior Alaska are evident from this study of activity patterns. The synchronization of the activity day with seasonal changes in the daily light cycle is one aspect of this adaptiveness. Such synchronization with the light cycle is essentially universal in living organisms but the timing and means of synchronization are unique to species and geographic locality. In interior Alaska, Black-capped Chickadees respond to different minimal levels of light intensity at different seasons of the year. In general, response to light intensities is such that activity days are longer in relation to daylength during the shorter, colder days of winter than at other seasons. In addition, the Fairbanks chickadees respond to lowest mean light intensities during the last half of November and the first half or more of December, with the result that their activity days are relatively even longer (1) during the November period of food caching and (2) prior to the winter solstice. While such synchronization is undoubtedly based on an evolutionary response to mean annual environmental conditions, it is noteworthy that during the warm December of 1960 chickadees responded directly with the longest mid-winter days of the study, beginning activities at the lowest light intensities of the study

Other responses which appear adaptive in nature are evident in relation to cold temperatures. Not only are there the general reactions of shorter activity days and greater feeding intensities with colder temperatures, but during mid-winter the amount of activity appears to decrease with extreme cold. These combined responses indicate that chickadees conserve energy by reducing activity during cold periods, especially during severe cold in mid-winter, through shorter feeding days and reduced activity; the fact that even slight increases in solar radiation in mid-winter tend to lengthen the activity day supports this contention.

With such responses, the tiny Black-capped Chickadee is better able to withstand the long nights and extreme cold of northern latitudes.

SUMMARY

Daily activity patterns of Black-capped Chickadees (*Parus atricapillus*) were studied about an artificial feeder near Fairbanks, Alaska, from September to May, 1960–1967. The daily light cycle was the dominant environmental factor determining the daily activity period. Activity days were longer relative to daylength before the winter solstice than after.

Light intensity was the second most influential factor. Chickadees began activity in the morning at lower light intensities than those at which they ended activity in the evening, and they began and ended activity at lower intensities during the last half of November and the first half of December than at other times of year.

At cold temperatures, chickadees had shorter activity days than when it was warmer, but their feeding intensity was greater; they apparently conserved energy by reducing activity during cold periods.

Even after accounting for the effects of light intensity, chickadees began activity in the morning earlier on clear than cloudy mornings. Solar radiation tended to result in shorter activity days during early and late winter, but longer activity days during mid-winter. Snow and wind appeared to have only slight effects on activity patterns.

The relative influence of several of the environmental factors appeared to change during the winter, and each factor exerted more influence on the timing of first activity than of last activity.

ACKNOWLEDGMENTS

I am pleased to acknowledge and express appreciation for the generous assistance I received from others during this study. Most notably, Raymond B. Roof, my late husband, built and maintained the light meter, feeder, and recording equipment; Thomas T. Wetmore IV piloted my data through the computer and often functioned as a valuable sounding board for my thoughts; Samuel J. Harbo guided me through the statistical analyses; and Heinrich K. Springer was of great assistance in literature translations. John T. Emlen, Donald S. Farner, Hermann Pohl, and George C. West read an earlier draft of the manuscript and made a number of helpful suggestions.

LITERATURE CITED

Aschoff, J., ed. 1965. Circadian clocks. North-Holland Publ. Co., Amsterdam.

———. 1967. Circadian rhythms in birds. Proc. XIV Int. Ornithol. Congr. p. 95–111.

——— AND R. WEVER. 1962. Beginn und Ende der täglichen Aktivität freilebender Vögel. J. Ornithol. 103:2–27.

CHAPLIN, S. B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus*, in winter. J. Comp. Physiol. 89:321–330.

COCHRAN, W. G. AND G. M. COX. 1957. Experimental design. 2nd ed. Wiley and Sons, Inc., New York.

DAVIS, G. J. AND J. F. LUSSENHOP. 1970. Roosting of Starlings (*Sturnus vulgaris*): A function of light and time. Anim. Behav. 18:362–365.

DIXON, W. J., ED. 1973. BMD Biomedical Computer Programs. 3rd ed. Univ. Calif. Press, Los Angeles.

DUNNETT, G. E. AND R. A. HINDE. 1953. The winter roosting and awakening behavior of captive Great Tits. J. Anim. Behav. 1:91–95.

ENRIGHT, J. T. 1966. Temperature and the free-running circadian rhythm of the House Finch. Comp. Biochem. Physiol. 18:463–475.

ESKIN, A. 1971. Some properties of the system controlling the circadian activity rhythm of sparrows, p 55–77. *In* M. Menaker, ed. Biochronometry. Natl. Acad. Sci., Washington, D.C.

FRANZ, J. 1943. Über Ernährung und Tagesrhythmus einiger Vögel im arktischen Winter. J. Ornithol. 91:154–165.

———. 1949. Jahres- und Tagesrhythmus einiger Vögel in Nordfinnland. Z. Tierpsychol. 6:309–329.

GROSSMAN, A. F. 1975. Metabolism and temperature regulation of winter acclimatized Black-capped Chickadees of interior Alaska. M.S. thesis, Univ. of Alaska.

HOFFMANN, K. 1959. Über den Tagesrhythmus der Singvögel im arktischen Sommer. J. Ornithol. 100:84–89.

JOHNSON, H. M. 1957. Winter microclimates of importance to Alaskan small mammals and birds. Arctic Aeromedical Lab. Tech. Report 57-2 U.S. Air Force.

KLUIJVER, H. N. 1950. Daily routines of the Great Tit, *Parus m. major* L. Ardea 38:99–135.

KRANTZ, P. E. AND S. A. GAUTHREAUX. 1975. Solar radiation, light intensity, and roosting behavior in birds. Wilson Bull. 87:91–95.

LAWRENCE, L. DE K. 1958. On regional movements and body weight of Black-capped Chickadees in winter. Auk 70:415–443.

LEOPOLD, A. 1949. A sand county almanac. Oxford Univ. Press, New York.

——— AND A. E. EYNON. 1961. Avian daybreak and evening song in relation to time and light intensity. Condor 63:269–293.

MARKGREN, G. 1963. Studies on wild geese in southernmost Sweden. Part I. Acta Vertebr. 2:299–418.

MENAKER, M., ED. 1971. Biochronometry. Natl. Acad. Sci., Washington, D.C.

MORTON, M. L. 1967a. Diurnal feeding patterns in White-crowned Sparrows, *Zonotrichia leucophrys gambelii*. Condor 69:491–512.

———. 1967b. The effects of insolation on the diurnal feeding pattern of White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Ecology 48:690–694.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee—3. Auk 59:499–531.

PAATELA, J. E. 1938. Beobachtungen über das Verhalten der Vögel in der Sommernacht. Ornis Fenn. 15:65–69.

PALMGREN, P. 1935. Über den Tagesrhythmus der Vögel im arktischen Sommer. Ornis Fenn. 12:107–121.

POHL, H. 1968a. Einfluss der Temperatur auf die freilaufende circadiane Aktivitätsperiodik bei Warmblütern. Z. Vgl. Physiol. 58:364–380.

———. 1968b. Wirkung der Temperatur auf die mit Licht synchronisierte Aktivitätsperiodik bei Warmblütern. Z. Vgl. Physiol. 58:381–394.

———. 1972. Seasonal change in light sensitivity in *Carduelis flammea.* Naturwissenschaften 59:1–2.

RAVELING, D. G., W. E. CREWS, AND W. D. KLIMSTRA. 1972. Activity patterns of Canada Geese during winter. Wilson Bull. 84:278–295.

U. S. DEPARTMENT OF COMMERCE. 1973. Local climatological data, 1972 annual summary with comparative data—Fairbanks, Alaska. Environmental Data Service, National Oceanic and Atmospheric Administration.

WAGNER, G. 1958. Beobachtungen über Fütterungsrhythmus und Nestlingsentwicklung bei Singvögeln im arktischen Sommer. Ornithol. Beob. 55:37–54.

WILLIAMS, L. 1941. Roosting habits of the Chestnut-backed Chickadee and the Bewick Wren. Condor 43:274–285.

UNIV. OF ALASKA, FAIRBANKS 99701. ACCEPTED 2 JAN. 1975.

REQUESTS FOR ASSISTANCE

Shorebirds.—In 1976 the Canadian Wildlife Service will again be carrying out extensive banding and color-marking of shorebirds in James Bay. Last year a highly successful program resulted in over 70 reports of color-marked birds in eastern North America and South America from amongst c. 4000 banded in southern James Bay. Much valuable information on migration routes is being obtained and observers are again asked to look out for and report any color-dyed or color-banded shorebirds that they may see. Reports should include details of species, place, date, color-marks, and, if possible, notes on the numbers of other shorebirds present. For color-dyed birds, please record the color and area of the bird that was dyed. For color bands and standard metal leg bands, please record which leg the bands were on, the colors involved, and the relative position of the bands if more than 1 was on a leg (e.g. right leg, blue over metal, etc.). All reports will be acknowledged and should be sent to: Dr. R.I.G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0H3.

Semipalmated and Least sandpipers.—In 1976 and 1977 the Surinam Forest Service plans to color-band large numbers of Semipalmated and Least sandpipers along the Surinam coast, northeastern South America. The objective of this study is to obtain more information about the origin of the birds visiting Surinam and about their migration routes to and from this country. All birds will be banded above the tarsus ("knee") with a standard aluminum Fish and Wildlife Service band and 2 orange color-bands of about the same size as the aluminum band. Should you see any of these birds, please write to: Arie L. Spaans, Surinam Forest Service, P.O. Box 436, Paramaribo, Surinam, South America. Mention species, location and date of observation, the position of the aluminum and color-bands (left or right, and, if more than 1 band is on a leg, which band is above and which below), and number of color-banded birds involved.

FORAGING BEHAVIOR AND HABITAT SELECTION OF THREE SPECIES OF VIREOS IN SOUTHERN ONTARIO

Ross D. James

The Red-eyed Vireo (*Vireo olivaceus*), the Warbling Vireo (*V. gilvus*) and the Yellow-throated Vireo (*V. flavifrons*) have completely overlapping ranges in southern Ontario. The Red-eyed and Warbling vireos generally occupy different habitats, but the Yellow-throated Vireo is reported to occupy the range of habitats occupied by the other two species (Sutton 1949, Bent 1950).

Hamilton (1962) has categorized all vireos as gleaners from foliage, although Kendeigh (1945) has indicated that the Solitary Vireo (*V. solitarius*), which is closely related to the Yellow-throated Vireo, searches branches for food. However, in the literature, the Yellow-throated Vireo is repeatedly characterized as a forager of the uppermost or crown-layer of trees, apparently supporting Hamilton's (1962) contention that they glean from leaves. Hamilton further indicates that, as a crown-layer forager, the Yellow-throated Vireo is able to share successfully the same habitat with the Red-eyed Vireo to the extent that the 2 forms forage in the same parts of trees.

The present report gives the results of a study in which I examined foraging behavior, habitat choice, the extent of sympatry, and some of the factors which facilitate sympatry in the genus *Vireo* in southern Ontario.

METHODS

Most observations were made between sunrise and noon, when the birds were most active. I spent about 500 hours observing in the field in the summers of 1966 and 1967. Observations were made with the aid of a 7 × 35 binocular.

This study was conducted in southern Ontario, in Toronto city, and surrounding regions within a general area having forest communities dominated by broadleaved trees. However, in southern Ontario the natural vegetation has been mostly reduced to farm woodlots, hedgerows, and remnant stands on soils too poor to farm (Rowe 1959:44).

Within this general region, vireos were studied in 5 specific localities: (1) Pickering-Ajax area 30 km E Toronto, Ontario Co., (2) north of Toronto, 8 km NW King City, York Co., (3) Don River Valley in Toronto (Glendon College Campus), York Co., (4) Campbellville district, 48 km W Toronto in the Halton Co. forest tracts and environs atop the Niagara escarpment, (5) Galt area, 96 km W Toronto (Dryden tract 6.5 km W Galt, and Wrigley Lake), Waterloo Co.

Foraging study.—When I saw a vireo foraging, I followed its progress until it flew out of sight, and for every successul foraging event, recorded the following:

(1) I categorized the method used to approach and secure the food item as (a) *Hawking*—where both the birds and prey were in flight. (b) *Hovering*—where a bird in

flight removed prey from a plant, or (c) *Stalking*—where both bird and prey were clutching a plant surface.

(2) The source of food I identified as a leaf or branch. A leaf source included the ends of small twigs bearing leaves, as well as any buds present. Branches comprised all tree parts from small twigs to large limbs, or all cases where no leaves were near the food source, including the trunk of the tree.

(3) The zone of the tree, in which an insect was caught I categorized as peripheral (the outer, or terminal portions, of the limbs where most of the leaves were concentrated), or central (the area from the trunk or center of a tree, radially outward, exclusive of the outer portions of branches, and characterized mainly by bare or dead limbs).

(4) The perch upon which a bird stood as it searched for food immediately prior to catching an insect I categorized as a dead or live branch, and, in the latter case, whether foliated (bird within or adjacent to leaves) or unfoliated.

(5) The height of the tree in which the bird was foraging and the height above the ground at which the bird was foraging when it secured a food item, I estimated to the nearest meter.

(6) The species of tree in which the bird was foraging was recorded.

When I observed foraging, but the source of food could not be determined, I only recorded the height of foraging, tree height, and the species of tree.

Habitat Study.—I regarded nest location as strongly indicative of habitat preference, since it was always within the habitat used by the vireos for all their activities throughout the nesting cycle. Data were collected on the habitat surrounding 8 Red-eyed, 9 Warbling, and 9 Yellow-throated vireo nests. The pairs of vireos associated with these nests were studied for sufficient periods of time to enable me to obtain a good approximation of the territory used for foraging throughout the nesting cycle.

In order to distinguish among the habitat types, I recorded the following criteria: (a) tree species present, (b) percentage of dead limbs on tree near the nest, (c) presence or absence of understory, and (d) percent of tree or canopy cover on a territory. In determining percentage of dead limbs on trees, I assessed as many as 5 trees which were used extensively for foraging in each territory, regardless of the tree species. The total number of major limbs were counted and the proportion of dead limbs noted. I estimated canopy cover with the aid of sketches, plotting the locations of all trees within the area. All continuous forests were recorded as 90% canopy cover (Park 1931).

I also compared the heights and positions of all nests, and the species of tree in which the vireos nested.

Interspecific reactions.—Tape recorded songs were used to compare responses of each species to congeneric and conspecific song. Songs were recorded in the field on a Uher 4000 Report-L tape recorder with the microphone affixed to a 60 cm aluminum parabolic reflector, at a tape speed of 19.05 cm per sec. I used a J. B. Lansing Signature Hi-fidelity speaker in field playback experiments.

During playback the speaker was placed on the ground below and within 15 m of a nest tree. Songs were played in the vicinity of 2 to 5 active nests of each species, in both the nest building and incubation phases of the nesting cycle. In the case of the Warbling Vireo additional experiments were performed when young birds were in the nest. For all experiments, songs of the 2 sympatric vireos were played for 1 min each, followed by a maximum of 1 min of conspecific song. The interval between songs was never less than 1 min or as long as 5 min. In addition, I observed several naturally occurring interspecific encounters.

TABLE 1

FORAGING, NESTING, AND HABITAT DIFFERENCES AMONG VIREOS IN SOUTHERN ONTARIO

	Red-eyed	Warbling	Yellow-throated
Foraging Method (%)			
Stalking	28.0	32.0	69.0***
Hovering	61.0	59.0	28.5***
Hawking	11.5	10.0	4.5
n	150	132	64
Food Source (%)			
Leaf	99.0	97.0	16.0***
Branch	1.0	3.0	84.0***
n	150	132	64
Tree Zone (%)			
Peripheral	93.5	88.0	19.5***
Upper	38.5	40.0	5.5
Middle	42.0	40.0	12.5
Lower	13.0	8.0	1.5
Central	6.5	12.0	80.5***
Upper	1.5	6.0	26.5
Middle	5.0	6.0	48.5
Lower	–	–	5.5
n	76	64	78
Foraging Perches (%)			
Unfoliated	65.0	51.5	21.5
Foliated	22.0	39.0	2.0
Dead	14.0	9.5	76.5***
n	150	132	64
Nest Height (m)			
Average	4.9	8.2	13.4
Range	2–15	6–15	9–15
n	10	10	10
Nest Placement			
Peripheral			
Upper	3	4	1
Middle	4	3	–
Lower	2	1	–
Central			
Upper	1	2	6
Middle	–	–	3
Lower	–	–	–

*** Significant differences ($P < .001$) between this and the other 2 species.

TABLE 1
(Continued)

	Red-eyed	Warbling	Yellow-throated
Canopy Cover (%)			
Average	78	34	62
Range	50–90+	10–70	30–90
n	8	9	9
Dead Limb Counts			
Average	11.1	9.3	19.8
Range	5–20	5–30	5–35
n (Trees)	22	29	25
n (Territories)	7	8	8

Bill morphology.—I measured bill length, from the anterior margin of the external nares to the tip of the bill, and depth and width of the bill at the anterior margin of the external nares on study skins. Ten males were measured for each of the 3 species as were 10 Red-eyed Vireo females but only 9 each of Warbling and Yellow-throated vireo females. All specimens were from existing Royal Ontario Museum collections and were taken in Ontario between the months of May and August.

Statistical analysis.—A statistical test of the equality of percentages (Sokal and Rohlf 1969:608) was used (unless otherwise indicated) to test foraging differences among the vireos. In all cases where a significant difference was indicated between percentages, I tested the percentages to determine what sample sizes would be required to detect a true difference between them (Sokal and Rohlf 1969:609). In all cases my sample sizes were sufficiently large to be 90% certain of detecting a true significant difference at the 5% level.

RESULTS

Foraging differences.—A breakdown by method of 346 successful foraging bouts for the 3 species is given in Table 1. Hovering was used to about the same extent by the Red-eyed and Warbling vireos to secure the major portion of their food. The Yellow-throated Vireo on the other hand took significantly more food by stalking. None of the species used hawking to any extent to obtain food.

The Red-eyed and Warbling vireos, clearly using the same source, took their food almost entirely from leaves. Although they secured a large proportion of their food by hovering, some food was obtained by hanging from the end of a branch and picking an invertebrate from a leaf. This method was included under stalking. In contrast, the Yellow-throated Vireo gleaned most of its food from the bark of trees.

The Yellow-throated Vireo foraged largely within the central zone of trees.

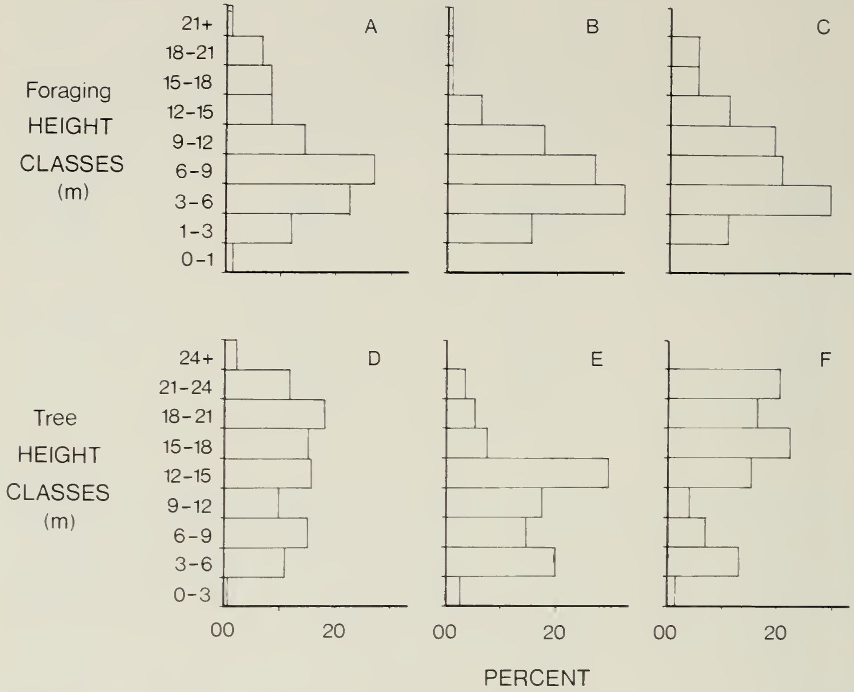

FIG. 1. A–C. The percentage of the total number of foraging actions recorded at different heights above the ground. A. *V. olivaceus* (n = 211; mean = 7.83 m); B. *V. gilvus* (n = 131; mean = 7.74 m); C. *V. flavifrons* (n = 228; mean = 9.26 m). D–F. The percentage of the number of trees of different height classes in which foraging actions were recorded. D. *V. olivaceus* (mean = 15.1 m); E. *V. gilvus* (mean = 10.0 m); F. *V. flavifrons* (mean = 16.2 m).

The Red-eyed and Warbling vireos, however, foraged significantly more in the peripheral areas. Yellow-throated Vireos often spent a protracted period in a tree before moving on to another. As it foraged on the basal portions of limbs, moving near and around the trunk in a spiral fashion, this vireo searched a higher percentage of dead limbs than the other species. Warbling Vireos like the Yellow-throated Vireos spent much time foraging in individual trees. Moving through the outer foliage Warbling Vireos restricted foraging largely to the tips of live branches. Red-eyed Vireos on the other hand moved rapidly from tree to tree in mature dense forest perching mainly on smaller live branches. Both Warbling and Red-eyed vireos searched peripheral leaves from perches on nearby twigs.

Figure 1 (a, b, c) shows the foraging heights of 570 foraging bouts for the species. The mean foraging heights for Red-eyed, Warbling, and Yellow-throated vireos were respectively 7.8, 7.7, and 9.3 m. No significant differences are apparent in foraging height ($P < .05$ using a single classification anova with unequal sample sizes, Sokal and Rohlf 1969:219) or in the heights of the trees in which these foraging bouts were recorded (Fig. 1: d, e, f). Mean tree heights for Red-eyed, Warbling and Yellow-throated vireos are respectively 15.1, 10.0, and 16.2 m.

The amount of foraging done in the lower, middle, or upper third of the peripheral or central zones of tree by each species is summarized in Table 1. Both Red-eyed and Warbling vireos foraged similarly in the peripheral zone and upper ⅔ of trees, different from Yellow-throated Vireos which largely foraged centrally although in the upper ⅔ of trees.

Average nest height for 10 nests of each species was 4.9, 8.2 and 13.4 m for the Red-eyed, Warbling and Yellow-throated vireos respectively. While these bear no relationship to mean foraging heights, the placement of nests in trees (Table 1) corresponds closely to preferred foraging positions ($r = .94$ for Red-eyed, .89 for Warbling and .89 for Yellow-throated using product-moment correlation coefficient for small samples, Sokal and Rohlf 1969:509).

Habitat differences.—In general, the vireos foraged in any tree within their territories (Table 2). However, over half the Yellow-throated territories had oaks (*Quercus* sp.) present and this was the only vireo to forage in conifers. The Red-eyed was the only species to make significant, and repeated, use of understory (Table 2b). The Warbling occasionally forages in short trees, but I did not consider these understory because of the open nature of the habitat this vireo occupied.

A comparison of the percent canopy cover on the territories of Red-eyed and Warbling vireos (Table 1) shows that Warbling Vireo habitat was significantly more open ($P < .001$) than that of the Red-eyed Vireo, consistent with reported habitat preferences (Bent 1950, James 1971). The percent canopy cover on Yellow-throated Vireo territories averaged between the values for the other species and is significantly different from either of them ($P < .05$, using a t-test for small samples).

Average figures for the dead limb estimates on territories of the different vireo species (Table 1), reveal a significantly higher value for the Yellow-throated Vireo over the other 2 species ($P < .05$). As much as 10% of the limbs on any tree were dead, and the increase shown in the Yellow-throated Vireo habitat indicates a preference for completely dead trees or trees such as oaks and aspens (*Populus* sp.) which often have large numbers of dead lower limbs.

In 1965 and 1966, pairs of Yellow-throated Vireos nested less than 100 m from a Warbling Vireo nest of 1967. Because of an open marsh to the north, and a young pine (*Pinus* sp.) plantation to the south which converged to the

TABLE 2
RELATIVE TREE SPECIES USE BY VIREOS*

(a)	Red-eyed (n = 7)			Warbling (n = 8)			Yellow-throated (n = 8)		
Overstory	(A)	(B)	(C)	(A)	(B)	(C)	(A)	(B)	(C)
Sugar maple (*Acer saccharum*)	6	6	4	5	5	2	5	5	1
White elm (*Ulmus americana*)	3	3	2	5	5	1	5	5	1
Red oak (*Quercus rubra*)	3	2		2	1		5	5	3
Balsam poplar (*Populus balsamifera*)	2	1	1	4	3	2	3	3	2
Trembling aspen (*Populus tremuloides*)				5	2	3	5	5	1
White birch (*Betula papyrifera*)	3	2		1	1		1	1	
Beech (*Fagus grandifolia*)	4	3	1	1			3	1	
Silver maple (*Acer saccharinum*)	2	1		2	2	2	1	1	1
Ash (*Fraxinus* sp.)	3	1		4	3		1		
Apple (*Malus* sp.)	1	1		4	2		2	1	
Basswood (*Tilia americana*)	1	1		3	3		1	1	
Ironwood (*Ostraya virginiana*)	1	1		2	2				
White pine (*Pinus strobus*)	1			3			3	3	
Hickory (*Carya ovata*)	2	2	1				2	1	
Hawthorn (*Crataegus* sp.)	1	1	1	1	1		2	1	
Walnut (*Juglans* sp.)	1			2	1		3	1	1
Cherry (*Prunus* sp.)				2	1				
Willow (*Salix* sp.)				3			1	1	
Spruce (*Picea glauca*)	1			1					
Cedar (*Thuja occidentalis*)	1						1		

* Tree species recorded in vireo territories, the number of territories each species was recorded in (Column A), the number of these territories in which the vireos were seen foraging in these trees (Column B) and the number of times each type of tree was used as a nest tree in 10 nestings of each species (Column C).

Table 2
(Continued)

(b) Understory	Red-eyed (n = 7)			Warbling (n = 8)			Yellow-throated (n = 8)		
	(A)	(B)	(C)	(A)	(B)	(C)	(A)	(B)	(C)
Maple (*Acer* sp.)	6	5							
Ironwood (*Ostraya virginiana*)	4	4							
Beech (*Fagus grandifolia*)	3	3							
Elm (*Ulmus americana*)	3	1							
Willow (*Salix* sp.)						2	1		
Dogwood (*Cornus* sp.)						4			
Poplars (*Populus* sp.)						3	1		

east of the Warbling Vireo nest, the Warbling and Yellow-throated vireos foraged in the same area, although in successive years.

In 1967, a Yellow-throated Vireo nested within 75 m of a Warbling Vireo with some observed overlap of foraging areas. In 1963 and 1965 a Yellow-throated Vireo nested in a tree whose branches intertwined with a tree in which a Warbling Vireo nested in 1967. In 1966, a Yellow-throated Vireo nested less than 50 m from Warbling Vireo nests of 1966 and 1967. Again, I observed overlap of foraging by these vireos in 1966.

In 1967, I observed 3 instances of Yellow-throated Vireos nesting within 100 m of Red-eyed Vireo nests, and in one case, not more than 25 m separated the nest trees. In all cases, where Yellow-throated Vireos nested near Warbling Vireos, the habitat was open. Where nests were near Red-eyed Vireos, twice they were in a mature forest, and once in a more open river valley with mature trees. From these observations it is evident that Yellow-throated Vireos can nest in a habitat similar to either of the other species. Several tree species used as nest trees are common to all 3 vireos (Table 1). The seeming preference for sugar maples (*Acer saccharum*) by the Red-eyed Vireo was probably a function of availability rather than preference. Yellow-throated Vireos seemingly demonstrated a proclivity for oaks, which were not plentiful in the study area.

Interspecific reactions.—None of the vireos responded strongly to playback of congeneric song. Playing of a congeneric vireo song resulted in a temporary

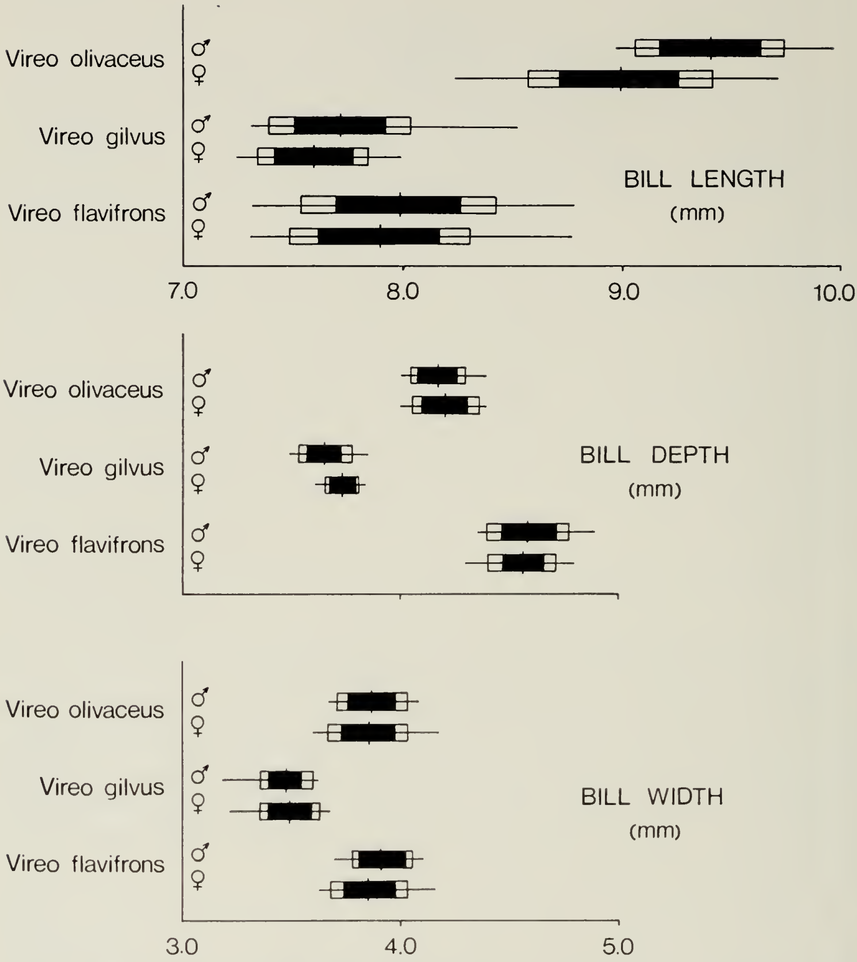

FIG. 2. Comparison of length, width, and depth of bill of the 3 vireos. Horizontal line represents the range, vertical line the mean, open bar 1 standard deviation on either side of the mean, and solid bar 2 standard errors on either side of the mean.

increase in the rate of song or a return to the nest tree by the male in whose territory tape recorded song was played. But never in 2 to 5 trials at any stage of the nesting cycle, did a vireo approach the speaker after 1 min of playback of a congeneric vireo song. On the other hand, a conspecific song invariably drew the bird to within 3 m of the speaker within 30 sec, and in as little as 5 sec, regardless of the stage of the nesting cycle.

On 2 occasions Red-eyed Vireos sang in areas used for foraging by Warbling Vireos, and on one occasion in an area used by Yellow-throated Vireos. On these occasions, and once when a Yellow-throated Vireo sang in the nesting area of a Warbling Vireo, there was no aggressive interaction between species. However, in all these cases the intruding bird was at some distance from the nest of the resident bird. Twice a Warbling Vireo passed through a Yellow-throated Vireo nest tree after having been attracted by tape recorded song. On these occasions the Warbling Vireo was chased immediately from the nest tree but continued to sing unmolested a short distance (within 30 m) from the nest tree. Other small passerines, such as warblers, were frequently chased from a nest tree by vireos. It appeared that the presence of a bird of any species was a greater stimulus for defense than a congeneric vireo song. The strongest stimulus for defense was, however, the conspecific song which rapidly drew a bird some distance from its nest.

Bill morphology.—Warbling and Red-eyed vireos have bills of similar proportions but all dimensions of Warbling Vireo bills are smaller than those of Red-eyed Vireos (Fig. 2). Yellow-throated Vireos have bills similar in length to that of Warbling Vireos but are both deeper and wider than either Warbling or Red-eyed vireo bills.

DISCUSSION

My observations support statements by others that the Red-eyed Vireo is a gleaner of arthropods from foliage (Kendeigh 1945, Bent 1950) and that its foraging encompasses not only the canopy but also the shrubby understory (Sutton 1949, Hamilton 1962). Although I did not color band birds, I noted no sexual differences in the foraging heights of male and female Red-eyed Vireos as demonstrated by Williamson (1971). However, she also points out that habitat configuration can promote much of this divergence and most of the forest in which my observations were made was second growth with a more uniform vertical distribution of foliage.

The Warbling Vireo has also been considered a gleaner of arthropods from foliage (Bent 1950, Root 1967), but one that prefers to forage in the tree tops (Sutton 1949, Hamilton 1962). I noted a significant use of the upper-most strata for feeding by Warbling Vireos; however, this vireo also forages in the lower parts of trees, and occasionally places a nest in the lower branches of tall trees.

My observations show Yellow-throated Vireos to be neither habitual treetop foragers nor habitual gleaners from foliage as suggested by Bent (1950), Hamilton (1962), or Williamson (1971). This vireo not only foraged on the lower limbs of trees but also showed as great a vertical foraging amplitude as the other 2 species. Again habitat characteristics may explain many of the differences. Williamson (1971) worked in mature climax forests. When Yellow-throated Vireos were observed in such habitat in Ontario, where trees reached 30 m in height, the birds tended to forage higher in the trees. But, much of the habitat was not climax forest but shorter, dispersed, second growth. I even noted Yellow-throated and Red-eyed vireos on the ground and Warbling Vireos within 15 cm of the ground. Sutton (1949) reported Yellow-throated Vireos nesting near the ground. Moreover, my study has indicated that the Yellow-throated has a foraging niche distinct from that of Warbling and Red-eyed vireos. The Yellow-throated Vireo forages in a manner similar to that suggested for the Solitary Vireo, searching the bases of horizontal branches and the numerous dead stubs that occur in a forest (Kendeigh 1945, 1947:56). It is not surprising to find such a resemblance between these 2 vireos when the suggested evolutionary origin of Yellow-throated from Solitary vireos is considered (Hamilton 1958). The habit of Yellow-throated Vireos, of spiralling upward about the trunk on the bases of branches, is also reminiscent of the actions of Bell Vireos (*V. bellii*), when foraging in large trees (Barlow 1962). The presence and importance of such distinct foraging niches has been clearly demonstrated among numerous other sympatric species (Hartley 1953, MacArthur 1958, Gibb 1960, Stallcup 1968).

Nine of 10 Red-eyed Vireo nests in my study area were placed in forests with abundant understory. This is consistent with the reported habitat requirements of this bird (Sutton 1949). One nest was placed in a small bush near a grove of taller trees, more typical of nest placement in more northern areas (Lawrence 1953) where they may nest in mixed forest, but still require a high percentage of broadleaved trees to which they largely confine their activities (Kendeigh 1945, 1947:56).

The Warbling Vireo was found nesting in open habitat ranging from open parkland with isolated trees and small groves where flights of up to 100 m might be made between foraging sites, to the open edge of forest inhabited by Red-eyed Vireos. The amounts of understory and canopy cover distinguished the habitats of Red-eyed and Warbling vireos on my study area, consistent with the reported preferences of these species (Bent 1950). The choice of habitat by Red-eyed and Warbling vireos appears to be on the basis of general habitat configuration, (similar to that reported by James, 1971, for these species), rather than tree species composition.

Yellow-throated Vireos occupied a greater range of habitat type than either of the other species. Bent (1950) and Sutton (1949) indicated that the Yellow-throated Vireo may forage and nest in habitats preferred by either of the other species. I recorded territorial overlap between Yellow-throated and both Warbling and Red-eyed vireos, although I noted no instance of Red-eyed or Warbling vireos nesting closely enough to overlap one another. An examination, then, of some of the factors facilitating this ecological overlap seems appropriate.

The habitat of Yellow-throated Vireos is usually somewhat different, although overlapping that of the other species. Yellow-throated Vireos generally occupy more open parts of woods (Sutton 1949) or areas with little understory when nesting near Red-eyed Vireos. The Yellow-throated Vireos were the only species to show a preference for large oak trees which were nesting sites or present in large numbers in 6 of 10 territories. The only species I saw foraging in white pines (*P. strobus*) and rarely in tamarack (*Larix laricina*) and norway spruce (*Picea abies*) was the Yellow-throated Vireo. On one territory white pines made up nearly 50% of the mature trees and such conifers are occasionally used for nesting sites by Yellow-throated Vireos (Bent 1950). Red-eyed Vireos have been reported nesting in conifers (Williams 1946) or making limited use of spruce trees for foraging (Kendeigh 1947:56), but the Solitary Vireo, more closely related to the Yellow-throated Vireo, is the only species which regularly nests in conifers. Tree species composition then may also be important in the habitat choice of Yellow-throated Vireos, as is the general habitat configuration.

Visual characteristics have been considered of lesser importance as isolating mechanisms than habitat separation, because vireos as a group have been considered to show little difference in coloration (Hamilton 1962). Vireos do possess distinct plumage patterns and the bright yellow breast and eye ring, and the white wing bars of Yellow-throated Vireos, must not be overlooked as possible recognition marks serving to reduce interspecific strife, as in other species (Kroodsma 1974).

The songs of vireos, however, seem to be far more important in interspecific recognition. Playback experiments with vireo song strongly suggest that the vireos were able to differentiate readily between songs, responding only to a conspecific song. Sutton (1949) considered song an adequate isolating mechanism in vireos because he had never seen fights between vireo species in 14 years of observations, although he had several times seen Yellow-throated Vireos in the same tree as one of the other vireos.

Just as playback of recorded congeneric song aroused little or no reaction, a territorial male vireo singing near the nest of another species provoked no defensive action on the part of the nesting vireo. Aggression resulted only if the intruding vireo actually landed in a nest tree. But the intruder was then chased from the nest tree as was any other small passerine entering the nest tree.

Food selection is apparently one of the most important single factors involved in competitive situations (Lack 1966). Many of the ways related species avoid competition seem to have a direct bearing on allowing the differential taking of foods (Lack 1961:55–72). The bills of these vireos show definite differences in size and proportion sufficient to suggest different prey selection (see Root 1967). The bills of male and female Red-eyed Vireos show considerable divergence in length and even this difference has been correlated with distinct foraging patterns of the sexes (Williamson 1971).

Chapin (1925) in his analysis of vireo stomach contents indicated little difference in the diet of the 3 vireos, except to point out that Yellow-throated Vireos took a large number of adult moths. Most moths (*Lepidoptera*) are nocturnal, concealing themselves during the day against a dark background such as the bark of trees. Hence, it is not surprising that a vireo searching the bark of trees, would find more moths than vireos searching leaves.

As birds are not dependent upon any specific food, as long as it belongs to a general type (Kendeigh 1947:56), little difference in insect species may be evident. However, arthropods of different sizes or different stages of growth might be chosen by the different vireos. It is unfortunate that Chapin (1925) did not differentiate adult or larval forms or the size of items he found in vireo stomachs.

I seldom observed 2 of these vireo species in the same tree. When observed, they were usually in the nest tree of one of the species, and antagonism was evident. Nevertheless, Yellow-throated Vireos have been observed in the same tree as one of the other species, both apparently unconcerned with the other. This response or lack of it, suggests that ecological isolation is functionally operative, and that territorial exclusion among congeners applies only to the immediate nest area as noted in the genus *Parus* in Europe (Hinde 1952 *in* Hamilton 1962).

SUMMARY

Three sympatric vireos, the Red-eyed, the Warbling, and the Yellow-throated, were the objects of this foraging and habitat study conducted in southern Ontario in the summer of 1966 and 1967.

The foraging behavior of Red-eyed and Warbling vireos was found to be very similar, both species hovering to obtain most of their food from leaves about the periphery of trees. Yellow-throated Vireos foraged in the interior of trees, stalking insects along the branches. A large vertical foraging range is displayed by all 3 vireos. The Yellow-throated Vireo avoids competition with the other species by lateral separation within trees, whereas the Red-eyed and Warbling vireos avoid overlap through habitat selection. Red-eyed prefer shady forests while Warbling Vireos inhabit more open areas, with a scattered assemblage of trees. The Yellow-throated Vireo may overlap both of the other species in habitat choice, and has been observed occupying at least parts of territories occupied by one or the other species. Data on interspecific reactions, and bill morphology tend to support the above results.

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LITERATURE CITED

Barlow, J. C. 1962. Natural history of the Bell Vireo. Univ. Kans. Publ. Mus. Nat. Hist. 12:241–296.

Bent, A. C. 1950. Life histories of North American Wagtails, Shrikes, Vireos and their allies. U.S. Natl. Mus. Bull. 197.

Chapin, E. A. 1925. Food habits of Vireos, a family of insectivorous birds. U.S. Dep. Agric. Bull. 1355.

Gibb, J. 1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis 102:163–208.

Hamilton, T. H. 1958. Adaptive variation in the genus *Vireo.* Wilson Bull. 70:307–346.

———. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo.* Condor 64:40–68.

Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22:261–288.

James, F. C. 1971. Ordinations of habitat relations among breeding birds. Wilson Bull. 83:215–236.

Kendeigh, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. Auk 62:418–436.

———. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ont. Dep. Lands and Forest, Biol. Bull. No. 1.

Kroodsma, R. L. 1974. Species-recognition behavior of territorial male Rose-breasted and Black-headed grosbeaks (*Pheucticus*). Auk 91:54–64.

Lack, D. 1961. Darwin's Finches. Harper and Row, N.Y.

———. 1966. Population studies of birds. Clarendon Press, Oxford.

Lawrence, L. de K. 1953. Nesting life and behaviour of the Red-eyed Vireo. Can. Field-Nat. 67:47–87.

MacArthur, R. H. 1958. Population ecology of some warblers of the northeastern coniferous forest. Ecology 39:599–619.

Park, O. 1931. The measurement of daylight in the Chicago area and its ecological significance. Ecol. Monogr. 1:189–230.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37:317–350.

Rowe, T. S. 1959. Forest regions of Canada. Dep. Northern Affairs and Natl. Resources, Forestry Branch, Bull. 123.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.

Stallcup, P. L. 1968. Spatio-temporal relationships of nuthatches and woodpeckers in ponderosa pine forests of Colorado. Ecology 49:831–843.

Sutton, G. M. 1949. Studies of the nesting birds of the Edwin S. George Reserve. Part 1. The Vireos. Univ. Mich. Mus. Zool. Misc. Publ. No. 74.

Williams, A. B. 1946. Red-eyed Vireo nesting in a hemlock. Auk 63:438–439.

Williamson, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129–152.

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MOLT IN LEACH'S AND ASHY STORM-PETRELS

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Broadly speaking, a bird's major energy-demanding activities during the yearly cycle are reproduction, molt, and in migratory species, migration. In many species, these activities do not overlap, presumably because of energy demands they each place upon a bird. Of particular interest to us are some species in the family Hydrobatidae. Harris (1969) felt the extended period required for molt in certain tropical storm-petrels prevents them from engaging in less-than-annual nesting cycles even though they are present in an environment that allows such regimes in other sympatric marine bird species. If molt can have such a governing effect on the energy budgeting of hydrobatids, its processes in this group should be of interest. Molt is relatively well known for only 6 storm-petrels—British, *Hydrobates pelagicus*: Scott (1970); Wilson's, *Oceanites oceanicus*: Roberts (1940), Beck (1970), Beck and Brown (1972); Harcourt's, *Oceanodroma castro*: Allen (1962), Harris (1969); Leach's, *Oceanodroma leucorhoa*: Harris (1974); Galapagos, *Oceanodroma tethys*: Harris (1969); and White-faced, *Pelagodroma marina*: Mayaud (1950), Browne *in* Palmer (1962)—but this information, with the exception of that for *H. pelagicus*, is confined largely to defining the extent of overlap among molt, nesting, and migration or post-breeding dispersal.

In an earlier paper (Ainley et al. 1974), we compared the life-histories of 2 species, the Leach's and the Ashy Storm-petrel (*O. homochroa*), that breed on the Farallon Islands, California. These 2 morphologically similar species were found to be similar in a few but different in most aspects of their life histories. In brief, Leach's Storm-petrels visit the Farallones for 7 months from late February to early September, and winter during intervening months in the tropical and subtropical waters of the eastern Central and North Pacific. They lay eggs during a 5½ week period from early May to mid-June. Ashy Storm-petrels visit the island for most of the year and usually remain within several hours flight of the island during all seasons. They lay eggs from late April to mid-July and sometimes later. We previously made some comparisons on molt (Ainley et al. 1974), explaining that it overlapped the pre-egg and chick stages of the annual cycle much more in the sedentary Ashy than in the migratory Leach's. In the present paper we present the full analysis of our work on the timing, sequences, and rates of molt in these 2 species.

METHODS

South Farallon, a rocky granitic island of 44 ha, is on the edge of the continental shelf at 37.4°N, 123.0°W, 43 km west of San Francisco, California. It and its neighboring islets harbor the largest breeding concentration of marine birds in the U.S., excluding Alaska and Hawaii. The 1600 breeding Leach's and 4000 breeding Ashy Storm-petrels largely confine themselves to the southern quarter of the island (Ainley and Lewis 1974). Both species nest in greatest concentration under rocks on the south-facing talus slope of Lighthouse Hill (elevation, 109m).

We caught storm-petrels at night, when they were active about the island, by playing tape-recorded calls of Leach's to attract both species to mist-nets placed on the talus slope. We divided the calendar year into 73 five-day periods and attempted to capture at least 30 birds of each species in every period. The data reported here were gathered from 321 Leach's and 981 Ashy Storm-petrels trapped whenever weather permitted between April 1972 and April 1973. After each capture session, we banded the birds and recorded observations and measurements. The birds were then released while it was still dark, within 2 hours of capture.

We recorded molt, weight, wing length, color, and stage of incubation patch development. One of us recorded while the other measured. Molt was scored using the system devised and computer programmed for shorebirds by G. W. Page of the Point Reyes Bird Observatory. For each of 6 body regions, the number of growing feathers was scored on a scale of 0 to 3. The body regions inspected were: head, throat, flanks, belly, back, and rump. The 0 score indicated no molting feathers in a region, 0.5 indicated 1–3 growing, 1 indicated several, 2 indicated about every fourth feather growing, and 3 indicated most feathers growing. This last score, although found often in shorebirds and songbirds, was rarely encountered in storm-petrels. Molt in tail and wing feathers was scored differently. The 12 rectrices were numbered outward 1–6 from the center of the tail; primaries were numbered from the carpal joint outward, 1–10 (the eleventh vestigial primary was ignored); and the secondaries were numbered inward from the carpal joint, 1–14. We looked at all flight feathers of one wing and all tail feathers. Each was characterized as old, missing, 1/10, 3/10, 5/10, 7/10, or 9/10 grown, new, or of unknown age. We used these scores to determine rates and sequences but not the timing and intensity of molt. The latter was determined by totaling body molt scores and the number of growing tail and wing feathers for each bird, and by determining the mean, range, and 95% confidence limits for the number of growing feathers of all birds captured in each period. Five-day periods were combined into 10-day periods to increase sample sizes. We compared resultant values to the time of year and to the stage of nesting. After the period from 6 to 15 April, all birds with a downy ventral apterium were defined as immature and were analyzed separately. The ages of these birds were not known but some birds were one year of age (Ainley et al. 1974).

We compared intensity of molt to the stage of nesting in those Ashy Storm-petrels whose nests were under observation (Table 3). We confined these observations to parents that on occasion remained during the day in the late chick period (chicks 46–83 days of age), rather than taking from burrows birds that were incubating eggs or brooding small chicks. In this way we minimized nest desertions due to our activities. No nests of Leach's Storm-petrels were accessible. The state of the incubation patch was useful in correlating stage of molt to the nesting cycle (see Ainley et al. 1974).

THE TIMING AND INTENSITY OF MOLT IN ADULTS

Body molt.—The molt began for both species with a renewal of body feathers. We first found body feathers in the nests of individual Ashy Storm-petrels at the time their eggs were hatching, sometimes a little before and sometimes

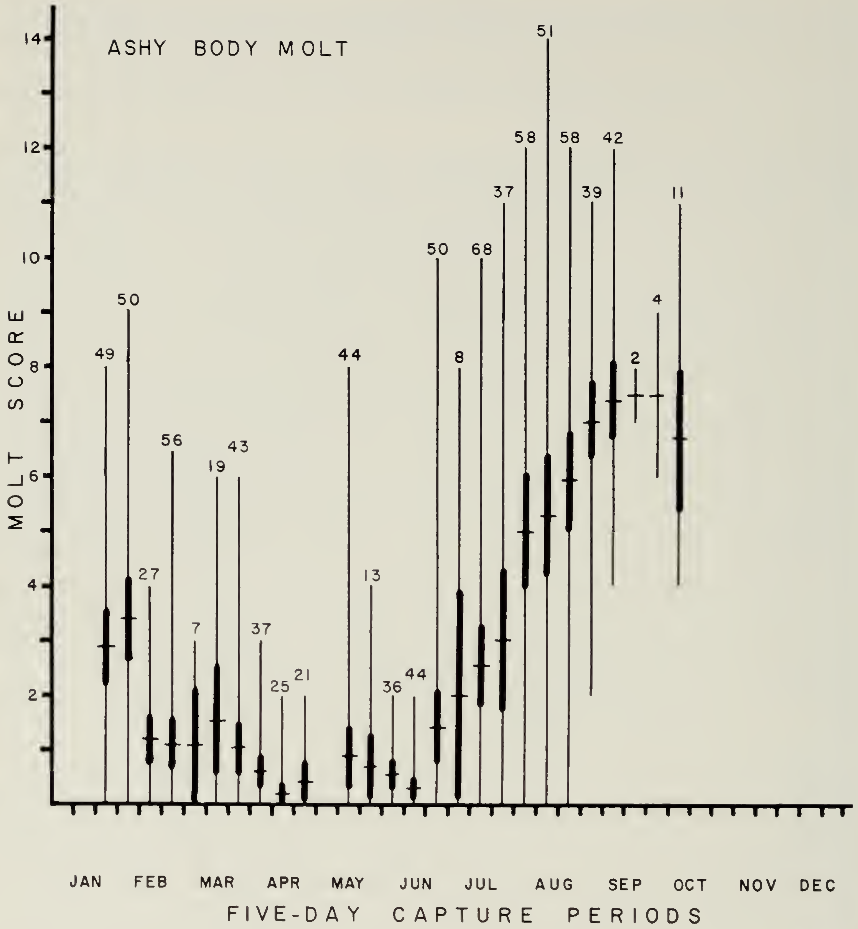

Fig. 1. The timing and intensity of body molt in adult Ashy Storm-petrels. Molt in the population during each 10-day period (combined 5-day periods) is described by the mean score, range, 95% confidence interval, and sample size.

a little after. Harris (1974) found the same in Leach's Storm-petrels nesting farther north in California. Leach's at the Farallones begin egg-laying a few days later than the Ashy, but their incubation period is a few days shorter. Thus for both species the first eggs hatch at the same time in the year (Ainley et al. 1974). In our netting sample, molting Ashy Storm-petrels first appeared between 15 and 19 June, and molting Leach's first appeared between 10 and 14 June (Figs. 1 and 2, Table 1).

Peak body molt scores in the Ashy were 12–14 and the highest mean scores

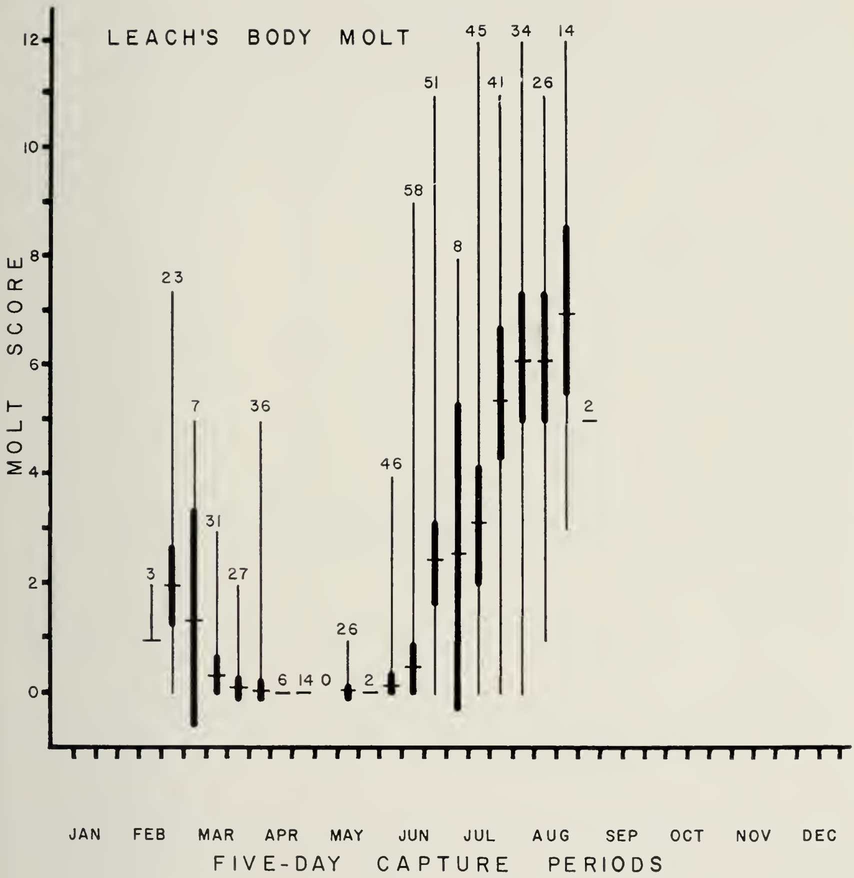

FIG. 2. The timing and intensity of body molt in adult Leach's Storm-petrels.

ranged from 7.0 ± 0.6 to 7.5 ±0.6 (Fig. 1, Table 1). Peak scores first occurred in the period from 4 to 13 August, about 50 days after body molt began. In an equal interval from the start of molt (ca. 40 days) both species reached a mean score of 7.04. We could not determine for sure if Leach's reached higher scores because we caught very few after the period when they reached the score of 7.04. The few we caught afterwards had lower scores and in the entire sample their peak scores ranged only 11–12, a lower range than in the Ashy. These facts and the fact that Leach's Storm-petrels require more time to complete body molt (see below) suggests a less intense body molt than in Ashy Storm-petrels.

Body molt continued coincidentally with molt in other feather groups. It

TABLE 1

A COMPARISON OF MOLT IN LEACH'S AND ASHY STORM-PETRELS

Comparison*	Species	Body	Tail	Primaries	Secondaries
1. Period Begun	L	32–33	36–37	46–47	52–53
	A	34–35	42–43	48–49	48–49
2. No. Periods from Previous Molt Phase	L	–	4	10	6
	A	–	8	6	0
3. No. Periods from Start of Body Molt	L	–	4	14	20
	A	–	8	14	14
4. Period of First Peak Score	L	40–41	40–41	–	–
	A	44–45	48–49	48–49	–
5. No. Periods, Start to Peak	L	8	4	–	–
	A	10	6	–	–
6. Four Highest Peak Scores	L	11–12	8–9	4	–
	A	12–14	7–9	6	12–14
7. Four Highest Mean Scores	L	5.4–7.0	4.4–5.25	–	–
	A	7.0–7.5	3.25–5.0	–	–
8. Days to Completion;	L	248–285	ca. 75	< 228	–
Mean		274	–	–	–
N (birds)		9	–	1	–
	A	228–283	–	166–181	124–160
		257	–	–	–
		12	–	4	4

* Data in comparisons 1, 4, 6, and 7 come from Figs. 1–7; in 8 from birds captured in molt during both the fall and spring (see Table 2); and in 2, 3, and 5 from other comparisons in this table.

was last to finish in the spring and did so about a week after the finish of molt in primaries and secondaries. It required slightly more time for completion in Leach's than in Ashy Storm-petrels ($P < 0.05$, t-test). In a sample of 9 Leach's caught both at the start of molt in the fall and its finish in the spring, the total time for completion ranged from 248 to 285 days (mean = 274 days, SD = 16). In a similar sample of 12 Ashies the elapsed time ranged from 228 to 283 days (mean = 257 days, SD = 17).

Tail molt.—Just before the start of true tail molt, rectrices were apparently lost easily, as indicated by birds having all tail feathers missing, or all on one side missing, etc. In this analysis, we considered tail molt to begin in the period immediately preceding that in which the first increase in mean tail molt score occurred. This was a few weeks after we first recorded adventitious molt. True rectrix molt began in Ashy Storm-petrels between 25 July and 3 August, about 40 days after the start of body molt (Fig. 3, Table 1), and coincided with or slightly preceded the attainment of peak intensity in the latter. This is also apparent in the case histories of recaptured birds (Table

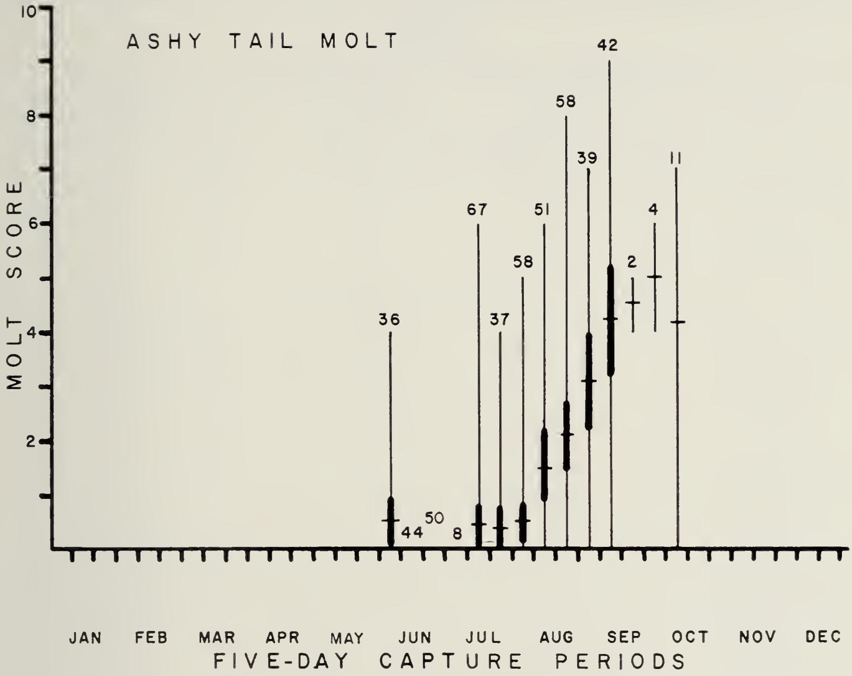

Fig. 3. The timing and intensity of tail molt in adult Ashy Storm-petrels.

2). Two Ashy parents with chicks 48 and 52 days old were the first found in tail molt, while one with a chick 46 days old had no tail molt (Table 3). That fits with what we observed in the netted birds. In contrast, Leach's began rectrix molt in the period from 25 June to 4 July, about 20 days after the start of body molt (Fig. 4, Table 1). Thus in this species, tail molt was begun earlier relative to the start of body molt and before attainment of peak body molt intensity.

In addition to beginning tail molt earlier, Leach's reached greater intensity of rectrix molt and did so much more quickly than Ashy Storm-petrels. Peak intensity of tail molt in the Ashy Storm-petrel was reached within 30 days after its start, but in the Leach's it was reached within 20 days. In the Ashy, high peak scores were 7–9 and high mean scores ranged from 3.25 ± 0.9 to 5.0 ± 1.0; whereas in the Leach's, high peak scores were 8–9 and high mean scores ranged from 4.4 ± 0.8 to 5.25 ± 0.7 (Table 1).

We have no direct measurements of the duration of tail molt, but apparently it required less time in Leach's than in Ashy Storm-petrels. This was suggested by the above information and by comparison of molt sequences (see below).

TABLE 2
MOLT SCORES OF BIRDS RECAPTURED SEVERAL TIMES

Date	Primary	Secondary	Tail	Body
Oceanodroma leucorhoa				
(1) 30 June	0	0	0	4
15 July	0	0	5	4
3 Aug	0	0	8	7
20 Mar	0	0	0	0
Oceanodroma homochroa				
(1) 9 Aug	0	0	0	8
15 Aug	0	0	0	8
26 Aug	0	0	1	7
9 Sept	4	0	1	4
6 Apr	0	0	0	2
(2) 3 Aug	0	0	0	7
26 Aug	0	0	0	7
9 Sept	0	0	1	10
18 Oct	4	0	6	6
6 Feb	6	14	0	4
6 Mar	2	6	0	2
(3) 30 June	0	0	0	5
15 July	0	0	3	10
7 Aug	0	0	5	7
30 Jan	2	2	0	3
11 Feb	0	0	0	0
(4) 26 June	0	0	0	0
19 Aug	0	0	0	4
9 Sept	0	0	2	11
16 Sept	0	0	3	6.5
18 Oct	4	0	7	9
2 Feb	6	12	0	7
(5) 25 May	0	0	0	1
15 July	0	0	0	6
7 Aug	0	0	0	12
18 Sept	0	0	2	6
17 Oct	4	0	5	6.5
4 Feb	6	12	0	3
18 Feb	4	0	0	1.5
(6) 26 June	0	0	0	3
15 Aug	2 missing	0	6	7
28 Aug	2	6	5	7
3 Sept	2	6	4	7
9 Sept	4	4	2	5
2 Feb	2	4	0	2

TABLE 3

MOLT SCORES OF ASHY STORM-PETRELS HAVING CHICKS OF KNOWN AGE

Chick Age		Parent's Molt Score			
Days of Age	Days to Fledging	Primary	Secondary	Tail	Body
46	34	0	0	0	8
48	33	0	0	6	9
52	27	2	0	5	5.5
53	—	4	0	new	5
57	23	4	0	new	5
67	16	4	0	4	7
73	6	0	0	4	5.5
75	2	6	2	4	6
78	0	4	0	8	11
79	1	0	0	2	9
83	0	6	0	4	10

Our best guess, based on comparisons of growth rates for individual feathers and molt sequences, was that for Leach's Storm-petrels tail molt was completed in about 75 days and for Ashy Storm-petrels in about 95 days. Tail molt in Leach's was almost fully completed before the start of wing molt (see below), and it was about ¾ completed when the chick fledged and the parent ceased to visit the island. In the Ashy Storm-petrel, it was usually about ½ completed at chick fledging.

Primary molt.—Our first records of molting primaries in Ashy Storm-petrels occurred during the period 24 August to 2 September, when peak intensity of tail molt was reached (Tables 1 and 2). In the nesting birds, primary molt first appeared in parents having chicks 52–80 days of age (Table 3). Thus in this species, primaries began to molt 55–70 days after the start of body molt and about 30 days after the start of tail molt, when the latter reached peak intensity. In the Leach's most birds had fledged their chick and ceased to visit the island before primary molt began. We thus have few data on primary molt in that species. First records for primary molt in Leach's Storm-petrels occurred in the period 14 to 23 August. As with the Ashy, this was about 70 days after the start of body molt; unlike the Ashy, this was well past attainment of peak intensity in rectrix molt.

Among netted birds, the peak score recorded for the Ashy was 6 and for the Leach's it was 4 (Table 1), meaning 3 and 2 growing primary feathers per wing, respectively. The same respective scores occurred in 12 Ashy and 7 Leach's Storm-petrels which we examined in the collection of the California Academy of Sciences. These birds had been collected at sea off California

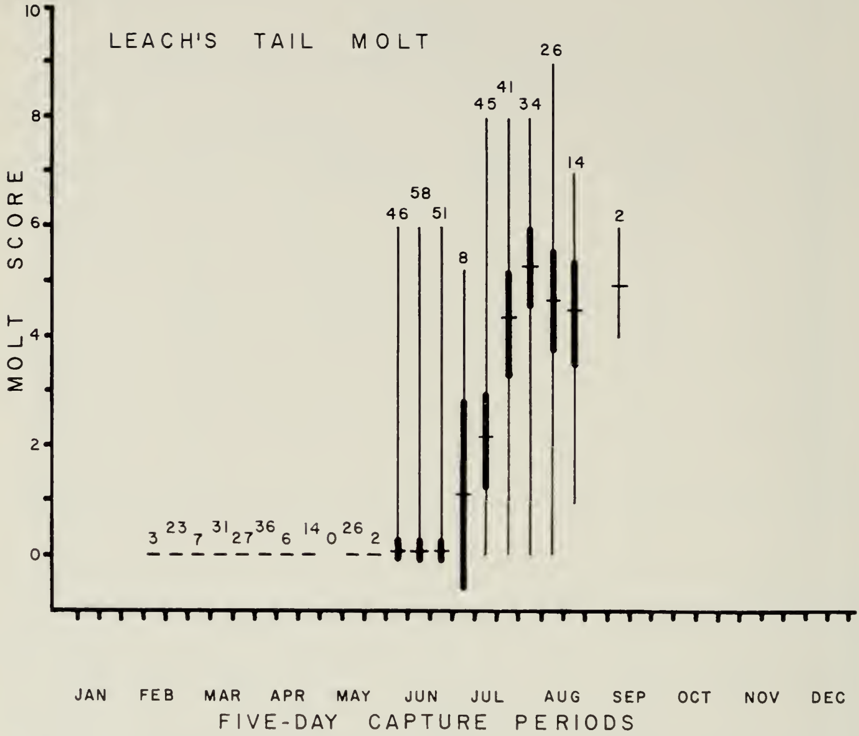

FIG. 4. The timing and intensity of tail molt in adult Leach's Storm-petrels.

during October and November of various years. Harris (1974) found only one Leach's Storm-petrel having 6 "molted" (= growing?) primaries in a sample of 53 molting birds. We recorded the peak score in the Ashy at the very start of primary molt during early fall, but we found the peak score in the Leach's (in the collected specimens) only during the late fall and early spring. Thus attainment of peak intensity of primary molt in Leach's Storm-petrel was delayed longer than in the Ashy, as well as being usually at a lower peak level.

Primary molt overlapped the period of visits during the pre-egg stage much more in the Ashy than in the Leach's Storm-petrel. Almost all Leach's (93% of 127 examined between 15 February and 15 April) had completed primary molt upon making their first spring visits to the island, and only 7% were still in the last stages of molt. In contrast, during the same period 25% of 189 Ashy Storm-petrels were in primary molt. This species, however, began visiting much earlier in the spring (Ainley et al. 1974), and of the 99 Ashy Storm-

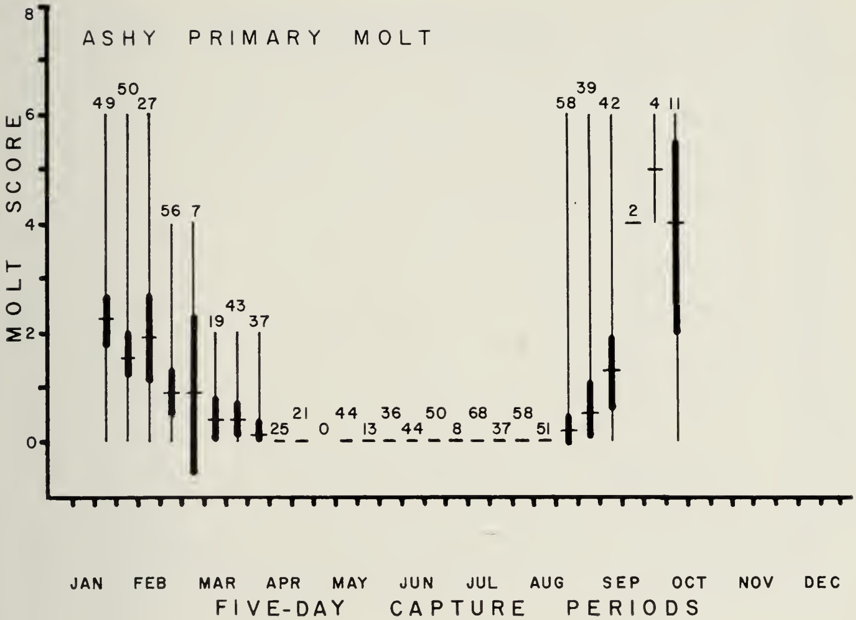

Fig. 5. The timing and intensity of primary molt in adult Ashy Storm-petrels.

petrels inspected between 26 January and 14 February, 68% were in primary molt. The last records of molt in primary feathers occurred for both species between 5 and 15 April (Figs. 5 and 6).

In a sample of 4 Ashy Storm-petrels caught in primary molt both during the fall and spring, the duration of molt ranged from 166 to 181 days. All that can be said here for Leach's Storm-petrels is that primary molt can last less than 228 days (n = 1 bird). Primary feather renewal may take a bit longer in the Leach's as indicated by the delay in attainment of peak intensity and the lower peak scores relative to those of the Ashy.

Secondary molt.—Ashy Storm-petrels began molting secondaries between 24 August and 2 September, coincident to the start of primary molt (Table 2, Fig. 7). In Leach's, on the other hand, secondary molt started at least 30 days after the start of primary molt (Table 1, Fig. 6). The first Leach's in secondary molt was caught in the period from 13 to 22 September.

Both species finished secondary molt coincidentally with the end of molt in primary feathers. Similarly to primary molt, then, the last birds of both species that were renewing secondaries were found between 6 and 15 April. In a sample of 4 Ashy Storm-petrels, the secondaries required 124 to 160 days for completion of molt, less time than required for primaries. The explanation

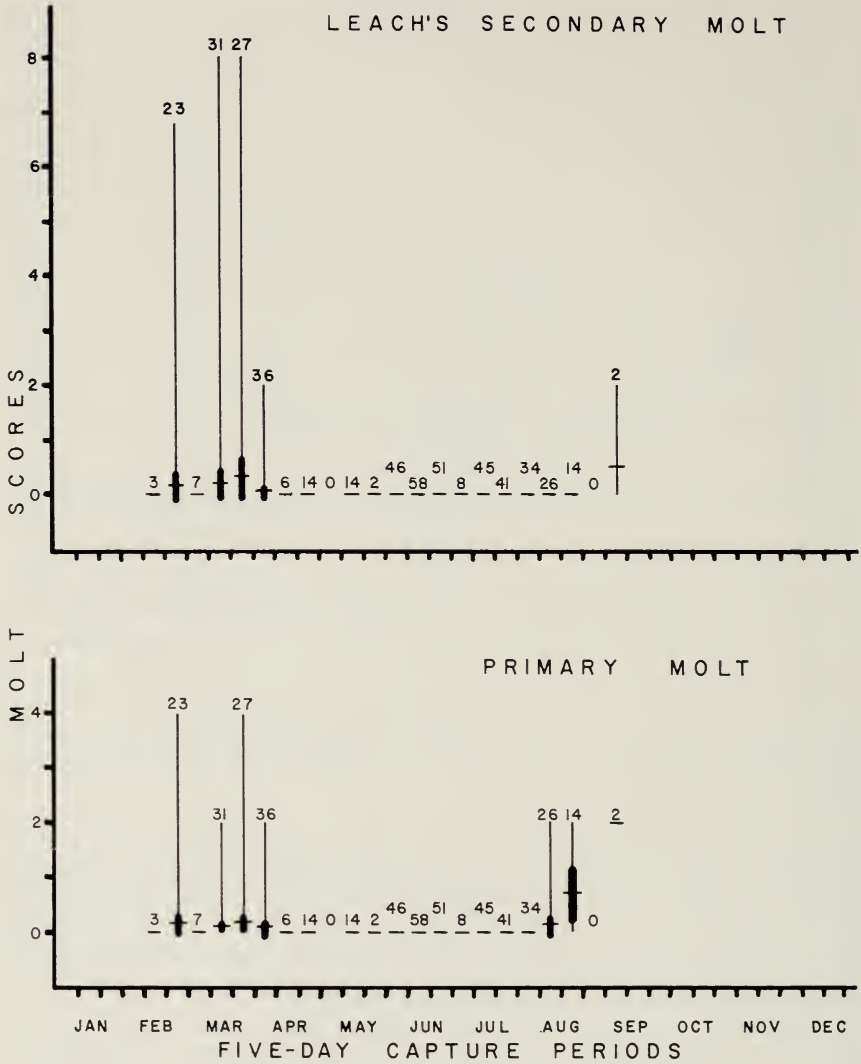

FIG. 6. The timing of primary and secondary molt in adult Leach's Storm-petrels.

for more rapid renewal of secondaries will become apparent in the section on molt sequences. We have no data on the duration of secondary molt in the Leach's but it must be shorter than in the Ashy because unlike in the latter, it began well after the start of primary molt yet ended at the same time. The peak secondary molt scores in the Ashy Storm-petrel were 12–14, or 6–7 grow-

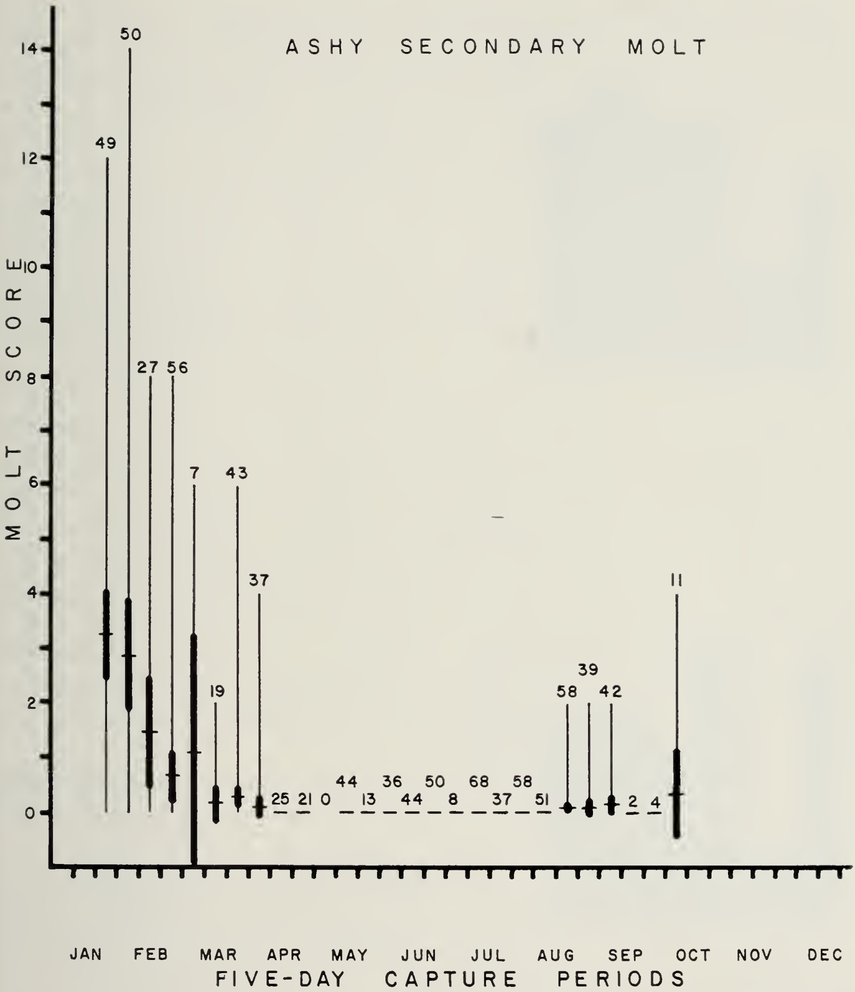

FIG. 7. The timing and intensity of secondary molt in adult Ashy Storm-petrels.

ing secondaries per wing; but all we can say for Leach's is that peak scores were somewhere above 8, or 4 growing secondaries per wing.

SEQUENCES OF MOLT

Body molt.—Little can be said about molt sequence in body feathers. The first body region in which molt began was usually the belly and the last to complete molt was usually the forward part of the head (the face).

Tail molt.—The sequences of feather loss and replacement were the same in both species, but a noticeable difference occurred in rate of sequence progression. In about a third of the birds checked, no clear pattern was discernible; but in the remainder the following sequence occurred with some variation. The most constant element of the sequence was that pair 5-5 (the next to outermost feathers on either side) was the last to be lost and the last to complete growth. This pair of feathers was dropped when the outermost pair (6-6) reached 7/10 to 9/10 growth. The outer pair was usually the first or second pair to be molted. This system insured use at all times of at least one pair of the longest, outermost feathers in the tail. The forked tail in these storm-petrels probably enhances balance and maneuverability in their characteristic darting and dipping flight.

Tail feathers were most commonly lost in the order: 6, 4, 2, 1, 3, 5 (Fig. 8). Thus every other feather on either side of the tail was lost in succession from the outside pair toward the center and then from the center toward the outside. The major difference between the species was that in Leach's Storm-petrels, feathers 1, 3, and 5 began their molt much sooner relative to growth in 6, 4, and 2. The result should be, and nothing suggested otherwise, that rectrix molt required less time for completion in the Leach's Storm-petrel. In fact because the shorter inner feathers required less time to complete growth (due to their shorter length, see below), the inner 4 feathers often completed growth before the 6-6 pair. It appeared in some individuals of Leach's that the 1-3-5 set began molt almost simultaneously to the 6-4-2 set. This was rarely the case in the Ashy.

The sequence just described differs from that in the British Storm-petrel, in which rectrices merely molt in pairs from the central ones outward (Scott 1970).

Primaries and secondaries.—The following sequence description was determined for Ashy Storm-petrels. Based on the 7 molting specimens of Leach's in the California Academy of Sciences, it is seemingly the same for that species also. The problem was that we caught Leach's Storm-petrels in the very beginning or the very end of primary molt but never in any intermediate stages of wing feather renewal. The major difference between the species appeared to be in rate of feather loss. Scott (1970) described about the same sequence in the British Storm-petrel.

Primaries 1 and 2 were dropped simultaneously. When these became ⅓ grown, primary 3 and secondary 12 were lost. Hereafter, once a primary became about ⅓ to ½ grown (with the previous one being ½ to ¾ grown) the next one was dropped. Secondaries 12 to 14 (the tertials) were lost very slowly and they also grew quite slowly, such that when primary 6 was dropped, secondary 12 was just about fully grown but 13 had not yet been lost. How-

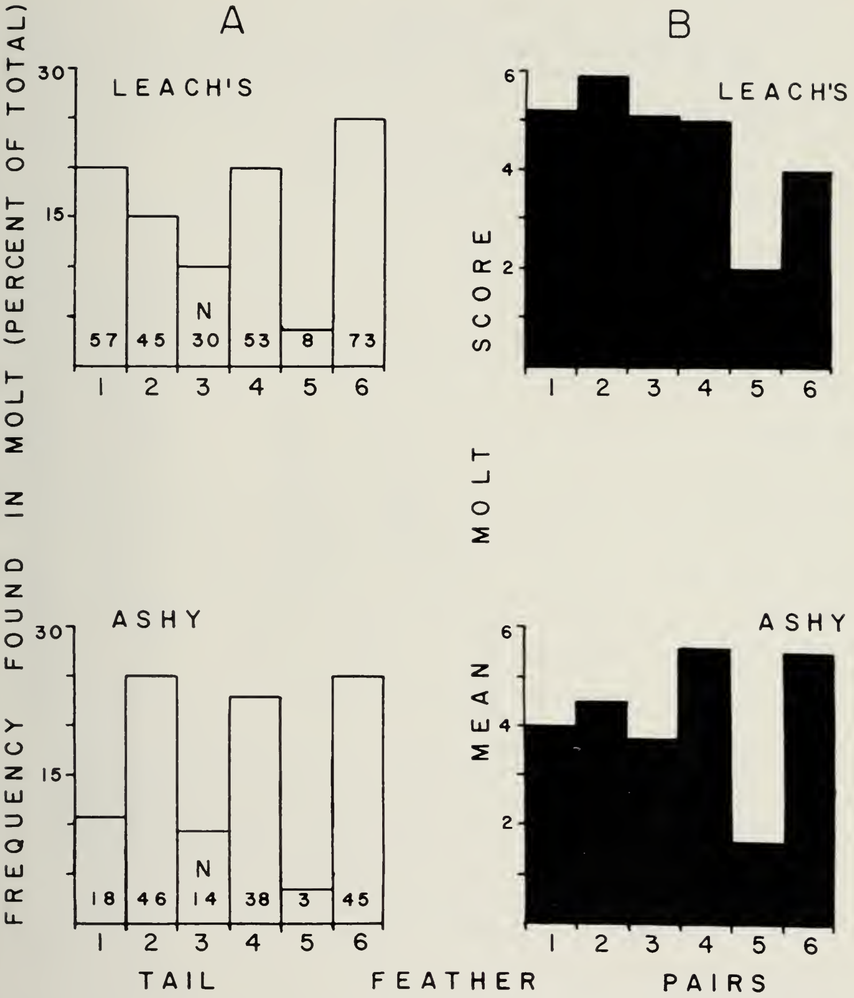

FIG. 8. The sequence of tail feather replacement in Leach's and Ashy storm-petrels, as shown by sample sizes (A) and molt scores (B) of feather pairs. The sequence of feather loss is evident in (A) assuming that feather pairs most often found in molt are first to start and pairs least often found in molt are last to start. Molt scores (B) indicate the rate of feather loss—one species relative to the other—by showing the extent of growth in each feather compared to others.

ever, when primaries 9 and 10 had reached full growth, secondaries 13 and 14 had completed their growth. When primary 7 was dropped so were secondaries 1 and 5. Secondary feather replacement then passed successively inward from these 2 centers. When primary 8 was lost so was secondary 11, and

TABLE 4

RATES OF FEATHER GROWTH IN BIRDS RECAPTURED DURING MOLT

Tail Feather	6	5	4	3	2	1
Oceanodroma homochroa						
Score change/day	.023	.023	.028	.035	.037	.035
N	23	3	12	7	16	8
Total days	44	44	36	29	27	29
Feather length (mm)	84	79	70	64	60	58
mm/day growth	1.9	1.8	2.0	2.2	2.2	2.0
Oceanodroma leucorhoa						
Score change/day	.023	.024	.027	.032	.036	.038
N	13	1	5	4	6	5
Total days	44	44	37	31	28	26

Primary Feather	10	9	4	3	2	1
Oceanodroma homochroa						
Score change/day	.022	.013	.017	.023	.026	.026
N	3	1	1	3	6	6
Total days	45	77	60	43	39	39
Feather length (mm)	93	107	78	69	61	55
mm/day growth	2.0	1.4	1.6	1.6	1.5	1.4

feather replacement then passed successively outward from 11 to 9. The last feathers to complete growth, just about simultaneously, were primary 10 and secondaries 4 and 9. In summary, primary feather molt passed outward from one center (the carpal joint) but secondary feather molt proceeded from 4 centers: the carpal joint inward, secondary 5 inward, and secondary 11 and 12, inward and outward, respectively. The greater number of growing feathers allowed the secondary molt to be completed in a time less than or equal to that of the primaries.

RATES OF FEATHER GROWTH

Rectrices.—Rate of change in the molt score (i.e., extent of growth) increased from .02 score points per day for feathers 5 and 6 to .04 score points per day for feathers 1 and 2 (Table 4). Considering the different lengths of the feathers, rate of growth was actually about the same for all tail feathers, about 2 mm per day. Thus, the longer, outer feathers required more time to complete growth than the shorter, inner ones: feathers 5 and 6 required 44 days, feather 4 required 36 days, and feathers 1, 2, and 3 required 27 to 29 days. These observations were for Ashy Storm-petrels, but similar growth

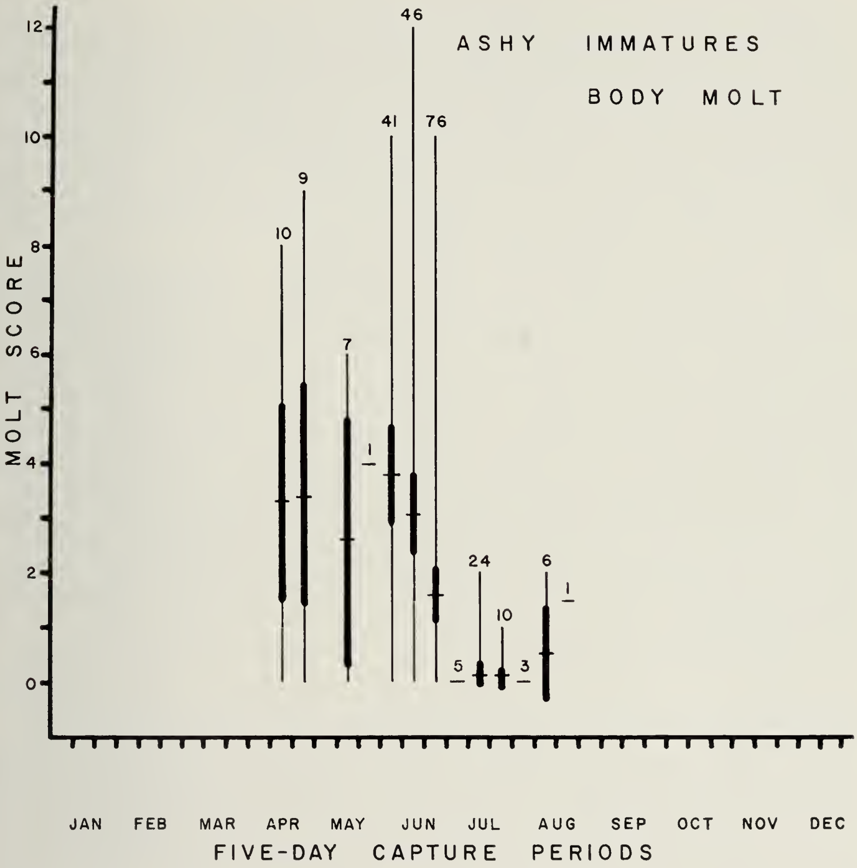

FIG. 9. The timing of body molt in immature Ashy Storm-petrels.

rates occurred in the tail feathers of Leach's Storm-petrels. It seems, therefore, that a faster rate of feather loss rather than faster growth accounts for the faster progression of rectrix molt in the Leach's compared to the Ashy.

Primaries.—Data were available only for determination of growth rates in the primaries of the Ashy Storm-petrel. The length of time required for completion of growth again depended on feather length. Changes in molt score in recaptured birds ranged from .03 points per day in the shortest, inner primaries to .01 in the longest, outer ones. Primary 9, the longest wing feather, required about 77 days to grow and primaries 1 and 2, the shortest, required about 39 days. The true growth rate of primaries was generally less than 2 mm per day, and thus was slower than in the rectrices.

MOLT IN IMMATURES

All birds of both species having no incubation patch (score of 0; Ainley et al. 1974) after period 20 (about 10 April) were considered immature. Probably some having a partially downy ventral apterium (score of 1) were also immature but we could not separate them from adults. These immatures probably accounted for the records of body molt in "adults" during the egg stage (see Figs. 1 and 2). In breeding adults, as shown earlier, body molt did not begin until about the time of egg-hatching.

Body molt began earlier in the year in immatures. We had a much larger sample of immature Ashy Storm-petrels with which to work (Fig. 9), but the few immature Leach's examined by us exhibited similar patterns. Most immature Leach's Storm-petrels apparently stopped visiting the island before beginning body molt, but most immature Ashy Storm-petrels visited while in body molt but ceased visiting prior to the start of tail molt. Immatures, however, made very few repeat visits (Ainley et al. 1974). We recorded heavy body molt in immature Ashy Storm-petrels during the period from 16 April to 4 July, the time of year to which their visits were restricted, and when little molt was recorded in adults. Assuming temporal patterns to be similar, immatures should also have begun molt in the tail and wings earlier in the year than adults.

Crossin (1974) discussed the incidence of molt in specimens of *O. l. leucorhoa* and *O. l. beali* (the Leach's subspecies breeding at the Farallones) collected at sea by the Pacific Ocean Biological Survey Program in the eastern Central and North Pacific Ocean. Assuming that molt regimes of both subspecies are similar relative to the breeding cycle, and considering that *O. l. leucorhoa* in Alaska lays eggs about a month later than *O. l. beali* at the Farallones (compare Bent 1922, with Ainley et al. 1974), then the individuals of both subspecies he found in primary molt during the spring were probably adults. The majority of collected specimens, and more so for *O. l. leucorhoa* than *O. l. beali*, however, had completed primary molt by November or December and sometimes by October. There seems little doubt that these birds, which apparently contributed large numbers to the Central Pacific populations, were non-breeders and probably immatures. Assuming that primary molt requires about 170 days for completion, the first adult *O. l. beali* found in primary molt at the Farallones should have finished this molt phase during the last week of January.

DISCUSSION

Comparison of the timing and intensity of molt and its various phases in the 2 storm-petrels reveals some interesting differences that agree with the general divergence in life styles outlined in a previous paper (see Ainley et al. 1974). In general, these relate to differences in the time and energy budgeting of a short-ranging, sedentary species—the Ashy Storm-petrel—and a long-ranging, migratory species—the Leach's Storm-petrel. In the Ashy, molt overlaps extensively with reproduction and with a limited post-breeding dispersal. In particular, much overlap exists between wing feather molt and the chick and pre-egg stages of successive nesting cycles. In the Leach's molt places a minimum of demand on energy budgeting during the pre- and post-breeding migrations, and in even greater contrast to the Ashy, wing feather molt barely overlaps any phase of reproduction.

Scott (1970) compared the molt regimes in petrels, except the albatrosses, by grouping 18 species and subspecies on the basis of (1) breeding latitude (high, temperate, tropical), (2) type of post-breeding movement (transequatorial migration or dispersal into adjacent seas), and (3) molt regime (*a*, molt after the wintering area had been reached; *b*, molt started at the breeding grounds and completed quickly before dispersal; *c*, molt started after breeding but completed slowly to end just before the next breeding cycle; and *d*, like the last but molt started at the breeding grounds). The second of these regimes has yet to be reported for a hydrobatid. His breakdown by breeding latitude was deemed important to the study of molt and post-breeding movement based on the widely accepted generality that ocean productivity, and thus food availability and the potential for energy uptake, declines from high to low latitudes.

In the sub-Antarctic and in temperate latitudes, species such as *Oceanites oceanicus* (Roberts 1940, Beck 1970, Beck and Brown 1972) and *Pelagodroma marina* (Mayaud 1950, Browne *in* Palmer 1962) finish breeding and then fly quickly to the wintering area where molt occurs (regime *a*). Tropical species such as *Oceanodroma castro* (Allan 1962, Harris 1969) and *Oceanodroma tethys* (Harris 1969), which disperse into adjacent seas after breeding, require the entire period between annual breeding cycles to complete the molt (regime *c*). Finally, the temperate species *Hydrobates pelagicus,* which winters across the equator in south temperate seas, begins its molt late in nesting, and then like tropical species, requires the entire period until the next breeding cycle for its completion (regime *d*; Scott 1970).

Leach's Storm-petrels from the Farallones are most similar to the British Storm-petrel in their patterns of reproduction, molt, and migration. One possible relating factor is that the subtropical waters inhabited by the Leach's during their breeding season (see Ainley et al. 1974) are similar in productivity to waters of the eastern North Atlantic and Mediterranean areas (see Gulland 1971) inhabited by the British Storm-petrels during their breeding season. Both then leave nesting areas to migrate into or across tropical waters for the winter.

The pattern of reproduction, molt, and post-breeding movement exhibited by Ashy Storm-petrels does not fit into any of Scott's categories. No other hydrobatid so far studied overlaps molt, and especially that of flight feathers, so extensively with both the chick stage of one nesting cycle and the pre-egg stage of the one following. The Ashy Storm-petrel, based on the knowledge available, is the most sedentary species in its family. Individuals are absent from the Farallones for less than 2 months each year, but even during that time they are within several hours' flight of the islands. Throughout the year they inhabit the subarctic waters of the California Current. Their sedentary nature and extensive overlap between molt and nesting correspond logically to the high productivity and food availability of the waters they inhabit; the California Current off central California is among the most productive ocean regions in the world (Gulland 1971).

SUMMARY

Molt in Ashy Storm-petrels proceeds rather regularly from one phase to another; when one phase reaches peak intensity the next begins. In adults, body molt starts at about egg-hatching, 40 days later rectrices begin their molt, 30 days after that primaries begin molt, followed by secondaries almost immediately. Most Ashy Storm-petrels have half-completed tail molt and are molting the first 2 or 3 primaries when their chick fledges. They are still molting the last 2 or 3 primaries on their first visits to the island in the following nesting cycle. The total time required for molt averages 257 days.

Molt in Leach's Storm-petrels proceeds in the same order but the intervals between start of the various phases differ. Tail molt begins only 20 days after start of body molt, 50 days later primaries begin molt, and about 30 days after that molt in the secondaries begins. When the chick fledges, parents have almost completed tail molt but usually have not begun wing molt. Most Leach's Storm-petrels complete molt before visiting the island in the following breeding cycle. Total time required for molt averages 274 days.

The sequences of feather replacement and the rates of growth in individual feathers are described.

Immatures begin molt earlier in the year than adults, starting about the time the latter are laying and incubating eggs.

Little overlap occurs between molt and migration, and between primary molt and breeding in the Leach's compared to extensive overlap between these activities in the Ashy Storm-petrel. The different molt regimes correspond to the overall divergence in life styles of the 2 species, Leach's being a long-ranging, migratory species of subtropical open-ocean waters and the Ashy being a short-ranging, sedentary species inhabiting subarctic coastal waters. Molt in the Leach's is similar in its timing and degree of overlap with other activities to the British Storm-petrel; but the molt regime in the Ashy is unique among storm-petrels so far studied.

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LITERATURE CITED

AINLEY, D. G. AND T. J. LEWIS. 1974. The history of Farallon Island marine bird populations, 1854–1972. Condor 76:432–446.

———, S. MORRELL, AND T. J. LEWIS. 1974. Patterns in the life-histories of storm petrels on the Farallon Islands. Living Bird 13:295–312.

ALLAN, R. G. 1962. The Madeiran Storm Petrel *Oceanodroma castro.* Ibis 103b:274–295.

BECK, J. R. 1970. Breeding seasons and moult in some smaller antarctic petrels, p. 542–550. *In* Antarctic ecology (M. W. Holdgate, ed.). Academic Press, London.

——— AND D. W. BROWN. 1972. The biology of Wilson's Storm Petrel, *Oceanites oceanicus* (Kuhl), at Signy Island, South Orkney Islands. Br. Antarct. Surv., Sci. Rep. No. 19.

BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. 121.

CROSSIN, R. S. 1974. The storm petrels (Hydrobatidae), p. 154–205. *In* Pelagic studies of seabirds in the central and eastern Pacific Ocean (W. B. King, ed.). Smithson. Contrib. Zool. 158.

GULLAND, J. 1971. The fish resources of the ocean. Fish Agri. Organ., United Nations, Rome.

HARRIS, M. P. 1969. The biology of storm petrels in the Galapagos Islands. Proc. Calif. Acad. Sci., 4th Ser. 37:95–166.

HARRIS, S. W. 1974. Status, chronology and ecology of nesting storm petrels in northwestern California. Condor 76:249–261.

MAYAUD, N. 1950. Contribution a l'etude de la mue des Procellariens. Alauda 17/18: 144–155, 222–233.

PALMER, R. S. (ED). 1962. Handbook of North American birds. Vol. I. Yale Univ. Press, New Haven.

ROBERTS, B. 1940. The life cycle of Wilson's Storm Petrel *Oceanites oceanicus* (Kuhl). Br. Grahamland Exped. 1934–37, Sci. Rep. 1:141–194.

SCOTT, D. A. 1970. The breeding biology of the Storm Petrel *Hydrobates pelagicus.* Ph. D. thesis, Oxford Univ.

POINT REYES BIRD OBSERVATORY, BOX 321, BOLINAS, CA 94924. ACCEPTED 21 FEB. 1975.

COMPARATIVE BREEDING BEHAVIOR AND ECOLOGY OF THE BUSHY-CRESTED AND NELSON SAN BLAS JAYS

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The Bushy-crested Jay (*Cyanocorax melanocyanea*) is a resident of open, mesic highland forests of Central America from Guatemala to Nicaragua. The Nelson San Blas Jay (*C. sanblasiana nelsoni*) occupies tropical deciduous woods and open palm wood plantations of foothills and lowlands of the Pacific slope of Mexico from Nayarit to Guerrero. Each species occurs in flocks throughout the year and is communal in reproductive habits. I have previously written of their systematic and phylogenetic relationships (Hardy 1961, 1969), their habits in following army ant swarms (Hardy 1974a), the ontogeny of plumage and softpart color change as well as sexual differences (Hardy 1973), and their displays and postures (1974b).

Communal breeding strategies are not rare in neotropical jays and this level of sociality may be primitive in the ornate line (Hardy 1974b). The studies reported here show that *C. melanocyanea* and *C. sanblasiana nelsoni* are socially reproductive, with helpers at the nest ranging from juveniles to adults, more than one adult incubating a single clutch, and mutual assistance in *C. s. nelsoni* by breeding pairs of the same social groups.

STUDY AREAS AND METHODS

Field study of the Bushy-crested Jay took place from 12 to 30 June 1969 on the grounds of the Hotel Santa Maria de Ostuma, 10 km north of Matagalpa, Nicaragua. I studied the Nelson San Blas Jay from 12 June to 1 July 1970 in lowlands near Las Varas, Nayarit, Mexico.

Nests were located and activity patterns studied at both sites. Birds were caught in mist nets and marked with paint for individual recognition. Some were recaptured later in the study for retention in captivity; the captives in an aviary provided information on reproductive roles not clearly revealed in the wild. Some young birds were also captured for examination. Specimens were collected for examination of stomach contents, reproductive status, sex, and for preservation as skins, skeletons, and in liquid. All specimens preserved are in the Moore Laboratory of Zoology, Occidental College. Besides direct observation, I made still and motion pictures of the birds' activities and recorded their voices. After mapping the physiographic and vegetational features of the study plots, I studied ranges of the flocks within them.

Bushy-crested Jay study area and habitat.—Santa Maria de Ostuma lies at 1200 m elevation on the Pacific complex at the western confluence of the Cordilleras Isabella and Dariense on the slopes of the mountain. Luxuriant cloud forest cloaks the Caribbean exposure and spills over the crest about 3 km up the mountain trail from the hotel, losing its tree fern component in the process and merging in ecotonal fashion with the mountain tropical evergreen forests at just below 1200 m. This is at the lower edge of the study area. Much of the study site has the large trees of the cloud forest, but the

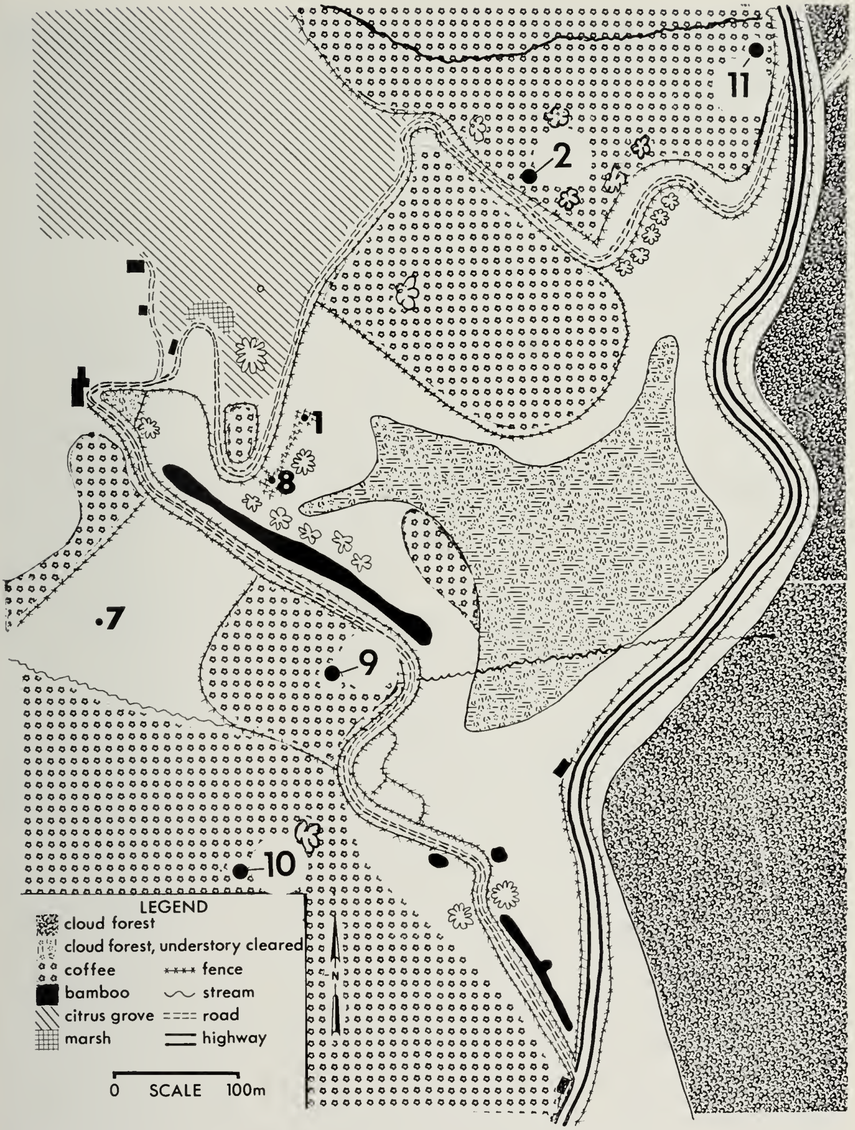

Fig. 1. Map of the Bushy-crested Jay study site at Santa Maria de Ostuma, Nicaragua.

subcanopy layers of vegetation have been removed and largely replaced by coffee trees (Fig. 1). I made no attempt to identify the tree species of the native forest.

The study site vegetation is evergeen and although there may be little rain from November through May, it can rain anytime and there is never a period that one could classify as a dry season (Vivo 1964:210–211). During this study the temperature was remarkably constant, between 19.5° and 22°C day and night. Rain fell almost daily, mainly as brief heavy showers in the afternoon or at night.

The Bushy-crested Jay was abundant in the disturbed forest and could be found less commonly at times around old clearings made for growing corn or along open cattle trails in the relatively undisturbed cloud forest, especially when flocks were feeding young. This jay did not occur in the undisturbed forest or, during the breeding season at least, in the tropical forest at lower elevations.

San Blas Jay study area and habitat.—Las Varas, Nayarit, is near sea level at the boundary between coastal lowlands and the low hills. The former area originally supported a luxurious tropical deciduous to semi-evergreen forest. Now the native palms, *Acrocomia mexicana* and *Orbignya cohune*, grow not only wild but are extensively planted and grow in partially wild stands reproducing themselves. There is also other cultivation, mostly corn and grazing land. Nuts of *O. cohune* are harvested for their oil. I estimated that more than half the lowland in the vicinity of the study area was in palm growth; the remainder was about half small, partially disturbed plots of forest (second growth, even here with some palms) and half corn fields and pasture. Small sluggish streams and bayous are scattered through the land. Fig. 2 shows the habitat at the same site.

The tropical deciduous woodland on the foothills may have a species composition much the same as that of the adjacent lowlands, but in the foothills the growth form is more tortuous and the trees shorter. Thorns characterize many species.

A distinct wet season runs from mid-June to November or December, and a dry season from January to June (Shelford 1963:445). In the dry season the native forest almost completely loses its leaves, except for larger trees in the lowlands, especially along water courses, and some trees along the arroyos in the foothills.

Until 22 July temperature rose daily to the low and mid-30s C in early afternoon and fell to the low 20's C at night. Thereafter cloud cover and rain narrowed the range from high to mid-20's. Prior to 22 June relative humidity always rose to above 90% at night and remained above 80% except for a short midday period when it fell to between 40 and 60%. Thereafter daily minima seldom went below 70% in midday. These fluctuations were great compared to those at the highland study locality. From 12 to 23 June no rain fell at the study area. From then on to the end of the study period rains fell almost daily as heavy afternoon and evening thundershowers. Shelford (1963:445) gives the summer maximum temperature as 39°C in this zone and the period February through April and November as the driest periods.

The Nelson San Blas Jay was common in the vicinity of Las Varas in the breeding season in the palm groves, especially where the groves were contiguous with open pasture and cultivation, and in thicket mixtures of cutover forest and palms. The birds were rare or absent in the heavier forest; at least near Las Varas my impression was that they occurred in the foothill woodland only as nonbreeding flocks; therefore they were uncommon there at the time of this study.

Vegetational composition of home ranges.—Bushy-crested Jay home ranges spanned virtually all available habitats except completely undisturbed cloud forest (Figs. 1 and 3). Coffee plantation composes from approximately 20 to over 50%. Open habitats such as citrus groves, roadside clearings, and ecotonal areas between them (clear zones on Fig. 1) are all represented. The least frequented habitat was cloud forest with understory completely cleared (not planted in coffee, probably grazed heavily). Even where group 2 ranged into otherwise undisturbed cloud forest this was only near the edge and along

FIG. 2. Representative woodland of the San Blas Jay study area.

open trails into the forest. Bushy-crested Jays simply did not inhabit completely undisturbed cloud forest.

Nelson San Blas Jay groups 1 and 2 remained almost entirely within the mixed palm-native broadleaf woodland. Group 1's nest was on the thicket edge adjacent to an open corn field. The birds frequently flew out into the field to forage and also retired into the woodland, keeping higher in the trees. The woodland habitat of group 1 was dense, with canopy of native trees. That of group 2 was open in the area most frequented, palms being the tallest trees and other trees comprising the young second growth (Fig. 2). Group 3 inhabited severely disturbed acacia thicket with scattered palms mingled with small plots of pasture and roadside thicket. A summary characterization of the preferred situation based on these 3 groups suggests either variety by contiguity of different habitats or by internal disturbance of open palm-native broadleaf woodland. Accentuating this, our patrols of undisturbed foothill woodland revealed only occasional small groups of clearly nonbreeding jays, while patrols in lowlands several km away from our study sites, in situations having the variety of several artificial habitats plus roadsides, revealed other breeding jays. As with the areas of occurrence of the Bushy-crested Jay, the patches of undisturbed native forest had no Nelson San Blas Jays.

The native woodland in the foothills is virtually leafless in the dry season while the lowland forests provide the evergreen palms and generally more mesic aspect of the native woodland. Although the lowland broadleaved forest had adequate cover, it apparently lacked sufficient diversity and edge for these jays.

Field determination of age, sex, and individual identity.—The nature of ontogeny (Hardy 1973) in these jays makes it possible to distinguish age and sometimes sex and individual identity in the field—a boon to accurate study even when birds cannot all be captured and marked. In *C. melanocyanea,* juveniles have a dull grayish cast to the plumage, horn-colored bills, and dark irides. Yearlings have black bills and dark brown irides. Two-year-olds and older birds have black bills and yellow irides. In the hand, 2-year-olds can probably always be distinguished from older birds by the presence of a particolored bill interiorly. Older birds have solid black bills inside and out. Juvenile *C. s. nelsoni* have a yellowish horn-colored bill, dark irides, a tall erect fronto-nasal crest, and the grayish cast to the plumage. Yearlings have a particolored bill, the tall crest, and dark irides. Three-year-olds seemingly still have dark irides but these begin to change and may be slightly lighter than iris color in 2-year-olds. Though the bill is black exteriorly, it is pale or particolored interiorly. Adults may have no crest or 1 or 2 wispy crest feathers (a highly variable feature often useful in distinguishing individuals in a communal group) and black bills inside and out. Adult females have pure yellow irides, while males have brownish or greenish-yellow irides. This difference is sometimes visible through a binocular and useful when one becomes acquainted with a group under study. Non-overlapping weight differences of adult males and females (males more than 117 g, females 92–113 g) facilitate sexing captured birds.

BREEDING BIOLOGY

General Pattern of Breeding Behavior

The Bushy-crested and Nelson San Blas jays exhibit communal social systems in reproduction. A nucleus pair presumed to be the functionally reproductive pair, was sometimes detectable with respect to a nest. In *C. melanocyanea,* the adult flock size of the best studied group seems to have been 11,

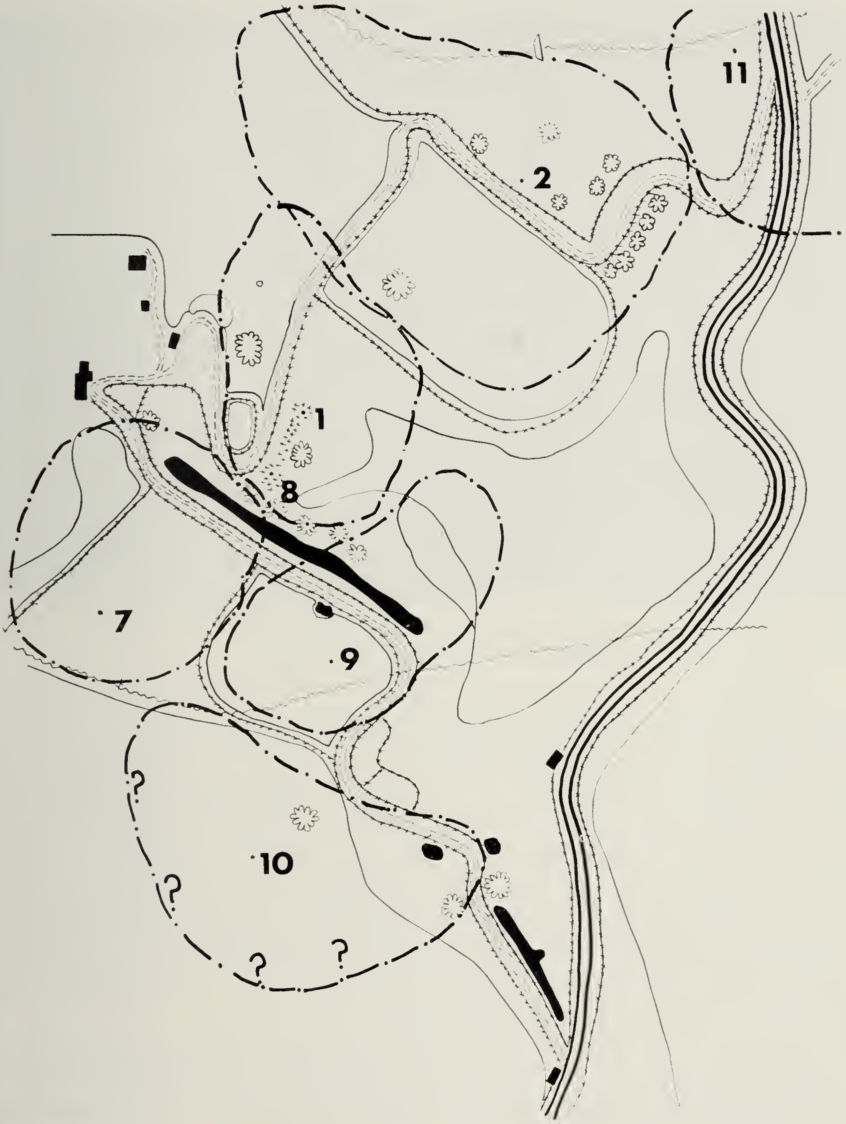

Fig. 3. Boundaries of communal group ranges of the Bushy-crested Jay.

based upon the estimated number of birds beyond juvenile age feeding young at nest 2. Other approximately equal numbers of adult and first year birds formed neighboring flocks, in the other areas shown on Fig. 3. At nest 2 of *C. s. nelsoni,* 4 or 5 adults (including at least 2 males and 2 females) formed the main group, while at nest 3, 2 adult males and 2 adult females formed the basic communal group. Each group also had a yearling member. The fifth adult at nest 2 was rarely seen. It is probable that each of these groups had suffered some diminution by trapping, as I saw a trapper in the vicinity of number 2. Thus, at least 5 or 6 birds normally form these flocks.

Communal groups in both species have at least 2 partly overlapping nesting periods in the breeding season. I have no evidence for more than 2. I studied both species toward the end of the first period and while the second was well underway. At the beginning of each study period in early June, nestbuilding or incubation was underway, while nestlings or fledglings were being cared for by the same communal groups. The communal group seems to center its attention around one nest at a time but in the Bushy-crested Jay, nests 1 and 8 were simultaneous second-period nests of a flock caring for a single brood of fledglings. At nest 2 four grown fledglings were partially dependent on the communal group for food, and this group of 11 adults plus the 4 juveniles (or at least 3 of them) were attending a nest containing 4 young. At San Blas Jay nest 2, I suspected that the one adult female who rarely appeared at the nest was incubating at another nest nearby, but I was unable to verify this. At nest 3 the incubating female represented the second nesting of the group, for her attendants plus another adult female that occasionally replaced her on the nest were caring for fledglings in the immediate vicinity.

Nestbuilding.—In both species each nest was built mostly by the female that laid the eggs in it. In captivity at Occidental College females were closely accompanied by their presumed mates who also brought nest material to the nests but played lesser roles in actual construction. Indeed, it seemed that nucleus females may have been entirely responsible for nest construction most of the time. Other jays in the aviaries carried nest material around, visited the nests, and sometimes removed nest materials, but they contributed little if anything to nest construction. It seemed to me from this fact that the aviaries were creating artificial situations to a certain extent, by forcing individuals that would not have been normally involved in nestbuilding in the wild into proximity of the nests during their construction.

The nests of both species are simple accumulations of sticks with finer twigs composing the lining. The nests are very sparsely built and in the Bushy-crest may virtually disintegrate by the time the young fledge. The nest of the San Blas Jay is slightly sturdier than that of the Bushy-crest and composed of half again as much material.

Nest 2 (Fig. 4) of the Bushy-crested Jay was collected after the young fledged. It was typical of the ones we saw and measured as follows: total width, 17–20 cm: width of cup, 10 cm: maximum depth of cup, 5 cm (but probably slightly deeper when new): total nest depth, less than 10 cm but

FIG. 4. Nest of Bushy-crested Jay in a coffee tree.

nest 8 was much deeper, for nest situation determines this. This nest was constructed totally of twigs and coarse rootlets. There was no grass, moss, or plant fiber. The outer shell of coarse sticks was 2–5 mm in diameter and 10–30 cm in length. The rounded inner portion was composed of finer sticks 5–15 cm long and 1–3 mm in diameter and finer rootlets—but not so fine as to make a soft cup lining. The depth at center was approximately 2.5 cm. The nest generally appeared very flimsy and small for the bird. Except at center bottom of the cup where eggs rest, one could see through even the new nest.

Table 1 gives heights of nests of both species.

All active nests of the Bushy-crested Jay were in coffee trees within plantations. Nest 1 was in a young plantation where the trees were densely planted and from 2 to 4 m in height. Nests 2 and 8 were in a plantation where the trees were 3 to 6 m apart and from 3 to 6 m in height. Nest 10 was in an abandoned plantation being reclaimed by native understory vegetation. All but one of the inactive nests, none of which was definitely known to be a jay nest (although all were strongly believed to be), were at edges of clearings in the forest (3–7). Number 9 was near 10 in an overgrown coffee plantation.

TABLE 1

HEIGHTS OF NESTS (M) OF NELSON SAN BLAS AND BUSHY-CRESTED JAYS

	Nest Number									
Species	1	2	3	4	5	6*	7*	8*	9*	10*
San Blas	5.5	3.0	3.0							
Bushy-crested	3.8	2.4	4.0	5.5	4.0	4.0	3.8	4.3	1.5	5.9

* Inactive or unsuccessful nests.

Nest 1 of the San Blas Jay was in a tangle of vines near the top of a thicket-edge tree of the palm woodland within 1.5 m of a corn field. Nest 2 was in a crevice at the base of dead fronds of a palm standing in acacia thicket surrounded by second-growth woodland and pasture.

Egg-laying and the clutch.—The clutch in both species is produced by one female at each nest, judging from the small clutch size and observations of laying in one female of each species in captivity in aviaries containing other adult females. From data on captive birds, eggs seem to be laid partly on successive days or every other day, even within the same clutch. The shell colors of the 2 species (as well as of other species in the subgenus *Cissilopha*) are probably unique in New World jays. They are a pale pinkish buff base overlaid with irregular stippling and mottling of reddish-brown.

In the 2 nests of the Bushy-crested Jay (1 and 8) containing full clutches being incubated, the clutch sizes were 4 and 3, respectively. A third nest contained 4 nestlings. No nests containing eggs in the Nelson San Blas Jay were examined in the wild. The nest (1) where incubation behavior was watched at length could not be checked without chance of dislodging it. Nest 2 was discovered with 4 nestlings. Nest 3 was not checked until after the young hatched when it had 3 hatchlings.

Care of Eggs and Young in the Nelson San Blas Jay

Incubation and associated activities.—There are few data on length of incubation of the Nelson San Blas Jay. One female in captivity took 17 days to incubate 2 eggs successfully. Observations of Yucatan Jays, *C. yucatanica* (Raitt and Hardy, ms), suggest 17–18 days as a probable incubation period for that species.

I studied 2 nests of this species during incubation in the wild in 1970 (nests 1 and 3). At each of these the participating individuals were distinguishable by phenotypic features, so that our failure to capture and mark any but the nucleus female and a male at nest 3 was mitigated. Observation at nest 1 spanned the period 12–29 June from late nestbuilding phase, and at nest 3 the period 23 June–1 July, late incubation through hatching. At nest 1 the flock size had seemingly been greatly reduced by a bird trapper a few weeks before my study. (I personally verified his success by visiting his home to observe no fewer than 20 jays that he insisted came from near the location of my camp!) Thus our impressions of early incubation are probably distorted by the anomalous character of the group being studied. At this nest, there were only 3 birds, an adult female, her mate, probably a 2- or 3-year-old male, and a yearling. The female was discovered building the nest on 12 June and on 14 June completed it. She had begun to sit for short periods on 13 June and began prolonged nest-sitting on 14 June. I do not know when the eggs were laid, as the nest was situated in vines that precluded examination without severe disturbance. Presumably, eggs were laid in the first days after the last nest construction was seen (14 June). At this nest in a total of 1990 min of watch, only the female sat, for 1605 min (86.5% of total observation time). There were 17 exchanges, in which the male perched on the nest rim or very near the nest virtually the entire time the female was away (79.4% of total observation time). The nest was unattended in this period for only 79 min. The male made 41 visits to the nest and fed the female at or near the nest 28 times. The yearling bird often accompanied one or both of the adults, but did not participate in the nesting activities. It visited the nest 8 times, frequently begged food, and was fed by an adult.

Nest 3 was discovered about one week before hatching and incubation was observed from 23 to 27 June. The communal group at nest 3 had 4 consistently active participants. The facts that none of the attendant birds at nest 3 was marked until 29 June, and that variation in light and obstructions to our vision at the nest existed, precluded consistent identification of the attendants. The presumed female parent and the most frequent presumed male attendant were trapped on 30 June and verified as to sex by weight and iris color (see Hardy 1973). The few data gathered do not warrant tabular presentation or analysis. Data on participation in care of young at nest 2 where the 4 regular attendants were marked suggest that our general conclusions about attendance at nest 3 are valid. These tentative conclusions are as follows: There were 2 adults of each sex, plus a yearling. Most incubation was by an adult female distinguishable by 1 or 2 wispy crest feathers. Another female was her occasional replacement for periods of a few minutes as well as her occasional feeder. She had no discernible crest. The latter bird was the principal caretaker of 4 fledglings in the vicinity, 3 together and one alone. Presumably, she was their female parent. Two adult male attendants were distinguishable as males by "impure" yellow irides and in good light from each other by slightly different tint to iris color—brownish-yellow vs greenish-yellow. These birds also visited the nest and fed the nest sitter and fledglings. Finally, a yearling bird with a tall stiff crest and some white on the bill frequented the vicinity and rarely visited the nest. It also fed the fledglings.

Hatching and early nestling care.—By the behavior of the adults, hatching was known to have occurred by 27 June. By 30 June the frequency of visits to the nest by attendants had increased greatly and seemingly involved the same birds in approximately the same proportions and roles: the presumed female parent adult performed most brooding, being occasionally spelled by the other adult female. On one occasion another adult, thought to be one of the presumed males, brooded the young for a few minutes. All 5 birds fed the young either directly or by delivering food to a female adult attendant.

Care of young to fledging.—On 15 June, nest 2 with half grown nestlings was discovered. Preliminary observations were made of unmarked attendants on 16 June. On 17 June the 4 principal adult attendants, by iris color and weight 2 females and 2 males, were captured and marked with paint in early morning hours. The remaining attendants seemed to be 1 additional adult female and a yearling and were distinguishable without being marked. On the day of fledging, 24 June, the color-marked birds were recaptured and their sexual identity verified by gonadal examination. They were prepared as study skins (JWH 765–768).

Number of attendants and their contribution.—Figure 5 summarizes the participation of these 6 birds in nestling care. Note that the 2 principal females were the only brooders, recalling nest 2 of the Bushy-crested Jay, and that they were the chief food-bringers as well. One male, L, made approximately twice as many visits as the other, J, and perhaps was the male parent. The 2 females, N and R, about half the time made prolonged visits in which they poked around the nest contents, examined the undersides of the nest and merely sat in apparent guard duty. Almost all times males visited the nest they were joined by one of the females or one of them was already there. The female then helped *distribute* the food and occasionally ate some of it herself. This habit persisted to fledging. The third female made 3 visits on 17 June and 3 on 18 June, but none later. The yearling visited the nest only the first day, 16 June. Neither of these birds was seen in the vicinity on succeeding days. No record was kept of fecal sac removal differences among the adults.

The attendants at nest 2 were remarkably tame; therefore, I think our observation without blind or other cover in no way altered frequency or character of attendance here. What happened to the unmarked adult and the yearling after 18 June? I speculate that it was the adult incubating at a nest that we failed to find, perhaps as at nest 1, being accompanied by the yearling. As there was no evidence that the marked adults were engaged in care of

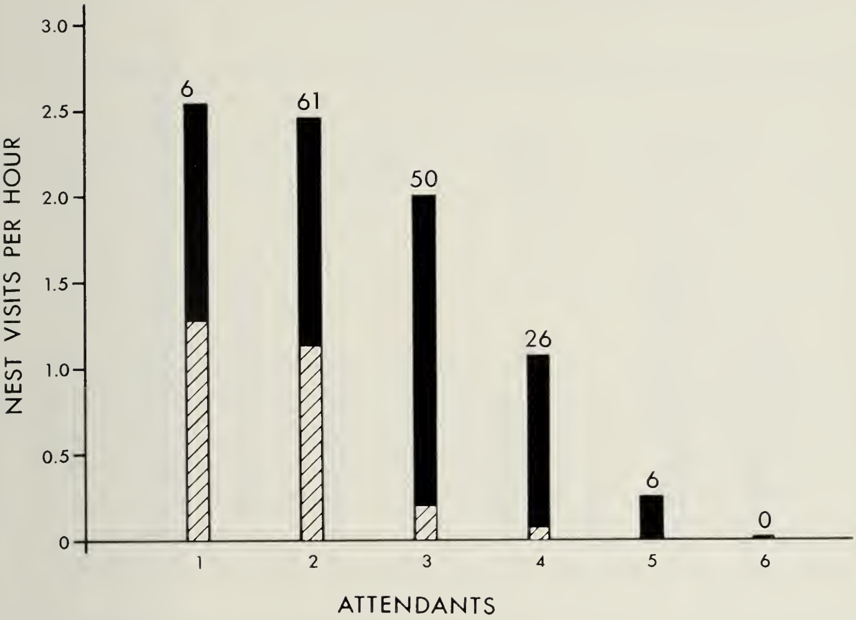

FIG. 5. Frequency of feeding visits to nest by 6 birds (5 adults, 1 yearling) at nest 2 of *C. sanblasiana nelsoni.* Numbers above each column = total visits. Cross-hatched areas of columns indicate frequency of nest visits more than 1 min long; solid areas less than 1 min. Letter symbols used in text (suggested by color markings, sex, or age in field studies) follow their figure number equivalents: 1 (N); 2 (C); 3 (L); 4 (J); 5 (third female); 6 (yearling). Birds 1, 4, and 5 were females, 2 and 3 males, and 6 was of unknown sex.

fledglings in the vicinity of nest 3, I presume that this was the first nesting of the year for this group.

I observed care of fledglings in the vicinity of nest 2. As previously stated, all birds attending the young in nest 3, except the presumed parent at the nest, were noted feeding these 4 fledglings. Three of these were together most of the time and the fourth was alone. They gave frequent location calls. These young were not over one week out of the nest when discovered on 24 June. I have no data on care or behavior of grown juveniles. Presumably their partial dependence on the adults for care is protracted, as the yearlings at both nests 1 and 3 begged and in the former case received food from an adult.

Care of Eggs and Young in the Bushy-crested Jay

Incubation and associated activites.—Incubation behavior in Bushy-crested Jays was studied at 2 nests, at which no birds were marked for individual

TABLE 2

SUMMARY OF ATTENTIVE BEHAVIOR DURING INCUBATION AT 2 NESTS OF THE BUSHY-CRESTED JAY

Nest	Total Time in min (no. periods)	% Time Eggs Covered	No. of Exchanges (with ceremony)	No. Times Sitter Fed (by juv.)	Minimum Total Adult Attendants (juvs.)
1	2050 (25)	98.3	15 (8)	16 (1)	4 (2)
8	756 (8)	87.5	3 (1)	1 (0)	4 (2)

identification (Table 2). At nest 1, 25 observation periods totaled 2050 min. At nest 8, 8 observation periods totaled 756 min. Observations at nest 1 began before the last of 4 eggs was laid, and continued past hatching. Observations at nest 8 were begun approximately half-way through incubation and continued past hatching. The total minutes and periods are for those times when only eggs were in the nest.

At nest 1, on 13 June, in an 87 min period, the sitting bird, presumably the nucleus female, was fed 4 times by adults and once by a juvenile with no begging or display. Because no birds were marked it was impossible to know how many attending adults there were. At one point on this day, however, 5 birds gathered at the nest; at least 2 of these were juveniles and 2 were adults. On 21 June, 1 bird fed the sitter, then replaced it on the nest. Immediately after the first sitter had departed, another adult flew to the nest and fed the new sitter. These activities verify that more than 2 adults visited the nest and suggest the possibility that more than 2 adults sit on the eggs.

Early in incubation exchanges at nest 8 were generally without ceremony whether accompanied by feeding of the sitter or not. But from 15 June onward, visits to the nest often were accompanied by wing-fluttering and vocal begging by the sitter, or sometimes just by slight fluttering. In the 5 observation periods within which 2 exchanges of adults at the nest occurred, one exchange involved begging ceremony while the other involved none or only slight wing fluttering. This suggests that a male and female were involved, full begging ceremony occurring when the female was relieved.

At nest 8, also, at least 2 adults sat on the eggs, and other birds, including juveniles, occasionally visited the nest. But there it seemed that one bird performed most of the sitting, although again, without marked birds, this cannot be certain. For the most part, as is suggested by the few exchanges of duties, the sitter merely left the nest unattended at times to feed and rest. This is also reflected in the smaller percentage of time the eggs were covered. The incubation period was not ascertained.

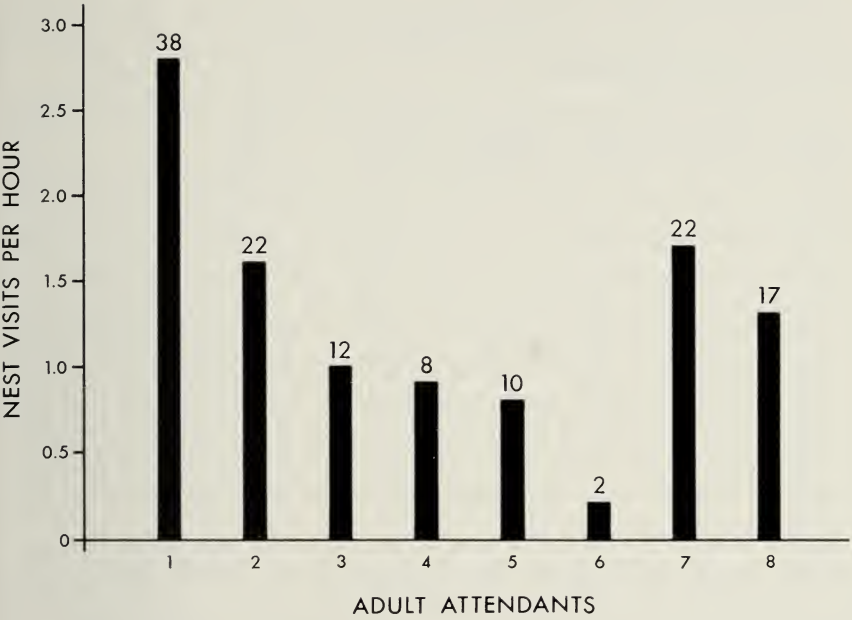

Fig. 6. Frequency of feeding visits to nest by adults at nest 2 of *C. melanocyanea.* Letter symbols used in the text (suggested by color markings employed in the field studies) follow their figure number equivalents: 1 (T); 2 (E); 3 (Y); 4; 5 (C); 6 (A); 7 (M); 8 (W). Birds 1–4 were males; 5–6, sex unknown; 7–8 females.

Hatching and early care of young.—I studied hatching and early care of young at nests 1 and 8. At least 2 birds continued to perform nest-sitting duties at each nest. Even before the clutches completely hatched, nest visitations by other birds increased. Hatching began first at nest 8 on 27 June. This was marked by the sitter getting up often, peering down into the nest and poking around, by increased begging by the sitter, and by the appearance of several juveniles near or at the nest. The juveniles begged and were fed by other adults. On 29 June when there were 2 young and one egg in nest 8 these juveniles begged the sitter and crouched beside it on the nest. Sometimes the sitter begged and at other times poked at these birds, but they were not intimidated and did not leave. At least 5 other adults were in the vicinity with the group of 3 or 4 juveniles. Four adults were seen simultaneously at or near nest 8. In the afternoon at one point when no adult was at the nest, 2 juveniles huddled on the nest rim and finally one of them actually brooded the young!

At nest 1 the group of 5 or 6 adults with 3 or 4 juveniles trouped past on

30 June when the eggs were beginning to hatch. One of these came out of the group and fed the adult on the nest. The juveniles were not seen at this nest during the hatching period.

On 30 June no birds were near nest 8 and it was empty. We made no further observations at either nest 1 or 8 after 1 July.

Later care of young.—We discovered nest 2 on 14 June when the 3 young were approximately 2 weeks old. We made almost daily morning and afternoon study of activities there and in the immediate vicinity. We color-marked 8 adults and 2 juveniles near the nest from 17–20 June and retrapped 5 of these adults plus one unmarked juvenile on 25 June as the young were leaving the nest. From 18 through 24 June, in a total of 1028 min, we gathered data on the contributions of these marked birds plus some unmarked ones. Figure 6 shows the nest visits of the 8 marked adults. No visits by the 2 marked juveniles were recorded, although they were seen in the vicinity. Unmarked juveniles did visit the nest 15 times in the period 14–25 June to feed the young. Four or 5 juveniles in the home range (Fig. 6) of the flock were involved in care of the young in nest 2.

Number of attending adults.—Probably 11 adults regularly visited nest 2; including the 8 marked birds. From 21–24 June, the 8 marked adults made 49 recorded visits (mean 6.1) and the unmarked adults made 20 visits. Assuming that unmarked adults averaged the same number of visits as marked ones, the suggestion is that 3 adults were involved, giving a mean of 6.7 visits per bird. We usually saw only one unmarked bird at a time at or near the nest, occasionally 2. Once I saw 3 such adults, one at the nest, one just leaving, and one just arriving. Therefore I believe that 3 unmarked adults were involved.

Differences in contribution by attendants.—Only one unmarked adult was significantly below the range of 1–3 visits/hr to the nest; this bird was very shy. It was frequently seen in the home range and made abortive approaches to the nest with food. Perhaps it had been frightened by capture, for we saw it feed the young only twice after being marked.

We watched this nest from a distance of approximately 20 m, without a blind or other cover. Although most of the time the birds seemed to pay only cursory attention to us, at irregular intervals individuals showed shyness by carrying food and not going to the nest. At these times, several jays scolded us briefly. These periods usually lasted only a few minutes. I concluded that our presence had some effect on the total attendance at the nest, but except for the one bird the proportionate attendance did not seem to be affected.

Frequency of visits to nest.—Total feeding visits per hour ranged from 5 to 28 (mean 13.3). Although the 2 busiest hours were recorded in "early"

TABLE 3

VISITS BY FEEDER ADULT AND JUVENILE BUSHY-CRESTED JAYS TO NEST 2

Dates in June	Time of observation in min	Length of observation (min)	Juvenile feedings	Adult feedings	Total feedings	Feedings per hour
14	09:20–09:45	25	1	4	5	12
15	09:25–10:25	60	0	5	5	5
16	08:10–09:25	75	3	9	12	9
17	06:05–06:55	50	0	3	3	3
18	11:10–12:00	50	4	5	9	11
18	15:00–16:05	65	0	13	13	12
19	08:05–10:15	130	0	14	14	7
19	17:05–18:05	60	0	25	25	25
20	05:15–06:50	95	2	21	23	15
20	16:20–16:55	35	0	9	9	15
20	08:43–10:43	120	2	30	32	17
21	16:02–17:02	60	0	16	16	16
22	09:00–10:00	60	2	11	13	13
24	08:15–09:15	60	0	28	28	28
		1028 min	15	207	222	

morning (28 feedings, 08:15–09:15, 24 June) and at dusk (25 feedings, 17:05–18:05, 19 June), I have no evidence otherwise for greater frequency early or late. Frequencies of 11 to 17 feedings/hr occurred after mid-afternoon; one evening when a light rain fell on 15 June, only 3 visits occurred in the final hour before brooding began near dark. Table 3 summarizes nest visitation data.

Division of nest visitation duties.—We tried to determine on behavioral grounds which birds were the nucleus pair. Two birds were the only ones seen to brood the young, mostly in late evening hours and presumably all night when the nestlings were young. Based upon our assumptions about the sexual identity of the principal attendants in incubation at nests 1 and 8, we predicted these 2 would prove to be male and female. Laparotomy later showed both to be females. This feature of breeding is also found in the San Blas Jay (see earlier description). Besides brooding, these 2 birds also performed nest "poking." In nest poking, the bird perches below the nest and probes its interstices. At times the work seems to be directed toward slight nest repair, but at other times it is as if the birds were searching for something, perhaps ants, or other insects that we could not see. We have noted this behavior in the Yucatan and San Blas jays, and Jerram Brown (pers. comm.) has recorded it in Mexican Jays (*Aphelocoma ultramarina*) and believes the birds may be pecking at organisms such as ants or lice that infest the nest.

The most frequent feeder of the young was T by a wide margin. I collected this bird, having failed to recapture it, and it proved to be a male. In my view the putative nucleus pair was T and M, because of their prominent feeding and brooding duties, respectively.

Fecal sac removal was dominated by E (5 observed times), followed by M and T, (3 times each). Y and W each were seen to remove one fecal sac.

Prolonged nest rim sitting, as if guarding, was a special activity also observed for one bird. This was C, who averaged 3–4 min/hr from 18–24 June in this capacity, although he was the next to the least frequent feeder.

The data are few, of course, but the suggestion that there might be some division of activities in care of the young is one that should be pursued in further work on this and other communal species.

Role of juveniles in care of nestlings.—Contribution of the partially dependent juveniles to care of young is seemingly minor. We observed a juvenile brooding briefly at nest 8 and feeding nestlings at nest 2. Unmarked juveniles fed the young 15 times between 14 and 24 June and never interfered with the work of the adults or behaved in a way that might have been conspicuous to predators. At nest 10, however, where 4 juveniles frequented the vicinity of the nest, one of them stationed itself for approximately an hour near the nest and intercepted food being brought to the nest by adults. This would seem nonadaptive to the survival of the nestlings.

Sex ratio of adults in communal flocks.—The sex ratio of adult birds captured on the final day at nest 2 was 4 males, 2 females. C, A, and the 3 unmarked adults were not captured at this time. Unless females are more difficult to trap, for which there is no evidence, and unless 4 of the 5 adults uncaptured were females, there was an unbalanced sex ratio in the adult nest attendants at nest 2. Woolfenden (1975) discovered a similar and well-documented imbalance in the Scrub Jay (*A. coerulescens*) in Florida, with males favored by 15%. He attributed this to earlier mortality and greater dispersal of females.

Prevalence of helpers.—All evidence points to the likelihood that strongly communal habits in breeding are the rule in the Bushy-crested Jay. The adults at nest 10 were not marked, but our impression was that a number similar to that at nest 2 were involved in care of young. We estimated at first 6 adults at nest 10 which is the same number that seemed involved at nest 2 prior to marking of adults. The number of adults with juveniles frequenting the vicinity of and occasionally visiting nests 1 and 8 further support this estimate.

Summary of Participation of Flock Members in Incubation and Care of Young

In both the Bushy-crested and San Blas jays, more than 1 adult may incubate the eggs. In the Bushy-crested Jay evidence from brooding participation suggests that 2 females may incubate, but evidence directly from incubatory behavior is equivocal and leaves open the possibility that the nucleus male may participate. I have found no evidence that male New World jays incubate, outside of *Cissilopha.* I have seen an adult male captive Yucatan Jay incubate (Raitt and Hardy ms). Juveniles and other adults may visit the nest but their roles seem minor. In the San Blas Jay, the nucleus female was assisted in incubation on occasion by another adult female of the flock, and the sitting bird was fed by other flock members. In Bushy-crested Jays, 2 females may brood young, and other adults may show some emphasis in contribution such as fecal sac removal and guarding the nest or domination in bringing food. Seemingly the entire communal flock helps feed the brood. Even juveniles help sporadically in this way. In San Blas Jays, all members of the communal group may feed the young. At the 1 San Blas Jay nest studied in detail, 2 adult females brooded and also "supervised" the dispersal of food to the young by the contributing 2 male birds.

Group Dispersion

Communal home ranges.—Figure 3 shows the group home ranges of Bushy-crested Jays at Santa Maria de Ostuma. Their sizes in hectares were as follows: "1–8," 2.7; 2, 7.1; 7, 2.9; 9, 2.5; and 10, 3.8. Based on estimates of all ranges studied, some of which were uncertain, the mean size was 3.9 ha. If the area is determined using data only from ranges of groups 1–8, 2, 7, and 9, those ranges that I am most confident were measured correctly, the mean remains 3.9 ha. If data only from 1–8 and 2, in which the ranges were definitely known, are used, the mean size of group ranges is 4.9 ha.

Communal group home range in the Nelson San Blas Jay was measured only for the group at nest 2. The area where the birds foraged regularly measured approximately 3.1 ha, comparable to group range in the Bushy-crested Jay. Careful study revealed no instances of the birds foraging south of the home range. Most activity took place between the nest and the stream bed to the west, with limited activity immediately east and southeast of the nest. Our observation station was east of the nest, however, and this may have discouraged the birds from flying directly east and distorted our estimates of activity in that direction. Because of the smaller group size in the groups we studied, it might seem logical to predict a smaller group home range. The general low density of birds in the population could have resulted in the larger area of occupancy. The flock was seen to move out of the home range only once, when it flew north across the old field and into another woodlot chasing a Wood Owl (*Ciccaba virgata*). Except for the old field, immediately surrounding areas had scattered trees and cultivated fields in which the corn was just sprouting or in which no crop had as yet appeared. Perhaps this discouraged the birds from moving outside the shown home range.

Territoriality.—I have deliberately used the term home range above. If territory is allowed in the broad sense of Kaufmann (1971) to include an exclusively occupied area maintained as such even by passive avoidance, then territory may be the better term for the areas occupied by the communal groups of both jays. In the Bushy-crested Jay I observed what I interpreted as a territorial skirmish at the boundary between the areas of groups 1–8 and 2. Here the group feeding grown juveniles of 2 was met by adults of 1–8. An adult of 1–8 briefly chased a juvenile. The 2 groups immediately departed from the "boundary" with no further chasing. Passive avoidance by my interpretation would almost necessitate rare reinforcement by such brief skirmishes. I think that typically such an event might involve (as this one did) an inexperienced juvenile bird.

Boundary skirmish is common in western Scrub Jays, *Aphelocoma coerulescens woodhouseii* (Hardy 1961). Certainly "passive avoidance" and spatial use that might be termed exclusive home range are typical of Blue Jays, *Cyanocitta cristata* (Hardy 1961) and Steller's Jays, *C. stelleri* (Brown 1963). The latter species according to Brown has a territory that can be conceived of as a dominance phenomenon strongest at the nest site and decreasing in all directions from the nest, so that aggressiveness is least at the perimeter. This results in passive avoidance and little territorial behavior in the classic sense.

FOOD, FORAGING, AND CLIMATE

Stomach content analysis for specimens taken at the time of the studies (Table 4) bear out our field observations about the food of these species. We were impressed that foraging Bushy-crested Jays spent approximately one-half their time just above ground level in open places foraging for beetles in herbaceous growth. The remaining time spent feeding in the trees seemed to involve mostly foraging on the small figs (*Ficus* sp.) of the native forest. We did not see figs fed to young. It appeared to us that young were fed mostly beetles and grasshoppers. In contrast, we were surprised to find adult Nelson San Blas Jays bringing not only insects but parts of lizards and pieces of the orange fleshy pericarp of the cocoa-palm fruit to the nestlings. We verified the fruit delivery by netting adults on the way to the nest.

Insect populations useful to jays as food multiply with the onset of the rainy season in climates characterized by a wet and a dry season. The locality where we studied Bushy-crested Jays may technically have a wet and a dry season but the latter is moist in the cloud forest (see Vivo 1964:210–211). I see no reason to believe that there is significant fluctuation in the insect foods of the Bushy-crested Jay at Santa Maria de Ostuma. In Nayarit, however, the climate

TABLE 4

ANALYSIS OF STOMACH CONTENTS OF BUSHY-CRESTED AND NELSON SAN BLAS JAYS

Specimen	Date Collected	Beetle	Ant	Fly	Cockroach	Plant, Misc.
Bushy-crested						
JWH731 (yearling)	14 June 1969	60% (Tenebrionidae Scarabaeidae, et al.)	10%	10%		20% (detritus, incl. stones)
JWH732 (adult)	14 June 1969	80% (Carabidae, et al.)				20% (detritus)
JWH733 (juvenile)	15 June 1969	30%			60%	10% (detritus)
JWH734 (juvenile)	15 June 1969	70% (1 Tenebrionidae, darkling beetle, 1 Scarabaeidae, June beetle)				30% (22 fig seeds, 7 orange "banana-shaped" seeds, detritus)
JWH735 (adult)	26 June 1969	65% (Scarabaeidae, et al.)	10%			24% (detritus) 1% 2 small seeds (fig?)
JWH737 (nestling)	28 June 1969	100% (Scarabaeidae 30%; Weevil 70%)				
San Blas						
JWH766 (adult)	25 June 1970				"primarily"	
JWH643* (yearling)	27 April 1968	40% (Scarabaeidae)				40% kernels (corn?) 20% unidentified & misc., incl. feather

* This specimen collected 6 km SW Compostela, Nayarit.

is characterized by an almost totally dry season from November through early June and by a very wet season from mid-June to November (Vivo 1964:212). We made no quantitative studies of insect populations, but our general observations in the dry period immediately preceding the rainy season indicated few large insects or caterpillar larvae that the jays might eat or feed to young. That we found them bringing lizards and vegetable material to the nestlings suggests possible food shortages. The vegetation of the understory and ground level was almost leafless in the forage area near nest 2, and thus I feel our chances of seeing available insect prey were excellent.

In the San Blas Jays we studied it is probably adaptive for the over-lapping nestings to span the dry to wet season change. Young of the first nest were just requiring larger insects, and young of the second nesting at nest 3 (that we did not long observe) hatched just as the rains began. They too would have had the advantage of the first flush of insect abundance that occurs with the rains.

It seems likely that a marked dry-wet season character supports the communal habit as follows. Both nestings begin in the dry season when the adults need forage only for themselves and there is no loss of eggs by rain and storm. Young of the first nesting can have larger insects that appear with the first rains when they need them. Young of the second nesting, though having increased chance of mortality from rain, do not suffer from lack of food in any way, an advantage that may balance the rain mortality. Over-lapping of the 2 nesting attempts thus took maximum advantage of both wet and dry seasons and minimized negative factors of both.

PREDATION

In late incubation stage at nest 8 of the Bushy-crested Jay, the nest was abandoned and the eggs were missing. The egg predator here was not identified, but there are 3 prime candidates. The wren *Campylorhynchus zonatus* moved about in flocks in the canopy and subcanopy of the forest and was abundant. A small tree squirrel, *Sciurus* sp., was fairly common and the Emerald Toucanet, *Aulocorhynchus prasinus*, was common. All are known egg eaters.

While watching the communal group feed fledglings at nest 3 of the San Blas Jay, I suddenly heard one of the young give a squawk. I rushed to where it had been perched on a large limb in the subcanopy of a spreading tree in a pasture. At first I could not find the bird, but after about 5 min, I spied its legs hanging from the mouth of an iguana (*Iguana iguana*) about 70 cm long. I can find no published records of these arboreal lizards eating birds, their diet being principally vegetable matter. Alvarez del Toro (1972:61) discusses the food of the iguana with no mention of avian prey, although he does state that the diet includes insects and frogs.

I saw no evidence of predation on adult jays of either species. We saw no hawks such as *Micrastur* spp. or *Accipiter* spp. at either study tract. The age composition of the communal groups seemed to suggest low mortality and predation pressure on adults. This is probably due to the buffering effect of group activity when lone individuals are more vulnerable to being taken by a hawk. When 4 to 12 birds are feeding in a loose flock the scene is constantly being monitored by at least one pair of eyes. One individual can then sound the predator alarm and all benefit.

Predator buffering effects of the communal group with regard to nest protection are uncertain from our studies. In home ranges we frequently saw the communal groups mob such animals as large tree lizards (*Iguana* sp., *Ctenosaurus* sp.), foxes (*Urocyon cinereoargenteus*), squirrels (*Sciurus* sp.), and predators invisible to us lodged in hollow cavities in trees. In other words, the jays were vigilant in patrolling and quick to come to terms with potential dangers to themselves. We saw no predators approach nests, but when we examined nest contents we were surprised, especially when they contained young, that we were not mobbed.

We found most of the study nests by their conspicuousness because of the presence of the communal group, and I expect that predators also find jay nests easily by the same means. Whether this effect is balanced by the increased efficiency of predator detection provided by so many adults is still a moot point.

THE BASIS OF COMMUNAL SOCIAL STRUCTURE

As I found both the Bushy-crested and San Blas jays breeding in edge situations provided by disturbed forest or woodland habitats, they do not support Brown's (1974) assertion, although I admit its logic, that "we should expect to find communal breeding among species inhabiting stable, climax vegetation forms more frequently than among species characteristic of transient environments." Moreover the Yucatan Jay (Raitt and Hardy ms) also is an edge and disturbed forest inhabitant. All evidence available to me suggests that these 3 jay species exist in groups of generally old age structure and are K-selected (little population fluctuation and existing at carrying capacity) as Brown believes is characteristic of species having communal kinship-based reproductive habits. Furthermore, it can be said that the disturbed transient nature of the lowland environments preferred by *C. yucatanica* and *C. sanblasiana* have prevailed since at least 1950 B.P. (Willey et al. 1964:446). Although the evidence is sparse and scattered, it seems reasonable to conclude that some kind of agricultural activity has been widespread throughout lowland Middle America since at least 4000 and possibly 8950 B.P. (Mangelsdorf 1964:427–428). Moreover although agriculture doubtless involved some clearing of woodland, it seems probable that it capitalized in the beginning upon the existence of a savannah climate-vegetation regime that had evolved in the glaciation period between 20,000 and 10,000 years B.P. Tsukada (in Cowgill and Hutchinson 1966) certainly concludes this for the Petenxil area, Guatemala, where corn planting dates from about 4000 years ago. Thus Yucatan and San Blas jays have had available, and possibly have been inhabitants of, patchy and transient habitats throughout this period. We know less about the history of montane environments of Central America, where the Bushy-crested Jay lives. It seems probable that this species has faced more uniformly natural environments of forests and less disturbance of these by man. In short it is difficult to correlate persistence or origin of communal habits in Bushy-crested, Nelson San Blas, and Yucatan jays with the same factors. Millicent Ficken, one of the referees of this paper, points out that some workers early drew correlations between group size in certain primates and composition of habitat, but that when more data became available these correlations were weakened. I therefore decline to speculate further on the origin and ecological basis of communal social behavior in these jays until at least current studies by Raitt and myself on *C. s. sanblasiana* and *C. beecheii* are completed.

SUMMARY

Bushy-crested and Nelson San Blas jays were studied in captivity and in the field in montane Nicaragua and lowland Nayarit, Mexico, respectively. Bushy-crested Jays inhabit disturbed cloud forest and are especially common in coffee plantations. The species flocks at all seasons and is communal in breeding. The breeding season consisted of 2 overlapping nesting periods, with either one or 2 nests in each. Two or 3 birds attended nests during incubation and at least 2 birds incubated. Other flock members visited the nests toward time of hatching. Nests were mostly in coffee trees, in the understory of the forest. Care of young at one nest was probably by 11 adults plus juveniles of a first nesting of the year. Two adult females brooded the young.

Nelson San Blas Jays inhabit mixed palm and tropical deciduous forest in the breeding season in Nayarit and are communal in reproduction. Five adults plus a yearling attended one nest and 4 adults plus a yearling attended another nest. There are 2 overlapping nesting periods for a communal group. The presumed female parent of fledglings occasionally left her charges to incubate briefly at a second nest at which another adult female was the principal incubator. Two adult males and a yearling fed both the fledglings and the incubating birds.

Home ranges of the birds were mapped for both species; best data suggest these varied from 3 to 4 ha. These ranges may correspond to territories in the passive sense, but only one possible instance of territorial behavior was seen—in the Bushy-crested Jay.

Bushy-crested Jays fed on beetles, grasshoppers, and figs. Young were fed insects. San Blas Jays fed on insects and lizards, feeding the young these as well as fleshy portions of palm fruit. Food was seemingly not a limiting factor in nesting success of Bushy-crested Jays, which experience no marked dry/wet season. In Nelson San Blas Jays, the breeding

season began in the severe dry season when insects seemed to be in short supply (hence the presence of lizards and vegetable materials in the diet provided the young) and ended in the rainy season when insects were abundant.

Possible predators are listed for the Bushy-crested Jay; an arboreal iguana was recorded as a predator on fledglings in the Nelson San Blas Jay. The adaptive value of communal groups in predator detection and buffering is equivocal.

Communal reproductive habits in these jays do not seem correlated with the same basic historical and ecological factors and thus it is premature to speculate on the origin and basis for persistence of communal social behavior or on its temporal relationship to a lesser degree of sociality.

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LITERATURE CITED

Alvarez del Toro, M. 1972. Los reptiles de Chiapas. Estado de Chiapas, Tuxtla Gutierrez, Chiapas.

Brown, J. L. 1963. Aggressiveness, dominance and social organization in the Steller Jay. Condor 65:460–484.

———. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63–80.

Cowgill, U. M. and G. E. Hutchinson. 1966. The history of the Petenxil basin. Memoirs Connecticut Acad. Arts and Sciences 17:121–126.

Hardy, J. W. 1961. Studies in behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kansas Sci. Bull. 42:13–149.

———. 1967. Behavior, habitat and relationship of jays of the genus *Cyanolyca*. Occ. Papers Adams Center Ecol. Stud. 11:1–13.

———. 1969. A taxonomic revision of the New World Jays. Condor 71:360–375.

———. 1973. Age and sex differences in the black-and-blue jays of Middle America. Bird-Banding 44:81–90.

———. 1974a. Jays as army ant followers. Condor 76:102–103.

———. 1974b. Behavior and its evolution in neotropical jays (*Cissilopha*). Bird-Banding 45: 253–268.

Kaufmann, J. H. 1971. Is territoriality definable? *In* Behavior and Environment (Esser, E. H., ed.), Plenum Press, New York.

Mangelsdorf, P. C., R. S. MacNish, and G. R. Willey. 1964. Origins of agriculture in Middle America. *In* Natural environment and early cultures (West, R. C., ed.), Handbook of Middle American Indians, vol. 1, Univ. of Texas Press, Austin.

Shelford, V. W. 1963. The ecology of North America. Univ. of Illinois Press, Urbana.

Vivo, J. A. E. 1964. Weather and climate of Mexico and Central America. *In* Natural environment and early cultures (West, R. C., ed.), Handbook of Middle American Indians, vol. 1, Univ. of Texas Press, Austin.

Willey, G. R., G. F. Ekholm, and R. F. Millon. 1964. The patterns of farming life and civilization. *In* Natural environment and early cultures (West, R. C., ed.), Handbook of Middle American Indians, vol. 1, Univ. of Texas Press, Austin.

Woolfenden, G. E. 1975. Florida Scrub Jay helpers at the nest. Auk 92:1–15.

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REQUESTS FOR ASSISTANCE

Gyrfalcon.—Winter Gyrfalcon sightings are wanted. Information on the age and sex of clearly identified Gyrfalcons is needed in conjunction with research being done on nesting Yukon Gyrfalcons. Please send sightings along with date and general location to: Joseph B. Platt, Laboratory of Ornithology, Cornell University, Ithaca, NY 14853.

Shorebirds.—A cooperative International Shorebird Survey was started in 1975 to obtain information on shorebird migration and to identify and document areas of major importance. This scheme has been highly successful, with much very valuable information on shorebird distribution and migration coming from contributors throughout eastern Canada and the U.S., the Caribbean Islands, and Central and South America. In 1976 we are anxious to continue and extend the scheme in as many areas as possible. Any observer who may be able to participate in regular survey counts of shorebirds during spring and autumn migration periods, as well as during the winter in shorebird wintering areas, is asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome.

For areas in Canada: Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0H3.

For areas in the U.S., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, MA 02345.

SOME DYNAMICS OF A BREEDING COLONY OF LAYSAN ALBATROSSES

Harvey I. Fisher

The purpose of this paper is to present data gathered over a 13-year period (1960–73) on Eastern Island of Midway Atoll, North Pacific Ocean, on certain aspects of the biology of breeding Laysan Albatrosses, *Diomedea immutabilis.*

Special attention is given to the close attachment to the home colony, the age composition of the breeding colony, the ingress of new breeders, and the frequency and patterns of breeding. These are analyzed in the light of published and unpublished information on this species, but the scarcity of valid, comparable data for other procellariiform species makes it unprofitable to attempt much intra-ordinal comparison.

METHODS

Our techniques for capturing, marking, and banding albatrosses and for keeping detailed records on each bird are described in other publications and will not be repeated here. Only one aspect of our search for banded birds has not been noted. Early investigations showed that Laysans had a close affinity for the site of their first nest and, indeed, for the nest site where they had been hatched (Fisher and Fisher 1969; Fisher 1971b). But since this affinity was so important in studying breeding dynamics, we wanted to verify it specifically for the plot used in this study.

In 9 of the 12 seasons we checked twice a week for any of our birds that might have moved into a strip some 50 m wide that bordered our plot on the north, south, and west. The eastern border was paved runway unsuitable for nesting. In 3 seasons we also recaptured all breeding birds in the "triangle" (Fisher and Fisher 1969:218, Fig. 6) which represented all adjoining suitable habitat.

The banding of chicks which began in 1956 and continued thereafter, the banding of juveniles which were centering their activities in our study area, and the banding of all breeders each year, starting with the 1960–61 season, made us confident that we had identified virtually all Laysan Albatrosses using this part of Eastern Island. This was verified by the fact that after the 1963–64 season no more than 7 unknown breeding albatrosses were captured in any succeeding year.

The population studied thus consisted of birds whose ages: (1) were known; (2) could be calculated with a good degree of accuracy on the basis of their first entry into the breeding population; and (3) were unknown and could only be stated in minimal values.

When the exact age of a bird was not known, an age was assigned as follows: First-time breeders were assigned to year classes on the basis of the percentages of males and females known to initiate breeding at various known ages (Van Ryzin and H. I. Fisher, ms). Applying these percentages to the new breeders found in any season, 1963–64 for example, we assumed that certain percentages of them were hatched each year between 1952–53 and 1957–58. All breeders banded in the plot between 1959–60 and 1962–63 seasons were assigned a minimum age of 8 years, since the mean and modal ages for both sexes at first breeding are between 8 and 9 years. However, this group was believed to include disproportionately large numbers of birds 12 or fewer years of age and of birds 20 or more years old. Dates of egg deposition (Fisher 1969) added credence to this view.

The greatest fallibility in these assignments of age may lie in the assumption that there was no significant annual variation in mortality, in the ages at which young birds first began to breed, or in the production of young which later became breeders. We know such variations exist, but there was no certain way to assess their magnitude in each of the 13 seasons of observations or in the years earlier when chicks were hatched that later became part of our study. However, the "cyclic" recurrence of these variations, the length of the study and the sizes of the samples mitigate against significant, cumulative errors.

RESULTS

Attachment to site.—Of the 49 non-breeders of unknown age that frequented the plot each season between 1962 and 1965, 20 males first bred a mean distance of 15 m (1 to 46) from the site of first capture and banding, and the 22 females 18 m (2 to 46). Only 6 of the first-nesting sites (4 of females and 2 of males) were outside the plot; they were within the 50 m border. Seven birds were never caught again.

Of the 1288 plot breeders of 1960 to 1963, only 3 males and 7 females were discovered breeding outside the plot. The males were 2 to 3 m outside, and 2 of them were with new mates. All 7 females had new mates: 6 were on nests a mean 14 m (5 to 32) from the nearest plot border, and the seventh female was incubating some 90 m from her former nest site.

Just 2 males and 1 female of 1078 fledged in the plot and of an age to breed were found nesting beyond its borders—the males 6 and 13 m outside and the female 7 m away. Fifty-six males were incubating a mean distance of 19 m and 49 females 26 m from their natal nests. One plot fledgling of 1960 was temporarily on a nest on Kure Island on 8 January 1969, but we could not be certain it was truly breeding there. Vernon Kleen, who found it, also reported 2 additional 1960 chicks of ours from Midway, but not from the plot, nesting on Kure that same year. These 2 were verified by me as actual breeders on 1 February 1969.

Age composition of the breeding colony.—I wish to emphasize again that many of the ages used are minimal, calculated on the basis of presumed age at first breeding. To minimize possible errors, data in Table 1 are presented in 5-year spans of ages, except in the instances of the 8- and 9-year-old birds. Many of these were of known age, and the estimated ages of others probably varied from true ages by no more than a year or so.

Birds 8 or fewer years of age constituted approximately 10% of the breeders each year (Tables 1 and 2). Nine-year-olds made up a mean 6.3% (2.5 to

TABLE 1

MEAN AGE DISTRIBUTION OF LAYSAN ALBATROSSES BREEDING IN THE PLOT, 1963 TO 1972, INCLUSIVE

		Age					
Years	n	8 or less	9	10–14	15–19		20 or more
1963	1392	8.5%	2.5%	44.1%		45.3%	
1964	722	14.5	2.8	40.0		43.3	
1965	1445	9.5	9.5	50.2		30.0	
1966	1243	9.3	5.7	54.9		29.4	
1967	1332	12.0	5.0	56.5		27.5	
1968	939	11.5	9.8	41.6	33.1		3.5
1969	1455	9.3	8.5	20.7	51.2		10.6
1970	1383	9.7	8.5	22.2	42.6		16.0
1971	1660	8.4	5.0	24.0	35.0		28.0
1972	2208	9.3	5.8	23.6	30.0		31.5

9.8) of the breeding population. Birds 10 to 14 years of age averaged 37.9% of the breeders each year, but the range was great—20.7 to 56.5%.

Data on breeders judged to be a minimum of 15 years old are combined until 1967; we started the study in 1959–60 with many birds of unknown age—birds which did not reach the more reliably ascertained 15- to 19-year group until 1968. However, birds of a minimum of 15 years of age constituted from 27.5 to 45.3% of the population prior to 1968 and from 30.0 to 51.2% after that. The 20- or more-year-olds made up 3.5 to 31.5% of the breeders between 1968 and 1972.

The observable trends lend some credence to the validity of the method of assigning ages. There is less variation in the percentages involving birds of the 2 younger categories, and at least some of the variations are explicable. Note that the low percentages of birds 9 or fewer years old in the first 2 years are reflected in the higher percentages of 10- to 14-year birds in 1965–67 and in the increased percentages of 15- to 19-year birds in 1969–70 and, still further, in the larger percentages of birds more than 20 years old in the period of 1969 to 1972.

Seventeen to 20% of the breeders were fewer than 9 years old in 1964 and 1965, and 19 to 22% were of this age in 1968 and 1969; these percentages were higher than those in any other years. The 1964–65 season showed a drop of 5% in the 10- to 14-year-old class, and in 1965–66 there was a 10% increase. This same age group showed a major drop in relative numbers between the 1967 and 1968 seasons and remained at the lower level for the remainder of the study. Although the numbers in the 15- to 19-year class increased dramatically between 1968 and 1969, they declined thereafter. Birds

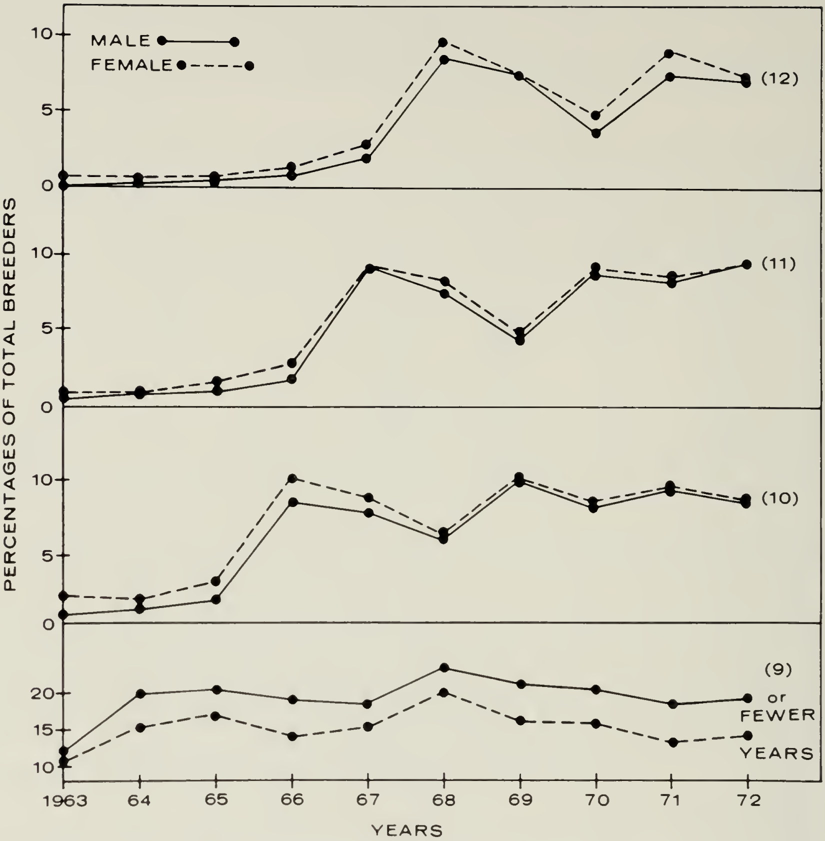

FIG. 1. Percentages of young breeders in a Laysan Albatross colony during a 10-year period.

identifiable as at least 20 years of age were relatively few in 1968, as compared to 1969 when their numbers began to increase.

The changes in the relative numbers of breeders to age 12 are illustrated in Fig. 1. Despite some significant, annual variations in the numbers of birds 9 or fewer years of age, many of them in their first breeding, this age group constituted a fairly uniform 15 to 17% of the breeding population during the 10-year period. The relative numbers of 10-year-olds rose greatly in 1966, and this showed up as increases in 11-year-olds and 12-year-olds in following years.

The drop in numbers of 10-year-olds in 1968 was reflected in fewer 11-year birds in 1969 and in fewer 12-year-olds in 1970. Once the numbers of each of these 3 age classes recovered from the decreases, they stabilized until

TABLE 2

MEAN AGE COMPOSITION, BY SEX, OF 13,849 LAYSAN ALBATROSSES BREEDING IN THE PLOT, 1963 TO 1972, INCLUSIVE

Age (years)	Males			Females		
	n	Mean	Range	n	Mean	Range
6	63	0.9%	0.4– 1.5	21	0.3%	0.1– 0.4
7	223	3.2	1.7– 5.7	152	2.2	1.6– 3.7
8	486	7.0	3.9–12.6	373	5.4	3.7– 9.0
9	438	6.3	2.5– 9.8	421	6.1	2.8– 9.5
10	438	6.3	1.2–10.1	489	7.1	2.2–10.3
11	362	5.2	0.5– 9.6	379	5.5	0.8– 9.4
12	264	3.8	0.2– 8.7	304	4.4	0.3– 9.8
13	195	2.8	0.1– 7.6	234	3.4	0.2– 8.9
more than 13	4485	64.5%		4422	65.6%	

the end of observation in the 1972–73 season—the 10-year and 11-year birds at approximately 9% of the breeders, and the 12-year-olds at 7 or 8%.

There was also sexual variation associated with the age variation in composition. Figure 1 and data in Table 2 indicate the greater percentages of males of ages through 9 years. Considering all birds 10 or fewer years old in the breeding population (Fig. 2), males predominated by 2 to 4% from

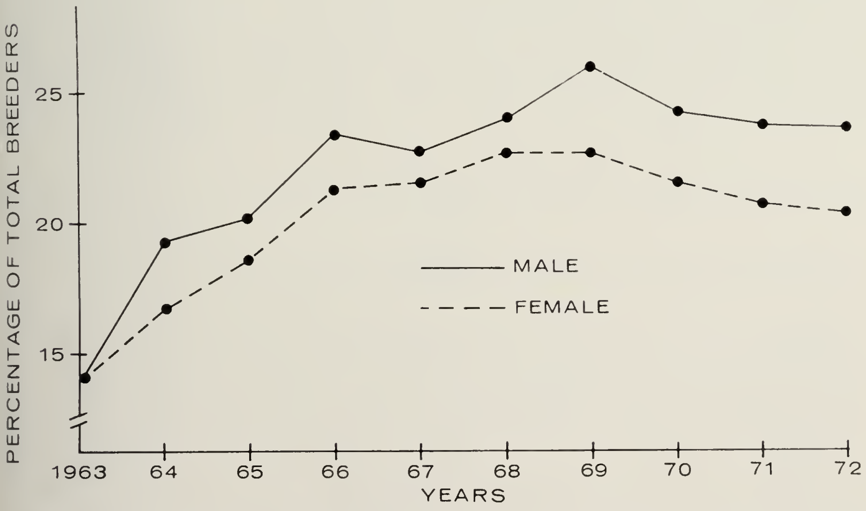

FIG. 2. Sexual variation in the numbers of breeding Laysan Albatrosses 10 or fewer years old.

TABLE 3

INGRESS OF FIRST-TIME BREEDERS INTO A LAYSAN ALBATROSS COLONY, EXPRESSED AS PERCENT OF TOTAL BREEDERS EACH YEAR

Age (years)*	1963	64	65	66	67	68	69	70	71	72
8 or less	8	14	10	9	12	12	10	10	8	9
9 or less	11	17	19	15	17	21	19	18	14	15

* See table 1 for sample sizes.

1964 onward, and by a constant 3% from 1969. By age 10 and thereafter, at least to age 13, the number of females was greater in each age class (Table 2). Birds 13 or fewer years old were equal in sex representation and constituted a mean one-third of all breeders.

Ingress of first-time breeders.—First-time breeders (8 or fewer years old) made up a mean, annual 10% (8 to 14) of the total breeding population during a 10-year period, 1963 to 1972 (Table 3). If the 9-year-old birds observed breeding for the first time are included, the mean, annual percentage of new breeders is 17 (14 to 21). Male breeders 9 or fewer years old consistently made up 2 to 5% more of the breeding population than did females of these ages, but this sexual difference was not present in the older age groups (Fig. 1).

Frequency of breeding.—The frequency of breeding by experienced birds in 212 constant pair bonds is shown in Table 4. Eighty-two pairs known from the 1960–61 to the 1972–73 season bred a mean 91% (43 to 100) of the time. Comparable data on 64 pairs known from 1961 to 1972 were a mean 84% (47 to 100), on 36 pairs known from 1962 to 1972 a mean 79% (47 to 100), and a mean 80% (40 to 100) for 30 pairs known from 1963 to 1972.

TABLE 4

PERCENT OF PAIRS* OF LAYSAN ALBATROSSES BREEDING EACH YEAR OF 10- TO 13-YEAR SPANS

Banded as breeders in:	No. pairs	Percent breeding in:												
		1960	61	62	63	64	65	66	67	68	69	70	71	72
1960	82	100	100	99	95	43	94	79	85	55	85	78	84	100
1961	64	—	100	100	91	47	97	72	84	59	87	77	88	100
1962	36	—	—	100	75	47	94	89	78	56	78	69	78	100
1963	30	—	—	—	100	40	97	67	93	57	83	87	80	100
Averages				96		44		86		57		81		

* Constant pair bond for period indicated; age unknown.

FIG. 3. Frequency of breeding by 212 constant pairs of Laysan Albatrosses during 10- to 13-year periods.

In each instance the lowest percentage occurred in the 1964–65 season and the next lowest in 1968–69, the "poor seasons" mentioned previously. The mean percentage of all 212 pairs that bred in these 2 seasons was 44 and 57, respectively (Table 4). Note also that 95 and 94% of the 1960 sample, 91 and 97% of the 1961 birds, 75 and 94% of the 1962 pairs, and 100 and 97% of the birds banded in 1963 nested in the season before and the season after 1964–65. The same relationships exist for the 1968–69 season, although the percentages are lower.

A mean 96% of these 212 pairs bred in the 1960–61 to 1963–64 seasons, inclusive, 86% during the 1965–66 to 1967–68 seasons, and 81% bred from 1969–70 to 1972–73.

All 82 pairs banded as breeders in 1960 also bred in 1961, and all 64 pairs banded in 1961 bred in 1962.

Figure 3 shows that the 212 constant pairs of unknown age contributed 2041 nestings during these years. The mean frequency of breeding per pair per year ranged from 0.82 to 0.86. The pairs in the 11-, 12-, and 13-year samples exhibited a more or less normal distribution in the total number of times they bred.

There were 3094 nestings by 366 birds involved in 2 or more pair bonds (Table 5). These birds had a mean frequency of breeding per year of 0.71 (0.64 to 0.78). The mean frequency was 0.64 (0.55 to 0.70) for birds with

TABLE 5

FREQUENCY OF BREEDING BY LAYSAN ALBATROSSES WHICH HAD TWO OR MORE MATES DURING 10- TO 13-YEAR SPANS

Span of years	No. birds	Total no. breedings in variable no. pair bonds				Mean frequency per bird per year in variable no. pair bonds			
		2	3	4	5	2	3	4	5
Ten:									
males	24	156	—	—	—	0.65	—	—	—
	1	—	7	—	—	—	0.70	—	—
females	30	194	—	—	—	0.65	—	—	—
	2	—	11	—	—	—	0.55	—	—
Eleven:									
males	27	214	—	—	—	0.72	—	—	—
	8	—	58	—	—	—	0.66	—	—
females	29	205	—	—	—	0.64	—	—	—
	5	—	34	—	—	—	0.62	—	—
	2	—	—	13	—	—	—	0.59	—
Twelve:									
males	50	453	—	—	—	0.76	—	—	—
	11	—	86	—	—	—	0.65	—	—
females	39	346	—	—	—	0.74	—	—	—
	4	—	31	—	—	—	0.65	—	—
	1	—	—	6	—	—	—	0.50	—
Thirteen:									
males	55	561	—	—	—	0.78	—	—	—
	18	—	163	—	—	—	0.70	—	—
	4	—	—	39	—	—	—	0.75	—
females	46	445	—	—	—	0.74	—	—	—
	7	—	53	—	—	—	0.58	—	—
	1	—	—	6	—	—	—	0.46	—
	1	—	—	—	7	—	—	—	0.54
Means	—	—	—	—	—	0.71	0.64	0.57	0.54
Totals	366	2574	443	70	7	—	—	—	—

3 different mates, and 0.57 (0.46 to 0.75) for 9 albatrosses with 4 successive mates. Only one bird was known to have 5 mates in 13 years, and it bred only half the time.

Males with 2 successive mates bred a mean 68% of the seasons and females only 60%.

Data on the number of breedings per pair bond are presented in 3 ways

Table 6

The Number of Breedings Per Pair Bond in Laysan Albatrosses

	Minimal Number of Breedings During Bond, All Ages, 13-Year Span[1]												
No. birds	1	2	3	4	5	6	7	8	9	10	11	12	13
12,396	1,363	2,167	1,051	494	326	216	144	106	101	102	76	42	10
Percent of bonds	22	34	16	8	6	4	2	2	2	2	—	—	—

	Number of Breedings During Bonds, All Ages, 9-Year Span[2]								
No. birds	1	2	3	4	5	6	7	8	9
1,968	335	275	173	99	58	32	8	4	0
Percent of bonds	34	28	18	10	6	3	1	—	—

	Minimal Number of Breedings During First Five Years of First Bond				
No. birds	1	2	3	4	5
128	12	9	14	18	9
Percent of bonds	19	14	24	28	14

[1] Minimal because bond was present at beginning of study or still intact at end of study, or both.

[2] Bond consummated and broken during study.

(Table 6). The top part of the table shows that 56% of the 12,396 breeders whose bonds were in force at the beginning or at the end of the study, or at both times, had a minimum of 1 or 2 matings with a mate and that 80% had 4 or fewer. This is very gross information, but the data in the middle of Table 6, on 1968 birds whose lengths of pair bond (or bonds) were known definitely, revealed similar percentages—62% had 1 or 2 breedings with a mate and 90% had 4 or fewer.

The mean frequency of breeding in their first 5 years by 64 pairs made up of 2 inexperienced birds was 0.59 per year, 189 attempts in 320 pair-years (Table 6, bottom). Nineteen percent of the pairs disappeared after their first attempt, but 9 pairs (14%) bred in each of these 5 years. However, in a sample of 27 inexperienced females and 18 inexperienced males paired with experienced birds of various ages, there was a mean frequency of breeding per bird per year of 0.80 for both sexes. One inexperienced female began breeding at age 5 with an experienced male and laid an egg each season for 4 more years.

Seventy-five percent of the 619 breeding pairs of 1961–62 also bred in 1962–63. Sixty-eight percent of the 417 pairs which fledged chicks in the summer of 1962 returned to breed that winter, and 81% of 202 pairs which failed to rear a chick in the 1961–62 season bred the next year.

Patterns of breeding.—The only "patterns" of breeding by 65 constant

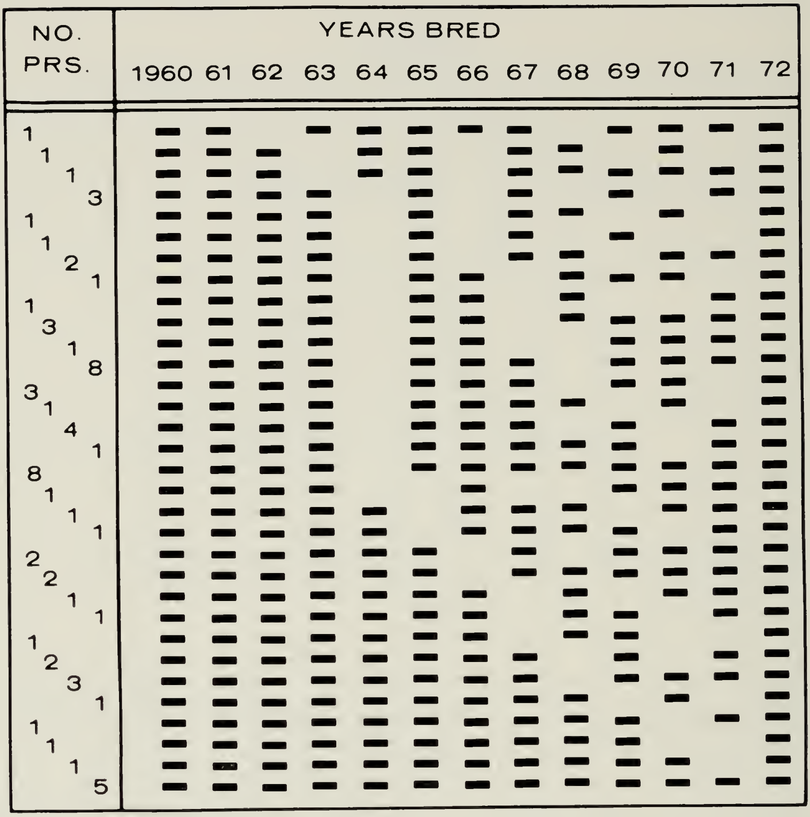

FIG. 4. The breeding patterns of 65 constant pairs of Laysan Albatrosses during a 13-year period.

pairs of experienced breeding birds of unknown age is that, generally, they bred every year (Fig. 4). In 1964 and 1968 many failed to breed, as indicated earlier. Twenty-six pairs bred each year, with the exception of one or both of these seasons. There were 60 instances of pairs breeding 4 successive years, 7 instances of 5 successive years, 7 of 6 years, 3 of 7 years, 13 of 8 successive years, 1 of 9 years, 2 of 10 years, 1 of 11 years, and 5 pairs bred in each of these 13 years. In only 7 instances did a pair fail to breed in as many as 2 successive seasons.

Sixty-four pairs of inexperienced birds (Table 6) whose exact ages were known exhibited no discernible patterns in breeding after the first 2 years of a 5-year span. Thirty-five pairs (55%) failed to breed the season after the first attempt, and 2 pairs skipped the second and third years as well before resuming breeding. Eight pairs bred in the first and second years and then

Table 7

Breeding Seasons Lost by Laysan Albatrosses Because of the Loss of a Mate

No. seasons lost	Males (168)		Females (124)	
	Number	Percent	Number	Percent
0	3	2	0	0
1	112	67	59	48
2	37	22	39	31
3	12	7	13	10
4	4	2	9	7
5	0	0	4	3
Mean seasons lost	1.4		1.9	

missed one or more seasons. Only 5 pairs bred in 3 consecutive years before missing a season. One pair bred the first 4 years, and 9 pairs bred in each of the 5 seasons of this phase of our investigations.

I found no evidence that age of mate or age at which breeding commenced affected either the pattern or the frequency with which these young breeders attempted to nest.

Studies of the pattern of breeding among 366 birds involved with 2 or more mates (Table 5) revealed that 363 (99%) failed to breed the season after their mates disappeared. These results were confirmed by, and other information gleaned from, an additional 292 birds which formed more than one pair bond during the study (Table 7). Only 1% bred the season following the mate's disappearance. Two-thirds of the males and half of the females failed to breed only in the first season after the mate was lost. An additional fifth of the males and a third of the females did not nest in the first or second seasons. Ten percent of the males and 20% of the females failed to breed for 3 to 5 years after the disappearance of their mates. Females lost a mean of 1.9 seasons and males a mean of 1.4 seasons during the 5 seasons after the original pairs were first identified.

DISCUSSION

Attachment to site.—Laysan Albatrosses are firmly attached to their home island, colony and nest site, and with few exceptions they return there regularly (Fisher and Fisher 1969; Fisher 1971b). Data from this study substantiate these findings for the birds in the study plot and elaborate on the distances that exceptional birds may move.

The Fishers (1969:197) found that 16% of 986 juveniles visiting an area eventually nested within 100 m of the site of first banding. The present data on more closely observed juveniles revealed that 85% later bred in the plot.

Fewer than 1% of 1288 established breeders moved their nests significantly in later years, and then only when there was a change of mates. There was sexual difference in this movement. The 3 males that moved short distances are thought to have shifted within their original territories primarily in response to different nest sites selected by subsequent mates. The 7 widowed females moved significant distances as a result of pairing with different territorial males.

The data on location of first nests of breeders fledged in the plot are identical to those I gave earlier (1971b:394, Table 2) and support the preliminary views expressed by Fisher and Fisher (1969:197). Males settle to breed a mean of some 15 m from their nests of origin, and females locate about 26 m away. The sexual difference comes about because it is the males that establish territories; they can exert considerable influence on their location. Females, on the other hand, are dependent upon finding a suitable, unpaired male on a territory.

We undoubtedly did not discover all of the more distant nesting sites of our birds, but the one 1960 plot chick at least temporarily incubating on Kure Island and the 2 other Midway chicks actually nesting there are the only acceptable records we have of any of our chicks nesting on other islands. Despite these instances it is evident that both sexes of Laysan Albatrosses make an attempt to locate permanently near their natal nests.

One result of such close affinity for a site would be intense inbreeding within an island's population or within colonies isolated on an island. There is, apparently, very little genetic exchange between island populations of these birds. Fisher and Fisher (1969:197–201) discussed the available records of inter-island movements and concluded that most were of juveniles banded as they island hopped to their home colonies. They most likely did not represent chicks reared on one island and breeding on another. The banding of miscellaneous juveniles or of birds in migration, as done all too frequently, has obscured the true picture of the degree of breeding isolation of this and other species.

With a high degree of inbreeding, one might expect divergence among the colonies of birds nesting on the series of small islands used by this species, and even among colonies on the same island. Intense inbreeding, even within different parts of the same, large colony, may have produced the "subcolony associations" we found earlier (1969) in the time of egg-laying, the feeding of chicks, and the grouping of chicks at first departure from the colony. Further evidence may be the groups of "dwarfs" found among Laysan fledglings in the same areas in successive years (Fisher 1967:381).

The effect of rigorous site attachment on genetic isolation of the Laysan Albatross merits detailed investigation.

Age composition of the breeding colony.—Previously, I have alluded in general terms to the atypical nature of Midway's Laysan colonies, but some specific, historical facts are pertinent here. Few albatrosses could possibly have bred in the study plot between 1940 and 1946. There were few chicks when I first visited the area in May of 1945 (Fisher and Baldwin 1946) and few nests were found during my visit in the winter of 1946 (Fisher 1949). The blacktop paving and wooden, rock-covered bunkers probably prevented much reproduction until at least 1948.

Therefore, by 1960 when the current, detailed investigation began, the breeders must have consisted largely of birds hatched prior to 1940, and thus at least 20 years old, and of birds hatched in 1948 or later years, and thus 12 or fewer years of age. The data in Table 1 tend to support this hypothesis, but, unfortunately, there was no way even to estimate the sizes of these components of the breeding colony.

The percentage of breeding birds 8 or fewer years of age is not highly variable from year to year. If one omits the percentages for 1964 and 1968, which were inflated because of major decreases in the actual numbers of older birds, the mean percentage is 9.6 (8.4–12.0). Much the same can be said for the 9-year-old group—a mean 6.3% (2.5–9.5) of the breeding population. The lower number of 9-year birds, compared to 8-year-olds, is because the majority of Laysans begin to breed at 8 years and many of these do not attempt to breed in their ninth year.

As increased numbers of young produced in the mid-1950s entered the breeding colony, there was a shift toward an older average age among the breeders, demonstrated first by the 10- to 14-year classes from 1965 to 1967, a few years later by the 15- to 19-year group, and, finally, by the relative numbers of birds 20 or more years of age after about 1969.

Recognizing that breeders 9 or fewer years of age tend to be a fairly constant proportion of all breeders, it appears that breeders belonging to the 10- to 14-year class had dropped by 1972 to perhaps half their 1963 numbers (Table 1). They made up a nearly constant 21 to 24% of all breeders in the last 4 years, indicating that their relative numbers may have stabilized. The detailed analysis of breeders in the 10- to 12-year-old classes demonstrated that their relative numbers stabilized between 1970 and 1972 (Fig. 1).

The primary continuing changes in age composition among the breeders are in the 2 groups 15 or more years old. Together, they made up 61.8% of all breeders in 1969 and approximately the same percentage in all years since. As the 15- to 19-year-olds declined in relative numbers, the older component among the breeders increased in size. It appears that the changes are slowing, however, and, considering the information available on mortality and longevity, they may be expected to cease in the next 2 or 3 years.

For purposes of discussion, I consider the age composition of the breeding colony essentially stabilized in 1972. This population of Laysan Albatrosses may be said to consist of: (1) a group of learners, birds 9 or fewer years old and breeding for the first or second time but making little significant reproductive contribution, and forming 15% of the breeding colony; (2) the prime, reproductive birds, aged 10 to 19 years, upon which the maintenance of the species may really depend and which constitute 54% of all breeding birds; and (3) birds of 20 or more years, composing 31% of the breeders, which are in the last third of their expected 16 to 20 reproductive years (H. I. Fisher, ms). This last component, birds experienced in survival and reproduction, probably makes an important contribution, for in a study still in progress I find that three-fourths of the birds more than 30 years of age are still reproductively active.

There is sexual variation within the age variation in the composition of the breeding colony. Males predominate within the 6- to 9-year classes, and the females are more numerous among breeders age 10 through 13 years. However, because of the preponderance of males in the early years, they still are more numerous among all breeders 10 or fewer years old. These differences in sexual representation come about because females generally initiate breeding a year later.

Ingress of first-time breeders.—The true percentage of naive, young breeders entering the breeding population in an "average" year probably is greater than the 10% observed for birds 8 or fewer years old. However, it is equally inappropriate to accept without question the observed 17% ingress of new breeders, based upon the inclusion of 9-year-olds.

We know that 47% of the young Laysans do not begin to breed until at least the ninth year (Van Ryzin and H. I. Fisher, ms); more females than males delay until this time. Also established are the facts that: (1) 18% of the males and 14% of the females first breed at 7 years; (2) relatively few inexperienced birds complete incubation of their first egg; and (3) approximately half of them do not attempt to breed the following year. Considering all these, it is probable that some birds initiating at 7 years were undetected then because they deserted before capture, and they could not be recaptured in their eighth year because they did not come to the colony during the egg season. They were thus first observed breeding in the ninth year. My best estimate of their numbers is about 2 or 3% of all breeders.

Consequently, if these are added to the 10% first found breeding at 8 or fewer years, approximately 13% of the breeders are new each year. The 3% must also be subtracted from the observed 17% for all birds 9 or fewer years old. The resulting 14% includes the above 13%, plus the approximate 1% of the breeders which begin to breed at age 9.

An annual recruitment of 14% is surprisingly high, considering the 5 to 6% annual mortality among breeding birds and expected 16 to 20 years of reproductive life.

Not all of the indicated increase in the breeding population on Midway can be attributed to this rate of recruitment. The growth of the colony is probably not typical of undisturbed Laysan Albatross colonies. Rice and Kenyon (1962) discussed the history of the Midway colony and the factors influencing its numbers up to 1957. The trend has been generally upward since 1903, largely, they thought, because of increased protective vegetation on Sand Island, but with some depressions in the years of World War II. Part of the post-war increase on Eastern Island (sometimes called Green Island in early accounts) may be attributed to the war-time opening up of the vegetation which may have been too dense for maximum use by Laysans. However, the virtual cessation of human disturbance must be a primary factor in the continuing "explosion" in numbers on both islands since the early 1960s. The resulting decrease in mortality makes possible increased life expectancies for aged, breeding birds and increased survival of juveniles to be recruited into the breeding population. Since these recruits were raised in the Midway colony and did not originate from other colonies, as Robertson (1973) believed may have happened with the Royal Albatross colony on Tairoroa Head, New Zealand, the impact of the increased survival of juveniles is more evident.

Frequency and patterns of breeding.—The evidence presented here and in other studies of procellariiformes indicates that these birds are physiologically capable of breeding each year. That is, the basic reproductive cycle is an annual one, and it is important in this discussion to keep in mind the difference between observed frequencies of breeding and potential capabilities for reproduction. Murphy (1936:664) seemingly did not when he suggested that longer than annual reproductive cycling of the individual procellariiform may have developed to permit multiple use of the very limited space in the colony. We know now, at least for the Laysan Albatross, that experienced birds not currently breeding return to the colony frequently enough to maintain their territories and to prevent their use by other pairs. It also seems improbable that space is a limiting factor in most albatross colonies.

Most individuals of some procellariiform species breed in successive seasons (Laysan, Rice and Kenyon 1962, and this study; Black-browed, *D. melanophris*, Tickell and Pinder 1967; Waved, *D. irrorata*, Harris 1973; and Black-footed albatrosses, *D. nigripes*, Rice and Kenyon 1962; and the Fulmar *F. glacialis*, J. Fisher 1952). However, the Wandering (*D. exulans*), Royal (*D. epomophora*), and Gray-headed (*D. chrysostoma*) (Tickell and Pinder op. cit.) and the Yellow-nosed albatross (*D. chlororhynchus*) (Elliott 1970) are regarded as biennial breeders. These views have been developed from gross information on the colony-wide return to breed in successive years and, in general, without consideration of the possible effects of several, major, biological factors—namely, mortality, food supply, nature of the formation of the pair bond (and its constancy), and influence of the age and experience of the members of the pair upon their patterns or frequencies of breeding.

The factors usually discussed are body size and the energy required for the successful rearing of a chick; the biennial cycle in some species is attributed to the long period of parental care which may be correlated in part with larger body size. The deviations from the annual reproduction expected in other species are often said to result from the exigencies of fledging a chick.

For example, Rice (1959:6) observed that 33% of the nesting Laysans failed to breed the next season and, more specifically, that only 63% of the successful breeders nested the next year, and that 87% which lost the egg early in incubation bred the following season. Rice and Kenyon (1962:521) reiterated these conclusions and further indicated that 87% of the pairs with "sterile" eggs bred the year following. This latter is puzzling because Laysans do not abandon sterile eggs. Indeed, a Laysan may incubate such an egg for weeks past its expected hatching date (Fisher 1971a:51). They are not released from the energy requirements of incubation, and one would expect the percentages of such pairs that returned to breed the next year to approximate the 75 to 79% Rice and Kenyon gave for pairs losing the egg late in incubation or the chick during the guard phase.

Richdale's view, expressed in 1952, that successful pairs of Royal Albatrosses breed in alternate years and that early nest failures enable pairs to breed the next season has been accepted (Carrick et al. 1960) and extended by Tickell (1960, 1968) and Tickell and Pinder (1967). These papers also corroborated Mathew's observation (1929) that the Wandering Albatross can breed only every second year, if it is successful in fledging a chick. Further, Tickell and Gibson (1968) noted that 60% of the Wanderers breed each year, and Tickell (1968:12) wrote that 55% of them did. Tickell and Pinder (1967) recorded 76% of 50 pairs of Black-broweds breeding in 2 successive years. Harris (1973:497) indicated that 90% of the Waved Albatrosses that reared a chick and 87% that lost eggs bred the next season. He thought, however, that all surviving pairs bred both seasons.

Underlying these observations, except those of Harris, is the theme of "necessary rest" for the parents (Richdale 1954:251). The necessary rest presumably spans a period during which the annual molt occurs and the bird not only regains any weight lost in fledging a chick, but also adds the usual pre-breeding fat. Most Laysans have a minimum of 3 months between the successful rearing of a chick and the beginning of the movement toward the breeding colonies for the next reproductive season. In most instances this seems to be ample time, especially since I showed (1967) that incubating Laysans can regain a 20% loss of weight in approximately 3 weeks at sea. Net losses after incubation are less than 20%. It is unfortunate that we know so little of the timing or energy requirements of the molt in the Laysan.

The Gray-headed Albatross is also small-bodied and has a rest period similar to that in the Laysan, but it is considered a biennial breeder by Tickell and Pinder (1967). If this is true, neither body size nor length of parental care can be considered the sole or perhaps even primary factor determining whether pairs of albatrosses breed in successive years.

A further analysis of the percentages of Laysan Albatrosses that breed in successive years emphasizes the possible effects of raising a chick. Although 75% of the 619 pairs that bred in 1961–62 also nested the following season, the simple observation is misleading, as it is in most published accounts. The 6% annual mortality of experienced breeders, the 2% mortality of young breeders, and the 14% constituency of young breeders in the population must be considered.

If mortality was evenly distributed among the pairs that did not return, and evenly between one or both members of a pair, there were only 568 viable pairs to return. However, 14% or 87 of the 619 breeding pairs were probably made up of first-time breeders, of which 60% (52 pairs) would not attempt reproduction the second year. Subtracting these 52 pairs, only 516 pairs could possibly have been available to breed. The second year 464 pairs (90%) did breed, which is in contrast with the observed 75%.

The 417 pairs which fledged chicks in the summer of 1962 probably included no more than 10 of the 87 young pairs. The 417 pairs then became 407 pairs available for the next season, but these were reduced to 377 pairs by mortality. The 284 pairs that did return thus represented 76%, versus the 68% originally stated.

There were 202 pairs of failed breeders in the 1961–62 season. We assumed that the remaining 77 pairs of first-time breeders were among them. Only 40% or 31 pairs of the latter might be expected to attempt reproduction in 1962–63, if the pairs consisted of 2 young birds. However, 45 of the 77 pairs probably consisted of a young bird and an experienced bird, and 80% of these mixed pairs do attempt reproduction in the season following their first. (All mixed pairs are included here, rather than with the successful breeders because seldom do they raise a chick in their first breeding attempts.) Therefore, 36 mixed pairs and 13 pairs consisting of 2 young birds might have nested. The 202 pairs of failed breeders were thus reduced to 174, and to

162 pairs when mortality was considered. Since 164 of the 202 pairs were observed breeding in the second season, it is obvious that the application of overall means to a specific sample produced a minor statistical anomaly. However, it is equally obvious that essentially all failed breeders of 1961–62, alive and eligible to breed in 1962–63, did attempt reproduction in the latter season. This is similar to Tickell's observation (1968:9) that the entire Wandering Albatross population may breed the season following a catastrophic destruction of all eggs.

Availability of food must be assumed to be a major factor influencing reproduction, but, because of our ignorance of oceanic food chains and of annual or seasonal variations in oceanic conditions, for the most part we can only speculate about its role. There is, however, considerable circumstantial evidence that the size of annual breeding populations of the Laysan Albatrosses on Midway Atoll, and on Kure as well, may be greatly influenced by "anomalies" in North Pacific Ocean conditions (H. I. Fisher, ms). Briefly, it appears possible to correlate the highs and lows in breeding numbers with shifts in major water masses, aberrancies in sea-surface temperatures, variations in salinities, and with several kinds of data on evaporation. All these variables may well influence the availability of food in the usual foraging areas, and data from Midway and Kure atolls in 1964–65 and 1968–69 indicated that the albatrosses and some other avian species were short of food.

Lack (1966:243) suggested that young females of several avian species may lay eggs later in the season than experienced females because of the need to accumulate energy reserves to form the egg. Since this pre-egg energy stress is short lived, and since Laysans can regain lost weight very rapidly, it appears that the critical food period, as far as affecting reproductive attempts is concerned, is the 2 or 3 weeks immediately preceding egg-laying. For most Laysan Albatrosses this is the last 3 weeks in November.

In the 1964–65 and 1968–69 seasons of presumed food scarcity, it was the experienced breeding birds that failed to attempt reproduction. The numbers of first-time breeders did not decline. The unanswerable question raised by these observations is whether experience is the only determining factor and, if so, in what way does it operate?

Major fluctuations in the breeding numbers of various high-latitude birds have been known for years, and Bertram et al. (1934:827) commented ". . . it is clear that periodic extensive non-breeding is not uncommon in the Arctic among certain birds." They believed one major reason was the variable food supply, and Johnsen as long ago as 1929 suggested that these "cycles" perhaps depended upon climatic "pulsations" which influenced the availability of food.

Harris (1969) chronicled some massive failures in breeding by the Waved

Albatross on the Galapagos Islands; in other instances this species did not attempt to breed in its usual numbers. He found a correlation between breeding failure and heavier than average rainfall, a condition that may well have affected or been associated with other events that affected the food supply adversely.

As J. Fisher and Lockley (1954:124) stated, it is doubtful that climate ever completely prevented mature sea birds from breeding by direct action upon the birds' glands, but they also viewed the poor years as being simply due to ". . . bad weather closing down the food-supply." Although the Laysan Albatross does not support Wynne-Edward's (1939:127) view that irregular breeding may be characteristic of all deep-sea birds, his suggestion does have the intimation that major fluctuations in the breeding of birds are not limited to the Arctic. They do occur in albatrosses in the temperate and subtropical latitudes.

The frequency of reproduction by Laysan Albatrosses is dependent also upon several, more predictable circumstances. If the pair bond remains intact, the pair of young breeders may attempt breeding in 59% of their first 5 years and in from 82 to 86% of the years thereafter. More than half of these young pairs failed to breed in the season following their first attempt. Although age of mate and age at which breeding is first attempted apparently do not affect the frequency of reproduction in these early years, previous breeding experience in one member of the pair may raise the frequency, from 59% to 80%.

Birds with 2 mates during spans of 10 to 13 years have a mean frequency of breeding of 71%, those with 3 mates 64%, and Laysans with 4 mates may breed only 57% of the time. The trend is further indicated by one bird which had 5 mates and bred only 7 times. Of the birds which lose mates, 99% do not attempt to nest the following season. Females thereby lose 1.9 seasons in 5 and males 1.4 seasons.

These figures emphasize the importance of a continuous pair bond to the reproductive potential of the species. With each additional mate during the 10- to 13-year span of observations there was a decrease of from 7 to 11% in the years in which the bird attempted to breed. The loss in reproduction is a direct result of the one or more seasons required for the formation of each pair bond. The death of a paired, breeding bird eliminates not only its future reproductive capability but also approximately 5 to 10% of the lifetime potential contribution of the mate it left. And not to be forgotten, since both parents are necessary throughout the season for successful fledging of the chick, is the loss of the reproductive contribution during the season a mate dies.

In view of the significance of the continuous bond for the reproductive potential of the species, it is surprising to find that perhaps 60% of the Laysans breed only once or twice with each mate and that 80 to 90% breed 4 or fewer times with each mate. Considering these facts, nest success, and mortality at various ages, it is apparent that the Laysan Albatross "needs" the 16 to 20 years of reproductive life I have suggested elsewhere.

SUMMARY

Attachment to site.—Chicks hatched in an area frequent that site for territory acquisition and pair formation in the 3 or 4 years immediately preceding first breeding. They attempt to establish themselves and to nest near the natal nest—males within perhaps 15 m and females less than 30 m distant. The young male has a greater influence on his location because he actively seeks a territory and establishes himself. The female can only search out an unattached male during her limited travels of the pre-pair bond period.

Breeding males do not change territories during their lifetimes, though they may accommodate to different nest sites of different mates within their territories. Females are just as consistently attached to their male's territory, but when the mate dies they may be forced to move significant distances to obtain a new mate.

Age composition of the breeding colony.—It is not certain that the colony of Laysan Albatrosses on Midway is typical for the species or that its age composition has yet completely stabilized. Human interference during World War II may have almost eliminated certain age groups. In 1960 the breeding population was believed to consist largely of experienced breeders a minimum of 20 years of age and of young breeders a maximum of 12 years old.

Despite major annual fluctuations in total breeding numbers and despite a doubling in breeding numbers between 1960 and 1972, the percentage of breeders 9 or fewer years old remained fairly constant at approximately 15%. After undergoing significant increases in the early years of the investigation, the group of breeders 10 to 14 years old settled down to a uniform 21 to 24% of total breeders in the last 5 years. The early increases in this group caused a major surge in the relative numbers of 15- to 19-year-old breeders midway in the study, which in turn is now reflected in increased percentages of breeders more than 20 years of age.

However, the changes in relative numbers of the older groups are slowing, and it is suggested that the following, stabilized population may be present: (1) 15% young breeders of no great current reproductive significance; (2) 54% prime, reproductive birds, 10 to 19 years old; and (3) 31% breeders 20 or more years of age.

Males predominate in each class through 9 years, females in age classes 10 through 13 years. By the latter ages the sexes are equally represented in the total numbers of these younger breeders. The differences in sexual representation are caused by males initiating reproduction a year sooner than females.

Ingress of first-time breeders.—In the rapidly growing population on Midway Atoll there is an approximate, mean 14% annual recruitment of new breeders. This is exceptionally high for a species which exhibits only 5 to 6% annual mortality during the 16 to 20 years of reproductive life. The historical and current conditions on Midway may have resulted in unnaturally high rates of recruitment. There has been a major decrease in human-induced mortality in the last 10 to 15 years.

Of particular note is the belief that all new breeders are recruited from the Midway colony itself, rather than from any other colonies.

Frequency and patterns of breeding.—The frequency with which the individual Laysan Albatross attempts to reproduce is influenced by: (1) the available food; (2) the strictly monogamous nature of the pair bond; (3) the number and length of the successive pair bonds formed over a period of time; (4) the time required to form each bond; (5) the age of the pair bond; (6) the mate's previous experience in breeding; (7) its success in fledging a chick; and (8) perhaps its sex.

Notwithstanding all these potential influences on the frequency of reproduction, the Laysan Albatross is physiologically and behaviorally capable of breeding each year after the second season of its reproductive life, and many do.

The mean, breeding frequency per pair per year ranges from 0.82 to 0.86 when the pair bond is maintained for 10 to 13 years. When an albatross has 2 mates during this span of years, the breeding frequency drops to 0.71, with 3 mates to 0.64, and with 4 mates to 0.57 times per year. Loss of a mate during the breeding season means the loss of the egg or chick of that year, as well as the loss of 1 or 2 breeding seasons by the survivor while it forms a new pair bond. Males which lose mates may form new bonds sooner than widowed females, indicated by a 68% frequency of breeding during 10 to 13 years by males with 2 mates, versus 60% for females which formed second bonds.

In the first 5 years of the bond between inexperienced birds, reproduction is attempted only in a mean 59% of the seasons. More than half of these young pairs do not attempt to breed the season after the first attempt. However, if the inexperienced bird pairs with an experienced one, the pair may attempt reproduction in 4 of the first 5 years.

A scarcity of food in the weeks immediately preceding egg-laying may prevent 50% of the mature, breeding population from even attempting to nest. In the years before and after such occasions 81 to 96% of the same pairs may breed.

When mortality and differential breeding patterns are considered in average or normal years, the colony-wide return of the eligible breeders of one season to breed the following season is 90%. Seventy-six percent of the breeders successful in fledging a chick return to attempt reproduction the following year, and all the failed breeders may nest the next season.

ACKNOWLEDGMENTS

Space does not permit me to acknowledge in each report resulting from a long-term investigation of the biology of the Laysan Albatross the financial, physical and mental assistance provided by literally dozens of individuals and agencies. I refer the reader to my paper (in press) on mortality in this species for a complete list of those who helped in many ways, and I reiterate here my appreciation of their valuable assistance.

LITERATURE CITED

Bertram, G. C. L., D. Lack, and B. B. Roberts. 1934. Notes on East Greenland birds, with a discussion of periodic non-breeding among Arctic birds. Ibis, Ser. 13:816–831.

Carrick, R., K. Keith, and A. M. Gwynn. 1960. Fact and fiction on the breeding of the Wandering Albatross. Nature 188 (4745):112–114.

Elliott, C. C. H. 1970. Additional note on the sea-birds of Gough Island. Ibis 112: 112–114.

Fisher, H. I. 1949. Populations of birds on Midway and the man-made factors affecting them. Pac. Sci. 3:103–110.

———. 1967. Body weights in Laysan Albatrosses *Diomedea immutabilis.* Ibis 109: 373–382.

———. 1969. Eggs and egg-laying in the Laysan Albatross, *Diomedea immutabilis.* Condor 71:102–112.

———. 1971a. The Laysan Albatross: its incubation, hatching, and associated behaviors. Living Bird 10:19–78.

———. 1971b. Experiments on homing in Laysan Albatrosses, *Diomedea immutabilis.* Condor 73:389–400.

———. In press. Mortality and survival in the Laysan Albatross, *Diomedea immutabilis.* Pac. Sci.

——— AND P. H. BALDWIN. 1946. War and the birds of Midway Atoll. Condor 48:3–15.

——— AND M. L. FISHER. 1969. The visits of Laysan Albatrosses to the breeding colony. Micronesica 5:173–221.

FISHER, J. 1952. The Fulmar. Collins, London.

——— AND R. M. LOCKLEY. 1954. Sea-birds. Houghton-Mifflin, Boston.

HARRIS, M. P. 1969. Age at breeding and other observations on the Waved Albatross *Diomedea irrorata.* Ibis 111:97–98.

———. 1973. The biology of the Waved Albatross *Diomedea irrorata* of Hood Island, Galapagos. Ibis 115:483–510.

JOHNSEN, S. 1929. Rovdyr- og rovfuglostatistikken i Norge. Bergens Mus. Arbok, Naturvid. rekke 1929 (2) :1–140.

LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford.

MATHEWS, L. W. 1929. Birds of South Georgia. Discovery Rep. 1:561–592.

MURPHY, R. C. 1936. Oceanic birds of South America. Vol. 2. Macmillan Co., New York.

RICE, D. W. 1959. Birds and aircraft on Midway Islands, 1957–58 investigations. U. S. Fish and Wildl. Serv., Spec. Sci. Rep.: Wildl. No. 44.

——— AND K. W. KENYON. 1962. Breeding cycles and behavior of Laysan and Black-footed albatrosses. Auk 79:517–567.

RICHDALE, L. E. 1952. Post-egg period in albatrosses. Biol. Monogr. No. 4, Otago Daily Times and Witness Newspapers Co., Dunedin, New Zealand.

———. 1954. The starvation theory in albatrosses. Auk 71:239–252.

ROBERTSON, C. J. R. 1973. Royal Albatross. Wildl. Rev., New Zealand, 1973 (4): 10–12.

TICKELL, W. L. N. 1960. Chick feeding in the Wandering Albatross *Diomedea exulans* Linnaeus. Nature 185(4706) :116–117.

———. 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora.* Antarct. Res. Ser. 12:1–55.

——— AND J. D. GIBSON. 1968. Movements of Wandering Albatrosses *Diomedea exulans.* Emu 68:7–20.

——— AND R. PINDER. 1967. Breeding frequency in the albatrosses *Diomedea melanophris* and *D. chrysostoma.* Nature 213(5073) :315–316.

VAN RYZIN, M. T. AND H. I. FISHER. In press. The age at which Laysan Albatrosses, *Diomedea immutabilis,* begin to breed. Condor.

WYNNE-EDWARDS, V. C. 1939. Intermittent breeding of the Fulmar (*Fulmarus glacialis* (L.)), with some general observations on non-breeding in sea birds. Proc. Zool. Soc. Lond. A, 109:127–132.

DEPT. OF ZOOLOGY AND SCHOOL OF MEDICINE, SOUTHERN ILLINOIS UNIV., CARBONDALE 62901 (PRESENT ADDRESS: FENWOOD TOFT, TRIPLETT, MO 65286). ACCEPTED 18 DEC. 1974.

GENERAL NOTES

Notes on the behavior of captive Great Cormorants.—General observations have been made on the maintenance activities of cormorants in the field (Lewis, The Natural History of the Double-crested Cormorant, Ru-Mi-Lou Books, Ottawa, 1929; Bartholomew, Condor 44:13–21, 1942 and 45:3–18, 1943; Stonehouse, Ibis 109:600–605, 1967; Owre, Adaptations for Locomotion and Feeding in the Anhinga and Double-crested Cormorant, Ornithol. Monogr. No. 6, A.O.U., 1967) and in captivity (Portielje, Ardea 16:107–123, 1927; Stolpe, J. Ornithol. 80:161–247, 1932; Kortlandt, Ardea 27:1–40, 1938). However, there has been little underwater observation of these birds and none in water bodies of the depth regularly used in the wild. I observed and filmed 2 juvenile Great Cormorants (*Phalacrocorax c. carbo*) kept in a large indoor pool, and noted particularly their feeding and plumage care behaviors.

Three fledglings were removed from nests on 25 June 1972, and kept in an outdoor cage (1.25 × 1.25 × 2.5 m) until 7 September, during which time one died. The remaining 2 were then moved to the pool and stayed in excellent condition up to their release on 2 October. The pool was a circular tank (15 m diameter × 3.5 m depth) and had many underwater viewing ports. The area was illuminated by bright artificial light for 11 hours per day; no sunlight was visible. At night, a weak light was left on at the side of the tank. Air temperature was approximately 16° C; water temperature was approximately 12° C. A raft with a perching branch attached provided a resting spot for the birds although they could also fly up to the rim of the tank. They were fed chopped herring (*Clupea harengus*) supplemented with vitamins, while caged, and live fish, mostly cunner (*Tautogolabrus adspersus*), while in the pool.

Surface swimming.—When entering the water, the birds usually jumped or flew down (feet first) from their perches (30 cm from water). Head-first dives were noted only during feeding frenzies which were initiated when fish were introduced while the birds were perched.

The cormorants, when entering the water quietly, swam around slowly, gently flapped their wings, and dipped their heads and necks in the water—undoubtedly to facilitate soaking. Surface swimming was executed by the alternate stroking of the legs at approximately 30° from the vertical. Steering was performed by the feet, although the tail appeared to be used in sharper turns. The head and neck were usually held in a relaxed S-shape except prior to diving, when the neck was straightened and the head angled slightly downward. The birds entered the water only to escape capture or to fish.

Diving.—There were 2 ways of submerging. Usually, the cormorant jumped clear of the water to dive in headfirst. To do this, its feet were brought forward and stroked down and back together, propelling the bird out of the water. The head and neck were pointed straight forward and then arched down to meet the water. Concomitant with the kicking of the feet was a quick depression of the tail, probably adding further vertical force. Just prior to the dive there was an audible exhalation and a dorsoventral flattening of the body, accomplished by angling of the elbows of the wings slightly outward and by some compaction of the plumage. In the second type of dive, the bird did not clear the water but lunged forward and down in a more quiet and graceful movement. This dive was noted only after extended bouts of fruitless fishing.

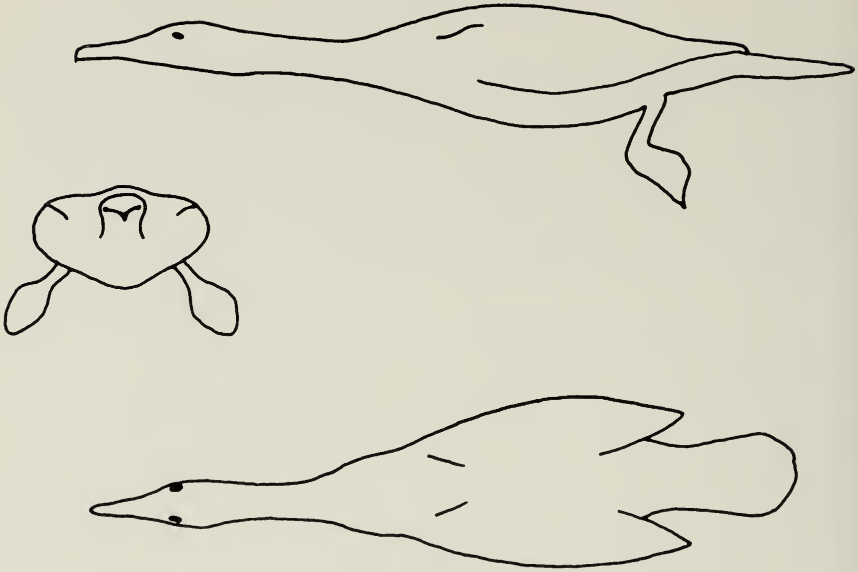

Fig. 1. Configuration of cormorant swimming underwater.

Once underwater, the cormorant usually proceeded downward at a 45° angle, although occasionally diving more steeply when a fish was sighted. The neck was held either straight forward or with a slight crook. The wings continued to be held slightly away from the body, acting as a down-forcing, planing surface, counteracting the upward components of propulsion and buoyancy. Propulsion was provided by the simultaneous kicking of the legs (Fig. 1), with which was integrated an up-and-down motion of the tail giving the bird's movement a slightly undulating appearance. Rates of kicking usually varied between 2 and 3 per sec although this could be doubled during a chase. Underwater speeds ranged from 1.5 to 2 m per sec. However, in one case, a bird was estimated to move at twice the speed of a mackerel (*Scomber scombrus*) it was pursuing; a mackerel is capable of approximately 3 m per sec in bursts (K. MacKay, pers. comm.). Directional control underwater was accomplished mainly with the feet and the long stiff tail (as noted by Stolpe, op. cit.) although, on very fast, sharp turns, the inside wing was angled out farther.

Braking involved primarily the feet; however, for quick stops, the wings were partially extended and the tail opened and brought up over the back.

When surfacing, the cormorant usually rose slowly, using its buoyancy. If, however, a large fish was caught for which the other bird was competing, a powered ascent was used, in which case the legs were stroked alternately as in surface swimming.

At the end of a feeding session and just prior to leaving the water, the bird rapidly shuffled its wings over its back and wagged its head and neck underwater. This possibly results in some beneficial rearrangement of the feathers. Finally, it raised its upper body clear of the surface, flapped its wings vigorously, and left the water.

Feeding.—The cormorants caught fish after a direct chase in which no special tactics were used. The neck was held in a slight S-shape, allowing maneuvering of the head when grabbing the prey. In all cases, the cormorant took the fish to the surface and swallowed it headfirst. If prey was not visible, the bird would cruise along the bottom, investigating hiding places such as drain holes.

Drying.—On leaving the water, the bird flapped its wings periodically for about 10 min. As drying took place, actual flapping became less frequent and the wings were gently waved in a characteristic outspread position. Body-shaking, head-shaking, head-flicking, and tail-wagging were regularly noted at this time (terminology from McKinney, Behaviour 25:120–220, 1965). Shivering was occasionally observed.

Preening.—Preening began once the concerted flapping had subsided. This behavior, which could last as long as 30 min, was usually associated with the drying procedure; the water would understandably cause feather matting. Completely dry birds preened less and with reduced intensity.

The neck and breast were invariably preened first. The neck was held erect and beak inserted down into the lower neck feathers, which were pushed, nibbled, and finally stroked into place. The bird worked in the same way down the breast, belly, and sides, often dislodging much down. Following this, the bird reached along the underside of its wings to stroke the individual primaries and secondaries, although all were not treated in a given session. The head was next twisted around to reach the back, the feathers of which were preened in a similar manner to those of the breast. The rectrices were treated like the wing feathers. Preening at the base of the tail often involved its deflection to one side, possibly associated with release of oil from the uropygial gland. There was apparently no widespread distribution of oil during any given preening bout. After this procedure, the cormorant rubbed its head over its back and under its wings. Although the various sections of the body were initially treated in this order, some areas were preened several times. Body-shaking then ensued, followed by a slow settling of the feathers into place.

Scratching.—The neck was lowered and stretched to one side and the nearest foot brought up to scratch the ear area. This behavior was not necessarily associated with preening.

I am indebted to Dr. E. L. Mills, Dalhousie University, for his valuable advice throughout this study. I would also like to thank Mr. Eldon Pace of the Nova Scotia Provincial Wildlife Park for taking care of the cormorants during their first 3 weeks of captivity.—
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Adaptiveness of foraging in the Cattle Egret.—Heatwole (Anim. Behav. 13:79–83, 1965) and Dinsmore (Am. Midl. Nat. 89:242–246, 1973) have shown that Cattle Egrets (*Bulbulcus ibis*) feeding in close association with cattle catch insect prey at a significantly higher rate and expend less energy than do those foraging alone. The purpose of this study is to confirm their results and to evaluate the adaptiveness of the Cattle Egrets' site tenacity about a cow's head and muzzle, and their defense of cows against conspecifics.

Observations were made of egrets foraging with black angus cattle over a Bermuda

TABLE 1

FORAGING EFFICIENCIES OF CATTLE EGRETS FORAGING WITH A COW, WHILE SHARING A COW WITH ONE OTHER EGRET, AND ALONE

	With cow	Sharing cow	Alone
Minutes watched	225	185	145
Captures	462	147	84
Steps	6336	6467	6425
Steps/minute	28.2	34.0	44.3
Steps/capture	13.7	44.0	76.5
Captures/minute	2.0	0.8	0.6
Efficiency ratio	6.8	55.0	127.5

grass pasture at the north end of St. Catherine's Island, off the coast of Georgia from 07:00–10:00 and 17:00–20:00 during August 1974. Grasshoppers (Orthoptera), the dominant component in the diet of Cattle Egrets in neighboring northern Florida (Jenni, Auk 90:821–826, 1973), were abundant in the pasture.

The Cattle Egrets always jerked back the head characteristically when swallowing prey. I tallied number of head-jerk swallows and number of steps per unit time as measures of energy intake and energy expenditure, respectively. Cattle Egrets fed away from cattle, fed solitarily within 2 m of a cow, or shared a cow. The feeding sites within 2 m of a cow were scored according to whether the egret's eyes were in front of the cow's shoulders, between the shoulders and the hips, or behind the hips. Because an egret foraging near a cow often attacked a conspecific joining it, I recorded the events which followed within 5 min of an egret's arrival within 2 m of a cow already attended by another bird.

Analyses were performed with the distribution-free Kruskal-Wallis test with Dunn's multiple comparison (Hollander and Wolfe, Nonparametric Statistical Methods, John Wiley, N. Y., 1973) and were confined to the activities of birds in adult (nuptial) plumage, but of unknown sex.

Egrets within 2 m of a cow almost never foraged for 5 consecutive min in just one zone (near head, side, or rear of cow). Because the egrets often made short quick dashes into another zone after an insect, and then returned to their original zone, the time intervals were short and variable. Ninety-nine egrets foraging alone with a cow foraged mostly about the head (79%), second most frequently along the cow's side (17%), and considerably less often about the rear (3%). Captures/minute were 2.0 for egrets feeding near the head (121.7 min), 0.7 for egrets feeding along the side (38.4 min), and 0.4 for those feeding near the rear (20.8 min). Thus, birds foraged most often in the most productive region about cows.

Twenty-two of 38 egrets (58%) flying to join another egret near a cow were driven off by the resident rather quickly ($\bar{x} = 7.8 \pm 4.6$ sec). Twelve arrivals (32%) left the cow within 5 min (mean = 86.5 ± 23.7 sec). The resident left once and was driven off by the arrival once in 2 of the 38 cases (32 and 8 sec, respectively). In only 2 instances were both egrets still foraging within 2 m of the same cow 5 min later.

TABLE 2

KRUSKAL-WALLIS TESTS WITH DUNN'S MULTIPLE COMPARISONS FOR CATTLE EGRETS FORAGING WITH A COW, WHILE SHARING A COW WITH ONE OTHER EGRET, AND ALONE

Comparisons		N	*P*
Steps/minute	With cow: sharing cow	82	.62
	With cow: alone	74	<.001
	Sharing cow: alone	66	.002
Captures/minute	With cow: sharing cow	82	<.001
	With cow: alone	74	<.001
	Sharing cow: alone	66	.63
Efficiency ratio	With cow: sharing cow	78	<.001
	With cow: alone	67	<.001
	Sharing cow: alone	59	.49

During 5-min observation periods, birds with exclusive access to a cow took fewer steps and caught significantly more prey per minute than did those sharing a cow (Tables 1 and 2). Egrets with exclusive "rights" to a cow had significantly better foraging efficiencies (steps/capture divided by captures/minute; Dinsmore, op. cit.) and caught slightly more prey per minute than did those foraging away from cattle, than did those sharing a cow. Clearly it is adaptive for an egret to defend its exclusive use of a cow. Those egrets sharing cows took significantly fewer steps resulting in a superior foraging efficiency, though not significantly so.

Neither Heatwole (op. cit.) nor Dinsmore (op. cit.) mentions egrets defending cattle, but the cattle-per-egret ratios between their study areas (as many as 5 egrets per cow) and mine (mean = 2.4 ± 1.2 cows egret, n = 12) were quite different. It is also clear that it pays an egret to share a cow rather than forage away from cattle completely. Apparently the tendency to defend a cow is weak and easily swamped by large influxes of egrets.

The function of aggression shown by these egrets appears uncommon. They were defending the space around another animal as the means to an end. A possibly similar case is the aggression of antbirds (Formicariidae) around army ant columns (Willis, Auk 85:253–264, 1968; Hilty, Wilson Bull. 86:479–481, 1974).

I assume that the egrets were defending the vicinity of cattle, but they could have been defending a critical individual distance (*sensu* Hediger, Wildtiere in Gefangenschaft, 1942, English ed. Wild Animals in Captivity, Butterworth, London, 1950). The latter interpretation is unlikely because many times the egrets fed peacefully less than a meter apart when away from cattle. Bird species dependent on food clumped in small discontinuous packets tend to be solitary, while those dependent on food evenly distributed tend toward group-dwelling (Crook, Symp. Zool. Soc. Lond. 14:181–

218, 1965). If differential prey vulnerability is analogous to differential prey abundance, the Cattle Egret behavior conforms nicely to Crook's model. When prey is highly vulnerable locally (around cattle) a solitary (antisocial) system emerges from the group feeding socially in the absence of cattle on homogeneously vulnerable prey.

I thank E. H. Burtt, J. J. Dinsmore, J. F. Downhower, and W. M. Shields for commenting on an earlier draft. G. C. White provided analytic computer programs. This study was conducted during a period of research funded by the Edward John Noble Foundation.—Thomas C. Grubb, Jr., *Dept. of Zoology, Ohio State Univ., Columbus 43210.* *Accepted 30 Jan. 1975.*

Wood Duck incubates eggless clutch.—While checking Wood Duck (*Aix sponsa*) nest boxes on the Great Meadows National Wildlife Refuge (Concord, Massachusetts) on 21 May 1970, we found a box in which down was mixed in with the box shavings but no eggs were present. Normally down is not added to a Wood Duck clutch until 5 or more eggs are laid. The box was rechecked on 28 May and a large depression was noted in the down and shavings mixture. On 4 June, the condition was the same except that duck fecal matter was present in the box. There was no further use of the box that year.

On 21 May 1971, the same box was again discovered to have a mixture of down and shavings but no eggs. When checked 3 June, a hen was incubating. The hen was left undisturbed until 22 June when it was captured on the nest. There were no eggs in the box but there was a large quantity of down. The hen had been previously trapped and banded as an immature female at Great Meadows in September 1966. The bird was returned to the box and not checked again that year.

On 28 April 1972, the same box was found to contain a large amount of down but no eggs. It was in the same condition 1 May when we added 4 hollow plastic eggs. On 6 May, there was no evidence of change and the plastic eggs were replaced with 7 Wood Duck eggs gathered from an abandoned nest.

By 9 May a hen was observed incubating in the box. The hen was captured 17 May and proved to be the same hen handled in 1971. She had not added any eggs to the clutch. The 7 eggs were replaced with 14 fresh game-farm Wood Duck eggs. The hen was returned to the box and left undisturbed until 8 June when the eggs were checked for signs of hatch. Thirteen of the eggs hatched 12 June and 10 ducklings were web-tagged.

One of the web-tagged ducklings was captured later that summer indicating at least partial brood survival. The hen was not found in later years.

We do not know the reason for this hen's peculiar behavior. Dane (Reproductive Endocrinology—Discussion: 195, *in* Breeding Biology of Birds, D. S. Farner, ed., Natl. Acad. Sci., Wash. D. C., 1973) suggests that among indeterminate layers, some stimulus such as number of eggs or surface area of eggs leads to specific clutch size. Welty (The Life of Birds, W. B. Saunders Co., Philadelphia, 1962) adds that the feel of enough eggs against the bird's belly may stimulate the pituitary gland to suppress ovulation and initiate incubation behavior. In the case of this hen, however, no eggs were present to cause such stimulation. Other factors must have initiated the incubation response.—H. W. Heusmann and Peter R. Pekkala, *Massachusetts Division of Fisheries and Game, Westboro 01581.* *Accepted 7 Feb. 1975.*

Extremes of sexual dimorphism in size in birds.—Current theories relating sexual dimorphism, breeding system, and ecological factors are based largely on avian data. As part of an attempt to assess the extent to which these theories account for the degree and distribution of sexual dimorphism in mammals, I became interested in comparing the range of sexual dimorphism in size in birds with that in mammals.

For birds, I at first used the extreme cases given by Lack (Ecological Adaptations for Breeding in Birds, Methuen, London, 1968:161). The biggest difference between the sexes in birds, he says, occurs in an Australian passerine, *Cincloramphus cruralis*, the Brown Song-lark. He gives the Australian Goshawk, *Accipiter fasciatus*, as an extreme case of sexual dimorphism in which the female is larger than the male. In both cases he sites Amadon (Proc. Am. Phil. Soc. 103:531–536, 1959) as his source of data. Lack's figures (Table 1) yield a female/male ratio of about .45 for the Brown Song-lark and 1.77 for the Australian Goshawk. If they were correct, and if wing length is a fair measure of size in birds, there would be more extreme cases of sexual dimorphism in birds favoring both males and females than in mammals. The range of sexual dimorphism in size would thus be much greater in birds than in mammals.

However, the figures Lack gives are not in the paper by Amadon which he cites. Furthermore, the figures given in Serventy and Whittell (Birds of Western Australia, Paterson Brokensha, Perth, 1951) for the Brown Song-lark suggest that it is not nearly as sexually dimorphic as Lack states. They give the total length of males as 9¾ to 10½ in (248–267 mm) and of females as 7½ in (191 mm) and the weight of males as 2½ to 3 oz (71–85 g) and of females as 1 oz (28 g). If the mid-points of the male ranges are used as average male values, the female/male ratio is .74 by total length and .71 by the cube root of weight.

Because of the conflict between the 2 sets of figures, I measured 7 females and 7 of the largest males (all in breeding plumage) of the Brown Song-lark at the American Museum of Natural History. Dr. D. W. Snow kindly measured the 4 females and 7 males at the British Museum of Natural History for me. My measurements on wings (Table 1) yield a female/male ratio of .74; Snow's one of .78. Since Serventy and Whittell give no data on wings, I also measured total length. The mean total length of males was 241 mm, of females 176, yielding a female/male ratio of .73. All of these estimates of the degree of sexual dimorphism are in line with those based on Serventy and Whittell's figures. Lack's figures are incorrect.

The Brown Song-lark is an extreme case of sexual dimorphism in size favoring males in birds, but it is of the same order of magnitude as other extreme cases such as the Capercaillie, *Tetrao urogallus.* In this species the average female/male ratio is .77 by the length of the 10th primary (Helminen, Papers on Game Research, Helsinki, No. 23:1–124, 1963) and .78 by the cube root of weight (Koskimies, Ornis Fenn. 35:1–18, 1958).

Lack's figures for the Australian Goshawk are also incorrect. According to the figures in Wattel (Publ. Nuttall Ornithol. Club No. 13:1–231, 1973) (Table 1), the female/male wing length ratio of this species is only 1.15 rather than the 1.77 indi-

TABLE 1

WING MEASUREMENTS OF *C. CRURALIS* AND *A. FASCIATUS*

Species and authority	Wing length, mm ♂	Wing length, mm ♀
Cinclorhampus cruralis		
Lack (1968)	65–68	28–32
Ralls (pers. observ.)	112	83
Snow (pers. comm.)	107	83
Accipiter fasciatus		
Lack (1968)	269	477
Wattel (1973)	262	302
Brown and Amadon (1968)	264	302
Ralls (pers. observ.)	261	299

cated by Lack. Data for one specimen of each sex that I measured and specimens measured by Brown and Amadon (Eagles, Hawks, and Falcons of the World, vol. 2, Hamlyn Publ. Group Ltd., Feltham, England, 1968) are similar to those of Wattel (Table 1). It seems probable that the most extreme case of sexual dimorphism in size favoring females in birds is a member of the genus *Accipiter* but it is not clear whether or not it is *A. fasciatus.* Several other species have more extreme female/male ratios by wing length according to the figures in Wattel. The most extreme case in North America is *A. striatus.* This species has a female/male ratio of 1.19 by wing length and 1.21 by the cube root of weight (Snyder and Wiley, Ornithol. Monogr., in press).

Amadon was correct when he said in 1959 that more extreme cases of sexual dimorphism in size favoring males occurred in mammals than in birds: the elephant seal, *Mirounga leonina,* is a much more extreme case than either the Brown Songlark or the Capercaillie (Bryden, Growth 33:531–536; Bryden *in* Harrison, ed., Growth and Development of Marine Mammals, vol. 1, Academic Press, New York, 1972). The most extreme cases favoring females in birds probably exceed those found in mammals.

I thank John Bull and Mary Le Croy for help at the American Museum of Natural History, D. W. Snow for measuring the specimens at the British Museum of Natural History, R. C. Banks, C. O. Handley, Jr., M. Howe, and H. Wiley for advice, and the Smithsonian Institution and the Radcliffe Institute for financial support.—KATHERINE RALLS. *Division of Mammals, Room 398 NHB, Smithsonian Institution, Washington, D.C., 20560.* *Accepted 25 Feb. 1975.*

New bird records for El Salvador.—During June of 1964 I accompanied the late Merriam L. Miles on an ornithological trip to El Salvador. Considering the paucity of ornithological investigations in El Salvador, it was not surprising that during our 18-day trip we collected 3 previously unrecorded species. The specimens were deposited in the Louisiana State University Museum of Zoology. The species are as follows:

Ruddy Duck (*Oxyura jamaicensis*).—Four of these ducks were observed on 18 June 1964, on Laguna de Chanmico, Dept. Libertad; a female was collected (LSUMZ 50481).

Least Tern (*Sterna albifrons*).—A pair of Least Terns was observed on 27 June 1964, at the small coastal fishing village of La Herradura, Dept. La Paz; a female was collected (LSUMZ 50503).

Melodious Blackbird (*Dives dives*).—This species was observed twice; a female (LSUMZ 50677) was collected on 13 June, 21 km W. of Libertad, Dept. Libertad, and a male (LSUMZ 50676) on 28 June 1964, at Laguna de Chanmico, Dept. Libertad.

I thank John P. O'Neill for providing information about these specimens.—ALAN FEDUCCIA, *Dept. of Zoology, Univ. of North Carolina, Chapel Hill, 27514.* *Accepted 13 Jan. 1975.*

The impact of an underground nuclear fracturing experiment on cliff-nesting raptors.—Almost any development and use of a natural resource has concomitant impacts on resident wildlife; stimulation of natural gas wells with nuclear fracturing techniques is no exception. On 17 May 1973, three 30-kiloton nuclear explosives were detonated 1900 m below the earth's surface in Rio Blanco County, Colorado in a U.S. Atomic Energy Commission-CER Geonuclear sponsored experiment called Project Rio Blanco. This note deals with the effects of ground motion resulting from that experiment on cliff-nesting hawks and eagles.

If nuclear stimulation of natural gas fields is to become a part of a national energy program, associated environmental costs must be carefully weighed. Two nuclear stimulation tests were conducted prior to Project Rio Blanco but environmental studies were not performed concurrently. The environment, including raptor populations, was studied before and after 2 underground nuclear tests on Amchitka Island, Alaska. Project Milrow damaged a cliff containing a Peregrine Falcon (*Falco peregrinus*) eyrie (White et al., Bioscience 21:623–627, 1971) and Project Cannikan destroyed or damaged 3 Peregrine Falcon and 6 Bald Eagle (*Haliaeetus leucocephalus*) nest sites (Kirkwood and Fuller, USAEC Report BMI-171-147, 1972). However, these tests differed from Project Rio Blanco in 3 important aspects. First, they were weapons tests and not nuclear fracturing experiments. They were 100 times more powerful and were closer to the surface; therefore, vertical displacement and damage were much greater. Finally, both tests were conducted in late fall, long after the raptor breeding season.

The nuclear devices of project Rio Blanco were detonated during the raptor nesting season. Red-tailed Hawk (*Buteo jamaicensis*) nests in the area contained eggs or newly hatched young; Golden Eagle (*Aquila chrysaetos*) young were 2–4 weeks old. In order to ascertain the impact of ground motion on active raptor nests, we searched for nests on cliffs within 16 km of the test site. On 15 May active nests found in an April 1973 survey conducted by Colorado Division of Wildlife were checked by helicopter. Additional cliffs were also visited and contents (eggs, young) of each active nest were noted. Portions of the study area not flown were searched from the ground on 16 May; nests located were examined and contents recorded. Nine Red-tailed Hawk and 3 Golden Eagle nests within the study area and 2 Red-tailed Hawk nests beyond the 16 km perimeter were documented prior to detonation (Table 1). All active nests were again examined by helicopter within 4 hours post-detonation; general condition

TABLE 1

RAPTOR NESTS OBSERVED NEAR PROJECT RIO BLANCO, 15–18 MAY 1973.

Nest no.	Species	Distance (km) and Direction from test site	Pre-detonation Survey	Post-detonation Survey
1	Red-tailed Hawk	1 SW	2 eggs	deserted
2	Red-tailed Hawk	2.5 SW	1 egg	destroyed
3	Red-tailed Hawk	5.5 W	2 eggs	minor rockfalls
4	Red-tailed Hawk	10 NE	2 young	no change
5	Red-tailed Hawk	11 E	1 young	no change
6	Red-tailed Hawk	13 W	1 young 1 egg	no change
7	Red-tailed Hawk	13 NE	3 young	minor rockfalls
8	Red-tailed Hawk	16 E-NE	1 young	no change
9	Red-tailed Hawk	16 NE	1 egg	deserted
10	Red-tailed Hawk	18 NE	fresh nest material	no change
11	Red-tailed Hawk	19 NE	recently deserted	destroyed
12	Golden Eagle	11 W	1 young 1 egg	no change
13	Golden Eagle	11 NE	2 eggs deserted	no change
14	Golden Eagle	16 E	1 young	no change

of the site, contents of the nest, and behavior of adult birds were recorded. Nests observed without adults on the aerial survey were examined from the ground on 17–18 May. While our documentation was the result of intensive air and ground searches, we do not imply that all cliff nests were located. Approximately 90% of the cliffs in the study area were searched and we feel at least an equal proportion of nests was found.

A Red-tailed Hawk nest (Nest 8) 16 km east-northeast of the test site was under observation at detonation. Prior to detonation the female was brooding a week-old chick and the male was perched in a treetop 0.5 km away. As the shock wave passed the cliff, several large rocks were dislodged and the female leaped from the nest, screaming. The male joined her and they soared above the nest for several min, screaming periodically, before landing in piñon pines (*Pinus edulis*) above the cliff. They screamed intermittently and changed perches several times. The female's agitation gradually subsided, and 10 min after detonation she returned to the nest. Another Red-tailed Hawk nest (#2) 2.5 km from the test site was not observed during detonation but the female was seen hovering above the ruined nest by aerial observers 5 min after detonation. This female was still in the immediate vicinity on 18 May.

On post-detonation helicopter surveys, more raptors were observed in the air than were seen in comparable pre-detonation surveys. It is possible that all raptors remained in an excited state for some time after detonation. Another possibility is that birds began active hunting in direct response to increased small mammal activity associated with ground motion and habitat alteration (Alldredge et al., 4th Symp. Radioecology, in press). We also realize that increased raptor activity could have been caused by stimuli unrelated to Project Rio Blanco.

On the post-detonation flight, no observable changes had occurred at the eagle nests; however, 6 of the Red-tailed Hawk nest sites were altered. Nest 1, containing 2 eggs, was 1 km from the test site. The female soared and screamed during documentation efforts at her nest. This nest was not destroyed by the shock wave although many sticks from it were scattered on the slope below and much of the cliff face was altered. Vertical displacement 1 km from the test site was expected to be between 8 and 16 cm according to the USAEC environmental impact report. The nest area was visited by helicopter and twice on foot after the detonation. No adults were observed and the nest was considered abandoned. Increased human activity, including that of the environmental analysis team, may have contributed to desertion.

The sandstone cliff on which Nest 2 was situated was also heavily damaged by the shock wave. A portion of the cliff above the nest fell, filling the nest with rocks and debris. The egg was probably crushed and was certainly inaccessible to the adults. Nest 11, 19 km from the test site, fell from the cliff and shattered on the ground below. Displacement was predicted to be 0.3 cm. It is quite possible, however, that the next severe wind would have had the same effect. The nest had contained 2 eggs on 27 April 1973, but the eggs had disappeared and the nest was abandoned on 16 May.

Cliffs on which 2 nests were located sustained observable damage but the nests and their contents were not harmed. At Nest 3, 5.5 km from the test site, portions of the cliff were dislodged by ground motion. Nest 7, 13 km from the test site, contained three 2–3 day old young. A slight overhang protected the back ⅔ of the nest. Several rocks 5–10 cm in diameter were in the front portion of the nest before detonation. Fragments, this size or larger, were dislodged from above the nest by the shock wave. The chicks would probably have been killed or injured by the falling debris had it not been diverted by the overhang.

An adult female was incubating one egg at Nest 9 prior to detonation. She was not seen during the post-detonation aerial survey, and the egg was cold on 18 May. It is difficult to ascertain whether the desertion of Nest 9 was due to ground motion, increased traffic on a road 50 m away, or our activities in documentation. Therefore, it was deleted from the affected nests in the following analysis.

Within 16 km of the test site, 3 eggs in 2 Red-tailed Hawk nests were lost, of 15 eggs and young in 9 nests, resulting in a 20% reduction in potential fledglings and a 22% loss of nests. However, nesting cliffs were not damaged so extensively that new nests could not be built on them in future breeding seasons. Unfortunately, we were unable to study this in 1974 or 1975. Since nesting was interrupted when eggs were near hatching, we doubt that renesting occurred in 1973.

Golden Eagle nests were not damaged, possibly because they were farther from the test site than Red-tailed Hawk nests that incurred the greatest damage. Also, they were located on large unbroken cliff faces whereas Red-tailed Hawk sites were smaller cliffs with numerous cracks and were more easily broken by ground motion. All eagle nests had an overhang above them that would have diverted any falling debris from the nest.

Project Rio Blanco had an observable impact on nests and behavior of Red-tailed Hawks. Damage was most severe within 2.5 km of the test site, where both documented Red-tailed Hawk nests were destroyed or deserted. However, an unstable nest site 19 km away (Nest 11) was also destroyed. The long-range impact of the test upon hawks and eagles could not be ascertained from cursory short-term observations but it appeared to be minimal. Damage to raptor nests from natural erosion or strong winds undoubtedly occurs each year, but we have no baseline data to document such events. While damage to nests resulting from ground motion associated with Project Rio Blanco might have occurred, in time, from natural causes, the Project likely accelerated the frequency of occurrence. Although the overall impact of Project Rio Blanco on cliff nesting raptors appeared quite small, we recommend that future nuclear fracturing experiments not be conducted during the nesting season and that they be carefully monitored to ascertain all possible environmental impacts.

The field work reported herein was funded in part by CER Geonuclear Corporation, Las Vegas, Nevada. Colorado Division of Wildlife Raptor Project W-124-R funded Stahlecker's participation. Several other Division employees also assisted with field work as did personnel from Colorado State University's Department of Radiology and Radiation Biology. E. D. Campbell, Las Vegas Operations Office, ERDA is gratefully acknowledged for assistance in logistical matters. The pertinent pages of Kirkwood and Fuller 1972 (cited herein), have been deposited in the Josselyn Van Tyne Memorial Library.—DALE W. STAHLECKER, *Dept. of Fishery and Wildlife Biology, Colorado State Univ., Fort Collins 80523;* and A. WILLIAM ALLDREDGE, *Dept. of Radiology and Radiation Biology, Colorado State Univ., Fort Collins 80523.* *Accepted 22 Sept. 1975. Page costs paid.*

Natal pterylosis of *Sporophila* finches.—Finches of the genus *Sporophila* (Emberizidae) are a familiar part of the avifauna of many parts of the Neotropics. The only information on the natal pterylosis of these finches is confined to unquantified statements for the Variable Seedeater (*S. americana*) which is reported as having "sparse gray down" (Skutch, Pac. Coast. Avif. 83:1–448, 1951) or "Dark Neutral Gray (down) blending to Lighter Neutral Gray at the tips" (Gross, Auk 69:433–446, 1952) present in 6 tracts. This paper presents data on the natal pterylosis of 4 of the approximately 30 species presently included in this genus: the Ruddy-breasted Seedeater (*S. minuta*), Yellow-bellied Seedeater (*S. nigricollis*), Gray Seedeater (*S. intermedia*), and Dull-colored Seedeater (*S. obscura*). Hopefully it will stimulate similar studies of additional species. As noted earlier (Collins, Bird-Banding 34:36–38, 1963; Bull. Br. Ornithol. Club 93: 155–157, 1973) absence of the details of the natal down distribution patterns unfortunately is typical for most Neotropical species.

We examined the following fluid-preserved specimens: 2 *S. minuta* and 1 each of *S. nigricollis* and *S. obscura*. The specimens of *S. minuta* were collected (by CTC) on 17 August 1964 near Cacandee Village, Caroni Co., Trinidad. The specimens of *S. nigricollis* and *S. obscura* were collected respectively on 8 and 13 October 1966 near Estación Biológica de Rancho Grande, Est. Aragua, Venezuela by Paul Schwartz. All 4 individuals were newly hatched (Stage A, Wetherbee, Bull. Am. Mus. Nat. Hist. 113:339–436, 1957) and presumably had not lost any neossoptiles through abrasion. The nestling of *S. obscura* unfortunately was badly damaged when its container leaked and the specimen desiccated. We could see that it had a sparse complement of neossoptiles involving only 2 tracts, although the exact arrangement of these downs in the spinal tract could not be determined. In 1974 Paul Schwartz made observations on an additional 8 nestlings of *S. nigricollis* near Rancho Grande, 2 nestlings of *S. intermedia* near Guanare, Est. Portuguesa, and 9 nestlings of *S. obscura* at El Limon, near Maracay, Est. Aragua.

The downs of *S. minuta* and *S. nigricollis* ranged in total number from 80 to 134. Their

TABLE 1

DISTRIBUTION OF NEOSSOPTILES IN *SPOROPHILA* FINCHES

Tract	*S. minuta*		*S. nigricollis*	*S. intermedia*[a]	*S. americana*[b]	*S. obscura*	
Coronal (right)	5	6	5	+	+		0–3(1)
(left)	5	6	5	+			0–2(1)
Occipital (right)	3	3	4	+	+	2	1–3(2)
(left)	3	0	3	+		2	1–3(2)
Spinal (upper)							
(right)	2	0	5	+	+	10	2–4(3)
(left)	3	2	4	+			2–4(3)
Spinal (lower)[e]	8	1	9	+			0–2(1)
Scapular (right)	5	4	2	+	+		0–4(2)
(left)	5	4	5	+			1–4(2)
Femoral (right)	6	4	8	+	?		
(left)	6	7	8	+			
Ventral (right)	7	0	11	+	+		
(left)	0	4	9	+			
Crural (right)	4	3	7	+	+		
(left)	4	3	9	+			
Rectrices (right)	6	6	6	?			
(left)	6	6	6	?			
Greater Secondary Coverts							
(right)	8	8	8	+[f]			
(left)	6	6	8	+			
Middle Secondary Coverts							
(right)	6	4	6	+[f]			
(left)	5	3	6	+			
Totals	103	80	134	?	?	14[c]	11–23(17)[d]

[a] Downs reported for these tracts, but no counts. (Schwartz, see text).
[b] Downs recorded for these tracts but no counts. (Gross 1952:443).
[c] Data may not be complete; damaged specimen (see text).
[d] Range and average number for 6 nestlings (see text).
[e] Unpaired tract along midline; all others paired.
[f] Downs present on some coverts but it is uncertain which set was involved.

color in life is medium to light gray for *S. minuta* and pale or smoky gray with a buffy brown tint for *S. nigricollis* (Schwartz, pers. comm.). The distribution of these neossoptiles is given in Table 1. The nestlings of *S. nigricollis* examined by Schwartz (pers. comm.) had neossoptiles present in the same tracts indicated in Table 1. Approximately 164 neossoptiles were present on a recently hatched nestling; a late stage embryo had only 100 neossoptiles excluding those of the crural tract which could not be counted. The 2 nestlings of *S. intermedia* had neossoptiles (color in life: light gray with rufescent brown tint) present on the same tracts as others of the genus (Table 1) although exact counts were not made. The small number of specimens as well as the variation among individuals makes it unwise at present to propose a typical number or distribution pattern for the genus *Sporophila.* Even so the total number of neossoptiles is smaller than the numbers reported for most temperate zone finches (Wetherbee, loc. cit.). As a reduced number of neossoptiles also seems to be characteristic of other Neotropical groups (Collins unpubl.) it may represent a trend in latitudinal variation. This will have to be confirmed when more specimens of more species have been studied.

The single specimen of *S. obscura* we examined had appreciably fewer neossoptiles present and only on the occipital and spinal tracts (Table 1). Schwartz stated (pers. comm.) that this paucity of downs (color in life: pale gray with buffy or brownish tint) is typical of *S. obscura.* Of the 9 individuals of *S. obscura* he observed in 1974, exact counts of neossoptiles were made on 2 preserved and 4 living nestlings. Total neossoptile counts ranged from 11 to 23, average 17, and usually also included the coronal and scapular tracts (Table 1). Observations made by M. Dale Arvey (pers. comm.) of *S. obscura* nestlings in Colombia also indicate that neossoptiles in this species are sparse and confined to the "capital tract and a few long filamentous feathers on the dorsal tract." As these data are in general agreement, it is apparent that the number of neossoptiles is substantially reduced in *S. obscura* compared with the other *Sporophila* finches examined thus far.

That *S. obscura* has a reduced complement of neossoptiles is important because it has been suggested by Schwartz (Acta IV Congr. Latin. Zool. 1:207–217, 1970; and *in* Paynter and Storer, Checklist of Birds of the World, Mus. Comp. Zool., Cambridge, 1970:141) that *S. obscura* should be transferred from *Sporophila* to *Tiaris.* Hatchlings of the Black-faced Grassquit (*T. bicolor*) in Venezuela have a very sparse natal down covering rather similar to that noted for *S. obscura.* Two nestlings and a late stage embryo of *T. bicolor* from Cata, Est. Aragua had sparse complements of neossoptiles on the coronal, occipital, spinal (upper and lower), scapular, and femoral tracts as well as rectrices and some wing coverts. The total number of neossoptiles were 32 and 64 for the 2 birds examined in detail. Field observations by Arvey (pers. comm.) in Colombia of *Tiaris* nestlings also indicated that the pattern of neossoptiles is highly similar to that noted here for *S. obscura.* This is further confirmed by Arvey's notes on aviary-raised young of the Yellow-faced Grassquit (*T. olivacea*) which had only "very sparse. elongated down feathers" on the capital and spinal tracts. Skutch (op. cit.) reported that *T. olivacea* hatchlings are "utterly devoid of natal down." Similarly. the absence of downs has been recorded for aviary-raised young of *T. olivacea*, *T. bicolor.* and the Cuban Grassquit (*T. canora*) by Goodwin (Avic. Mag. 65:131–134. 1959) and for 6 newly-hatched young of *T. canora* by Luis Baptista (pers. comm.). This apparent difference within *Tiaris* may simply be the result of individual variation (e.g., Schwartz. pers. comm. informs us that hatchlings of the Blue-black Grassquit, *Volatinea jacarina* may have very sparse natal down, as noted for *S. obscura.* or lack it completely). Arvey, in his field studies of *S. obscura*, and in captive-raised *T. olivacea*, also notes that sometimes the neossoptiles "disappear in a matter of 2–3 days after hatching", presumably by abrasion. However, 2 nestlings of *S. obscura* examined by Schwartz on day 1 and again on day 5 showed the loss of but a single neossoptile. Early losses of natal downs to abrasion have not been considered significant by other workers.

These data on the number and distribution of neossoptiles are in agreement with the suggestion that *S. obscura* should be included in *Tiaris* and not *Sporophila*. A complete analysis of the relationship of *S. obscura* is in preparation by Schwartz. More information on additional species of *Sporophila* is needed before an exact pattern of neossoptile distribution can be established for this genus. *Tiaris*, on the other hand, seems to be typified by a sparse complement of neossoptiles (sometimes none) frequently confined to the occipital and spinal tracts, but variably present also on the coronal, scapular, and femoral tracts, and wing coverts.

Field studies of the senior author in Trinidad were supported by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History, New York. We are grateful to M. Dale Arvey and Luis F. Baptista for providing unpublished data from their notes. We are greatly indebted to Paul Schwartz for contributing his personal knowledge, specimens, and field notes to this study, and particularly for sharing his unpublished data on the relationships of *S. obscura*.—CHARLES T. COLLINS AND MICHAEL H. KEMP, *Dept. of Biology, California State Univ., Long Beach 90840.* *Accepted 25 Feb. 1975.*

Cedar Waxwing feeding from spider web.—On 12 September 1974 at 08:40 C.D.T. we noticed a lone Cedar Waxwing (*Bombycilla cedrorum*) near the top of a dead, leafless tree on the Goose Pond Audubon Refuge, Columbia Co., Wisconsin. The bird landed on a limb, and hopped to another directly in front of a vertically-oriented spider web in which numerous specks, presumably insects, were visible. While perched the bird removed 8 of these specks with 8 pecks. The bird then flew about 2 m to another part of the same tree, perched by another spider web, and removed 2 specks from it. The bird last flew to a perch by a third web, and pecked once into the web. The waxwing never hovered by a web, and we never observed a spider on any web.

Between pecks the waxwing sat with its body's long axis 20° forward of vertical, the head, body, and tail aligned, the wings folded at the sides. When pecking toward the spider web the body rotated forward an additional 25° and the tail was raised 30° putting it slightly above the long axis of the body; then the head was thrust forward 0.5–1 cm. The peck and recoil involved the neck only; the wings were not moved nor were the feet. During each bout the pecks occurred at about 1/sec.

In a search of relevant literature we found no previous accounts of Cedar Waxwings or other passerines feeding from spider webs. McAtee (Roosevelt Wildlife Bull. 4:68, 1926) notes that waxwings very occasionally consume spiders and more frequently feed on tent caterpillars (Lasiocampidae). DuBois (*in* Bent, U.S. Natl. Mus. Bull. 197:91, 1950) observed waxwings seize geometrid caterpillars (Geometridae) that hung from twigs on gossamer thread. These observations suggest that waxwings may be preadapted to searching for prey in insect silk. However, many passerines consume spiders (e.g., Wetmore, U.S. Dept. Agr. Bull. 326:1–133, 1916) or use spider silk for nest construction (e.g., Bent, U.S. Natl. Mus. Bull. 203:1–734, 1953). Therefore one might expect cleptoparasitic web-feeding to be widely used by passerines, especially since such behavior obviates the need to capture prey. The apparent rarity of web-feeding may be due to the difficulty of discovering webs or the difficulty in extracting prey from the web without the bird's becoming entangled itself. However, the ease with which the waxwing picked out the prey renders the latter explanation unlikely. Another difficulty is the behavior of web-building spiders; these usually do not allow prey to remain long in the web (Savory, The Biology of Spiders, Macmillan Co., N.Y., 1928). Furthermore, orb web-builders spin a new web daily (Savory, op. cit.). It is possible, then, that opportunities for web-feeding are actually rare. We may have seen long-abandoned webs with an unusual abundance of prey available to the opportunistic waxwing.—EDWARD H. BURTT, JR., B. DENNIS SUSTARE, AND JACK P. HAILMAN, *Dept. of Zoology, Univ. of Wisconsin, Madison 53706. Accepted 26 Feb. 1975.*

Autumnal breeding in Chinese Spotted Doves.—On 31 October 1973, Paul Marsden, a student at Occidental College, Los Angeles, California, found a juvenile Chinese Spotted Dove (*Streptopelia chinensis*), which was being harassed by a house cat in the backyard of a home near the campus. The bird died, was prepared as a study skin, and deposited in the Moore Laboratory of Zoology, Occidental College (♀, 66262). The basal ¼ of its rectrices and remiges were still ensheathed, suggesting that this dove had either recently fledged or had fallen prematurely out of its nest. A second fall juvenile of this species is in the collection of the Los Angeles County Museum (♀, 18892). This individual was taken on 26 October 1937. It appeared slightly older than the first specimen, only the bases of the remiges being still ensheathed.

As an established feral, exotic bird in southern California, this species has been known to nest "from March at least through May" (Hardy, Wilson Bull. 85:506–512, 1973). Assuming that the observations reported herein are the result of breeding by feral parents and that these are not isolated incidents, the known outside breeding dates can be expanded to include the period between March and November in southern California where mild temperatures prevail. Fall breeding is known to occur in other avian species in California (Orians, Auk 77:379–398, 1960) and should be expected of the Chinese Spotted Dove as well. In many parts of its range of Thailand, Ceylon, Burma, and Java, the Chinese Spotted Dove breeds throughout the year (Herbert, J. Siam Soc. Nat. Hist. Suppl. 6:334, 1926; Deignan, U.S. Natl. Mus. Bull. 186:154, 1945; Wait, Manual of the Birds of Ceylon, Dulau and Co., London, 1925; Smythies, The Birds of Burma, Oliver and Boyd, Edinburgh, 1953; Voous, Ibis 92:283, 1950).

Circumannual breeding may have contributed to the success of this exotic in becoming established in southern California. On the Hawaiian Islands where feral populations of this dove also occur, nesting is known from February to October, but the species is also thought to nest throughout the year (Schwartz and Schwartz, The Game Birds in Hawaii, Board of Commissioners of Agriculture and Forestry, Honolulu, 1949).

I thank James Northern for the use of specimens under his care at the Los Angeles County Museum.—LUIS F. BAPTISTA, *Moore Laboratory of Zoology, Occidental College, Los Angeles, CA 90041. Accepted 25 Feb. 1975.*

EDITORIAL

Blackbirds, Scare Tactics, and Irresponsible Legislation

A friend of mine once commented that there are only 2 ways that a legislator can responsibly vote on legislation: (1) he can vote according to the expressed wishes of his constituency, or (2) he can vote following his own convictions after having thoroughly studied the pros and cons of a particular bill. On 27 January 1976 a bill was introduced into both houses of Congress that would allow Kentucky and Tennessee to bypass environmental laws so that they might eliminate millions of blackbirds by spraying them on their roosts with the pesticide Tergitol. The bill was passed by the Senate and House on the day it was introduced and was quickly signed into law by President Ford. Since there was no opportunity for citizens to express their feelings to their legislators and since the bill was passed without legislators having an opportunity to study both sides of the issue, I can only conclude that a majority of our legislators voted irresponsibly.

Environmental groups have expressed serious concern over the passage of this bill because it allows a special interest group to circumvent the National Environmental Policy Act and other federal laws. A dangerous precedent has been set. Recognizing the seriousness of these broader implications of the blackbird bill, I would like to comment on the specific problem which precipitated this legislation.

Few people would want a blackbird roost in their back yard or perhaps even within a kilometer of their residence. Blackbird roosts smell, an accumulation of excrement may kill vegetation in the roost, there may be a health hazard due to the growth of the fungus *Histoplasma capsulatum* in the nitrogen-rich soil beneath the roost, and some blackbird species feed on agricultural crops. The first two negative effects of a blackbird roost are obvious, but do not have dangerous or enduring consequences. The second 2 effects are controversial, but are continually recited in the popular press and on radio and television in attempts to gain support for blackbird "eradication" programs. We hear a lot about the dangers of histoplasmosis associated with blackbird roosts, but no one has quantified this danger nor has the relative importance of blackbird roosts as reservoirs for the fungus been examined. Unfortunately most of the literature concerning histoplasmosis is in medical journals, though I have elsewhere summarized and interpreted some of this literature as it relates to birds (Jackson, Inland Bird Banding News 45:52–57, 1973). The spores of *Histoplasma* are dispersed from the soil by the wind and the fungus grows not only in blackbird roosts, but anywhere there is a high concentration of nitrogen in the soil. Poultry farms are important natural reservoirs for the fungus. They tend to be much more permanent than blackbird roosts and the ground is often bare, thus increasing the likelihood of growth of the fungus and dispersal of the spores. Cattle feedlots would also seem to be optimum areas for growth and dispersal of *Histoplasma*, though I know of no studies that document this. In short, I suspect that the seasonal, frequently moved blackbird roosts present much less of a hazard than do other situations which we have readily accepted. Why aren't the potential hazards of poultry farms and the like subject to as much public attention? Perhaps it is a matter of economics—we are willing to tolerate the danger of histoplasmosis if it means dollars in the pocket. On the other hand, perhaps it is because the disease-causing fungus is ubiquitous and the elimination of individual reservoirs of the fungus is meaningless in terms of the general presence of the spores in the air. The real answer may be somewhere in between. It is of interest that skin tests indicate that up to 90% of adults in the states where the disease is most common have been exposed to the pathogen (Ajello, *in* Histoplasmosis, p. 88–98, Charles C. Thomas, Publisher, Springfield, Ill., 1960; Negroni, Histoplasmosis, diagnosis and treatment, Charles C. Thomas, Publisher, Springfield, Ill., 1965), and that in most people the disease is apparently little worse than the common cold.

The second "serious" consequence of blackbird roosts is also generally aired by the news media from only one point of view—the number of dollars worth of grain consumed by the hoards of blackbirds. What weed seed and overwintering insects do blackbirds also eat and what dollar value do we place on the birds' control of these pests? Both sides of the ledger need to be completed before the books can be closed. Furthermore, what will be the long term effects of destroying millions of blackbirds? These birds feed arthropods to their nestlings. If fewer blackbirds return north in spring to nest, might not northern farmers have greater problems with crop pests? And what of the reproductive potential of blackbirds? We know that when other species' populations are reduced they "bounce" right back as a result of increased production and survival of young. We have no reason to suspect that blackbird populations are any different. Blackbird roosts are a part of our environment and they are likely to remain so because of the innate behavior of the birds and the ways in which we manage the land. Attempts to rid ourselves of blackbird roosts will only result in destruction of wildlife, degradation of the environment, the dispersal of some roosts for part of a winter season, and the continual expenditure of large sums of money. If the birds don't return to the same roost the following year, it doesn't mean a problem has been solved; it means only that the problem has gone somewhere else—and perhaps it is even more of a problem there.

Blackbird roosts near human population centers may be bad, but when the birds roost on public land away from human population centers, let's leave them alone. Instead of spending money and energy on anti-blackbird campaigns using scare tactics based on half-truths, let us assemble what knowledge we have of the birds and the problems they supposedly cause, find out what we don't know, then spend our money on research to answer some of the presently many unanswered questions. Perhaps then we will be able to understand and reasonably manage the birds rather than merely destroy them. —Jerome A. Jackson.

(As a sad footnote to this editorial, I have learned that on 27 and 28 January, the Tennessee Department of Agriculture directed the spraying of Fenthion from National Guard helicopters at a blackbird roost at Henry Horton State Park. The kill from this spraying was apparently insignificant and on 9 February a second spraying was done using methyl parathion. The Audubon Council of Tennessee reports that only a few dozen blackbirds were killed, but that Cardinals, Song Sparrows, Mockingbirds, Screech Owls, Red-tailed Hawks, and Marsh Hawks were also found dead.)

ORNITHOLOGICAL NEWS

THE 1976 WILSON ORNITHOLOGICAL SOCIETY ANNUAL MEETING

The 1976 meeting of the Society will be held on the Cornell University campus from Thursday, June 3, to Sunday, June 6, and is being hosted by the Laboratory of Ornithology and the Cayuga Bird Club. The chairman of the local committee for arrangements is Dr. Douglas A. Lancaster, Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14853.

In the heart of the Finger Lakes Region, a summer resort area of New York state, Ithaca has a good variety of restaurants and lodging accommodations. The meeting headquarters will be Cornell's North Campus Union with adjacent dormitory facilities.

Alexander Wilson found this region so attractive that he made several visits by foot all the way from Philadelphia. He memorialized his experiences in a book in verse, "The Foresters." As with Wilson, you, too, can enjoy finding many of the 325 species recorded for the Cayuga Lake basin. Varied local habitats will yield such birds as Blue-winged and Golden-winged warblers along with their hybrids. Other warblers include Black-throated Green, Cerulean, Mourning, and Canada. The woods in the area resound with the songs of the Hermit Thrush, Veery, and Wood Thrush in early June. In the cool woods and gorges live both species of waterthrushes and an occasional Winter Wren. In addition to breeding waterfowl, of special interest at the Montezuma National Wildlife Refuge, north of Ithaca, are Prothonotary Warblers and a colony of Black Terns.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in the memory of the late Aaron M. Bagg, former president of the Society. The Student Membership Committee has designated the award recipients for 1976 as follows: John H. Alway, University of Alberta; Richard Balcomb, State University of New York at Albany; Gregory D. Bentz, University of Pittsburgh; Robert Bertin, University of Connecticut; Randall J. Breitwisch, University of Miami, Florida; Charles R. Brown, Sherman High School, Sherman, Texas; Carolyn Engel, Fort Lewis College, Colorado; Patricia A. Gowaty, University of Georgia; Juan Guzman, University of Calgary, Alberta; Barbara Lensing, University of Louisville, Kentucky; Stephen J. Maxson, University of North Dakota; Terry C. Maxwell, Texas A&M University; Richard E. McCamant, Texas A&I University; Linda Miller, University of Illinois; David J. Moriarty, University of Illinois; Mike Mossman, University of Wisconsin; Thomas L. Ritchie, University of Florida; Douglas W. Schemske, University of Illinois; James R. Sillman, University of Arizona; Gerald A. Smith, State University of New York at Oswego; Philip Unitt, San Diego State University; Daniel E. Varland, Eastern Illinois University.—Douglas James, Chairman, Student Membership Committee.

SYMPOSIUM ON AVIAN VOCALIZATIONS

One of the highlights of the 1976 Wilson Meeting at Cornell University will be a symposium on avian vocalizations. The symposium has been organized by John William Hardy and will include a series of invited papers.

SOUND ANALYSIS LABORATORY

The Museum of Vertebrate Zoology announces the opening of a sound analysis laboratory funded by the National Science Foundation. The laboratory will emphasize research on geographic variation in vocalizations of birds in conjunction with studies of morphological variation. The facility will be available for use by qualified investigators engaged in studies of this type. Address inquiries to Dr. Mercedes S. Foster, Curatorial Associate in Ornithology, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720.

SURVEY OF AVIAN SOUND RECORDINGS

The committee on collections of the American Ornithologists' Union is commencing a survey of collections in North America of tape recordings of avian vocalizations and sounds. The committee will be grateful for the help of all recordists, professional and amateur, who have or are curators of such collections. Both research and nonresearch collections are of interest to the committee. For more information please contact: AOU committee on Collections, c/o Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14853.

MANAGEMENT PRACTICES ON WILDLIFE REFUGES

The Wilson Ornithological Society, through its Conservation Committee, intends to examine management practices on National and selected State Wildlife Refuges. In particular, the Committee is interested in learning of practices that have either beneficial or deleterious impacts on bird populations. All correspondence will be confidential and anonymous letters are solicited, provided that the data or allegations can be supported. Correspondence should be directed to: Clait E. Braun, Chairman, Conservation Committee, The Wilson Ornithological Society, P. O. Box 2287, Ft. Collins, CO 80522.

HAWK MIGRATION CONFERENCE

The Hawk Migration Association of North America will hold its 1976 Conference at the University of Minnesota, Duluth Campus. The campus is within a 10 minute drive of Hawk Ridge, one of the great hawk migration lookouts. Dates of the conference will be September 2-5. Further details may be obtained from Dr. P. B. Hofslund, Biology Dept. UMD, Duluth, MN 55812.

NORTH AMERICAN WADING BIRD CONFERENCE

The National Audubon Society and the U.S. Fish and Wildlife Service are sponsoring a conference on wading birds (herons, egrets, ibis, storks, spoonbills) in North America. The conference is scheduled for 14–17 October 1976 at the Mills Hyatt House in Charleston, S.C. There will be 4 general sessions on the broad topics of: Behavior, Conservation and Management, Populations and Surveys, and Ecology. Each session will contain several invited papers, followed by submitted papers in the appropriate fields. A series of workshops is also planned. It is further expected that a "Working Group on Wading Birds" will be organized to facilitate information exchanges and further studies on wading birds. For further information write: Research Department, National Audubon Society, 115 Indian Mound Trail, Tavernier, FL 33070, or Mr. Don Woodard, National Coastal Ecosystems Team, U.S. Fish and Wildlife Service, National Space Technical Laboratories, Bay St. Louis, MS 39520.

Colonial Bird Register

The National Audubon Society and the Cornell Laboratory of Ornithology have organized the Colonial Bird Register to facilitate the collection and dissemination of information concerning the location and productivity of colonies of birds in wetlands throughout North and Central America and the Caribbean. Individuals and agencies working with colonially nesting species are asked to contribute to the success of the Register by completing and submitting field survey forms detailing the location of colonies, their sizes, species composition, habitat, disturbance factors, and other information. For further information contact: Dr. Donald A. McCrimmon, Director, Colonial Bird Register, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14853.

NSF/AOU Workshop on a National Plan for Ornithology

The National Science Foundation is supporting a 2-year project, sponsored by the American Ornithologists' Union, entitled "A Workshop on a National Plan for Ornithology." The Workshop, financially administered by Washington State University and coordinated by James R. King and Walter J. Bock, will include 25 participants from throughout the U.S. and Canada. Its purpose is to inventory the resources, both intellectual and physical, of North American ornithology, to identify current strengths and weaknesses, and to recommend guidelines for its future development and support. The first conference session of the Workshop will convene at the 94th Stated Meeting of the AOU, at Philadelphia, in August 1976. This will be followed by 2 meetings of each of the 6 Workshop Panels (The Role of the Ornithological Societies and the Amateur Ornithologist, Ornithological Education, Communications Resources, Special Data Banks, and Obtaining and Using Birds), and will conclude with a final conference meeting for the integration and summary of results in a report to the National Science Foundation and the ornithological community at large. Part of the Workshop inventory will consist of a questionnaire to be circulated as widely as possible among North American ornithologists. The success of the Workshop will be greatly aided by thoughtful and thorough responses from professionals and amateurs alike. An important goal of the Workshop will be an assessment of the role of amateur ornithologists, who are an important but underused scientific resource.

The Workshop plan was originated by the AOU, but it is hoped that it will be regarded as a joint effort of all of the ornithological societies and of the ornithological community at large. It represents a unique opportunity for introspection, critical assessment, and identification of future directions.

XVII International Ornithological Congress

On the occasion of the XVI International Congress in Canberra, the International Ornithological Committee accepted the invitation of the Deutsche Ornithologen-Gesellschaft to hold the XVII Congress in Germany. It elected Professor Donald S. Farner (Seattle) as president of the Congress. In consultation with the President the German members of the International Ornithological Committee decided to hold the Congress in the Kongresshalle in Berlin (West) from June 4–11, 1978; Mr. Rolf Nöhring of the Berlin Zoological Garden was designated as Secretary-General.

Those interested in participating in the Congress are urged to inform the Secretariate as early as possible in order to obtain more detailed information and communications concerning the Congress. Communications should be addressed to the: Secretary-General Rolf Nöhring, Zoologischer Garten, Hardenbergplatz 8, 1 Berlin 30, Germany.

North American Bird Bander

The Eastern and Western Bird Banding Associations have entered into a cooperative venture of publishing their quarterly journals together. *EBBA News* and *Western Bird Bander* have been suspended; instead, a new periodical has emerged: *North American Bird Bander.*

In order to receive this publication, join either EBBA or WBBA (but not both). Active membership dues of $6.00 for 1976 may be mailed to Mr. Davis H. Corkran, EBBA Treasurer, 154 Lake Ave., Fair Haven, NJ 07701 or Mrs. Shirley S. Spitler, P. O. Box 3128, Y.P.G., Yuma, AZ 85364.

Sandhill Crane Data

Dr. Lawrence H. Walkinshaw has deposited a copy of his field notes on Sandhill Cranes in the southeastern United States and Cuba in the Archbold Biological Station Library. These field notes mainly relate to Florida during 1966–1974 but also cover Mississippi, Georgia, and Cuba during 1938–1974. The crane data include nesting season and habitat, nest site and construction, adult behavior at the nest, eggs, young, nest success, and local movements. Also included are some census data for other birds occurring in Sandhill Crane habitat in Florida, Mississippi, and Cuba. For further information write: Librarian, Archbold Biological Station, Rt. 2 Box 180, Lake Placid, FL 33852.

Birds Banded in Asia

Single copies of the book entitled "Birds banded in Asia during the MAPS Program, by locality from 1965 through 1971" can be obtained free by writing to: Colonel Douglas J. Beach, Director, United States Medical Component, SEATO Medical Research Project, APO San Francisco 96346.

Range Expansion of Animals

The Smithsonian Institution has had translated from Polish and published in paperback *The Range Expansion of Animals and its Causes* (as demonstrated by 28 presently spreading species from Europe) by Eugeniusz Nowak. It was originally published under the title, "O rozprzestrzenianiu sie zwierzgt i jego przyczynach—na przykladzie 28 wspolczesnie rozprzestrzeniajqcych sie gatunkow z terenu Europy" in *Zeszyty Naukowe,* No. 3, 1971, pp. 1–255. The work covers 7 mammals, 8 birds, 8 insects, 3 crustaceans and 2 mollusks and includes 388 references. Copies are available from the U.S. Department of Commerce, National Technical Information Service, Springfield, VA 22151 at $6.75 domestic and $9.25 foreign. Cite publication no. TT 74–54005. A limited number of free copies are available from the Smithsonian Institution. Send a sturdy preaddressed envelope at least 10 × 7½ inches to Translation Officer, Smithsonian Institution Library, Washington, D.C. 20560. For U.S. addresses please place 30 cents postage on the envelope; foreign requests will be mailed post free.

CONSERVATION COMMITTEE REPORT ON EFFECTS OF ALTERATION OF SAGEBRUSH COMMUNITIES ON THE ASSOCIATED AVIFAUNA

Sagebrush (*Artemisia* spp.), principally big sagebrush *A. tridentata*, is a conspicuous feature of the environment in the western United States. Prior to settlement, sagebrush-dominated rangelands occurred from the western Dakotas into southern Alberta, Montana, Idaho, Washington, Oregon, northern California, Nevada, Utah, Wyoming, and Colorado into northern New Mexico (Beetle 1960). Much of the land occupied by sagebrush is public domain administered by the Bureau of Land Management, U.S. Department of Interior; and the U.S. Forest Service, U.S. Department of Agriculture. Significant areas are in private ownership, having been acquired under a variety of homestead and mining acts and government grants. Many areas formerly occupied by sagebrush have been cleared for agriculture with the last large area to be affected being in the Columbia Basin.

Historically, livestock grazing has been the primary use of many sagebrush lands although recreational use has increased in recent years. Sagebrush has been considered by many land managers to have little value and special interest groups have successfully pressured government agencies into programs to "improve" western rangelands. Improvement has meant the reduction of sagebrush and reseeding with grass. Because of increased efforts in the late 1950's and 1960's to "control" sagebrush in the western states, and in view of the increasing demand for red meat and energy in the foreseeable future, the Conservation Committee of The Wilson Ornithological Society decided to review the available data on the effects of reducing sagebrush on the associated avifauna, especially those species presumed to be largely dependent on sagebrush communities during some portions of their annual cycle.

HISTORICAL RESUMÉ

Sagebrush has been a dominant feature of rangelands in western North America since before the advent of modern recorded history. Reports of early travelers through the west, when much of the vegetation was presumed to be in pristine condition, indicate that brush, particularly sagebrush, was common (Vale 1975). It has been variously estimated that sagebrush covered from 58.7 to 109.3 million ha of land at one time, with big sage comprising 58.3 million hectares of the total (Sturges 1973, Beetle 1960). Extent of area dominated by sagebrush prior to modern civilization is unknown but little evidence is available to support the widely held belief that present sagebrush ranges are the result of past overgrazing on most sagelands.

Much of the area once dominated by sagebrush has been altered by mechanical, chemical, and biological methods. Major reasons for this alteration were principally related to agriculture; the need for more cultivated land for grain and hay crops, and the desire to increase livestock forage production. Thus, by the early 1950's sagebrush on at least 0.6–0.8 million ha was reported as being successfully controlled (Pechanec et al. 1954). By 1966, Schneegas (1967) estimated that 2.0–2.4 million ha of sagebrush had been treated by some method. Estimates in 1974 were that about 30% of all sagebrush land in Colorado had received some treatment since 1900. The situation in this state is not indicative of the entire western United States but it is conservatively estimated that at least 10% of the sagebrush rangelands in the west have been altered.

Prior to the end of World War II, most treatment of sagebrush was by mechanical methods such as plowing, chaining, and disking, although fire and heavy grazing pressure (by sheep and goats) had been used in some areas prior to mechanical control. After the mid-1940's, use of herbicides, primarily 2,4-D, became an important tool in reducing the abundance of sagebrush (and inadvertently many other shrubs and forbs). The basic premise was that sagebrush was competing for nutrients, water, and space with more desirable grasses. Since sagebrush is relatively unpalatable to livestock, the reasoning was that once sagebrush was controlled, the rangelands could support more livestock due to the increased growth and density of the grasses. Lost in the rush to eliminate sagebrush was the value of this shrub to many forms of wild and domestic animals. Most programs designed to reduce sagebrush on public lands were supported with public funds. On private lands, some public funds were used through cost sharing programs of the Soil Conservation Service and Agriculture Stabilization and Conservation Service. Cost per hectare of brush control and re-seeding with grasses has been estimated to range from about $15.00 to $62.00 (Vale 1974).

Historically, little concern was expressed about potential effects of alteration of sagebrush habitats on wild animals. Patterson (1952) questioned sagebrush control projects as a serious threat to maintenance of huntable populations of Sage Grouse (*Centrocercus urophasianus*), pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). In 1954, Carhart suggested that at least 4 species of birds—Sage Grouse, Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*), and Brewer's Sparrow (*Spizella breweri*)—would be adversely affected if sagebrush were eradicated. In the early 1960's, with advent of large-scale control projects, conservation departments of the western states, under the auspices of the Association of Western State Game and Fish Commissioners, formed the Western States Sage Grouse Committee to coordinate documentation of sagebrush loss and to make recommendations for mitigation, if possible, of such loss. Little research has been or is being done on other birds dependent upon the sagebrush type except for 2 studies in Montana (Feist 1968, Best 1972).

AVIFAUNA OF SAGEBRUSH COMMUNITIES

Over 100 species of birds which forage and nest in sagebrush communities have been listed (Wetmore 1920, Gabrielson and Jewett 1940, Dumas 1950, Booth 1952, Huey and Travis 1961, Bailey and Niedrach 1965, Walcheck 1970, Behle and Perry 1975). Birds which are obligates (almost entirely dependent) of the sagebrush type are: Sage Grouse, Sage Thrasher, Sage Sparrow, and Brewer's Sparrow. Near obligates are Green-tailed Towhees (*Chlorura chlorura*) and Vesper Sparrows (*Pooecetes gramineus*). Other species that are conspicuous and locally important are: Ferruginous Hawk (*Buteo regalis*), Golden Eagle (*Aquila chrysaetos*), Prairie Falcon (*Falco mexicanus*), Sharp-tailed Grouse (*Pedioecetes phasianellus*), Mourning Dove (*Zenaida macroura*), Burrowing Owl (*Speotyto cunicularia*), Common Nighthawk (*Chordeiles minor*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Horned Lark (*Eremophila alpestris*), Western Meadowlark (*Sturnella neglecta*), and Brewer's Blackbird (*Euphagus cyanocephalus*).

PRESENT STATUS

Alteration of sagebrush rangelands is still occurring but at a much reduced level. Probably fewer than 20,000 ha are being treated each year. Use of herbicides to reduce sagebrush densities is at the lowest level since 1950. Reasons for reduced alteration of sagebrush habitats, especially on public lands, relate to questions concerning the effectiveness of such programs, economic conditions (cost vs return), requirements of the National Environmental Policy Act, and concern about herbicides as possible agents causing birth deformities (Vale 1974).

Research in recent years on the effects of alteration of sagebrush rangelands indicates that removal of sagebrush significantly reduces soil moisture loss (Sturges 1973), increases dry matter production by forbs that remain, and makes grass more readily available to livestock (Daubenmire 1970). Evidence now becoming available indicates that any control of sagebrush outside of continuous agricultural practices is short-lived (Harniss and Murray 1973, Thilenius and Brown 1974). Thus, to increase forage production for livestock, sagebrush control must be on a continuing basis. Despite the cost and obvious limitations, agencies such as the Soil Conservation Service still actively support sagebrush conversion projects citing not only benefits to domestic livestock but also to elk (*Cervus canadensis*), deer (*Odocoileus* spp.), grouse and other wildlife (Petersen 1971).

Numerous studies throughout the western states have amply demonstrated the dependence of Sage Grouse on sagebrush during all seasons (Patterson 1952, Klebenow 1969, Peterson 1970, Wallestad 1971, Eng and Schladweiler 1972, and many others). Studies of the effects of herbicide spraying on populations of Sage Grouse have been conducted (Carr and Glover 1970, Martin 1970), but available data do not present a clear pattern. It would appear from these studies that control of sagebrush in narrow strips (with wide strips of undisturbed sage) is not detrimental to Sage Grouse. Such alteration may even be beneficial as large monotypic stands are broken into smaller stands with more edge. It has also been observed that Sage Grouse prefer the leaves of seedling sagebrush plants and seek them out in disturbed areas. In contrast to the possible benefits of certain sagebrush alteration done in strips, control of sagebrush in large blocks (larger than 16 ha) appears to be detrimental.

While research on Sage Grouse has been relatively intensive and well-funded, research on non-game species dependent upon the sagebrush community has been almost nonexistent. Best (1972) found that in central Montana, Brewer's Sparrows relied on sagebrush for nesting sites and declined 54% one year after a plot was sprayed. Follow-up studies (Pyrah and Jorgensen 1974) on this same area revealed that 5 years after a total kill of sagebrush, Brewer's Sparrows were almost completely eliminated and replacement by other species had not occurred. This is in contrast to the results of a limited study in Wyoming (Scott et al. 1966) which indicated that total numbers of birds tend to increase with sagebrush spraying. First-year results from another study in Wyoming support Best's findings, as populations of Brewer's Sparrow decreased 67% one year after sagebrush spraying with 2,4-D (Schroeder and Sturges 1975).

Data presently available indicate that the 4 species of birds that are obligates of the sagebrush community are in no danger of elimination from large areas, although total populations probably are reduced from pristine levels. Other species of birds seasonally associated with the sagebrush community do not superficially appear to have been affected by sagebrush control programs. Many of these species appear to be adapted to the structure of the sagebrush community, not sagebrush itself. It is thus possible that disturbance of this community by overgrazing, spraying, or plowing, while improving the area for some species such as Horned Larks, Western Meadowlarks, Vesper Sparrows, Lark Sparrows (*Chondestes grammacus*), and Mourning Doves, may be detrimental to other species, especially raptors.

While direct control of sagebrush as a range "improvement" practice is at a low level, many sagebrush-dominated lands have potential for development of energy resources, especially coal. Large tracts of sagebrush range in Wyoming, Colorado, and to a lesser extent, Montana, are underlain by coal deposits. Strip mining of these deposits on a limited basis has been occurring for several years. Extensive mining of some deposits is now underway and it appears that strip mining will be a major disturbance in sagebrush areas for at least the next 40 years. Effects of mining will be apparent long after extraction has been completed as current reclamation attempts leave considerable doubt that disturbed lands can be restored to any semblance of their original condition. With increasing demands for energy, oil, gas, and geothermal exploration on public lands in the western United States has vastly expanded. Present effects of increased energy exploitation on bird life of the sagebrush type are not known. It is anticipated that most effects will be detrimental, especially those related to disposition of overburden, waste products, and road development. Research on the revegetation of these strip-mined lands with grasses and forbs is now underway but little attention has been given to reestablishment of sagebrush. Of considerable importance to the avifauna in areas surrounding energy extraction sites is the unknown but assumed detrimental effects of increased human populations living and working in the area.

SUMMARY

Sagebrush, long considered by land managers to be an undesirable shrub, has been reduced throughout its range in western North America. Conservative estimates are that at least 10% of the 58.7 to 109.3 million ha of sagebrush lands have been altered through biological, chemical, or mechanical methods. Four species of birds (Sage Grouse, Sage Thrasher, Sage Sparrow and Brewer's Sparrow) are heavily dependent on the sagebrush community. Adverse effects of sagebrush control are well documented for Sage Grouse and partially documented for Brewer's Sparrow. Effects on Sage Thrashers and Sage Sparrows have not been documented. It is probable that these 2 species have also been adversely affected by reduction of sagebrush. Many other birds have been affected by alteration of sagebrush rangelands, with some being positively affected, and others, especially raptors, being adversely affected. Alteration of sagebrush communities by mechanical and chemical methods for livestock grazing is presently at the lowest level since 1950. Overgrazing of this community on public and private lands is still a major problem and the outlook is not favorable. Development of energy resources, especially coal, will have major impact on sagebrush communities and dependent avifauna for at least the next 40 years. Concern about the effects of alteration of sagebrush communities on wild animals is increasing at both the state and national level. However, judging from past performance of various governmental agencies, wildlife use of such lands is not presently considered to have high value.

RECOMMENDATIONS

1. Sagebrush should be considered a worthwhile and desirable plant because: (a) it supplies food and cover for wildlife and livestock; (b) it is a desirable ground cover plant helping to prevent or reduce soil erosion, reduce drifting of snow, supply a large amount of humus, and tap a deep moisture supply thereby increasing the amount of herbage produced per hectare; (c) aesthetically, sagebrush is a very desirable plant and its alteration creates a displeasing blotch on the landscape.
2. It should be recognized that disturbed or treated sagebrush habitat is dynamic and is a temporary condition which is especially vulnerable to overgrazing.
3. Sagebrush treatment should be confined to only the most productive sites where the greatest favorable returns can be expected.
4. Sagebrush alteration should be confined to relatively small areas of 16 ha, preferably less. These should be in irregular strips which would give a maximum amount of edge for wildlife and maintain habitat diversity, and be aesthetically most pleasing. Such strips should be alternated with undisturbed strips of sagebrush about twice as wide, or more, and preferably at right angles to the prevailing wind and/or the slope of the land.
5. Grazing and browsing by wildlife and livestock is a desirable use of the sagebrush range. This use should be carefully controlled to encourgae maximum forage productivity and to prevent range deterioration.
6. Wildfires and all destructive uses of the sagebrush habitat should be discouraged and controlled and kept to a minimum amount. Prescribed burns may prove to be a good management tool in the future.
7. Sagebrush control programs should be scheduled so as to avoid the bird nesting season as much as possible. Late April, May, June, and early July are the main nesting months.

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LITERATURE CITED

Bailey, A. M. and R. J. Niedrach. 1965. Birds of Colorado. Denver Mus. Nat. Hist.

Beetle, A. A. 1960. A study of sagebrush. The section *Tridentatae* of *Artemisia.* Wyo. Agr. Expt. Sta. Bull. 368.

Behle, W. H. and M. L. Perry. 1975. Utah birds, guide, checklist and occurrence charts. Utah Mus. Nat. Hist. Salt Lake City.

Best, L. J. 1972. First year effects of sagebrush control on two sparrows. J. Wildl. Manage. 36:534–544.

Booth, E. S. 1952. Ecological distribution of the birds of the Blue Mountains Region of southeastern Washington and northeastern Oregon. Dept. Biol. Sci. Walla Walla College 7:65–107.

Carhart, A. H. 1954. Sagebrush is going! Audubon Mag. 56:200–204.

Carr, H. D. and F. A. Glover. 1970. Effects of sagebrush control on Sage Grouse. Trans. N. Am. Wildl. and Nat. Resour. Conf. 35:205–215.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington State Univ., Agr. Expt. Sta. Tech. Bull. 62:1–131.

Dumas, P. C. 1950. Habitat distribution of breeding birds in southeastern Washington. Condor 52:232–237.

Eng, R. and P. Schladweiler. 1972. Sage Grouse winter movements and habitat use in central Montana. J. Wildl. Manage. 36:141–146.

Feist, F. G. 1968. Breeding-bird populations on sagebrush-grassland habitat in central Montana. Audubon Field Notes 22:691–695.

Gabrielson, I. N. and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis.

Harniss, R. O. and R. B. Murray. 1973. 30 years of vegetal change following burning of sagebrush-grass range. J. Range Manage. 26:322–325.

Huey, W. S. and J. R. Travis. 1961. Burford Lake, New Mexico, revisited. Auk 78:607–626.

Klebenow, D. 1969. Sage Grouse nesting and brood habitat in Idaho. J. Wildl. Manage. 33:649–662.

Martin, N. S. 1970. Sagebrush control related to habitat and Sage Grouse occurrence. J. Wildl. Manage. 34:313–320.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Sage Books, Inc., Denver.

Pechanec, J. F., G. Stewart, A. P. Plummer, J. H. Robertson, and A. C. Hull, Jr. 1954. Controlling sagebrush on rangelands. U.S. Dept. Agr. Farmer's Bull. 2072.

Petersen, M. M. 1971. From sagebrush to waving grass. Soil Cons. 36:210–211.

Peterson, J. G. 1970. The food habits and summer distribution of juvenile Sage Grouse in central Montana. J. Wildl. Manage. 34:147–155.

Pyrah, D. and H. E. Jorgensen. 1974. Ecology of sagebrush control. Montana Fish and Game Dept. Job Progress Rept., Fed. Aid Proj. W–105–R–9. (A copy has been deposited in the Van Tyne Library—ed.)

Schneegas, E. R. 1967. Sage Grouse and sagebrush control. Trans. N. Am. Wildl. and Nat. Resour. Conf. 32:270–274.

Schroeder, M. H. and D. L. Sturges. 1975. The effect on the Brewer's Sparrow of spraying big sagebrush. J. Range Manage. 28:294–297.

Scott, O. K., H. H. Scott and G. C. Scott. 1966. Sagebrush foothills. Audubon Field Notes 20:657–658.

Sturges, D. L. 1973. Soil moisture response to spraying big sagebrush the year of treatment. J. Range Manage. 26:444–447.

Thilenius, J. F. and G. R. Brown. 1974. Long-term effects of chemical control of big sagebrush. J. Range Manage. 27:223–224.

Vale, T. R. 1974. Sagebrush conversion projects: an element of contemporary environmental change in the western United States. Biol. Cons. 6:274–284.

———. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. J. Range Manage. 28:32–36.

WALCHECK, K. C. 1970. Nesting bird ecology of four plant communities in the Missouri River Breaks, Montana. Wilson Bull. 82:370–382.

WALLESTAD, R. O. 1971. Summer movements and habitat use by Sage Grouse broods in central Montana. J. Wildl. Manage. 35:129–136.

WETMORE, A. 1920. Observations on the habits of birds at Lake Burford, New Mexico. Auk 37:221–247, 393–412.

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NEW LIFE MEMBER

Storrs L. Olson is a life member of the Wilson Ornithological Society. Dr. Olson is presently a zoologist at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. His interests in ornithology include evolution, systematics, and paleontology. Much of his work has dealt with island avifaunas, seabirds, and rails; he has published numerous papers on these subjects. The photograph of Dr. Olson was taken at the bottom of a fumarole on Ascension Island, the type locality of the extinct rail *Atlantisia elpenor*.

ORNITHOLOGICAL LITERATURE

Avian Biology, Vol. 4. By Donald S. Farner and James R. King (eds.). Academic Press, New York and London, 1974: xxii + 504 pp., many charts, graphs, drawings, and black and white photographs. $37.00.—Chapter 1, by Terence Bennett, deals with the peripheral and autonomic nervous systems. There is a brief review of the 12 cranial nerves (n. terminalis is absent in birds) giving their nuclei in the brain and their disposition, and a brief discussion of spinal nerves. Somatic afferent innervation is discussed with particular attention to muscle spindles, tendon organs, sensory capsules, and cutaneous receptors. Visceral afferent innervation is considered in terms of respiratory, cardiovascular, and gastrointestinal systems. The somatic efferent, somatic afferent, and visceral afferent innervation are considered together under the heading "peripheral nervous system", although the p.n.s. was earlier defined from a purely structural standpoint as comprising essentially the cranial and spinal nerves. There is thus some confusion between a strictly structural division of the nervous system (central and peripheral sections) and a functional division (somatic afferent, somatic efferent, visceral afferent, and visceral efferent), but this is apparently followed for convenience in writing, as the largest part of the chapter is devoted to the visceral efferent (autonomic) system. This is perhaps one reason why Bennett follows Campbell's definition of the autonomic system as those efferent pathways with peripheral ganglionic synapses. Caution is advised against assuming simple correlations between types of transmitter substances and sympathetic or parasympathetic systems. The distinctions between these systems are not always clear in birds, and the terms are avoided in this chapter. The bulk of this section is devoted to detailed descriptions of the autonomic ganglia, followed by reviews of the innervation to the cardiovascular, respiratory, digestive, excretory, genital, endocrine, and integumentary systems, and the eye. Under each system the component organs are discussed individually.

This chapter is largely an extensive literature review, and points up many areas where precise information is lacking. It also shows that most information on the avian nervous system is still based on the domestic chicken. Bennett has written an exhaustive literature review, giving more than 30 pages of references, but only one illustration. A remarkable amount of information is summarized here, but there is little attempt at a general synthesis.

In Chapter 2 M. Menaker and A. Oksche discuss the avian pineal organ. Several distinct structural types are recognized in different birds, but most of the work has been limited to a few species. Detailed accounts are given of pineal cell types, nervous apparatus, secretory apparatus, and vasculature. With respect to function, much experimental evidence is reviewed and found to be contradictory. This is attributed to a lack of experimental controls resulting from a failure to appreciate the complexity of the problem. The pineal appears to be involved in integrating photoreception, circadian rhythmicity, and long-term control of the reproductive cycle. Much of the problem may arise from the fact that a good deal of the experimental work has been done on the chicken, in which artificial selection has modified or eliminated the normal environmental control of reproduction. An understanding of the general function of the avian pineal has not yet been achieved.

In Chapter 3 Walter J. Bock discusses the avian skeletomuscular system. The 2 systems are considered together because of their close functional relationship. In

A. J. Marshall's *Biology and Comparative Physiology of Birds*, to which *Avian Biology* is a successor, separate chapters were devoted to these systems; Bock feels that a similar review is undesirable now because little new material has appeared since that work was published. Instead he devotes this chapter to "an inquiry into the foundations, methodology, and goals of evolutionary morphology as exemplified by the avian skeletomuscular system." He points out that despite the great volume of literature on descriptive morphology, much is not applicable to current problems because of inadequate detail. He urges that current workers not merely describe structure for its own sake, but base all descriptive studies on specific questions in avian biology. Nomenclatural problems are discussed, and Bock refers to the hoped-for establishment of a standardized nomenclature of avian anatomy by the International Committee on Avian Anatomical Nomenclature.

The functional morphology of the skeletomuscular system is considered at great length. Bock feels that most work to this time is inadequate because of poor understanding of the complexities of the system, especially the muscles. The biomechanics of the skeleton are analyzed with examples from Bock's own work, particularly on the skull. The physiology of muscle is treated in detail, and the point is made that so many aspects of muscle function are not apparent from gross examination, that simple description and measurement (e.g. of muscle mass as a measure of strength) do not permit a valid examination of the functional capabilities of the system. Bock discusses the kind of approach necessary to give a meaningful functional analysis of the skeletomuscular system. This includes the use of the engineering technique of free-body diagrams and the analysis of torques as well as linear forces. This method of analyzing the function of the skeleton should be studied by all workers planning such investigations. The analysis of muscle function is a more difficult problem. So many factors of muscle activity can only be determined by physiological experiments that a useful analysis would appear possible only when using a few species that can be studied experimentally. For instance the student who wishes to analyze evolutionary adaptations in a large group of birds for which only preserved specimens are available will be unable to attack most of these problems. We may then ask whether it is better to do what is possible with the material available or to abandon such studies altogether. I would favor the former approach, but some readers may find Bock's arguments discouraging.

In the section on comparative morphology and systematics Bock defines homologous features as those that "can be traced back phylogenetically to the same feature . . . in the immediate common ancestor . . ." Although this definition includes no methods of accomplishing this tracing, the use of the phase "can be traced back" is unfortunate. If taken literally it would make the concept of homology almost useless in practice, because there is no way to trace back features to a common ancestor with certainty; there are only various methods of inferring this relationship. In a formal theoretical definition it might be better to replace the phrase "can be traced back phylogenetically to . . ." with something like "have evolved from". This, however, might lead to circular reasoning in which homology and phylogeny are defined in terms of each other, a problem which Bock discusses and tries to avoid.

In Chapter 4 William A. Calder and James R. King review the thermal and caloric relations of birds. They discuss the physics of heat exchange and relate the theoretical model to the complex problems of a living bird in a variable environment. Much early physiological work was done with captive birds in controlled laboratory conditions, which are much simpler than the situation in nature. Nevertheless, the authors conclude that these studies form a reliable basis for analyzing the natural situation. The physiological responses to heat and cold are discussed at length, as is hypothermia. One important point that is brought out in this review is that birds are much more variable in their physiological rseponses to thermal stress than is generally appreciated, particularly in their ability to conserve energy by reducing metabolic activity under cold conditions.

Chapter 5, by M. Berger and J. S. Hart, deals with the physiology and energetics of flight. It opens with the old question of whether respiratory movements are coordinated with wing-beats. Recent work shows that they are coordinated in varying patterns, usually with several wing-beats to each respiratory movement. There are distinct patterns of coordination in different phases of flight, and in birds with different wing-loadings.

Respiratory rate increases during flight, but oxygen extraction decreases, showing that ventilation increases more rapidly than metabolic need requires. Fat is the main energy source in flight. Oxygen consumption is greatest during ascending flight, least during descent. Variations related to body size are discussed. A review of circulatory adaptations emphasizes heart rate and heart size relative to body weight in birds as compared to mammals. Other subjects considered include temperature regulation, water loss, and energy turnover during migration. The general approach is quantitative, and data from the literature are summarized in extensive tables.

The book ends with author, subject, and bird name indices. This volume, like others in the series, is marked by a high level of both scholarship and price.—ROBERT J. RAIKOW.

A FIELD GUIDE TO MEXICAN BIRDS. FIELD MARKS OF ALL SPECIES FOUND IN MEXICO, GUATEMALA, BELIZE (BRITISH HONDURAS), EL SALVADOR. By Roger Tory Peterson and Edward L. Chalif. Houghton Mifflin Co., Boston, 1973:xxii + 298 pp., 48 color plates, end-papers (maps). $8.95.—Peterson's long-awaited field guide to Mexican birds now exists as worn field copies, and we may try to assess it (and its predecessors) as contributions to ornithology and field identification. The full title makes one wonder whether even R. T. Peterson could cover this large, complex region and maintain his usual standards. Alas, he did not.

What the Peterson-Chalif guide (hereafter P&C) gives us is an erratic text and good plates of adults of strictly Mexican birds, i.e. species not, or only locally found in the U.S., supplemented by U.S. species in some problem genera. In the 48 crowded plates the general standards are high, but we found minor inaccuracies in bill shapes, colors, and patterns too numerous to list here.

One trouble is that omission of most northern birds from the plates makes P&C, like its predecessors, only a partially illustrated guide. Anyone wishing plates of all Mexican species must carry at least one additional guide. Confusing young of such birds as the Hepatic Tanager and Brown-headed Cowbird are not included. Further, major variations in a number of species are also omitted; for example, no female quail is illustrated. Field guides, too, need their "taxonomic editor" if produced by those unfamiliar with an area and its birds. Most unfortunate is the absence from the list of those who aided P&C, of all of the few bird students ever resident in Mexico and most of the more active recent visitors.

The text is rather disappointing. The authors treat 1038 species in only 260 pages, as compared to 606 pages in the still pocket-sized "Birds of Mexico" by Blake (1953). Families appear in the familiar Wetmore-A.O.U. order, and each is introduced by a brief but helpful paragraph with range, general characteristics, habits, and food. The number of species is given for the world and for Mexico.

Species then follow in the general Hellmayr-Blake order, with *Attila* still in the Cotingidae, the Coerebidae maintained, etc. Curiously, the Bald Eagle appears between the kites and harriers, which are followed by *Accipter*, with *Leucopternis* stuck in the middle. One wonders why P&C include such marginal species as *Puffinus nativitatis*, *Pterodroma phaeopygia*, Hawaiian Duck, and others, yet omit Thayer's Gull and Arctic Tern, which must surely occur regularly in Mexico.

Strictly Mexican species are treated in the usual Peterson style, under *Field marks*, *Similar species*, *Voice*, *Range* (general and in Mexico), and *Habitat*. Occasionally a *Note* section is added for some confusing aspect. A brief *Memo*, with one or 2 identifying clues, replaces *Field marks*, *Voice*, and usually *Habitat* for most species shared with the U.S. *Memo* descriptions are usually of breeding plumages (of northern subspecies) which may or may not be seen in the tropics. For example, the Western Bluebird is said to have a "Rusty patch on back (usually)", the Eastern Bluebird a "Blue back"; but one Mexican race of Western is blue-backed, while southern Easterns usually have some red on the back. The *Memos* are particularly inadequate for ducks (especially the mallard group), terns, and female blackbirds.

On the other hand, a few genera have been brought up to date, following the findings of studies on *Ortalis* (Vaurie), *Otus* (Marshall), *Myiarchus* (Lanyon), and *Hylochilus* (Crossin & Ely). Some accounts commendably present alternate viewpoints of differing authors, and not infrequently alternate common (English) names are given.

Names follow the Blake-Eisenmann choices in nearly all cases; thus the familiar Mearns, or Fool Quail now becomes "Montezuma (Harlequin) Quail". The Scarlet-headed Oriole (*Icterus pustulatus*) of the A.O.U. checklist appears in P&C as "Streak-backed Oriole, *Icterus sclateri*", with a "Note: Birds north of Isthmus of Tehuantepec are sometimes treated as a separate species, Flame-headed Oriole, *Icterus pustulatus*." Unless a birder pays unusual heed to scientific names, he will surely be fooled here. (Incidentally, the P&C combination is impossbile; *pustulatus* has priority.) However, while many birds are no more "scarlet-headed" than "Purple Finches" are purple, these latter-day changes gloss over the fact that others are not streaked-backed (*I. p. graysoni*), some birds of the adjacent Mexican mainland, and *contra* P&C, females and young of the northern form (*I. p. microstictus*)! Use of changed names results in an occasional *lapsus* like "Bushy-crested Jay of Chiapas" (p. 167) sending even experts scurrying to the index.

On the other hand, P&C are to be commended for maintaining the common names Pygmy-Owl and Screech-Owl for the genera *Glaucidium* and *Otus* (except, curiously, *O. flammeolus*)—even though *Otus* does not "screech". Names are handles, useful as long as their application is widely known, and we need names for genera with closely similar species. The Latin names must now serve the purpose since each recent book (including the A.O.U. checklist and P&C) has its own set of English names! If this forces birders to pay a little attention to scientific names, so much the better!

Voice usually describes the primary song, and is successful on the whole, considering the difficulty of verbal description. It is omitted for most U.S. species, except for some best told by voice (e.g. flycacthers). The person who provided the voice description is often identified. One might wish better coverage of the more usual call or location notes, but these are very hard to describe verbally. Occasionally some salient point is omitted, as for example the ear-splitting volume of the song of *Saltator atriceps*, or the strident quality of the Thick-billed Kingbird. On the whole, however, these are the best vocal descriptions of Mexican birds available.

Habitat is a real help. Altitudes are given sparingly, and not always accurately, particularly in the lower limits.

Ranges in Mexico are disappointing, particularly in view of the claim (p. ix) "we have researched every pertinent published source, including a large number of papers and notes in the ornithological journals, especially *The Auk, The Condor*, and *The Wilson Bulletin.* All important regional publications south to Panama were also consulted." In high hopes, therefore, we open the text, only to lay it down dismayed. Apparently the *only* foreign publication consulted was Alvarez del Toro's Chiapas list, and even this is not fully digested; the Varied Bunting is credited to "Pacific slope of Chiapas", whereas it actually inhabits only the arid interior, on the Caribbean slope; while the extremely localized *Tangara cabanisi* of the Sierra Madre (Pacific slope) warrants only "mts of Chiapas". Obviously, neither Mexican nor British journals nor the Zoological Record were consulted. Failure to cover foreign literature leads to complete omission of one species, *Sporophila* (*schistacea?*) Berlioz.

P&C's bibliography lists all bird-finding guides and U.S. field guides. Their distributions do not always agree with each other or with P&C's, which is not necessarily bad; we prefer *not* to find P&C repeating Alden's Sinaloa Green Jays or Davis's Chiapas nuthatches, and regret their inclusion of Alden's Nayarit Baltimore Orioles. Completely ignored are Wetmore, Peters, Hellmayr & Conover, and publications (other than Peterson's guide) from the much-better known U.S. border states. More technical works, even major U.S. journals, are poorly covered; and most museum publications are omitted.

Despite abundant inaccuracies in the text, the plates do make P&C indispensable. All other published illustrations are either outclassed or are in such specialized publications as to be hardly worth lugging along, since the birder is already loaded down with at least 2 books.

With the publication of this milestone, it is an opportune time to reassess the guide-type books available on Mexican and northern Central American birds. Chronologically, the others are: 1953, E. R. Blake, "Birds of Mexico" (Univ. Chicago Press); 1955, E. P. Edwards, "Finding Birds in Mexico" (E. P. Edwards, rev. 2nd. ed., 1968); 1966, F. B. Smithe, "The Birds of Tikal" (Natural History Press); 1968, P. Alden, "Finding the Birds in Western Mexico" (Univ. Arizona Press); 1970. H. C. Land, "Birds of Guatemala" (Livingston Publ. Co.); 1972, E. P. Edwards, "A Field Guide to the Birds of Mexico" (E. P. Edwards); and L. I. Davis, "A Field Guide to the Birds of Mexico and Central America (Univ. Texas Press). There is also the large format "Las Aves de Chiapas", by M. Alvarez del Toro, 1971 (publ. by the Chiapas State Government) with colored plates of many species of southern Mexico.

Of the general works, Davis's does not merit serious discussion; its only real merit, the plates, have now been largely supplanted by P&C. Alden provides locally useful maps and some superior plates, but deplorable inaccuracy in bird identifications.

Of the more useful books, Smithe's fine Tikal guide has now been supplanted, to a great extent, by Land's major contribution, with its excellent introduction and coverage of all Guatemala—except for Smithe's better-than-average voice descriptions. Still, it remains useful in and near the Peten as would Alvarez's in Chiapas were it available. Edwards' "finding" guide, though out-dated due to rapid changes in habitats, is probably essential for a person first exploring Mexico. His field guide is an excellent supplement to P&C, providing descriptions and additional (often better) information on ranges, altitudes, habitat, and behavior.

And lastly, that most under-rated contribution "Birds of Mexico", (Blake 1953) has been invaluable to field ornithologists. The shortcomings of all recent books on Mexico show that it was over criticized by all of us at the time. Its information, though often imperfect, has stimulated or even permitted the flowering of Mexican Ornithology (as far as this has yet occurred). It is still a must for an ornithologist working in Mexico today. A special Quetzalcoatl Award for pioneer Middle American field guide writing to Bob Blake!—ROBERT W. DICKERMAN AND ALLAN R. PHILLIPS.

BIRD GUIDE OF THAILAND, 2nd (revised) edition. By Boonsong Lekagul and Edward W. Cronin, Jr. Kurusapa Ladprao Press, Bangkok, 1974: 325 pp., 112 color plates. No price given. Order from Association for the Conservation of Wildlife, 4, Old Custom House Lane, Bangrak, Bangkok, Thailand.—This field guide to the birds of Thailand is similar in size and format to the Peterson series. The color plates by the senior author are scattered throughout the book so that illustrations are usually on the page facing the description or an adjacent page. For each of nearly 850 species there is a brief description emphasizing field characters, and beside each description is a small outline map of Thailand showing the known distribution. The authors warn, however, that the distributions of birds in Thailand are very incompletely known, and that amateur ornithologists can make a valuable contribution by adding to this information. The book ends with a bibliography, glossary, list of subspecies, list of synonyms, indices to scientific, English, and Thai names, and a list of names changed since the first edition. It is well constructed and clearly printed, and would seem to be an indispensable aid to birding in Thailand.—R. J. RAIKOW.

BIRDS OF NEW JERSEY: THEIR HABITS AND HABITATS. By Charles Leck. Rutgers University Press, New Brunswick, N.J., 1975: 190pp. $12.50.—This small book is intended to serve as a guide to birding areas in New Jersey. The title, which suggests a state bird book, is thus misleading. Two-thirds of the book is devoted to the description and location of various bird habitats, and the rest contains records of New Jersey birds, including an annotated checklist. There are a few black-and-white photographs of birds, which are superfluous because the book is meant to supplement field guides and not to replace them, and some more relevant photos of habitats as well as a few maps. The price is steep, but the book should prove useful to those unfamiliar with birding in New Jersey.—R. J. RAIKOW.

A CHECK-LIST OF OKLAHOMA BIRDS. By George M. Sutton. University of Oklahoma, Norman: 48 pp. $1.00. Order from The Stovall Museum, Univ. Oklahoma, Norman 73609.—This is a supplement to the author's book "Oklahoma Birds" (1967) and incorporates changes in nomenclature made in the 32nd Supplement to the A.O.U. Checklist of North American Birds. Entries for 394 species include dates and counties of past observations. A handy companion to a field guide.—R.J.R.

BIRDS OF THE WORLD ON STAMPS. By Willard F. Stanley, Beverly S. Ridgely, and Gustavs E. Eglajs. Handbook No. 82, American Topical Association, Milwaukee, 1974: 102 pp., black-and-white photos. Paper cover. $6.00.—Order from American Topical Association, 3308 North 50th St., Milwaukee, WI 53216.

LANDSCAPING FOR BIRDS. By Shirley A. Briggs (ed.). Audubon Naturalist Society of the Central Atlantic States, Inc., Washington D.C., 1973: 62 pp., many drawings. Paper cover. $2.00.—Order from the publisher at 8940 Jones Mill Rd., Washington DC 20015.

THE BIRDS OF CALIFORNIA. By Arnold Small. Winchester Press, N.Y., 1974: xxiv + 310 pp., 378 black-and-white photographs. $12.50.—This book includes the first complete annotated list of the birds of California since Grinnell and Miller's *The Distribution of the Birds of California* (Pacific Coast Avifauna No. 27, 1944), and if only for that reason should find a place in the library of anyone interested in the avifauna of the state. As the author indicates, however, "this book does not purport to revise or supplant that essential work, as its emphasis and thrust are different." Instead, it is designed to "serve as an introduction to the hobby and sport of bird study as well as provide a comprehensive overview of the spatial and temporal [and ecological] distribution of the birds of California." I suspect that it was also meant to showcase his excellent photographic efforts. Despite its shortcomings, the book achieves these goals.

The first section (15 p) is an unannotated "Checklist of the Birds of California." Chapter 1 (18 p), "California and Its Bird Life," is a broad survey of climate, bird distribution and the 11 land regions. Chapters 2–4 include, respectively, an excellent discussion of amateur bird study (11 p), an "Annotated List of the Birds of California" (106 p), and a detailed treatment of "California's Habitats for Birds" (164 p). The index, to bird names only, is quite complete.

The checklist, with checkboxes for tallying one's state list, contains the common and scientific names of the orders, families, and 518 species of birds recorded in California from 1900 to 1973. Rarities based on specimens or photographs are so indicated; reliable sight records are accepted. Subspecies are not treated except where former species have been lumped recently.

Having eagerly awaited the publication of this book, I must confess to more than a twinge of disappointment that the species accounts in the annotated list are so brief, averaging only about 5½ lines each. Only in the case of extreme rarities, for which all records are given, are the accounts complete. The author, however, had no intention of producing a monograph, so the prospective buyer should not expect one.

The warning that the annotated list "includes the *seasonal status* of *most* of the population of each species and takes no notice of extremes in date or range within California" (p 34) might well have been printed in bold-face type, for the unwary reader can be lulled into a false sense of security by the detailed factual treatment afforded some species and thus come to expect it for all. He should have been warned even more strongly not to attempt inferences from the absence of information. While not a fault in itself, the omission of data becomes tantamount to error when the presented information states or implies the contrary. Far too often, such is the case in this book.

Most species accounts are divided into seasonal status, habitat, and range in California. The habitat sections are generally complete, though they do not always stress preferred habitat. Examples of important omissions are the Pectoral Sandpiper's virtual restriction to fresh or slightly brackish waters and the Rufous-crowned Sparrow's preference for rocky areas. The Horned Grebe is not "confined exclusively to salt water."

Range in California, described on the basis of political divisions and major land forms, is necessarily brief, often being restricted to the phrase "length of state." Many of these summaries appear to be based on Grinnell and Miller (op. cit.). Notable omissions, where the opposite is stated or implied, include the following: the Manx Shearwater is far less common and regular in the northern half of the state; along the northern coast the Swainson's Hawk is very rare in migration and does not breed north of Monterey Co.; the Least Tern does not just "wander north to San Francisco Bay" but breeds there; the Spotted Owl occurs regularly in the mountains near Monterey, and its Muir Woods population is no more "isolated" than many others in the state.

The habitat and range sections are reasonably well done. The summaries of seasonal status, however, are another matter. Although the author has considered the proper 3 status categories—occurrence, abundance, and frequency—his terms are in some cases ill-conceived, poorly defined, and are not applied consistently.

For example, abundance terminology is confined to common, uncommon, and rare. The absence of additional categories has resulted in such anomalies as the very common Mallard and fairly common Red-breasted Merganser both being termed "common"; and perhaps has caused the reversal in terminology between the "rare" Rock Sandpiper and "uncommon" Solitary Sandpiper. "Abundant" is applied to the Sooty Shearwater and "very rare" to the Peregrine Falcon, but neither term is defined. Most importantly, *many* species accounts completely lack abundance terms! As a result, the birder cannot, for instance, determine his chances of picking a Royal Tern out of a flock of Elegants (or could it be vice versa?); the conservationist cannot learn that the once rare Snowy Egret has made a comeback and should now be considered fairly common; and the ornithologist can only guess at the current abundance of the rapidly-colonizing Cattle Egret.

Confined to such a limited format, the author probably should not have attempted to distinguish between "pure transients" (species that "migrate through the state" but "do not breed") and "complex transients" (species in which some individuals migrate through while others winter or breed). In any event, the attempt has failed, partly because the definition (p 35) of pure transient does not exclude wintering birds, but mostly because of incomplete application. The Spotted Sandpiper and Ruby-crowned Kinglet are used as examples of complex transients (p 19) but are not so termed in the annotated list. Additional species surely fall into this category (e.g. Sharp-shinned Hawk) but are not so listed; while other forms (e.g. Western Red-tailed Hawk) are so defined but not so designated. Use of the term "transient" for many of the vagrant eastern warblers is novel but not acceptable. A transient is a bird that migrates through an area between its regular breeding grounds and regular wintering grounds and is at all times within its normal range. To defend a transient status for such vagrant warbler species as Blackburnian and Black-throated Blue, and especially the southeastern-ranging Prairie and Hooded, would be difficult indeed.

"Perennial visitor," said to be restricted to "sea birds" but applied to the Willet, should have been used, if at all, for a number of other birds (e.g. Common Loon and Black-bellied Plover), but perhaps not for the Wandering Tattler, one of the rarest summer visitors.

Although the writing style is direct and readable, it frequently suffers from a weakness in organization that results in disconcerting and space-consuming repetition. One example must suffice. The statement on p 300 that "Western Gulls of the 'Yellow-legged' race from the Gulf of California regularly visit the Salton Sea in small numbers after their breeding season in Mexico is completed by August" is repeated almost verbatim on p 301.

Typographical errors are scarce except in scientific names; a cursory inspection revealed discrepancies involving 20 species. For 9 species the errors are repeated or compounded in the checklist, annotated list, and index (*Miniotitla*, *Mniotitla*, and *Minotitla* for the Black-and-white Warbler) and thus would not seem to be merely typographical in origin. The entire species account for the Cassin's Sparrow has been repeated under Field Sparrow. The only record of the latter is of a single bird that remained on Southeast Farallon Island from 17 June to 9 July 1969. Contradictions are more common—too much so for such a scholarly work. The Laysan Albatross, for example, is said to be most numerous off the California coast during "summer and fall" (p 144) and (correctly) "October through March" (p 38). The Cattle Egret is said (p 297) to have first nested in California in 1971; the species account gives the proper year, 1970.

The 341 closeup photographs of birds illustrate 304 species and all 65 California families. In such a profusely illustrated book I was amazed to find only one caption error—the Red-breasted Merganser (p 55) is not a female. Many of the 37 habitat photographs were so carefully executed that I had to look carefully to be sure they were not of museum dioramas! Although many of the bird photographs are quite small, the bird images are large enough that size detracts only in relation to "what might have been." The appreciable amount of blank space adjacent to the photos is attractive and adds a certain degree of sumptuousness. but I wonder if a tighter design might have produced financial savings that could have been used for higher quality reproduction. Despite these drawbacks, the photographs are pleasurable to view and are especially so because most were taken away from nests; Mr. Small must be an accomplished stalker.

The discussion of avian habitats (Chapter 4), by virtue of its completeness. is the most useful, interesting, and novel section of the book. Each of the 25 or so bird habitats is clearly described in relation to the dominant vegetation, physiography, geographic limits. climate. avian components. and effects of man. The mention of many specific birding localities makes this section a general but helpful bird-finding guide.

Because many species have been added to the state list since 1944, this book becomes the most complete and convenient source of information on rarities. The accounts of the commoner species are too brief and inaccurate for the ornithologist or ardent birder but will be of interest to others. Beginning birders or those unfamiliar with the state will find the discussions of birding and habitats very enlightening. But those who hoped for a thorough and up-to-date monograph of bird distribution in California will have to wait.—Laurence C. Binford.

THE OWLS OF NORTH AMERICA. Paintings and drawings by Karl E. Karalus, text by Allan W. Eckert. Doubleday, Garden City, N.Y., 1973: 9 × 12½ in. (boxed), xxii + 279 pp., 59 col. pls., 54 drawings, 59 range maps. $50.00.—Many behaviorally and/or morphologically distinct groups of birds have been immortalized by pen and brush. Although North American owls fit both categories, this is the first work addressed solely to them in which "all the species and subspecies . . . (are) . . . illustrated in color and fully described." With the authors' objectives thus stated, I will attempt to evaluate whether this work justifies their claim.

The overall design of this book is excellent. It is printed on high quality paper, color plates are vivid, binding and cover are sturdy, and the book has an attractive slipcase. The text is divided into 5 sections: introduction, natural history descriptions, comparison tables, glossary, and bibliography. The color plates are conveniently grouped in 4's; each cluster usually separated by 15 pages of text. Most of the drawings are located adjacent to that portion of the text to which they relate.

The introduction explains the format used in species descriptions and the type of material handled under the various headings. Although short, the introduction is an admirable Methods section and will greatly aid those readers unfamiliar with such matters as wing length, molt, sexual dimorphism, and topography.

The main body of the text includes descriptions of each owl species and subspecies found north of Mexico. The section dealing with each species begins with the bird's classification according to the A.O.U. sequence of order, family, subfamily (where relevant), genus, specific, and subspecific names. The natural history description for each species is based on the best known subspecies. All other subspecific descriptions present material "only insofar as they differ from the representative subspecies." Each description is divided into sections giving scientific name and original description; other names; and distinguishing physical, ecological, and behavioral features; young and family life characteristics; distribution in North America; migration; and economic influence. Following the main text 15 comparison tables summarize the species size relative to all other species. The glossary defines some 150 terms, many of them related to owl topography. The text ends with a bibliography of about 280 titles, followed by an index.

The paintings by Mr. Karalus are impressive. Not only are they beautiful, but it is obvious Mr. Karalus has spent considerable time observing his subjects. Plates VI and VII show *Strix occidentalis* in a crouched position, which is characteristic of some owls, but not often noted by owl-watchers. Most owls tend to look cuddly, whereas a real-life *Glaucidium gnoma* appears sinister; Plates XLV and XLVI capture this inherent ferocity. Although *most* of the paintings accurately depict subspecific variation, this is sometimes difficult to perceive due to the variation in scale and body position illustrated in the plates. Two somewhat common artistic errors (or liberties) are present in a few plates. Beak size and the amount visible appears excessive. Also the artist has incorporated components from both dorsal and lateral aspects into paintings with a predominantly lateral orientation (*Surnia ulula*, Plate XLI). Such a position seems improbable, even for a neck-swivelling owl. The *Otus trichopsis* figured in Plates XXXIII and XXXIV appear ill; I have yet to see an *O. trichopsis* painting that is an accurate representation of this bird. The white of the feathers in my copy seems dull or tainted. This, I hope, is a publishing error and not a fault of the original plates. On the whole, this is the finest collection of North American owl paintings to be found in any one work.

The text is pretentious, imprecise, inaccurate, and unscientific. I will labor at some length to illustrate my point, because, due to the (apparent) scientific organization and comprehensive nature of this book, someone may mistake it as an authoritative treatise.

A list of some indicative errors follows. The American Ornithologists' Union is referred to as the "American Ornithological Union." "Owls have two fovea for simultaneous focus at objects near and far"; owls possess only one fovea and are unique in that it is temporally located, also fovea is not plural. There is a "comblike organ in the back of the eye which acutely sharpens perception"; there is presently no factual basis to support such a conclusion with regard to the pecten. In topography sketch #3 of the introduction one finds "cere (nostrils)"; the cere is the fleshy unfeathered skin at the base of the upper mandible. In the topography sketch #2 of the Introduction one also finds "culmen (upper mandible)"; the culmen is the mid-dorsal ridge of the upper mandible. Throughout the text specific names (e.g., *alba*, *asio*, *cunicularia*) are referred to as "species" names; proper taxonomy stipulates the species name is a binomial consisting of both genus and specific names. In the drawing of an *Otus asio* skeleton (p. 101) the labeling of the radius and ulna is reversed. The wings of *Speotyto cunicularia* "are long and narrow and certainly reminiscent of the wings of a sparrow hawk"; this most certainly is not a common attitude of *S. cunicularia* wings. As a final example, the glossary defines a species as "a group of subspecies (or a distinct single race) with like characteristics among one another, but dissimilar in certain characteristics to others of the same Genus"; need any comment be made!?

The failure of the authors to comprehend the biological meaning of species and subspecies has resulted in an inaccurate text which will greatly confuse the literature. This is well illustrated with regard to *O. trichopsis*. The text delineates 2 subspecies of *O. trichopsis*, "*O. t. trichopsis*" and "*O. t. asperus*." The *trichopsis* race is said to reside most commonly at an altitude of 5500–6500 feet, whereas "*asperus*" resides only within a few hundred feet of the 7000 foot zone. "*Asperus*" can be distinguished from *trichopsis* by its "darker gray" color and bolder "streaking of both back and breast." The distribution of both races illustrated and discussed on p 154–155 indicates they are almost totally sympatric.

J. T. Marshall, Jr. in his analysis of North and Middle American Screech Owls (Western Found. Vert. Zool. Monogr. No. 1, 1967) makes no mention of altitudinal segregation between the *trichopsis* and *aspersus* races. He concludes that *trichopsis* is darker ("blackish") with broad, coarse crossbars and *trichopsis* and *aspersus* are totally allopatric. The A.O.U. checklist (1957) recognizes only *O. t. trichopsis*. Thus there are a number of incongruities among this book, the A.O.U., and J. T. Marshall, Jr. The authors have misspelled *aspersus* ("asperus"), reversed the distinguishing characters of darkness of color and width of feather bars and listed 2 allopatric races as sympatric, but altitudinally segregated. It is difficult to comprehend how things got so turned around when the authors were only reviewing existing data. The entire text is written with this belief that subspecies are discrete morphological units which can and do exist in sympatry.

In a more general vein, the text ignores much information readily available in the literature. Possibly the weakest section deals with *Micrathene whitneyi*. Under "young and family" Eckert professes "disappointingly little is known about the nest life of this dainty little owl." Of "courtship and mating" he concludes the data "are still largely wanting." The writer has neglected Ligon's comprehensive monograph "The Biology of the Elf Owl, *Micrathene whitneyi*" (Univ. Mich. Zool. Misc. Publ. 136, 1968). Many statements on "Ears and Hearing" are supported only by the author's observations on ear asymmetry and by *field experiments* such as breaking twigs and squealing. This methodology leads to conclusions such as hearing "is . . . more useful than vision" (*G. gnoma*), "hearing is the primary means of prey location" (*O. trichopsis*), and "the auditory sense is acute . . . a great deal of prey is located through the rustling of grass" (*S. cunicularia*). Although most owls do have excellent sound perception, there is little justification for such pronouncements. The important work of Payne (Living Bird 1:151–159, 1962) concerning owl hearing is not cited. In the section on *S. cunicularia*, Eckert asserts that "there are numerous strong superstitions and many more erroneous beliefs in regard to the Burrowing Owl." Most of his discussion does nothing to refute the superstitions or correct the errors; rather it propagates many. The range maps of subspecies do not include the total species' range (unless representing a monotypic species). These maps would have been more informative if all the subspecific distributions of each species had been incorporated into a full page composite or, at least, if each subspecies distribution had been delineated within the species' range. As is, it is difficult to appreciate the geographic relationships among subspecies. It is also disappointing to note that the text rarely mentions any of the strigiform physiological data published within the past decade.

A major failing is the lack of in-text citations except for one footnote crediting someone else's work and one in-text reference to A. C. Bent. The authors' justification for this omission is to "keep the text itself reasonably free of material which is chiefly extraneous or incidental." In a comprehensive work such as this where most of the information has not been gathered first-hand by the author, citations are important and mandatory. Without them, the text has little credence. The lack of citations also reduces the usefulness of the bibliography.

The bibliography is a sorrowful mess! A foreword presents the disturbing news that "often certain books, papers, theses . . . provided only a single minor datum which was incorporated into this volume; to list these . . . would be virtually pointless." The bibliographic style is not a standard form i.e., "Baldwin, S. P. VARIATIONS IN BIRD WEIGHTS (with S. Charles Kendeigh), *The Auk*, Vol. 55, 1938, pp. 416–17." Under the K's one will find the same publication listed, but now Baldwin's name is in parentheses. At least 36 such cases of cross-referencing occur. Yet, in at least 8 other works of multiple authorship, one author has not been cross-referenced. A rather amusing set of errors is that J. David Ligon (approx. age 34) is credited with a 1926 publication by J. Stokley Ligon yet he (J.D.L.) is not cited for his own work on *M. whitneyi*. A more useful arrangement of the bibliography would have been to list each owl species and then cite contributing publications. There are other errors in this bibliography.

I could continue with comments about the lack of listing catalog numbers and museum locations for the owl specimens measured; that much information contained in some of the works cited in the bibliography is not incorporated into the text; that I suspect the bibliography was compiled by a company specializing in such matters. In short, many other ills could have been singled out for attention, but I hope my opinion is clear—regardless of price, this book *isn't* worth it. The paintings are superb and Karl E. Karalus does establish himself as an excellent wildlife artist; but the text by Allan W. Eckert is a poor imitation of A. C. Bent's "Life Histories of North American Birds of Prey, Part 2." If procured, this book can add only to one's coffee table.—DENNIS J. MARTIN.

THE BOOK OF OWLS. By Lewis Wayne Walker. Alfred A. Knopf, Inc., New York. 1974: xiii + 255 pp., 96 black-and-white photos, one figure. $12.50.—Lewis Wayne Walker was a naturalist, ornithologist, conservationist (long before it was fashionable), and inveterate owl watcher. His death in 1971 was untimely not only because the scientific and lay communities lost an excellent talent, but because his legacy to owl investigators, this book, apparently was not yet complete. The book consists of 14 chapters, each of the first 13 discussing one owl species. These chapters begin with a general natural history discussion, including anecdotes of Walker's experiences with the species, and end with brief accounts of the species' measurements, vocalizations, nesting and feeding habits, and activity pattern. The last chapter is a "potpourri of facts" which does much to dispel many misconceptions surrounding owls. Throughout the text Walker emphasizes benefits accruing to mankind from owls' dietary preference for rodents. His presentation supports the belief that rarely are species which man considers aesthetically or economically valuable eaten by owls. Although there is no bibliography many comprehensive works concerning owls are mentioned in the text.

I feel that if Walker had survived until the completion of this book it would have been, as the jacket proclaims, "an authoritative guide to all major species of North American Owls." As it is this work totally neglects the Barred, Whiskered, and Ferruginous owls. A discussion of the Barred Owl was excluded because of its close relationship to the Spotted Owl, which is discussed. Although these species are closely related, their natural histories are sufficiently distinct to warrant separate discussions.

Some confusion arises from the omission of scientific names from the text. The "Screech Owls" chapter appears to consider only *Otus asio*, but one lonely paragraph on *O. flammeolus* is injected near the end. The chapter "Horned Owls" causes pause to contemplate whether one is speaking of horned (eared) owls in general or, as is the case, the Great Horned Owl specifically. These minor problems are more of style than content. What is disturbing is that much of the text either has not been written by Walker (i.e., Pygmy, Spotted, and Great Gray owls) or nearly all the substantive material was gleaned from the works of others (i.e., Snowy and Hawk owls).

The book's photographic content and the vividness of its reproductions are unmatched. Although all the photographs are black-and-white, they do adequate justice to their subjects, which are usually seen at night as black and white figures anyway. Of particular interest for their content are the photos of the protective posture of the Screech Owl (p 24) and the female and young Burrowing Owls in their burrow (p 121 & 123). The beauty of the photos of the juvenile Barn Owl (p 8) and the Spotted Owl (p 128) are indicative of Walker's artistic excellence with a camera. Some apparent off-set toning problems occurred during the printing of my copy, resulting in black smudges on many text pages. Fortunately this problem did not affect the half-tones.

The strength of this book lies not only in its information content, but in the naturalist-man, Lewis Wayne Walker, and the mystique of the owls he loved. For those who wish to understand why birds so fascinate man, need to re-kindle their investigative fires, or simply want to learn more about owls, this book is a fine investment.—DENNIS J. MARTIN.

WHERE TO FIND BIRDS IN WESTERN PENNSYLVANIA. By David B. Freeland (ed.). Audubon Society of Western Pennsylvania, Pittsburgh, 1975: 61 pp., 25 maps. Paper cover. $2.75. Order from Paul M. Wick, 24 Woodland Rd., Sewickley, PA 15143.—This useful guide contains detailed maps and instructions for finding birds in 23 areas of Western Pennsylvania. Each area is described by an experienced observer from the Audubon Society of Western Pennsylvania.—R.J.R.

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THE WILSON BULLETIN

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SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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Male Great Blue Heron at peak of Stretch.

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PAIR-FORMATION DISPLAYS OF THE GREAT BLUE HERON

Douglas W. Mock

The Great Blue Heron (*Ardea herodias*) offers many advantages for the study of communication. It is large-bodied, conspicuous, fairly slow-moving, and geographically widespread across North America. Like many other herons it is rather solitary in habits through much of the year so its social behavior is concentrated into the breeding season. At that time herons aggregate in large nesting colonies where, with due caution, they can be observed at close range. Despite these advantages the published literature on Great Blue Heron social behavior consists of only 3 general accounts (Cottrille and Cottrille 1958, Meyerriecks 1960, Meyerriecks 1962). By contrast, the Old World Grey Heron, *A. cinerea*, has been extensively studied (Huxley 1924, Selous 1927, Holstein 1927, Verwey 1930, Strijbos 1935, Percy 1951, Lowe 1954, Owen 1959, Baerends and Baerends-van Roon 1960, Baerends and van der Cingel 1962, Hudson 1965, Milstein et al. 1970). This paper presents descriptions and illustrations of the social signals used by Great Blue Herons in the colony, including 6 displays previously undescribed for this species.

MATERIALS AND METHODS

Great Blue Heron reproductive behavior was studied for 2 breeding seasons in Minnesota and 2 breeding seasons in Texas. In 1970 and 1971 a 15-m scaffolding tower-blind was erected in a treetop heronry near Lino Lakes, Anoka Co., Minnesota (Lat. 45°10′N., Long. 93°10′W.). Daily observations were made through fledging for periods of up to 10 hours. Long-term observations were made in a colony on Hog Island, Redfish Bay, Aransas Co., Texas (Lat. 27°50′N., Long. 97°00′W.), in 1973 and 1975. The Texas herons built their nests on 1–3 m saltcedars (*Tamarix* spp.). A small shed (about 2m × 2.5m × 2m) was constructed in the center of the horseshoe-shaped colony with heron nests 10–15 m away on 3 sides. I lived totally inside this blind for 2–4 days at a time without disturbing the birds.

Observations of the nearest individuals and pairs were normally made through a camera with an 8× telephoto lens. Written and dictated notes were augmented by several thousand still photographs plus approximately 300 m of super-8 movie film.

Both members of about 8 pairs (per season) were individually recognizable by facial plumage idiosyncracies (especially the irregular dark spots and smudge patterns on the anterior of the white forehead). These birds were scrutinized with a 60× spotting scope and sketched in an identification notebook. No artificial markings were needed. Sexes were identified on the basis of copulation position with the male assumed to take the top position (in pairs where several copulations were observed no reversals of position occurred).

In addition to qualitative descriptions, 30 hours of behavior sequences by Texas herons were dictated into a tape recorder and later plotted onto "timeline" sheets. The empirical data in this paper were derived from that sample. Temporal analyses of display function, made from these sequences, will be published elsewhere.

In this paper each signal will be treated separately in the following format: name, list of synonyms used by previous authors, description of a "typical" performance, observed variations, social contexts, and discussion. The discussion includes display design (sensory channels and morphological features that enhance transmission), "messages" (in the message-meaning system of Smith 1968: inferred primarily from contexts), evolutionary derivation from nonsignal motor patterns, and probable homologies in other species. Throughout the paper I use the term "homology" in the evolutionary sense, implying that the behavior was present in the common ancestor of the related species in which it is found today. Display terminology generally follows Meyerriecks (1960) except in the few cases where his names implied function or motivation (e.g., "Aggressive Upright" was renamed "Arched Neck"). Display names have been capitalized to distinguish them from non-social motor patterns (Moynihan 1955).

Breeding cycle chronology.—The Great Blue Heron's breeding cycle is similar to that of other herons (e.g., *A. cinerea*: Verwey 1930, Lowe 1954, Milstein et al. 1970) and will only be summarized here. The following chronological stages are my own convention:

(1) *Solo male stage.* An unpaired male heron chooses a site, usually containing an old nest, and defends it against all conspecifics. Typically such a solo male has seasonally bright-colored legs, lores, and bill (Meyerriecks 1960:104), but this is variable. Both in Minnesota and Texas populations the legs turn reddish, the irides develop a slightly deeper yellow, and the lores become bright cobalt-blue (see frontispiece), not lime-green as illustrated in Palmer (1962:366). The solo male displays "spontaneously" to the colony at large with no particular signal-receivers attending him.

(2) *Bachelor male stage.* I classify a male as "bachelor" when he has attracted one or more "satellite" females to his vicinity. His displaying then becomes oriented slightly more toward the attending female who approaches him hesitantly. If more than 1 satellite is present (maximum observed was 8), they may threaten one another; but generally they position themselves 3–10 m from the male and stand or preen. When a satellite female gets close to the male he performs agonistic displays and attacks, driving her away repeatedly. The bachelor stage is clearly a period of mutual assessment for the sexes: the male can reject the female by continuing to attack and she can reject him simply by leaving.

(3) *Paired stage.* Eventually the courting male allows 1 female onto his nest. The new alliance is very tense and ritualized Bill Duels erupt frequently. As the male's attack tendency wanes (over a span of several hours), mutual Bill Clappering increases. Copulations can occur any time after the female is accepted on the nest and are repeated

irregularly until the eggs are laid. During the first few days, the paired female spends most of her time away from the colony, presumably feeding. The male stays at the nest and defends it. When the mates are together on the nest they may loaf, perform displays, or engage in cooperative nest building (the male usually collects sticks and passes them to the female who inserts them).

(4) *Incubation stage.* Once the first egg is laid, male-female displaying decreases sharply. Incubation commences after the first or second egg (producing an asynchronous hatch), lasts 25–29 days (Pratt 1970), and is shared by both sexes. The nonincubating mate is usually absent, presumably foraging.

(5) *Parental stage.* After the eggs hatch, 1 adult broods the young chicks while the other hunts. Thus the 2 parents rarely interact and then only during nest-reliefs. When the chicks reach the age of 3–4 weeks their food demands peak, forcing both parents to hunt full-time to provision them. The youngest chick often starves to death by the 4th week. The parents' pair bond may weaken or disintegrate entirely by the time of fledging and independence of the young.

SOCIAL SIGNALS

Stretch

(1) *Synonyms*: *Reckbewegung* (Verwey 1930), Howling (Cottrille and Cottrille 1958), Bitterning (Milstein et al. 1970).

(2) *Typical performance.*—From a resting position with all feathers relaxed, the heron smoothly lifts its head and swings the closed bill toward vertical. During this ascent the lower neck plumes are fully erected, the scapular and occipital plumes relaxed, the torso inclines, and the head twists slightly to one side (Fig. 1: frames 0–63). At the peak (see frontispiece) the heron begins a long, moan-like call that continues through most of the descent. The hyoid apparatus can be seen moving beneath the tightly stretched skin of the throat. Descent begins as the legs flex at the "heels," the wrists move out from the body (about 6 cm), and the shoulders lower. During the descent the heron sways to the opposite side (and sometimes back again), as it shifts its weight from leg to leg. Neither crest nor scapular plumes are erected during the entire performance.

The Stretch lasts about 6 sec from start (when the bill is first lifted from horizontal resting position: Fig. 1, frame 0) to finish (the moment when the bill leaves its vertical apex: Fig. 1, frame 140). Mean Stretch durations for 2 males were 6.1 sec (N = 21, range = 4.5–8.3, S.E. = 0.21) and 5.5 sec (N = 28, range = 4.8–8.6, S.E. = 0.71).

(3) *Variations.*—The Stretch is probably the most stereotyped of Great Blue Heron displays, but there is noticeable individual variation. Each heron appears to have a distinctive form for its Stretch, so consistent that I learned to recognize individuals by display-form alone. For example, 5 of the 1975 Hog Island males were characterized as follows:

Male 2 — very little sway, no leg flex at all, downward motion of the bill

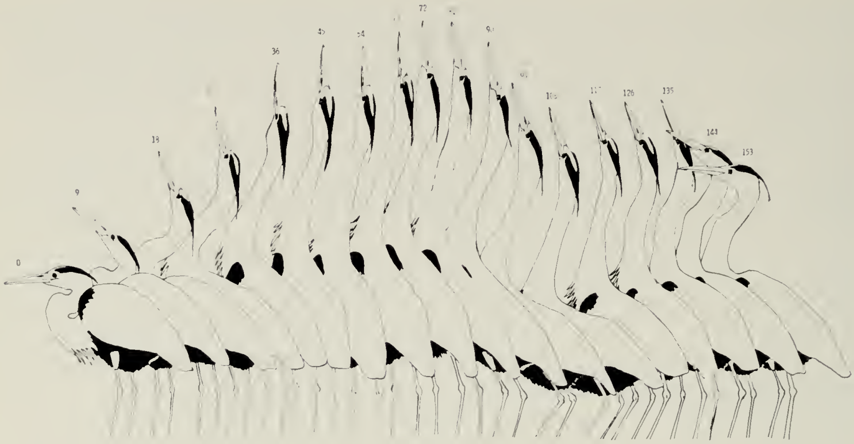

FIG. 1. Stop-action illustration of a complete Stretch. Each drawing was traced from movie film at 9-frame (½ sec) intervals. The vocalization began at frame 36; frontispiece position corresponds to frame 72. This individual does relatively little swaying or crouching in his Stretch.

only about 12 cm and due entirely to neck retraction, hyoid barely moves during call which is faint.

Male 15—all movements very stiff, no leg flex, body axis never dips below 25° above horizontal.

Male 16—at peak the bill passes vertical by 10–20° such that the heron is leaning over backwards slightly.

Male 18—choppy movements, performance ends suddenly after a very brief vocalization (sometimes no vocalization at all).

Male 20—unusually vertical body axis (never below 45°), legs flex deeply.

Components of the Stretch that show variation include: direction of the first lateral sway, amplitude of sway, angles of all axes (bill, torso, and legs), degree of neck-plume erection, speed and smoothness of performance, vocal characteristics (pitch, volume, duration, etc.), and degree of wing extension.

All herons, regardless of personal style, frequently give incomplete performances ("intention movements": Daanje 1950) of the Stretch. This usually consists of the bird raising its head as if beginning a full Stretch and then gently terminating the ascent after a second or 2 (to position of Fig. 1: frame 18). These intention movements are used in the same contexts as the full Stretch itself. They comprise 17% of the 850 Stretch performances in the timeline samples and become more common as the pairbond matures.

(4) *Contexts.*—The Stretch is performed in 4 distinct contexts, more than

any other Great Blue Heron display. It is the most common repertoire component of both solo and bachelor males. After pair-formation the Stretch is not discontinued as it is in many other heron species (e.g., Great Egret, *Casmerodius albus*: Wiese in press). It is given by a heron on the nest when its mate returns as part of the Nest Relief Ceremony and the Stick Transfer Ceremony. Finally, the Stretch is also used by the female when she has finished inserting one stick into the nest and is "sending" her mate off to collect another. Tomlinson (1974) briefly mentions the latter "sending off" context for the Stretch of the Purple Heron, *A. purpurea*, and Milstein et al. (1970) saw it 4 times in *A. cinerea*. It is in this "sending off" context that I most often saw the incomplete intention-to-Stretch functioning as a full Stretch. At first the male leaves the nest only after his mate does a full Stretch, but soon she begins abbreviating her performance. She repeats these intention-to-Stretch motions and mixes them with full performances until the male departs after the shortened version. Thus, the first phase of the Stretch display comes to replace the full performance as the mates get to know one another. Interestingly, in the Cattle Egret all female performances are abbreviated in form compared to the male's Stretch (Blaker 1969a: 86–87).

(5) *Discussion.*—The Stretch is the most conspicuous display in the Great Blue Heron repertoire. It also takes more time to perform than any other nonaerial display. The bright soft parts, especially the bill, are exhibited dramatically. The swaying motions are enhanced by the erection of the neck plumes. The wrists, normally tucked beneath a patch of black epaulet feathers, are held out revealing their chestnut lining. The accompanying vocalization calls attention to the visual effect and makes the display effective even at nightfall.

I believe that the Stretch encodes the messages of *identification* (probably individual), the *non-agonistic subset* ("I will not attack"), and the more general *bond-limited subset* in the message-meaning system of Smith (1969). In the solo male context the Stretch probably informs passing females of the male's availability for mating. During the bachelor stage it seems to be the invitation-to-approach that alternates with repelling attacks by the male. It is used in the paired stage in arrival situations when the mates are in close proximity to each other on the nest and attack tendencies are still high. In the fourth context, wherein the female apparently prescribes stick-collecting behavior for her mate, the message defies classification by Smith's scheme except in the loosely defined *bond-limited subset*. If this interpretation is correct, the signal probably facilitates cooperation between the mates in a shared task.

Various evolutionary origins of the Stretch have been suggested. Daanje

(1950) cited the Stretch of *A. cinerea* as a prime example of a ritualized intention movement (preflight take-off). Baerends and van der Cingel (1962) suggested that the display's form might be a mosaic of postural elements borrowed from conflicting drives to attack, flee, and settle-on-the-nest. In fact, herons show other motor patterns (e.g., the over-the-shoulder stick receiving posture of the female or certain active begging postures of nestlings) that bear as much physical similarity to the form of the Stretch as any published suggestion. Any of these hypotheses is plausible but, in my opinion, the origin of the Stretch is still an open question.

Homologous Stretch displays have been described for every member of the Ardeidae studied to date (see Blaker 1969a:87) except the Boat-billed Heron, *Cochlearius cochlearius* (Mock 1975a). Outside the family Ardeidae we should exercise great caution in suggesting Stretch homologies. Similar displays have been described for other members of the Ciconiiformes such as the White Stork, *C. ciconia* (Kahl 1972a), and the White Ibis, *Eudocimus albus* (Meyerriecks 1962). But equally similar-looking displays can be found in such unrelated taxa as penguins, albatrosses, gannets, ducks, gulls, terns, grackles, cowbirds, tits, and tanagers. Tinbergen (1959:62) notes that the abundance of bill-vertical postures in birds is surely complicated by convergence and he points out that there are a limited number of postures in which the primary weapon (bill) can be averted.

Snap

(1) *Synonyms*: *Schnappbewegung* (Verwey 1930), Bow-Snap (Milstein et al. 1970).

(2) *Typical performance.*—The plumes of the head, neck, breast, and back are erected as the head moves forward smoothly. When the neck is almost straight the heron suddenly flexes its legs at the "heels" and clacks its mandibles once loudly (Fig. 2).

(3) *Variations.*—The Snap is highly variable in form, involving neck angle, neck curvature, degree and distribution of feather erection, orientation of the display, leg flexion, twig-seizing, and lunging motions. The neck can be directed downward (as described above), upward, or anywhere in between. Low performances are by far the most common: of the 1352 Snaps in my timeline sample 72% had neck angles more than 20° below horizontal, 26% had neck angles between 20° below horizontal and 20° above, and only 2% had neck angles higher than 20° above horizontal.

Some of the higher Snaps resemble the Forward when they are performed without a vocalization (bill-clack only). Baerends and van der Cingel (1962) discriminated these 2 displays in *A. cinerea* on the basis of head orientation: high-neck performances facing conspecifics were considered Forwards, those

FIG. 2. Snap by Paired male as his mate watches (Hog Island, March 1973).

directed elsewhere were considered Snaps. This criterion generally fits my observations on *A. herodias* except that even low-neck Snaps are occasionally performed toward the receiver. The difference is probabilistic: Snaps *tend* to be done away while Forwards are always done toward the receiver. The importance of orientation is strongly suggested by performances that change in direction during mid-Snap. I have also seen males turn their necks to one side so as to Snap with the body facing the receiver but the head diverted by 30°. Baerends and van der Cingel's orientation criterion offers no clarification in the case of rare voiceless performances that are aimed at nobody but still bear components of the Forward (rocking lunge and wings held far from the body). Overall I believe that the Snap and Forward are separate displays which share several components but that intermediates do exist.

Another display that occasionally mixes components with the Snap is the Arched Neck. I have seen horizontal Snaps performed with a well-curved neck in both Minnesota and Texas. This variant seems to come in bursts: an individual may do a dozen curved Snaps and then discontinue it entirely.

Snaps commonly include the brief grasping and shaking of a twig on the nest's bush. This stifles the audible bill-clack and seems to intergrade with the form of yet another display, the Twig Shake. Usually Snaps that include twig-grasping are done much more gently and seem to follow bouts of stick manipulation. Meyerriecks (1960:99) also described a variant he termed the Low Bow which I have seen in neither Minnesota nor Texas.

Individualistic variations are not so marked in the Snap as in the Stretch though certain individuals seem to prefer low Snaps and others perform with little or no leg flexing. A sample of 75 Snaps by one Texas male showed that 68% of his performances were accompanied by strongly bent legs, 22% by moderately bent legs, and 10% by straight legs. In plumage 86% had full head and neck erection, 10% had moderate erection, and 4% had no erection at all.

(4) *Contexts.*—The Snap is a major part of the male's display repertoire during the solo and bachelor stages. After pair-formation it decreases quickly and is nearly absent by the time of egg-laying. Neither the form nor frequency of the Snap changes noticeably between the solo and bachelor stages.

Females perform Snaps too, but much less often than males. My timeline samples show 415 Snaps during the bachelor stage, of which 97% were performed by males; during the paired stage males performed 83% of the 291 total Snaps. This agrees with the data for *A. cinerea*: of 1977 Snaps, males did 96% (Baerends and van der Cingel 1962). Meyerriecks (1960:99) thought that *only* male Great Blue Herons did Snaps but he was not studying recognizable individuals. Snaps of males and females are very similar in form but females seem to prefer the horizontal neck angle, less leg flexion, and may be a little slower in overall performance.

(5) *Discussion.*—If a full spectrum of Snap variations were plotted, ranging from twig-grasping performances (resembling unritualized nest-building) on

one end and upward performances (resembling voiceless Forwards) on the other, the frequency distribution would be strongly unimodal at the "typical" low-necked Snap described above. But the atypical performances raise the possibility that the variability is conveying additional information. Because the variability is present in a continuum (with all intermediates) it can be considered "graded" in form.

The overall function of the Snap is difficult to assess. It is used in all contexts of courtship, with or without females attending, suggesting that it is a general advertisement, perhaps analogous to the territorial song of male passerines: it probably attracts unmated females and repels males. Approaching satellite females show little or no overt response to a male's Snap.

The Snap is thought to have evolved from fish-seizing (Verwey 1930), twig-grasping during nest-building (Meyerriecks 1960), or as "the direct result of the instincts activated" (namely ". . . to attack, to flee, and to settle down . . . ," Baerends and van der Cingel 1962). I favor Meyerriecks' view that the Snap evolved from twig-grasping and has been ritualized to the point of ignoring the stick in most, but not all, performances. It is possible that the upward performances are functionally and evolutionarily distinct from the more typical low Snaps and should be considered as variants of the Forward.

Homologous displays have been reported for every heron studied except the night-herons (Voisin 1970, Nelson 1975, Mock 1975a) and the Cattle Egret (Blaker 1969a, Lancaster 1970).

Wing Preen

(1) *Synonyms*: Wing Touch (Blaker 1969a), *Lissage des Plumes* (Voisin 1970), Wing-stroke (Wiese in press).

(2) *Typical performance.*—The heron leans forward, moves 1 wing a few cm down and out from the body, then runs its bill smoothly along the leading edge of the primaries (Fig. 3). This stropping motion is often repeated a second time before the heron resumes a standing position. The entire performance takes 2–4 sec. When doing Wing Preens herons usually orient themselves broadside to the signal receiver (80% of 142 performances in a sample); from that position they tend to choose the wing closest to the receiver (68% of the 113 broadside performances)—both these tendencies are statistically significant (χ^2 test, $P < .001$).

(3) *Variations.*—Wing Preens vary in stroke number, stroke placement, stroke length, and spatial orientation relative to the receiver. Usually there is either 1 stroke (55% of 620 Wing Preens in sample) or 2 strokes (40%), but performances of 3 or 4 strokes occur also (< 5% combined). While stroke number does not change significantly through the chronological stages

TABLE 1

INDIVIDUAL DIFFERENCES IN NUMBER OF WING PREEN STROKES FOR 4 MALE GREAT BLUE HERONS (HOG ISLAND, 1975)

Male	1-stroke	2-strokes	N
A	18%	66%	38
B	66%	32%	111
C	76%	24%	37
D	81%	19%	43

of pair-formation, certain individuals do show preferences for single-stroke and others for double-stroke Wing Preens (Table 1).

The tip of the bill, though typically passing along the wing's leading edge, sometimes runs several cm above that or even among the primary coverts. Occasionally it is even performed without touching the wing at all, merely sweeping parallel to the edge. Sometimes the bill chews at feathers during the display and may even pause while nibbling. Incomplete strokes are also quite frequent.

(4) *Contexts.*—The Wing Preen is a basic component of the male display repertoire throughout pair-formation. It is also performed by females but much less frequently: of the 513 Wing Preens sampled when both sexes were present (bachelor and paired stages), only 123 (24%) were done by females. Generally, Wing Preens can occur at any time that the male is displaying on his nest. It is one of the "spontaneous" displays used throughout pair-formation.

(5) *Discussion.*—As far as I know the ritualized Wing Preen has never been described before for an *Ardea* species. The oversight of previous workers can be readily understood in light of the similarity between this display and the normal preening motions from which it doubtlessly evolved. Once aware of it, however, I had no trouble distinguishing it: the heron always holds its wing the same way, preens it 1 or 2 strokes, and sometimes actually fails to touch it at all.

Once the Cattle Egret's Wing Preen was first described by Blaker (1969a) it has been found in many other species including: Great Egret (Wiese in press), Louisiana Heron (*Hydranassa tricolor*: Rodgers in press), Little Egret (*Egretta garzetta*: Blaker 1969b), Yellow-billed Egret (*E. intermedia*: Blaker 1969b), Snowy Egret (*E. thula*: pers. obs.), Little Blue Heron (*Florida caerulea*: pers. obs.), Black-crowned Night Heron (*Nycticorax nycticorax*: Voisin 1970, Nelson 1975), and possibly Boat-billed Heron (Mock 1975a). Somewhat similar displays also occur in the storks: Kahl (1972b) described Display Preening in the tribe Mycteriini.

FIG. 3. Wing Preen: male runs his bill-tip along the leading edge of his wing as his mate ignores him (Hog Island, March 1973).

The function of the Wing Preen is hard to assess. Its performance by courting unpaired males, approaching females, and members of newly-formed pairs suggests that it plays a role in pairbond formation but specific responses to the display's performance are not readily observable. The posture of the display, especially the directing of the bill toward the sender's own body, suggests Smith's (1969) *non-agonistic subset* ("I will not attack") which I suspect to be one of its messages.

Circle Flight

(1) *Synonyms*: circling nuptial flight (Selous 1927), Courtship Flight (Milstein et al. 1970).

(2) *Typical performance.*—Instead of retracting its neck against the shoulders as in normal flight, the heron keeps its neck fully extended throughout (Fig. 4) as it flies in a large (usually 50–75 m diameter) circle, ending back near its origin. The wingbeats are slightly slower and deeper than normal, producing an audible "whomp" with each stroke. The Circle Flight requires more time than any other display. Ten male performances ranged from 15–30 sec ($\bar{x} = 22.2$) and 8 female performances ranged from 16–50 sec ($\bar{x} = 28.1$).

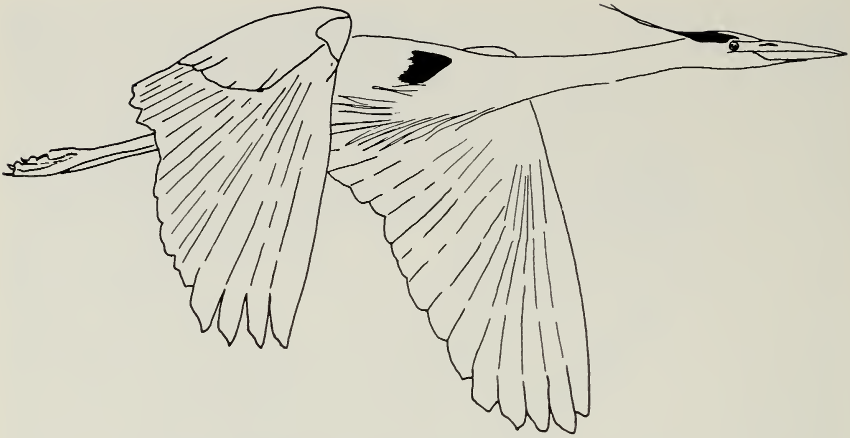

FIG. 4. Straight-necked flying position of the Circle Flight.

(3) *Variations.*—The Circle Flight is extremely variable in shape of flight-path, size of the circle flown, duration, and details of landing. Some flights have 2 laps instead of 1, some have a figure-8 pattern, and one was observed in which a male carried a stick in his bill. Wind conditions and heron traffic over the colony probably affect many flights.

One newly-paired male completed a Circle Flight by landing on his mate's back where he unsuccessfully attempted to copulate (she resisted by pecking at him). Female Cattle Egrets use the Circle Flight as a mounting tactic to subdue courting males (Lancaster 1970).

(4) *Contexts.*—In general, the Circle Flight is uncommon for either sex. Unpaired males normally use their nest-territory for both takeoff and landing but they occasionally use Circle Flights to move to an alternate display site (e.g., a vacant nearby nest). Satellite females tend to land closer to the courting male each time they do a Circle Flight: it serves as an approach technique. The final move onto the male's nest is sometimes achieved via a Circle Flight. During the first days of the pairbond, both sexes continue to perform infrequent Circle Flights.

On certain mornings Circle Flights are unusually frequent for the colony as a whole. This may be due to a form of display imitation ("social facilitation") or it may simply indicate that extrinsic conditions, especially wind, are especially suitable for aerial displaying.

(5) *Discussion.*—The Circle Flight has not been previously described for the Great Blue Heron though Meyerriecks (1960:102) suspected its existence. It has been noted in *A. cinerea* (Selous 1927, Verwey 1930,

Milstein et al. 1970), Great Egret (Wiese in press), Louisiana Heron (Rodgers in press), Snowy Egret, Reddish Egret (*Dichromonassa rufescens*), Green Heron (*Butorides virescens*) (Meyerriecks 1960), Cattle Egret (Blaker 1969a, Lancaster 1970), Little Egret and Yellow-billed Egret (Blaker 1969b). Meyerriecks noted that the small-bodied herons tended to perform more aerial displays than large-bodied herons. The infrequency of Great Blue Heron Circle Flights supports this idea: it comprises only 11% of the satellite female's meager display repertoire, 0.4% of the male's bachelor repertoire, and even less after pair-formation.

The functions of the Circle Flight seem to change in the different contexts. For solo and bachelor males it probably conveys the messages of *identification* and *locomotion* (Smith 1969). Like the other heron advertisement displays I suspect that the identification message provides quite detailed information on sex, species, and general vigor of the sender. Satellite females presumably use this information in deciding which males to approach. Circle Flights by satellite females, while giving that same kind of information to the males, also bring them physically closer to the nest. The fact that it is used in this manner suggests that the Circle Flight also carries an appeasement message (Smith's *non-agonistic subset*). Within the context of the new pairbond the Circle Flight may acquire a social-cohesion message (*bond-limited subset*: Smith 1969).

Landing Call

(1) *Synonyms*: Greeting call (Cottrille and Cottrille 1958), Alighting Display (North 1963, Milstein et al. 1970), Rick-rack (Blaker 1969a), Greeting Display (Rodgers in press).

(2) *Typical performance.*—When landing at its nest the heron fully extends its neck, erects its crest, and emits a series of low-pitched croaking notes. The call usually begins when the bird is braking about 10 m from the nest, and continues at 1-sec intervals until it lands.

(3) *Variations.*—The structural qualities of the Landing Call have not been recorded and studied in detail but I have the impression that there are considerable differences in pitch and tone and that these differences may be individualistic. Some notes are monosyllabic ("rok-rok-rok . . .") but most are di-syllabic ("arre-arre-arre . . .").

(4) *Contexts.*—Great Blue Herons use the Landing Call almost every time they land on the nest throughout the breeding season, especially if a mate is already present. Parents give it as they return to the nest to feed their chicks.

(5) *Discussion.*—The Landing Call has been described only as a part of the complex Greeting Ceremony and never as a complete display in itself. I

treat it as such because it includes a vocalization, it has a crest-raising component, and it occurs in social contexts.

I believe that the Landing Call provides information on individual recognition and announces the heron's arrival: Smith's (1969) messages of *identification* and *locomotion.* Mate-recognition is even possible to observe in the colony because non-mates who make the error of landing at the wrong nest are immediately attacked and driven away. I believe that Great Blue Herons can distinguish their mates at distances of at least 100 m: I have watched incubating herons rise suddenly, turn, and stare at an approaching mate long before it could have received an acoustic signal. It seems, therefore, that members of a mated pair are attuned to very subtle differences in flying motions. At closer distances the Landing Call serves to get the mate's attention if it has not been watching in the right direction. This recognition system is presumably important for a large, potentially dangerous bird like a heron that must coexist with its mate on a restricted nest site (see Nelson 1967 and 1971). The vegetation structure and spacing of nests usually obviates the simpler option of landing first, getting the mate's attention, and then proceeding to the nest. Similar vocal recognition has been demonstrated with play-back experiments for the colonial Northern Gannet (*Sula bassana*) which also nests in crowded colonies (White 1971, White et al. 1970).

Highly ritualized landing displays are present in other ardeid species such as Great Egret (Wiese in press), Snowy Egret (pers. obs.), Louisiana Heron (Rodgers in press), and Boat-billed Heron (Mock 1975a). Some of these are similar to the Great Blue Heron's Landing Call and may be homologous.

Twig Shake

(1) *Synonyms*: Twig Quivering (Baerends and van der Cingel 1962).

(2) *Typical performance.*—The heron extends its neck slowly, grasps a branch in its mandibles, and shakes it side-to-side or forwards-and-backwards. There are no accompanying vocalizations as found in the Twig Shake of the Cattle Egret (Blaker 1969a).

(3) *Variations.*—Many aspects of the Twig Shake show variability, including vigor of performance, orientation relative to the receiver, duration, neck angle, feather erection, grip, and choice of the twig. Usually the twig is part of the tree supporting the nest (in only 5% of 291 cases was the nest itself involved) and it is usually too thick or flexible to be broken off and added to the nest. Similar "tremble-shoving" movements, used when inserting a stick into the nest, are much gentler and longer in duration than the Twig Shake, which normally lasts only 1–3 sec.

As in the Snap, the neck angle in the Twig Shake can range from about 60° above to 60° below horizontal. Unlike the Cattle Egret (Blaker 1969a) the vast majority of Great Blue Heron Twig Shakes (95% of 291) are below horizontal.

The most conspicuous variability in the Twig Shake is in overall vigor of performance. Speed and amplitude range from gentle trembling to wild thrashing that can even cause the heron to lose its balance. This latter type of Twig Shake (collectively called *vigorous*) tends to replace the non-vigorous performances in social contexts (e.g., when a female approaches a displaying male). Thus the *vigorous* form accounted for only 32% of all solo male Twig Shakes (N = 114) but increased to 50% during the bachelor stage (N = 100) and 57% during the paired stage (N = 77).

Other variants of the Twig Shake include performances in which the stick is nibbled on (resembling the mandibulations of Bill Clappering). As mentioned earlier, a few very low performances intergrade with variants of the Snap and are virtually impossible to assign to either category.

(4) *Contexts.*—The Twig Shake is most commonly performed by the male: of 191 Twig Shakes recorded with both sexes present only 7% were done by females. The display is often given "spontaneously" by solo males (non-vigorous form) but increases in frequency when the male is being approached by a satellite female and when both sexes are first co-occupying the nest. At these times the male seems very nervous and excited and *vigorous* Twig Shakes predominate.

(5) *Discussion.*—The Twig Shake is not highly ritualized but I believe that it should be considered a display because the sticks involved are almost always inappropriate for nest-building purposes. The variability found in the Twig Shake's form may enable it to carry a large amount of "graded" information: because the *vigorous* forms appear under different social contexts from the non-vigorous forms, different information is probably being conveyed. *Vigorous* performances may well express redirected aggression.

The Twig Shake presumably evolved from nest-building motor patterns which it still resembles. It is probably homologous with the little-ritualized Twig Shakes of the Cattle Egret (Blaker 1969a, Lancaster 1970) and Boat-billed Heron (Mock 1975a) and may represent the primitive condition from which more highly ritualized displays evolved in the Great Egret (Bow: Wiese in press) and Black-crowned Night Heron (Twig Ceremony: Noble et al. 1938).

Crest Raising

(1) *Synonyms*: None.

(2) *Typical performance.*—The heron erects its black and white occipital plumes to a variable degree for a few seconds and relaxes. Displaying herons usually turn toward the stimulus that elicited the performance.

(3) *Variations.*—The form of Crest Raising varies continuously ("graded" in form) with respect to angle of erection, duration, orientation, and even the feathers raised. As Blaker (1969a) noted for the Cattle Egret, the anterior and posterior portions of the Great Blue Heron's crest can be erected independently.

(4) *Contexts.*—Crest Raising is both a signal performed by itself and one that is incorporated into other displays. Great Blue Heron displays which include a Crest Raising component are: Snap, Landing Call, Arched Neck, Forward, Supplant, Bill Duel, *Hard* Contact Bill Clappering, and *vigorous* Twig Shakes.

By itself, Crest Raising is performed by both sexes throughout the breeding season and is also used outside the colony on the foraging areas. Solo males seem nervous when they first claim a nest; they show Crest Raising in response to many stimuli (passing conspecifics, sudden noises, etc.). The display is most frequently used later, as a short-range signal between the sexes during pair-formation. At that time females perform Crest Raising about twice as often as males: they are reacting not only to their prospective mates but also to the same stimuli that elicited Crest Raising in solo males. New mates seem very nervous and commonly perform Crest Raising as a response to each other's movements. Female Crest Raising, when accompanied by head-elevation, quickly triggers male Bill Duel attacks at this time (see p. 210).

Great Blue Heron nestlings can perform Crest Raising by the age of 2 weeks (pin feathers of the head are about 1 cm long). They show it in response to a wide array of nest disturbances (e.g., parent landing on the rim) and as a component of the Forward.

(5) *Discussion.*—The optical effect of Crest Raising by adult Great Blue Herons is greatly enhanced by the contrast of a 2-tone crest. From the front a white-on-black pattern is produced when the full crest is erected and a white-only signal when the anterior portion is raised by itself. Accurate measurement of the possible message differences between these 2 signals was not attempted in this study. If Crest Raising *does* carry graded information its role as a component of 8 other Great Blue Heron displays should be re-evaluated. Conceivably it could modify all those messages and thereby greatly enrich the entire communication repertoire.

Crest Raising has been described, either as a separate display or as a component of other displays, in every ardeid species studied to date. It even occurs in the Great Egret which lacks specialized occipital plumes (pers. obs.).

All feather erection signals probably evolved initially from autonomic

Fig. 5. Female assumes Fluffed Neck as her mate brings a stick to the nest (Hog Island, March 1973).

responses promoting convection cooling (Morris 1956). Any visible autonomic response that reliably precedes (and therefore predicts) exertion can be selected for its communication function (Andrew 1972:194). In the case of feather erection the resulting increase in apparent body size presumably also contributed toward its evolution as a threat signal (Darwin 1872, Meyerriecks 1960).

Fluffed Neck

(1) *Synonyms*: Stiff-necked Upright Display and Aggressive Upright Display (Meyerriecks 1960), Erect Stance (Wiese in press), Aggressive pose (North 1963: fig. 5), and Upright (Rodgers in press).

(2) *Typical performance.*—The heron elevates its head to about ¾ maximum height and erects all the neck feathers to an extreme degree. The bill is usually open about 2 cm at the tip (some performances include a soft vocalization) and is either horizontal or slightly inclined (Fig. 5). The head may be drawn back slightly. The unique features of the Fluffed Neck are the horizontal angle of the bill and the extreme feather erection that encompasses the entire neck, not just the basal plumes as in most other displays.

(3) *Variations.*—The Fluffed Neck shows variability in the degree of vertical neck extension, the angle between the neck and bill, the erection of the occipital crest, and the vocalization.

(4) *Contexts.*—Great Blue Herons perform Fluffed Necks in 2 different contexts. It is used most commonly by paired females during cooperative nest-building. As the male repeatedly brings sticks to the nest the female sometimes greets him with the Fluffed Neck instead of the more usual Stretch or Arched Neck. I have also seen a heron give the Fluffed Neck when a Laughing Gull (*Larus atricilla*) swooped at it.

The Fluffed Neck is very rare in the Great Blue Heron but in the Great Egret it is the typical greeting signal between mates and is a general threat to others (Wiese in press). Displays that I consider as homologous with the Fluffed Neck have been described for a number of other heron species—unfortunately, under a confusing maze of synonyms. On the basis of display form, I recommend that Fluffed Neck, Arched Neck, and Upright displays be clearly distinguished (Table 2).

Upright

(1) *Synonyms*: None.

(2) *Typical performance.*—The heron raises its head forward and up until the neck and bill are very straight, pointing about 45° above horizontal. The crest may be either erect or sleeked. The heron holds this position for up to about 4 sec and then relaxes (or attacks).

(3) *Variations.*—Through variation in the angle and straightness of the neck, the Upright seems to grade into Arched Neck postures (see p. 204).

TABLE 2

CHART OF PROPOSED FLUFFED NECK HOMOLOGIES AND KEY TO SYNONYMS

	 Arched neck	 Fluffed neck	 Upright
Ardea cinerea	Aggressive Display[2]		
A. herodias	Aggressive Upright[3]	Fluffed Neck[8]	Upright[3]
A. melanocephala		Aggressive Pose[5]	
Casmerodius albus		Erect Stance[7]	Upright[7]
Egretta thula		Aggressive Upright[3]*	
Hydranassa tricolor		Upright[6]	
Dichromonassa rufescens		Aggressive Upright[3]*	
Butorides virescens		Stiff-necked Upright[3]	
Bubulcus ibis		Upright[1]	
Nycticorax nycticorax		Ruffle Neck[4]	

1 = Lancaster 1970, 2 = Lowe 1954, 3 = Meyerriecks 1960, 4 = Nelson 1975, 5 = North 1963 (fig. 5), 6 = Rodgers in press, 7 = Wiese in press, 8 = present paper. (*Meyerriecks' original descriptions indicate that the "Aggressive Upright" and the "Upright" intergrade as escape/attack tendencies vary—in lieu of further published detail I prefer to treat these as one variable display.)

In addition, the degree of crest erection is highly variable and the wings may be held several cm out from the body.

(4) *Contexts.*—I have seen the Upright only a few times in the colony, always in contexts similar to those of the Arched Neck when a conspecific lands nearby or flies close by.

(5) *Discussion.*—I have observed this display so infrequently that I initially considered it to be a minor variant of the Arched Neck. Meyerriecks (1960:94), however, in describing it for the Great Blue Heron said that it ". . . is most commonly seen where large numbers of *herodias* are feeding in close proximity . . . ." He also observed it during the "dancing ground" activities (see p. 223). Thus it may well be a distinct signal used primarily in special circumstances away from the colony.

This posture has been described as an agonistic display in several other heron species. It is a common colony display in the Great Egret (Wiese in press) but Meyerriecks' (1960) descriptions for the Reddish and Snowy egrets do not strongly resemble the oblique posture that I label as Upright: they sound very similar to my Fluffed Neck.

Arched Neck

(1) *Synonyms*: Aggressive Display (Lowe 1954), Aggressive Upright Display (Meyerriecks 1960), Arched-neck Greeting Display (Milstein et al. 1970).

(2) *Typical performance.*—Quickly the heron erects its plumes (crest, scapular, and basal portion of the neck) and curves its neck like a rainbow so that the closed bill usually points below horizontal (Fig. 6). It maintains this position up to 5 sec before relaxing to a standing posture.

(3) *Variations.*—The greatest sources of variability in the Arched Neck are the degree of neck curvature, degree of feather erection, and directional orientation of the performer. It is possible that individual herons perform consistently with respect to neck curvature. Occipital crests were sleeked during about ¼ of 272 male Arched Necks, but this variant was observed only once in 63 female performances. Furthermore, the males' sleeked variant virtually disappears after pair-formation (only 4% of all Arched Necks).

Less common variations include Arched Necks given from an incubating crouch, repetitions given quickly (even 1 triple performance), and 2 performances that included rocking stab-like motions resembling the Forward. The Arched Neck is ordinarily a noiseless display but one particular male added a grunt-like vocalization during some of his performances.

(4) *Contexts.*—Arched Necks usually occur in response to the movements of other herons in the colony—birds that are walking, landing, departing, or more commonly, just flying past. A heron landing within 2 to 10 m usually elicits an Arched Neck: herons landing farther away are mostly ignored: herons landing closer are typically attacked. Following an Arched Neck the performing heron either gives a Forward or Supplant (if the landing was close by) or relaxes (if the landing was farther away). When the moving heron is not landing but is merely flying low over the colony, the Arched Neck may be elicited at greater distances (up to 20 m).

Arched Necks are also performed in response to non-heron stimuli such as sudden loud noises (e.g., gunshot, boat-motor) or a human approaching the heronry. At these times many colony members may display simultaneously (Fig. 6), but each seems to be responding directly to the external stimulus rather than to other herons.

Although performed by both sexes during pair-formation, Arched Necks are given most frequently by unpaired males standing on their own nests. Satellite females begin doing it only when they have approached the male very closely; their usage then increases after the pairbond has formed. Thus, in the colony, the Arched Neck is closely associated with nest-territory ownership. Away from the colony it is used as a spacing signal on the "gathering ground" (see p. 223).

FIG. 6. Simultaneous Arched Necks given by bachelor male and satellite female as conspecific flies past. Note that male's crest is more erect than female's (Rice Lake, April 1971).

After pair-formation, Arched Necks are used irregularly during the arrivals and departures of both sexes, especially in the first days when both mates are still nervous around each other. It is usually followed by Bill Clappering.

(5) *Discussion.*—In contrast with the displays already described, the Arched Neck's context can be much more narrowly defined: it is almost always elicited by a moving heron. I believe that the Arched Neck functions as a relatively long-distance threat whose message (*attack*) might be paraphrased as "Keep your distance." This idea is supported by the fact that Arched Necks are most frequent during the early phases of the breeding cycle when the herons are defending new territories and are crowding into the colony for their first sustained social contact in months.

The Arched Neck probably evolved from a standing alert posture. It has been reported only for the first 2 species of Bock's *Ardea* superspecies (*cinerea–herodias–cocoi*: Bock 1956). It is also possible that the Arched Neck evolved as a variant of the ancestral Fluffed Neck (which I assume to be ancestral because that character-state is much more widely shared) that

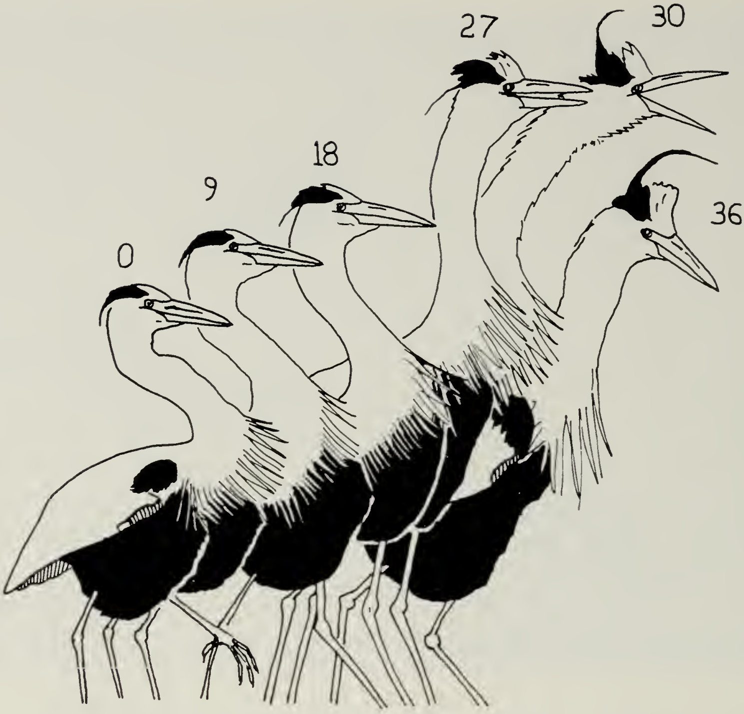

FIG. 7. Stop-action illustration of the Forward (from movie film shot at 18 fps). Frame numbers are given over each figure.

proved more effective/successful in evolutionary competition among signals (Moynihan 1970). Observations on other species of *Ardea* (especially *A. cocoi*) are needed to determine the taxonomic distribution of this display.

Forward

(1) *Synonyms*: *Stossbewegung* (Verwey 1930), Threat Display (Cottrille and Cottrille 1958), Forward Display and Full Forward Display (Meyerriecks 1960), Bill-snapping and Threat Display (Milstein et al. 1970), *La Menace* (Voisin 1970), Upward Snap (Birkhead 1973).

(2) *Typical performance.*—The heron moves its wrists out from the sides of the body, retracts its neck part way onto the shoulders, and erects all plumes of the head, neck, and back. In this position it either stabs at another bird or walks toward it before stabbing. The stab is performed with a rocking motion: the legs straighten, the neck extends, and the head passes

Fig. 8. Forward given by 3–4 week old chick (Danger Island, Texas, May 1974).

through a short arc as the heron emits a sharp "squawk" and clacks its bill at the point closest to its opponent (Fig. 7). After a Forward the heron pauses and, if the other bird has not moved away, it often repeats the Forward or continues advancing. On rare occasions the displaying heron gets close enough to make contact during the stab.

(3) *Variations.*—Almost everything about the Forward is variable—crest erection, walking motions, wing position, qualities of the call, etc. As described under the Snap, voiceless performances of the Forward are sometimes difficult to distinguish from high Snaps and are considered a distinct display, Bill-snapping, by Milstein et al. (1970).

(4) *Contexts.*—Forwards are usually performed from the nest as part of territorial defense. Solo males begin using it as soon as they have chosen a nest-site. Bachelor males do the most Forwards (in repelling satellite females) and paired males do relatively few. Female herons perform fewer Forwards than males and direct them primarily toward other satellite females during the bachelor and paired stages.

Less commonly, Great Blue Herons of both sexes direct Forwards at nearby commotions. These are usually social (e.g., neighbors fighting), but can actually be any heron-caused disturbance, such as a clumsy landing. Local arrivals typically elicit Arched Necks followed by Forwards. Forwards can be directed at herons up to 15 m away, but are usually used in closer situations (8 m or less).

Great Blue Heron chicks perform recognizable Forwards toward siblings when only a few days old. As time passes they use the Forward (and actual pecking) to repel competitive siblings at feeding times and, by the age of 2–3 weeks (Fig. 8), the chicks can defend the nest against conspecifics (wandering neighbor chicks and stick-stealing adults) and perhaps against certain predators (e.g., gulls and night-herons). Forwards by chicks tend to lack the vocal component, terminating most commonly in a loud bill-clack (as reported for *A. cinerea* by Baerends and van der Cingel 1962). The frantic competitive begging that occurs each time a parent returns with food usually includes many Forward-like lunges at the parent: apparently chicks attack everything in their environment and this attack behavior elicits a regurgitation response from the parents.

(5) *Discussion.*—The Forward is one of the few heron displays in which the signal's receiver is seldom in doubt. I felt that I could determine the receiver in 99.4% of 349 Forwards. The identity of the receivers changed through the pairing process, from any passing conspecific in the solo male stage to satellite females in the bachelor male stage and back to any passing conspecific in the paired male stage (Fig. 9).

The Forward is apparently a ritualized attack posture derived from the intention movement to deliver the blow. It has been described for all heron species studied to date with the only questionable homologies being the An-Snap of *Cochlearius* (Mock 1975a) and the *Pfahlstellung* of *Botaurus* (Portielje 1926).

The Forward conveys a strong *attack* message which can be represented as "Move away!" This function is served by the extreme conspicuousness of the overall display (visual and acoustic) and presumably by all the size-increasing components (feather erecting, wing-lifting, and physical advancing). The bill, which is the heron's primary weapon, is held foremost and is brightly colored during pair-formation.

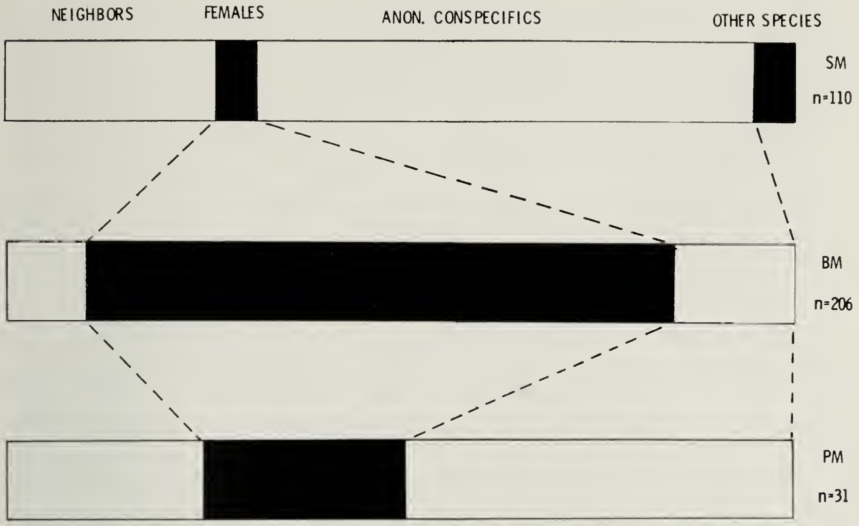

FIG. 9. Identity of receivers for 347 Forwards given by male Great Blue Herons throughout pair-formation. Each bar represents 100% of the Forwards for its pairing stage: SM = solo male stage, BM = bachelor male stage, PM = paired male stage.

Supplanting

(1) *Synonyms*: Supplanting Run (Blaker 1969a), *L'Attaque* (Voisin 1970).

(2) *Typical performance.*—The attacker flies directly at another heron, erecting all feathers and emitting a loud squawk. If the opponent does not flee it is landed on and pecked. Usually the attacker lands on the spot just vacated by its opponent, stands there for a variable period slowly relaxing its plumes, and then returns to its original perch.

(3) *Variations.*—Even more than the Forward, this display varies in all details, depending on such additional things as the distance flown and the opponent's reactions.

(4) *Contexts.*—Supplanting is seen most commonly when a satellite female has either come too close to a bachelor male's nest or has failed to move away after several Forwards by the male.

(5) *Discussion.*—Supplanting differs from totally unritualized attack only by the presence of a vocalization. The *attack* message is obvious and is immediately reinforced by the signaler's action. Similar flying attack signals have been reported in most other species. There is some doubt in my mind about whether Supplanting should be maintained as a display separate

FIG. 10. Bill Duel. Male stabs at female's open bill while she recoils and tries to catch his bill. Female succeeds in catching male's bill: the Duel ends in a clinch (Hog Island, March 1975).

from the Forward. I have distinguished the 2 solely on the basis of flying locomotion.

Bill Duel

(1) *Synonyms*: bill-sparring (Lowe 1954, Cottrille and Cottrille 1958, Meyerriecks 1960), inhibited mutual bill fighting (Baerends and van der Cingel 1962), stab-and-counterstab (Blaker 1969a).

(2) *Typical performance.*—If a newly-paired male sees his mate raise her head above her shoulders he usually attacks in a ritualized manner. He quickly erects all plumage (especially crest and neck), stands very tall, and then lunges at her face with wings held out and bill closed. The female avoids the stab by quickly retracting her neck so that his thrust ends just short of contacting her bill-tip (Fig. 10 left). Then the male retracts his neck for another stab and the female moves her head back to a normal position, watching him closely. This cycle of male stabbing and female pulling back often continues for about 4 repetitions, producing a seesaw action between the mates. The female usually keeps her bill open when the male thrusts

FIG. 11. Female (left) averts her bill when standing close to her new mate (Hog Island, March 1973).

and tries to seize his bill in the tips of her mandibles. If she succeeds and can hold on, she can end the Bill Duel in a clinch (Fig. 10 right). Bill Duels last 1–5 sec, depending on the number of male stabs and whether or not the female catches his bill-tip.

(3) *Variations.*—Because this mutual display has so many variable com-

ponents, it is simpler to discuss the common features of all Bill Duels which qualify it as a display and make it recognizable. First of all, it is almost always started by the male of the pair (115 of 118 Bill Duels). Second, the male's stab is always directed at the female's face or bill, never at her body. Finally, this behavior is easily recognized by the seesawing action and, in many cases, by the final bill grasping (which resembles a kiss). Virtually everything else varies: duration, number of stabs, relative positions of the mates, feather erections, etc. The male's stabbing is rarely accompanied by the harsh "squawk" vocalizations found in the Forward. And sometimes the female actually returns the stabs instead of just passively recovering.

Many Bill Duels never progress beyond the intention-movement stage of the male standing tall, fluffing out, and feinting a stab. These "face-offs" comprised 23% of the 115 male-initiated Bill Duels in the sample.

(4) *Contexts.*—The great majority of Bill Duels occur during the first few hours that a new pair is together on the nest. At this time the male is still very hostile and seems to be "nervously tolerating" the female who tries to avoid direct confrontations with him. The female keeps her eyes averted most of the time, either poking at twigs or facing away from the male (Fig. 11). She also keeps her crest sleeked and head low: head-raising elicits male attacks more than any other act. Gradually the male ceases his attacks and the female abandons her low-head, facing-away postures. The few female-initiated Bill Duels I saw came at this time, when the intra-pair dominance reached a balance.

(5) *Discussion.*—Bill Duels are highly ritualized if not rigidly stereotyped in form. The orientation of the stab toward the female's face allows her to avoid it easily—without fleeing. Her torso is usually much more vulnerable for serious pecking. By constrast, bachelor males sometimes peck satellite females on the body to drive them away.

The function of the Bill Duel is apparently to reduce the male's attack tendencies and thereby promote peaceful coexistence on the restricted nest-site. The male has to overcome his aggressiveness and the female must overcome her tendency to flee: both goals are attained through these ritualized fights.

Bill Duels are also waged between young siblings starting at about 1 week of age. It is possible that these originate as practice bill-grasping motions like those used for scissor-feeding from the parent's bill.

To my knowledge, elaborate Bill Duels have been described only for Great Blue Herons, Grey Herons (Baerends and van der Cingel 1962), and Cattle Egrets (Blaker 1969a, Lancaster 1970). Adult Cattle Egrets commonly Bill Duel with neighbors from adjacent nests—a situation not observed in Great Blue Herons. I have also seen Bill Duels performed by Great Egrets but they are less common than in the Great Blue Heron.

TABLE 3

RELATIVE FREQUENCIES OF BILL CLAPPERING VARIANTS IN MALE AND FEMALE GREAT BLUE HERONS (DATA FROM TIMELINE SAMPLES)

	Sex of sender			
	Male		Female	
Types of Bill Clappering	N	%	N	%
Aerial	146	25	153	39
Contact	396	67	240	61
Hard Contact	53	9	2	1
Totals:	595		395	

Bill Clappering

I distinguish 3 different forms of Bill Clappering, each of which has been described under various names in the literature: (a) Aerial Bill Clappering—no physical touching occurs between the sender's bill and the receiver's body; (b) Contact Bill Clappering—touching involves only the receiver's feathers; and (c) *Hard* Contact Bill Clappering—the sender's bill is pushed with such force that it passes through the receiver's feathers to the skin.

(1) *Synonyms*:

(a) Aerial Bill Clappering = "clappering" (Huxley 1924), Bill-snapping (Meyerriecks 1960), Bill-clappering (Hudson 1965).

(b) Contact Bill Clappering = mutual preening (Cottrille and Cottrille 1958), Feather-nibbling (Meyerriecks 1960, Baerends and van der Cingel 1962), allopreening (Milstein et al. 1970), *Mordillage* (Voisin 1970), Bill Nibbling (Rodgers in press), low-intensity Back-biting (Blaker 1969a).

(c) *Hard* Contact Bill Clappering = Back-biting (Blaker 1969a, Lancaster 1970).

(2) *Typical performances.*—

(a) Aerial Bill Clappering: The heron starts wagging the tip of its bill from side to side and extends its neck toward the mate (Fig. 12, above). Small nibbling mandibulations (amplitude 1 cm) are performed in mid-air, producing a rapid clicking noise sometimes audible as far as 10 m away. After 1–3 sec the heron retracts its neck to a normal standing position.

(b) Contact Bill Clappering: The heron smoothly extends its neck toward its mate (the lateral head-wags are optional) and nibbles on the mate's feathers (Fig. 12, below).

(c) *Hard* Contact Bill Clappering: The heron pushes its bill forcefully against the mate's body. The bill is usually closed, but lateral head

FIG. 12. Aerial Bill Clappering (above) by male over female's rump as she inserts a nest stick (Hog Island, February 1973). Contact Bill Clappering (below) of feathers on female's neck (Hog Island, February 1975).

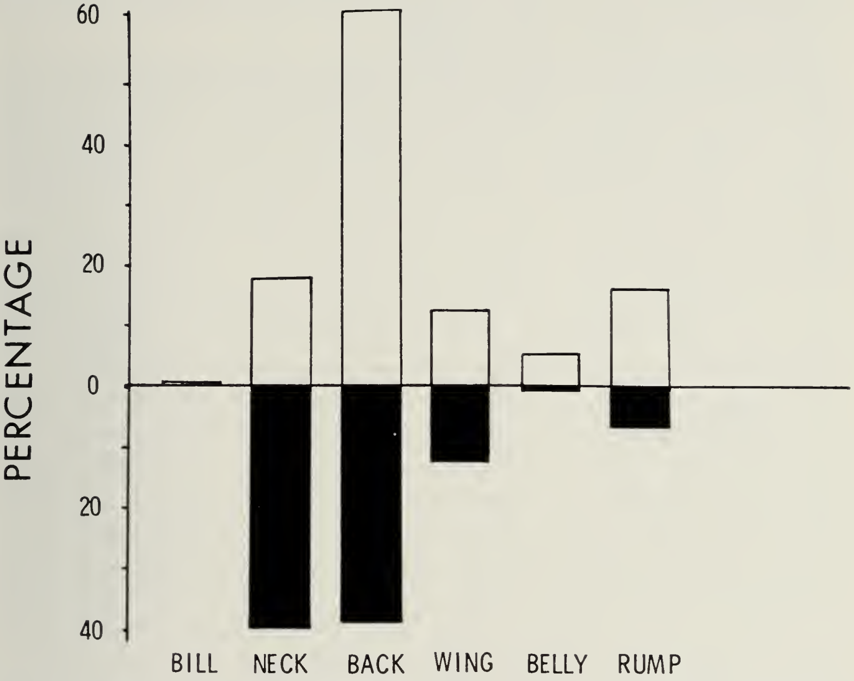

FIG. 13. Regions of the body receiving Contact Bill Clappering from the male (top graph—open bars) and from the female (bottom graph—solid bars).

twists may accompany the physical contact, causing the mate's body to move with the twists. On occasion the receiving bird (who is the female in 96% of my observations) is pushed so hard that it loses its balance and stumbles.

(3) *Variations.*—Contact Bill Clappering is the most common form for both sexes (Table 3), but Aerial Bill Clappering is more important in the female's repertoire than it is in the male's.

Contact Bill Clappering is directed to many different parts of the receiver's body. Males show a marked preference for the female's back while females orient more toward the male's neck (Fig. 13). Most (88% of sample) *Hard* Contact Bill Clappering is directed at the female's back.

Other sources of variability include duration of the display, details of body juxtaposition, body contacts other than the bill during Bill Clappering, and probably speed of mandibulating. On rare occasions a male heron may grasp the female's entire neck while Bill Clappering.

(4) *Contexts.*—Bill Clappering is by far the most common display during the paired stage. It is especially frequent when the mates are first together.

Although Bill Clappering is done by both sexes, males do slightly more (60% of total: data in Table 3) than females.

Bill Clappering may occur any time the mates are on the nest together, but certain activities are more likely to elicit its performance. Sudden movements, sudden changes of behavior, or any action that involves a horizontal neck extension (e.g., Twig Shake, Snap, or inserting nest sticks) often triggers Bill Clappering from the mate. It also occurs sometimes when the receiving mate has done nothing at all (even when it's asleep). Bill Clappering by 1 heron often elicits a Bill Clappering response from the mate: the resulting mutual performance can last up to 10 sec and occasionally ends with the mates' long necks intertwined. It is a common display both preceding and following copulations (as noted for *A. cinerea* by Milstein et al. 1970).

Bill Clappering plays an important role after Bill Duels. As soon as the attacking male ceases his thrusts the female often begins Bill Clappering. This apparently calms the male (his feathers quickly relax) and usually leads to mutual Bill Clappering. On other occasions imminent Bill Duels seem to be replaced by Bill Clappering. When the newly-accepted female elevates her head the male starts to attack but then suddenly Contact Bill Clappers her instead. The female usually reciprocates then and both herons quickly relax. In a similar context, satellite females often perform Aerial Bill Clappering toward a belligerent bachelor male while making the final approaches to his nest. Paired females predictably perform Contact Bill Clappering after their mates direct Forwards at neighbors and passers-by.

Even young chicks perform Aerial and Contact Bill Clappering after hostile events. I elicited this from nestlings at age 2 weeks or older: they first made several volleys of Forwards and then quickly gave mutual Bill Clappering when I backed away.

(5) *Discussion.*—Bill Clappering seems to convey 2 messages, the *non-agonistic* and *bond-limited subsets* (Smith 1969), both of which ultimately strengthen the pairbond. Bill Clappering apparently reduces the male's attack tendencies after he has first allowed a female onto his nest. The female employs 3 behavioral tactics at this time: keeping her head low, directing her bill away from him, and Bill Clappering him frequently (especially after Bill Duels). Second, the signal is used by both sexes to interrupt the mate's other activities, thereby drawing the mate's attention back to the signaller (the *bond-limited* message). For example, a female who is probing among the nest sticks may suddenly receive gentle Contact Bill Clappering from her mate. She immediately stops probing and engages in mutual Bill Clappering for several seconds. In general, Bill Clappering seems to help the pair adjust to the reproductive necessity of coexisting peacefully on a small nest.

Various forms of Bill Clappering have been described for 17 heron species

TABLE 4

SUMMARY OF BILL CLAPPERING HOMOLOGIES IN THE ARDEIDAE

	Aerial	Contact	References
Ardea cinerea	X	X	Hudson 1965
A. herodias	X	X	present paper
A. melanocephala	X	?	Symmes 1951
A. purpurea	X	X	Tomlinson 1974
Casmerodius albus	X	X	Wiese in press, pers. obs.
Egretta garzetta	X	X	Blaker 1969b
E. thula	X	X	Meyerriecks 1960
E. intermedia	X	X	Blaker 1969b
Florida caerulea	X	X	Meanley 1955, pers. obs.
Hydranassa tricolor	X	X	Rodgers in press
Dichromonassa rufescens	X	X	Meyerriecks 1960
Butorides virescens	X	X	Meyerriecks 1960
Bubulcus ibis	X	X	Blaker 1969a
Nycticorax nycticorax	X	X	Nelson 1975
Nyctanassa violacea	X	?	Harford 1951, Nelson 1975
Cochlearius cochlearius	X	X	Mock 1975a
Ixobrychus exilis	X	X	Weller 1961, pers. obs.

(Table 4). Similar mandibulating displays in storks (Up-Down of Kahl, 1972a) and ibises (see review in Hudson 1965) may even be homologous with heron Bill Clappering, but detailed evidence is lacking.

Bill Clappering is a composite display using up to 3 sensory modalities: auditory, visual, and tactile. The acoustic signals of Aerial Bill Clappering are not always audible over distance, especially if there is wind. It is possible that the faintness of this cue is a metacommunicative design feature serving to address the message to the nearby mate only (Bateson 1955, Hockett and Altmann 1968); certainly the tactile components serve this function. The 6 Great Blue Heron chicks that I hand-raised could always be heard when Aerial Bill Clappering at close range.

There are at least 2 plausible, but opposing, explanations for the evolution of Bill Clappering displays. "The Attack-Allopreen Hypothesis" has been presented in bits and pieces before but has not been organized into a comprehensive scheme. The "Autopreen Hypothesis" is new.

The idea that heron allopreening is inhibited attack behavior was first implied by Baerends and van der Cingel (1962) who asserted that Contact Bill Clappering was attack redirected from the mate's body to its feathers. The evolutionary link between inhibited attack and allopreening was developed more fully by Harrison (1965) who specified 2 basic preconditions that might have been important in the evolution of allopreening in herons: high levels of aggression and enforced close proximity of mates. Hudson's (1965) detailed account of heron Bill Clappering addressed only the final transition from Contact Bill Clappering (allopreening) to Aerial Bill Clappering. He did not speculate on how allopreening itself evolved. Blaker (1969a), however, adopted the "inhibited attack" line of reasoning which he thought contradicted Hudson's allopreening model directly. In fact the 2 ideas are not mutually exclusive but merely represent different stages in the same evolutionary argument.

Thus, according to the synthesized "Attack-Allopreen Hypothesis," selection favored a reduction in the vigor of attack pecking between mates to allow peaceful coexistence on the small nest platform. High levels of male aggression that were advantageous in territorial defense were disadvantageous if unchecked toward females. Because herons are bound by ecological constraints to share parental duties, it is crucial that the mates be able to tolerate each other on the nest. The first evolutionary stage, reduced or inhibited pecking (my *Hard* Contact Bill Clappering), is found in all herons to a greater or lesser extent. In Great Blue Herons it usually lacks the nibbling component and is a relatively infrequent form (only 10% of male, and less than 1% of female Bill Clappering). By contrast, this stage has apparently been favored in the communication system of the Cattle Egret where it is the most common variant (Blaker 1969a).

The second evolutionary stage, gentle Contact Bill Clappering, accordingly reflects continued selection for reduced aggression. This version is directed at the feathers, not the skin, and almost always includes the nibbling component. Nibbling may have been added secondarily as the bill-in-the-feathers position elicited a well-fixed preening response ("transitional action": Lind 1959).

Aerial Bill Clappering may have originated as metacommunication about Contact Bill Clappering, providing the message that "this is going to be ritualized peck-nibble, not an aggressive attack." Examples of similar early warnings being retained as signals themselves are known in monkeys where audible lip-smacking precedes social grooming (Andrew 1963). Alternatively Aerial Bill Clappering could have evolved without metacommunicative function simply as an intention movement to perform Contact Bill Clappering. Here the tactile cues are totally lacking but the mandibulations persist and, without the feathers to muffle them, became more audible. I have observed that Great Blue Herons perceive the differences between Aerial and Contact Bill Clappering and respond differently to these 2 signals.

The opposing "Autopreen Hypothesis" does not have as many obvious selective pressures supporting it. It is based mainly on the observation that

Great Blue Herons, at least occasionally, treat their own neck plumes with ritualized "clappering" that serves no apparent function in feather maintenance. Such performances could be relicts of an early stage in the evolution of Bill Clappering. The "Autopreen Hypothesis" argument is that preening of the neck plumes became ritualized for signal function (as did autopreening of the lead primaries in the case of the Wing Preen) to produce audible clicking sounds. Such a display would serve to maintain acoustic contact between mates and would surely inform the mate of the position and harmless occupation of the bill. Aerial Bill Clappering is the proposed second step, wherein selection favored moving the acoustic signal closer to the mate for better transmission. The addition of tactile cues apparently would have expanded the information content of the display, thus leading to Contact Bill Clappering. Variability in Contact Bill Clappering would provide the raw material for a final selective peak at *Hard* Contact Bill Clappering in those species where more aggressiveness between mates might be advantageous.

The 2 hypotheses thus reflect opposite views of the balance between tendencies for aggression and for closeness. In the "Attack-Allopreen Hypothesis" aggression is considered a holdover from territory defense and an obstacle to proper functioning of the pairbond. But the "Autopreen Hypothesis" envisions aggression as both the ultimate initiator of Bill Clappering evolution and as a secondary adaptive peak in some species like the Cattle Egret.

Advertising Call

Every student of pair-formation behavior in *Ardea cinerea* has described a conspicuous Advertising Call, consistently described as a loud "yelping" call given by unmated males in sporadic volleys from the moment they choose a nest site until the pairbond is formed (e.g., Milstein et al. 1970). There is no controversy over its existence in *A. cinerea*. By contrast, nothing resembling the Advertising Call has ever been described for *A. herodias*, though this species is so closely related to *A. cinerea* that some systematists have proposed lumping the 2 (Parkes 1955, Mayr and Short 1970).

Meyerriecks (1960:101) reported a few observations of Great Blue Heron males in Florida standing on nests and opening and closing their bills, but he was too distant to hear any calls. In 3 field seasons of watching closely for this display in *A. herodias* I have witnessed possible performances on only 3 occasions. These 3 observations are the only times I have seen Great Blue Herons emitting calls not accompanied by any special postures (i.e., not part of a Forward or Stretch). Each heron simply stood on its nest and gave a series of soft, high-pitched "en" vocalizations. The first time (on Hog Island, 1973) 8 irregularly-spaced notes were uttered. The second observation was made on the same nest the following morning (presumably involving the same male). Then the heron repeated "en" notes irregularly for about 3 min. My third observation (on Hog Island, 1975) consisted of about 8 soft, high-pitched "en" notes, spaced at roughly 1-min intervals. I believe that the true Advertising Call of *A. cinerea* is either totally absent or extremely rare in *A. herodias*. This discrepancy is the most notable repertoire difference yet described for these species.

Special Display Sequences

For the most part, Great Blue Heron displays are not rigidly organized into predictable sequences. This is true both for strings of behavioral events performed by 1 individual and for interactions between 2 herons. Perhaps because of this, heron ethologists have made special note of 3 relatively predictable interaction sequences and have sometimes even described them as displays (which, strictly speaking, they are not). The term "Ceremony" will be used here to connote these sequences.

(1) *Greeting ceremony.*—When 1 heron flies in to join its mate on the nest, it typically gives the Landing Call. The bird on the nest becomes alert and usually performs a full Stretch (less commonly it responds with an Arched Neck or Fluffed Neck) as the arriving mate lands on the rim. Wiese (in press) shows how similar interaction in the Great Egret help the arriving bird find its own nest in the colony: birds whose mates failed to answer the Landing Call tended to alight away from the nest and walk to it. Greeting ceremonies have been described for many herons (e.g., Verwey 1930, North 1963, Blaker 1969a, Rodgers in press, Wiese in press).

(2) *Stick transfer.*—When 1 heron (usually the male) brings sticks to its mate a similar sequence of interactions occurs. The Landing Call is usually omitted, perhaps because most sticks are stolen from nearby nests so the mates never lose visual contact with each other. As the male returns the female does a Stretch (or partial Stretch) then turns and takes the offered stick. Although the male is sometimes reluctant to release his stick he usually does so readily and Bill Clappers the female as she tremble-shoves the new stick into the nest.

(3) *Nest relief.*—During the incubation stage, a special sequence coordinates the mates' actions at changeovers. The arriving heron gives a Landing Call to which the incubating mate stands and performs a full Stretch. After landing nearby the new arrival walks to the nest and finally onto it as its mate exits. Often the pair stands close together for several minutes of Bill Clappering, preening, and even sleeping before the departing mate leaves.

FIG. 14. Pair in simultaneous Tall Alert postures (Hog Island, March 1973).

Miscellaneous Signals

In addition to the easily-recognized displays already described, Great Blue Herons have some less-ritualized behavior patterns that may well convey information.

(1) *Tall Alert.*—When alarmed a Great Blue Heron stands as tall as pos-

sible with bill horizontal, feathers sleeked, and head very still. It seems to rely on its wide peripheral vision to locate the source of the disturbance. This posture serves as a cue to other birds: many neighbors adopt Tall Alert stances even if they showed no overt response to the original stimulus (Fig. 14). Thus the Tall Alert has a social meaning which I believe is unintentional (the heron assuming a Tall Alert is probably trying to gather information for itself: other herons simply use that behavior as a useful piece of information for themselves).

(2) *Shoulder Nibble.*—Great Blue Herons touch their bills to their black epaulet patches from time to time, both between displays and while preening. The act is highly variable, ranging from lengthy nibble-preening to smooth, brief touching (which seems to have no feather-maintenance function and therefore may be a slightly ritualized social signal). No display preening of the epaulets has been described for any heron species to date.

(3) *Treadling.*—Courting male Great Blue Herons sometimes stand on their nests and sway slowly from side to side. This swaying usually takes about 2 sec, is about 20–30 cm in amplitude, and may be accompanied by slight lifting of the free foot with each sway. I do not know the social function of this behavior but it commonly occurs during periods of active displaying and may attract attention to its performer. Similar swaying has been reported for unpaired male Cattle Egrets (Blaker 1969a) and the highly ritualized Snap-Hiss of the Black-crowned Night Heron (Noble et al. 1938, Nelson 1975) may also have evolved from this motor pattern.

(4) *Static-optic Advertising.*—The mere existence of an unmated male heron on his nest-territory carries information to the rest of the colony. Although the Great Blue Heron's signal merely consists of standing, this presence is moderately ritualized in the Cattle Egret (special hunched posture with partial scapular erection: Blaker 1969a) and highly ritualized in the Great Egret (extreme hunched posture with bill pointing down, scapular aigrettes fully fanned: Wiese in press). Despite the simplicity of the posture, the male Great Blue Heron probably transmits a complex *identification* message by his being *on* the nest (unpaired females do not loaf on nests) with his bright-colored softparts and species-typical plumage. His message might be paraphrased as "I am a territory-holding male Great Blue Heron, physiologically ready to breed." Rather than overextend Moynihan's (1955) formal criteria for "display" status, I follow Estes (1969) in calling this type of signal "static-optic advertising."

Fighting

Actual physical combat lasting longer than 1 peck is very rare in Great Blue Heron colonies. Most fights are brief aerial clashes, accompanied by very loud screams, but producing no injuries. Many seem to result from disputed nest ownership.

Gathering Ground "Dance"

Early accounts of heron breeding behavior often included vague descriptions of herons forming flocks on the ground near the colony and "dancing" (e.g., Bent 1926, Lowe 1954). More recent authors have expressed doubt about the social nature of these aggregations (Baerends and van der Cingel 1962, Milstein et al. 1970, Birkhead 1973).

In March 1971 I watched a group of over 100 Great Blue Herons standing in the snow beside the Rice Lake heronry. Though I watched them for several hours a day during the 4 days before they ascended to the nesting trees, I never saw "dancing." The herons mostly stood still with their heads drawn tightly against their shoulders. The total social activity consisted of occasional Forwards and Arched Necks directed at landing herons.

I believe that those Minnesota herons were merely waiting for environmental conditions to permit colony occupation and nesting. Early migrants are usually confronted with very cold temperatures and almost solidly frozen lakes. For several weeks I saw large numbers of herons scavenging for frozen fish at the lake's melting edge. Others flew long distances toward the Mississippi River and were absent for much of the days. The gathering-ground flocks consistently stayed where weather conditions were most favorable. Several times, when the wind shifted direction, the flock moved to stay on the lee side of the heronry's knoll. The herons spent most of their time standing on 1 foot in the snow with the other foot tucked tightly against the breast feathers.

In the nonmigratory coastal Texas population, breeding is much less synchronized than in Minnesota. Eggs may be found in nests from early January to mid-July (Mock 1975b) with most clutches starting in late February–early March. Accordingly, occupation of the nesting colonies is less synchronous. Some herons can be found roosting in the island colonies at any time of the year, but I have never observed anything like the gathering-ground flocks of northern heronries.

Copulation

Great Blue Heron pairs copulate repeatedly throughout the paired stage and even after 1 or 2 eggs have been laid. I estimate that each pair copulates 10–20 times during this period. A similar estimate of 20 copulations was made by Blaker (1969a) for the Cattle Egret.

I saw no instances of rape (forced copulation with resisting females) or

FIG. 15. Copulation. The female crouches as the male grasps her head and flaps his wings for balance.

extramarital copulations in the Great Blue Herons, either in Minnesota or Texas. Rape has been reported for this species (Cottrille and Cottrille 1958, Michael Brandman pers. comm.), in *A. cinerea* (Verwey 1930) and in 5 other heron species (Taylor 1948, Meanley 1955, Lorenz 1966, Blaker 1969a, Lancaster 1970, Wiese in press), but it seems to be very rare in most herons.

Most copulations occur in the morning and evening hours (females forage away from the colony during midday) and a few occur at night. Every copulation I have seen occurred on the pair's nest, though Cottrille and Cottrille (1958) report that adjacent limbs may be used instead.

As in other herons, little or no overt signaling precedes a Great Blue Heron copulation. Sometimes a male performs Bill Clappering prior to a mounting attempt, but more often he simply walks slowly around the female and steps onto her back. I once saw a successful copulation occur just 10 sec after the male had reared up in an intention-to-Bill-Duel motion.

The male is apparently always on top (see Materials and Methods). He lifts 1 foot and places it gently on the center of the female's back, sometimes raising and lowering the foot several times before finally mounting. For copulation to be successful the female must lean forward and bend her legs slightly. In addition, she holds her wrists a few cm from her sides but not so far as to form a platform (as reported for *Cochlearius*: Mock 1975a). Uncooperative females do not crouch at all and may continue with some other activity like nest-building. One female turned on her mate and made 4 gentle stabs at him to disrupt a mounting attempt. Once on top the male treadles briefly, grasps the female's humeri with his toes, and lowers himself onto his tarsi. This motion is usually accompanied by wing-flapping for balance. The female moves her rectrices to 1 side and the male wags his lowered tail over the cloaca. The male nearly always grasps the female's head or neck in his mandibles and retains that grip through copulation (Fig. 15). By contrast, male Cattle Egrets rarely hold the female's head (Blaker 1969a) and male Great Egrets never do (Wiese in press).

Sperm transfer presumably occurs when the 2 cloacas are in transitory contact at the midpoint of the male's lateral wags. At the extreme sideways end of the wag the female's cloaca is totally uncovered. Total mount times average about 20 sec, but the 6–10 lateral wags take only about 11 sec and actual cloacal contact is probably less than half of this. Following the final wag the male rises from his tarsal crouch and either steps or flies from the female's back. His departure is often clumsy and may cause the female to stumble.

DISCUSSION AND CONCLUSIONS

Sensory modalities.—So far as is known, Great Blue Herons communicate using only 3 sensory modalities: visual, acoustic, and tactile. Of these, the visual modality is most important. While all 14 described displays have unique and conspicuous visual components (6 are entirely visual), only 6 have acoustic and 4 have tactile components (Table 5). The Great Blue Heron's reliance on visual signals is well suited to its open-nesting habits and diurnality: by contrast, the Boat-billed Heron, which nests in dense mangrove thickets, uses signals that are primarily acoustic (Mock 1975a).

Visual communication has the unique disadvantage of a signal channel that is not permanently open. Visual signals can only reach the intended receiver if that individual is oriented (with eyes open) toward the sender (Wilson 1975). One of the main functions of Great Blue Heron acoustic signals seems to be the maintenance of an open *visual* channel (to draw attention to the performer). This may explain why totally visual signals, like the Wing Preen and Twig Shake, are usually sandwiched into a series of displays that contain acoustic cues. The 3 silent agonistic displays (Fluffed Neck, Upright, and Arched Neck) are employed primarily when the intended receiver is landing nearby and therefore already scanning the area.

Redundancy and multiple functions.—Each message of heron communication is apparently encoded into several different signals (intra-repertoire

TABLE 5

A RANKING OF THE SENSORY MODALITIES OF EACH GREAT BLUE HERON DISPLAY

	Sensory modality*		
	Visual	Acoustic	Tactile
Stretch	1	2	–
Snap	1	2	–
Wing Preen	1	–	–
Circle Flight	1	2	–
Landing Call	2	1	–
Twig Shake	1	–	–
Crest Raising	1	–	–
Fluffed Neck	1	–	–
Upright	1	–	–
Arched Neck	1	–	–
Forward	1	2	3
Supplanting	1	2	3
Bill Duel	1	3	2
Bill Clappering	3	2	1

* 1 = most important, 2 = second most important, 3 = least important, dash = non-existent.

redundancy) and, reciprocally, each signal carries more than 1 message (multiple function: Beer 1975). This redundancy is increased by a high rate of display repetition in many contexts (e.g., a solo male heron may give over a hundred performances of only 6 displays without stopping). Although redundancy and multiple function may in part be artifacts of the ethological units chosen for study, it is likely that both are significant features of heron communication (Table 6).

Redundancy (and repetition) of a message should improve its chances for reaching the intended receivers, especially if they are as mobile as "prospecting" female herons. Furthermore, redundancy allows a message to be expressed in different forms which, by using different sensory modalities, should make it more conspicuous. This signal variety may also help combat habituation in the receiver ("Anti-monotony Principle": Hartshorne 1973). In all these hypothetical ways, redundancy can emphasize those messages which are critical to reproductive success. Someone knowing little about heron courtship would probably predict that the 2 key tasks of an unpaired male are attracting females and defending a nest-territory from other males. Accordingly those functions—male advertisement and nest defense—are served by more displays than any others (Table 6).

TABLE 6

CONTEXTS AND MESSAGES OF GREAT BLUE HERON DISPLAYS

	Displays														
	Stretch	Snap	Wing Preen	Circle Flight	Landing Call	Twig Shake	Crest Raising	Fluffed Neck	Arched Neck	Forward	Supplanting	Bill Duel	Bill Clappering	Tall Alert	Static-optic
I. Uses/Contexts:															
External Disturbances							X	X	X					X	
Nest Defense							X	X	X	X	X			X	X
Male Advertisement	X	X	X	X		X	X								X
Female-female Encounters							X		X	X	X			X	
Greetings at nest*	X				X		X	X	X				X		
Intra-pair Appeasement	X				X								X		
Intra-pair Aggression							X					X			
II. Messages (Smith 1969)															
Identification	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Probability	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
General Set							X								
Locomotion					X	X	X				X				
Attack							X	X	X	X	X	X			
Escape							X								
Nonagonistic	X												X		
Association	X	X	X	X									X		
Bond-limited	X		X		X								X		
Play															
Copulation															
Frustration															

* Includes Greeting Ceremony, Nest Relief Ceremony, and Stick Transfer Ceremony.

The multiple functions feature allows the signal repertoire to remain fairly small (and therefore less ambiguous: Moynihan 1970), without sacrificing content. This multiplicity is possible because the sender's message is usually modified en route by various aspects of the context (Smith 1968, Beer 1975).

Thus the combination of intra-repertoire redundancy and multiple functions can, theoretically, provide an enormous amount of flexibility plus desirable simplicity for a communication repertoire.

SUMMARY

The communication of Great Blue Herons during pair-formation was studied for 4 breeding seasons (2 each) in Minnesota and Texas. Each signal is described for form, variability, and contexts and interpreted for probable functions and evolutionary derivation. An attempt was made to apply the message classification system of Smith (1968, 1969) to heron displays. Six displays are described for the first time in this species. Overall, the communication system of the Great Blue Heron can be characterized as a visual one with acoustic cues serving for reinforcement. Intra-repertoire redundancy and multiple functions of the signals are probably also important.

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LITERATURE CITED

Andrew, R. J. 1963. The origins and evolution of the calls and facial expressions of the primates. Behaviour 20:1–109.

———. 1972. The information potentially available in mammal displays. *In* Nonverbal Communication (R. A. Hinde, ed.), Cambridge Univ. Press, England.

Baerends, G. P. and J. M. Baerends-van Roon. 1960. Ueber die schnappbewegung des fischreihers (*Ardea cinerea* L.). Ardea 48:136–150.

——— and N. A. van der Cingel. 1962. On the phylogenetic origin of the Snap display in the Common Heron (*Ardea cinerea* L.). Symp. Zool. Soc. Lond. 8:7–24.

Bateson, G. 1955. A theory of play and fantasy. Psychiatr. Res. Rep. 2:39–51.

Beer, C. G. 1975. Multiple functions and gull displays. *In* Function and Evolution in Behaviour (G. Baerends, C. Beer, and A. Manning, eds.), Clarendon Press, Oxford, England.

Bent, A. C. 1926. Life histories of North American Marsh Birds. U. S. Natl. Mus. Bull. No. 135.

Birkhead, T. R. 1973. Observations at a standing-ground adjoining a heronry. Naturalist 924:13–19.

Blaker, D. 1969a. Behaviour of the Cattle Egret, *Ardeola ibis*. Ostrich 40:75–129.

———. 1969b. The behaviour of *Egretta garzetta* and *E. intermedia*. Ostrich 40:150–155.

Bock, W. J. 1956. A generic review of the family Ardeidae (Aves). Am. Mus. Novit. no. 1779.

Cottrille, W. P. and B. D. Cottrille. 1958. Great Blue Heron: behavior at the nest. Misc. Publ. Mus. Zool. Univ. Mich. no. 102.

DAANJE, A. 1950. On locomotory movements in birds and the intention movements derived from them. Behaviour 3:48–98.

DARWIN, C. 1872. The expression of the emotions in man and the animals. John Murray, London.

ESTES, R. D. 1969. Territorial behavior of the Wildebeest (*Connochaetes taurinus* Burchell, 1823). Z. Tierpsychol. 26:284–370.

HARFORD, H. M. 1951. Nest of the Yellow-crowned Night Heron *Nyctanassa violacea* in Kansas City, Mo. Auk 68:235–236.

HARRISON, C. J. O. 1965. Allopreening as agonistic behaviour. Behaviour 24:161–209.

HARTSHORNE, C. 1973. Born to sing. Indiana Univ. Press, Bloomington.

HOCKETT, C. F. AND S. A. ALTMANN. 1968. A note on design features. *In* Animal Communication (T. A. Sebeok, ed.), Indiana Univ. Press, Bloomington.

HOLSTEIN, V. 1927. Fiskehejren. Gads Forlag, Kopenhagen.

HUDSON, M. J. 1965. Bill-clappering display in the Common Heron *Ardea cinerea.* Ibis 107:460–465.

HUXLEY, J. S. 1924. Some points in the breeding behaviour of the Common Heron. Br. Birds 18:155–163.

KAHL, M. P. 1972a. Comparative ethology of the Ciconiidae. Part 4. The "typical" storks (genera *Ciconia*, *Sphenorhynchus*, *Dissoura*, and *Euxenura*). Z. Tierpsychol. 30:225–252.

———. 1972b. Comparative ethology of the Ciconiidae. The Wood-storks (genera *Mycteria* and *Ibis*). Ibis 114:15–29.

LANCASTER, D. A. 1970. Breeding behavior of the Cattle Egret in Colombia. Living Bird 9:167–194.

LIND, H. 1959. The activation of an instinct caused by a "transitional action." Behaviour 14:123–135.

LORENZ, K. 1966. On aggression. Methuen, London.

LOWE, F. A. 1954. The heron. London: Collins New Nat. Monogr., no. 11.

MAYR, E. AND L. L. SHORT. 1970. Species taxa of North American birds, a contribution to comparative systematics. Publ. Nuttal Ornithol. Club no. 9.

MEANLEY, B. 1955. A nesting study of the Little Blue Heron in eastern Arkansas. Wilson Bull. 67:84–99.

MEYERRIECKS, A. J. 1960. Comparative breeding behavior of four species of North American herons. Publ. Nuttal Ornithol. Club no. 2.

———. 1962. *In* Handbook of North American Birds (R. S. Palmer, ed.), Yale Univ. Press, New Haven, Connecticut.

MILSTEIN, P. LES., I. PRESTT, AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. Ardea 58:171–258.

MOCK, D. W. 1975a. Social behavior of the Boat-billed Heron. Living Bird 14:185–214.

———. 1975b. New early egg-date record for Great Blue Herons in Texas. Tex. Ornithol. Soc. Bull. 8:10.

MORRIS, D. 1956. The feather postures of birds and the problem of the origins of social signals. Behaviour 11:1–12.

MOYNIHAN, M. 1955. Remarks on the original sources of displays. Auk 72:240–246.

———. 1970. Control, suppression, decay, disappearance, and replacement of displays. J. Theor. Biol. 29:85–112.

NELSON, J. B. 1967. Colonial and cliff-nesting in the Gannet. Ardea 55:60–90.

———. 1971. The biology of Abbott's Booby *Sula abbotti.* Ibis 113:429–467.

Nelson, D. 1975. Pair formation behavior of the Black-crowned Night Heron. Honors Thesis, College of Biol. Sci., Univ. of Minnesota, Twin Cities.

Noble, G. K., M. Wurm, and A. Schmidt. 1938. The social behavior of the Black-crowned Night Heron. Auk 55:7–40.

North, M. E. W. 1963. Breeding of the Black-headed Heron at Nairobi, Kenya, 1958–62. J. East Afr. Nat. Hist. Soc. Natl. Mus. 24:33–63.

Owen, D. F. 1959. Some aspects of the behaviour of immature herons, *Ardea cinerea*, in the breeding season. Ardea 47:187–191.

Palmer, R. S. (ed.) 1962. Handbook of North American birds. Vol. I. Yale Univ. Press, New Haven, Connecticut.

Parkes, K. C. 1955. Systematic notes of North American birds. 1. Herons and ibises. Ann. Carnegie Mus. 33:287–293.

Percy, Lord W. 1951. Three studies in bird character. Country Life, Ltd. London.

Portielje, A. F. J. 1926. Zur ethologie bezw. psychologie von *Botaurus stellaris*. Ardea 15:1–15.

Pratt, H. M. 1970. Breeding biology of Great Blue Herons and Common Egrets in central California. Condor 72:407–416.

Rodgers, J. A., Jr. Breeding displays of the Louisiana Heron. Wilson Bull., in press.

Selous, E. 1927. Realities of bird life. Constable & Co., Ltd. London.

Smith, W. J. 1968. Message-meaning analysis. *In* Animal Communication (T. A. Sebeok. ed.), Indiana Univ. Press, Bloomington.

———. 1969. Messages of vertebrate communication. Science 165:145–150.

Strijbos, J. P. 1935. De Blauwe Reiger. L. J. Veen, Amsterdam.

Symmes, T. C. L. 1951. Display of the Black-necked Heron. Ostrich 22:38.

Taylor, J. S. 1948. Notes on the nesting and feeding habits of *Ardea melanocephala*. Ostrich 19:203–210.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae) : a progress report. Behaviour 15:1–70.

Tomlinson, D. N. S. 1974. Studies of the Purple Heron, part 2: behaviour patterns. Ostrich 45:209–223.

Verwey, J. 1930. Die paarungsbiologie des fischreihers. Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere. 48:1–120.

Voisin, C. 1970. Observations sur le comportement du heron bihoreau *Nycticorax n. nycticorax* en periode de reproduction. Oiseau 40:307–339.

Weller, M. W. 1961. Breeding biology of the Least Bittern. Wilson Bull. 73:11–35.

White, S. J. 1971. Selective responsiveness by the Gannet to played-back calls. Anim. Behav. 19:125–131.

———, R. E. C. White, and W. H. Thorpe. 1970. Acoustic basis for individual recognition in the Gannet. Nature 225:1156–1158.

Wiese, J. H. 1976. Courtship and pair formation in the Great Egret. Auk, in press.

Wilson, E. O. 1975. Sociobiology, the new synthesis. Belknap/Harvard Univ. Press, Cambridge, Massachusetts.

J. F. BELL MUSEUM OF NATURAL HISTORY, UNIV. OF MINNESOTA, MINNEAPOLIS 55455. ACCEPTED 15 MAR. 1976.

BEHAVIORAL INTERACTIONS OF BLUE-WINGED AND GOLDEN-WINGED WARBLERS

Bertram G. Murray, Jr. and Frank B. Gill

The interactions of populations in recently established zones of secondary contact are of interest from many points of view (Mayr 1963). The degree of hybridization will determine the future evolutionary independence of the 2 populations (Mayr 1963, 1970; Short 1969), and the degree of ecological overlap and competition will affect their future coexistence in the same community (Lack 1944, 1971). These long-term evolutionary and ecological consequences are mediated through daily behavioral interactions that are based, in part, on what is often called "species discrimination." If individuals fail to discriminate in selecting mates (Sibley 1957, Mayr 1963) or in establishing territories (Murray 1971), and if the failure to discriminate is reproductively disadvantageous, there will be selection for greater discrimination in responding to different phenotypes.

The behavior of hybridizing populations has been increasingly studied (Ficken and Ficken 1967, 1968a,b, 1969; Gill and Murray 1972a,b; Kroodsma 1974; Emlen et al. 1975) with the development of the "playback experiment." Species-specific characteristics sometimes occur in combination in hybrid individuals, the study of which may provide clues to the nature and effectiveness of isolating mechanisms.

We have already presented the results of our experimental work on hybridizing Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*) in southern Michigan (Gill and Murray 1972a,b). The present paper reports the behavior of these warblers in natural circumstances, especially their intraspecific and interspecific aggression. Some of our results bear on the ontogeny of species discrimination and on the nature of hybridization between these species.

METHODS

We studied marked individuals in 1969, 1970, and 1971 in 2 areas of Michigan: Island Lake Recreational Area near Brighton, Livingston County, and near Burke Lake in the Rose Lake Wildlife Research Area in Clinton County, about 16 km east-northeast of Lansing (Ingham Co.). These 2 sites are about 60 km apart.

Blue-winged are more numerous than Golden-winged warblers but range into drier habitats. In wetter habitats where Golden-winged Warblers are most common, both species occur in equal abundance.

In 1969 we observed the birds almost daily from 5 May through 24 June at Island Lake, and on only 3 days at Burke Lake. In 1970 we began observations on 30 April at Island Lake and on 3 May at Burke Lake. FBG noted activity primarily at Island

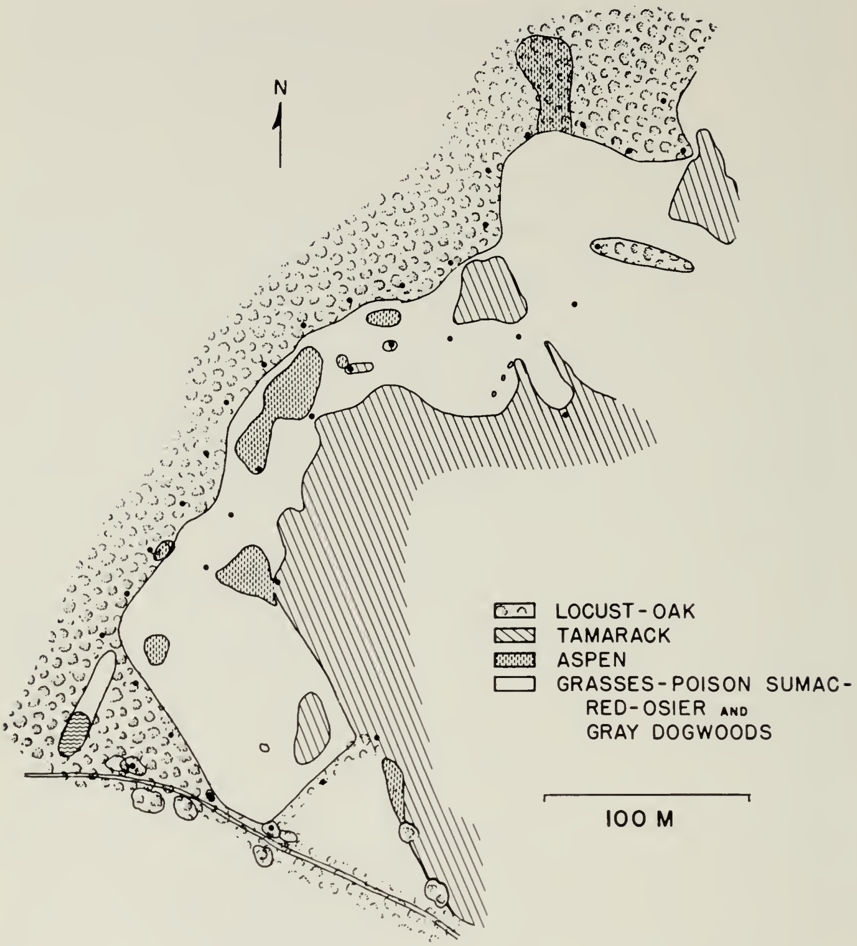

Fig. 1. Habitat map of the main study area at the Island Lake Recreational Area.

Lake while engaged in experimental work, while BGM concentrated on mapping territories, dividing his time about equally between both areas. We were in the field almost daily throughout May. In June BGM continued daily observations at Burke Lake and made 3 visits to Island Lake. In 1971 BGM began observations at Burke Lake on 28 April and continued almost daily observations there through May, while visiting Island Lake only once.

Additional but casual observations (with respect to data presented in this paper) were made in surrounding areas, especially in Hartland Township, Livingston County.

For our work on territoriality we concentrated on 2 small areas that were each occupied by about 12 individuals. The Island Lake area (Fig. 1) is a narrow, low

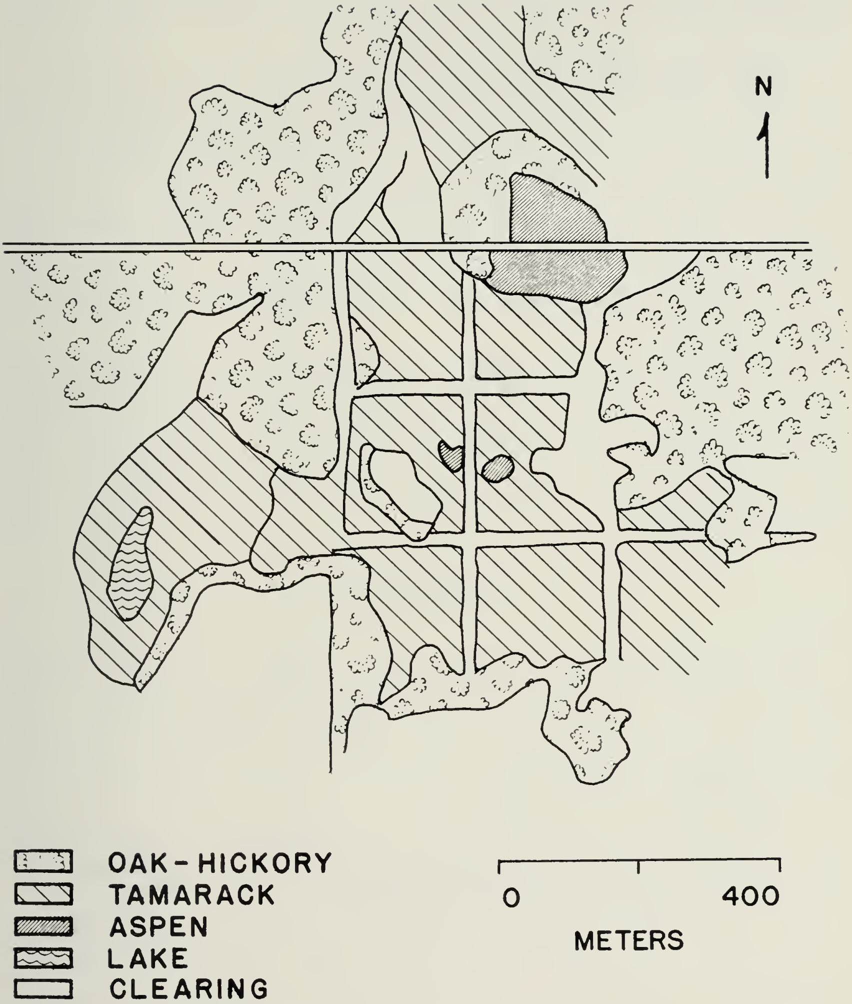

Fig. 2. Habitat map of the main study area near Burke Lake on the Rose Lake Wildlife Research Area. The map is drawn from one provided by Gordon Zorb of the State of Michigan Department of Wildlife Resources.

swamp of tamarack (*Larix laricina*), poison sumac (*Rhus vernix*), red-osier and gray dogwoods (*Cornus stolonifera* and *C. racemosa*), and poplars (*Populus deltoides*). It is bordered on the west by a dry upland deciduous forest of oaks (*Quercus* spp.) and locust (*Robinia pseudo-acacia*); on the east by a tamarack forest bordering the Huron River. We mapped this area by laying out 2 transects marked at 30.5 m intervals and by triangulation.

The Burke Lake area (Fig. 2) is an extensive tamarack swamp surrounded by higher, drier oak-hickory woodlands. The swamp is crisscrossed by several man-made clearings, which we used as trails. The forest has been thinned in recent years as a result of the larch sawfly (*Pristiphora erichsonii*).

We color-banded almost all the males occupying these areas. A few birds were mist-netted by simply setting nets in likely spots. Our usual technique was to attract a selected bird to a net by using both models and tape-recorded songs. We were able to net most birds within 30 min. In addition to banding the birds with a Fish and Wildlife Service aluminum band and 2 colored, plastic bands, we examined each bird for signs of introgression according to criteria established by Short (1963) and slightly modified by us (Gill and Murray 1972b).

In the text we refer to individuals by the initials of the species name and the color of the bands. For instance, B-RW refers to a Blue-winged Warbler with 1 red band above 1 white band.

Each individual's activity was plotted on a composite map, and a line was drawn around the activity points. We calculated the area of a territory by tracing the territory onto graph paper and counting the squares. We saw few intraspecific encounters at these boundaries. Nevertheless, we think the boundaries of these activity spaces accurately delineate territories because from our experimental work we know that within these areas a particular male responds aggressively toward playbacks of intraspecific song.

RESULTS

Arrival

Male Blue-winged and Golden-winged warblers arrived in southern Michigan in late April and early May. In both 1969 and 1970 at Island Lake some resident male Blue-winged Warblers were already on territory when we began observations on 5 May and 30 April, respectively, but both Blue-winged and Golden-winged warblers continued to arrive throughout May and even into June (Table 1). A few Blue-winged Warblers arrived only slightly earlier than did Golden-winged Warblers. There appears to be broad overlap in arrival dates of these 2 species.

The same was observed at Burke Lake, where our coverage was not so intense as at Island Lake except in 1971. Then, with almost daily coverage from 28 April on, the first 2 Blue-winged Warblers arrived on 6 May, and the first Golden-winged Warbler on 7 May. Arrivals of banded birds were: G-RW, 7 May; Lawrence's (L-RR), 10 May; G-GR, 11 May; Brewster's (Br-YY), 13 May*; G-YG, 14 May; G-GW, 15 May; B-GR, 20 May*; and G-RP, 22 May*. (Starred birds may have arrived, at most, one day earlier.)

We have reported here and in Table 1 only those birds whose appearance we are certain about because of the intensity of our coverage of a particular area, the distinctiveness of an individual's song, and our use of color bands.

Some of the later "arrivals" may have moved in from surrounding areas rather than having just returned on migration from their winter range.

Table 1

Arrival Dates of Territorial *Vermivora* at Island Lake Recreation Area, Michigan[a]

	1969	1970
	Blue-winged Warblers	
B-RR	5 May	——
B-WW	5 May (+1)[b]	1 May
B-BB	5 May (+1)	1 May
B-GG	5 May (+7)	1 May
B-GY	31 May	——
B-BG	9 June	——
B-RG	(banded 7 June)	30 April
B-YY	13 May (+14)[c]	——
B-WG	——	3 May[d]
B-YR	——	4 May[d]
B-BY	——	11 May[e]
B-BW	——	14 May[e]
B-WB	——	18 May
	Golden-winged Warblers	
G-YY	7 May[f]	——
G-RR	7 May[f]	(between 12 and 19 May)
G-GG	7 May	4 May
G-BB	4 June (+3)	——
G-BY	——	11 May[e]
G-WR	——	18 May (+1)
G-RG	——	20 May (+1)
G-RY	——	21 May (+1)

[a] Observations began on the morning of 5 May 1969 and late afternoon of 30 April 1970.
[b] Number in parentheses indicates the number of days later that a bird was banded.
[c] Distinctive song.
[d] At another closely watched site.
[e] May have been present the previous day when we did not cover area.
[f] One of these was present on 5 May.

Territorial Establishment

During the first week or so after arrival, male Blue-winged and Golden-winged warblers usually sing infrequently and respond poorly to playback. We could have passed these birds over as transients had they not been marked. At this time most birds restricted their activity to those areas where they later became more conspicuous in their singing, display, and aggressiveness.

As territories were being established, there were some changes in the area occupied by some birds, more so by Golden-winged Warblers. In 1969 at Island Lake one Blue-winged Warbler (B-BB) was first netted over

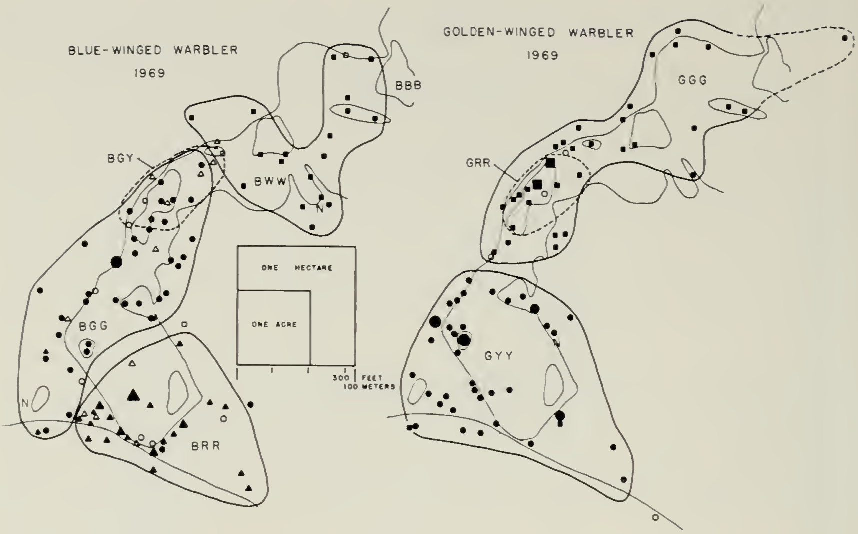

FIG. 3. Territories of Blue-winged and Golden-winged warblers at Island Lake in 1969. The territories are indicated by the heavy lines superimposed over the lighter lines outlining the major features of the habitat (see Fig. 1). The activity of each individual is shown by symbols: B-RR, triangles; B-GG, circles; B-WW, squares; G-YY, circles; G-GG, squares. There are two exceptions: only the outline of the territory is shown for B-GY and for G-RR, represented by dashed lines. Blackened symbols represent observations of singing birds, and the white symbols represent observations of non-singing birds. The larger symbols represent many observations at a single singing perch. The "N" indicates the position of the nests.

180 m from where he finally established his territory. A Golden-winged Warbler (G-RR) sang regularly from 7 to 12 May at Island Lake before it inexplicably disappeared. FBG found him in 1970 on the east side of the Huron River, about 400 m away. At Burke Lake in 1970 we banded a Golden-winged Warbler (G-RW) in another's (G-GR) territory, and another Golden-winged Warbler (G-GW) near the boundary of G-RW's territory, neither of which was seen in these spots again. In 1970 G-GG returned to Island Lake on 5 May and sang throughout the area before disappearing on 15 May. So far as we know he was never challenged. He was subsequently replaced by 2 new Golden-winged Warblers, G-RG on 18 May and G-WR on 20 May. Both remained at least until we last visited the area on 18 June. On 22 May 1970 at Island Lake we accidentally killed a Golden-winged Warbler that was first detected the previous evening. Within an hour he was replaced by another Golden-winged Warbler that sang from the same singing perches.

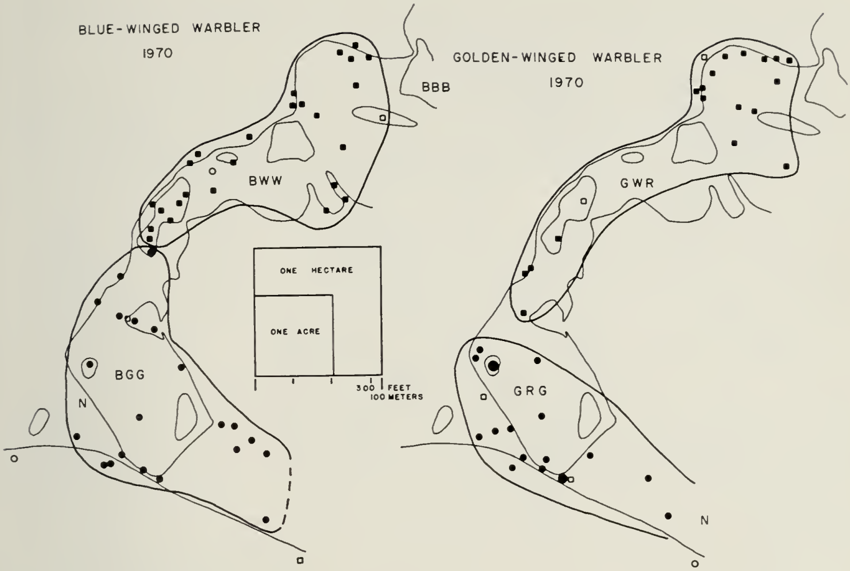

Fig. 4. Territories of Blue-winged and Golden-winged warblers at Island Lake in 1970. The symbols are the same as in Fig. 3, except that the Golden-winged Warblers are different birds. In 1970 G-GG sang throughout the area before disappearing just before the arrival of G-RG and G-WR.

Territory establishment continued through late May and early June. Later arrivals must either establish territories in peripheral, unoccupied areas or challenge already established territory holders. We observed both. The earlier arrivals (Table 1) occupied the central areas (Figs. 3 to 5), whereas most later arrivals occupied the periphery. We did observe 2 major challenges to territory holders in the swamp area. At Island Lake on 31 May 1969 a new male (later banded B-GY) appeared in B-GG's territory. After about one hour's encounter of continuous singing of muted Type I and Type II songs and chasing, B-GY established a small territory from which he excluded B-GG (Fig. 3), where he remained at least until we ceased observations in late June. On 9 June 1969 we watched another prolonged encounter, this time between B-RR and an intruder (later banded B-BG). B-BG apparently established dominance over B-RR because the former sang for a half hour or so without interruption and B-RR was unobserved. We set up a net and caught B-BG, unfortunately while he was being chased by B-RR who had reappeared. B-BG was not seen again, perhaps because of our interference.

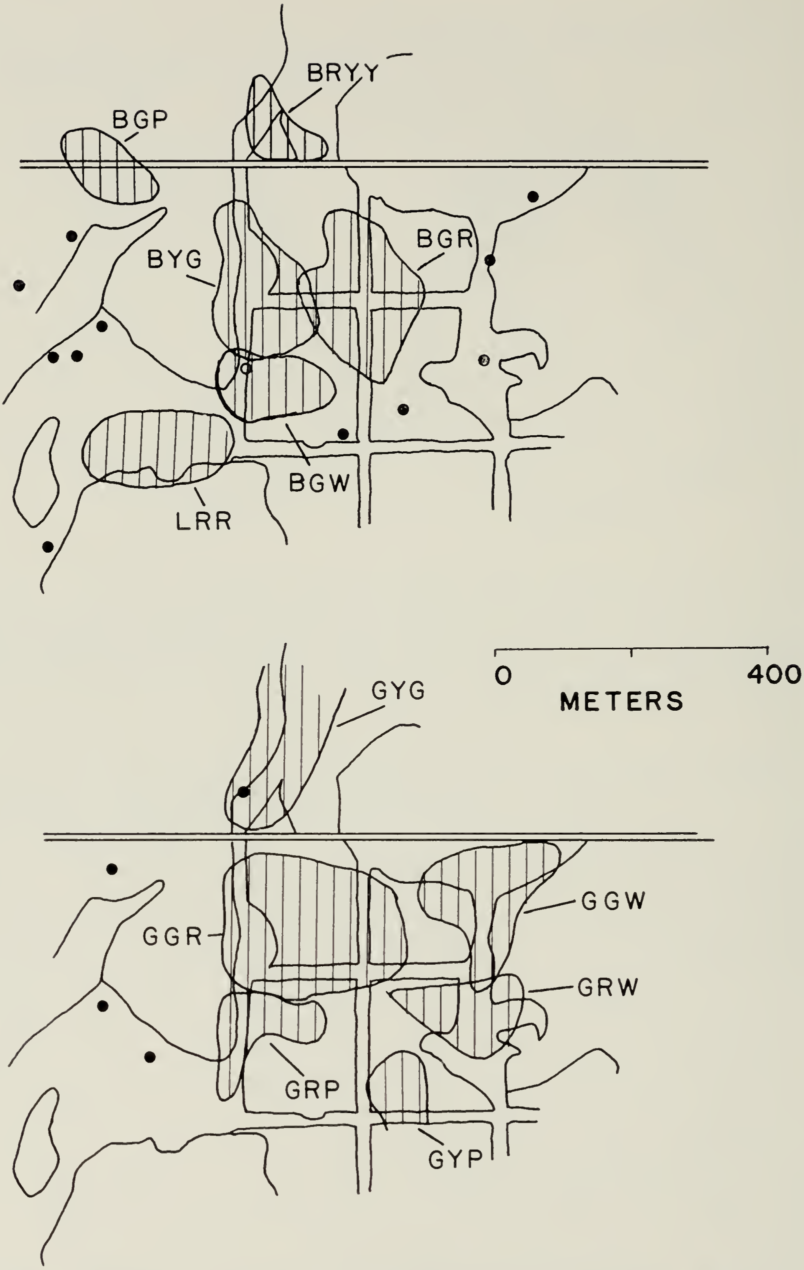

FIG. 5. Territories of *Vermivora* at the Burke Lake area in 1970. The territories are shaded areas superimposed over light lines outlining the major features of the habitat (see Fig. 2). The black dots represent sightings of unmarked Blue-winged Warblers (upper) and Golden-winged Warblers (lower).

TABLE 2

TERRITORY SIZE (HECTARES) OF *VERMIVORA* IN MICHIGAN

Blue-winged Warbler			Golden-winged Warbler		
			Island Lake		
	1969	1970		1969	1970
B-RR	1.5	—	G-YY	2.4	—
B-GG	1.9	2.1	G-GG	2.0	—
B-WW	1.3	1.6	G-RG	—	1.6
G-GY[a]	0.4	—	G-WR	—	1.7
			Burke Lake		
B-GR	—	3.0	G-GR	—	5.2
B-YG	—	2.6	G-GW	—	2.6
B-GW	—	1.5	G-YG	—	2.4+
B-GP	—	1.1	G-RW	—	1.6
			G-RP	—	1.4
			G-YP	—	0.8+
Lawrence's Warbler			Brewster's Warbler		
		2.2			0.9

[a] Established territory on 31 May in a portion of B-GG's territory.

Spatial Relationships

Blue-winged, Golden-winged, Brewster's, and Lawrence's warblers maintained typical Type A territories (Nice 1941) to which the males confined most, if not all, of their activities. As mentioned earlier, the territories of Blue-winged and Golden-winged warblers overlapped extensively (Figs. 3 to 5). The hybrids did not overlap with birds singing the same song—in these cases, the Blue-winged Warbler song. There was, however, a tendency for Blue-winged and Golden-winged warblers to sing primarily from different singing perches, as previously noted by Ficken and Ficken (1968a), despite our observations of individuals of both species at times singing near each other without apparent conflict. At times early in the season we did observe newly arrived Golden-winged Warblers to cause a shift in the singing perches of already established Blue-winged Warblers. This separation of primary singing areas within mutually held territories deserves further study.

Territories in Michigan are large, ranging from 1.3 to 5.2 ha (Table 2). At Island Lake where our measurement of territory size was more accurate than at Burke Lake, the average size of a Blue-winged Warbler territory was 1.8 ha and of a Golden-winged Warbler territory, 1.9 ha. At Burke

Lake territories averaged 2.0 to 2.7 ha, respectively, for Blue-winged and Golden-winged warblers.

At Island Lake we occasionally saw a Blue-winged Warbler or a Golden-winged Warbler trespassing on adjacent territories (Figs. 3 and 4). Sometimes a bird would be over 400 m from its own territory. These trespassing birds rarely sang and then never more than a few songs. One Golden-winged Warbler (G-YY) left his territory apparently to watch a fight between 2 Blue-winged Warblers on 31 May 1969.

We observed one other unusual incident. On 12 June 1969 we found B-RR singing normal Type I songs from near the center of his territory. He finally flew off and disappeared in the direction of B-GG's territory. After about 5 min he returned to his singing perch. This behavior was repeated several times during the next hour. We followed him and found that he was singing muted Type I songs at the southern edge of B-GG's territory, where a female Blue-winged Warbler was completing a nest. He swooped down at her on a 45° angle to the nest site and then returned to the center of his territory, where he continued singing normal Type I songs. Either B-RR was courting B-GG's female or his female was building in B-GG's territory. Whatever the case we did not see B-RR at this spot again, and a few days later the nest was deserted.

At Burke Lake each male restricted all of his activities to within his territory's boundaries. The only trespassing we recorded was by newly arrived birds; at least we sometimes originally caught a bird outside the area in which he subsequently established a territory.

By plotting activity spaces at Island Lake for each week in 1969 (Fig. 6) we note that the apparent activity space for each individual changes, which might imply changes in the boundaries of territories. These changes, though, seem to be the result of the males changing the places from which they sang most frequently because the entire season's activity spaces barely overlap (Fig. 3). If territory boundaries shifted during the season, we would expect to see broad overlap in the birds' seasonal activity spaces, as is the case in the one proved territory boundary change—B-GY's encroachment of B-GG's territory (Figs. 3 and 6). Such results emphasize the need for long-term intensive observation in studies of territorial behavior in birds.

Territorial Aggression

In natural encounters between Blue-winged Warblers, between Golden-winged Warblers, and interspecifically, the form in which aggression was expressed is characterized only by its diversity. Encounters varied in length from a few seconds to at least an hour, in activity from simply sing-

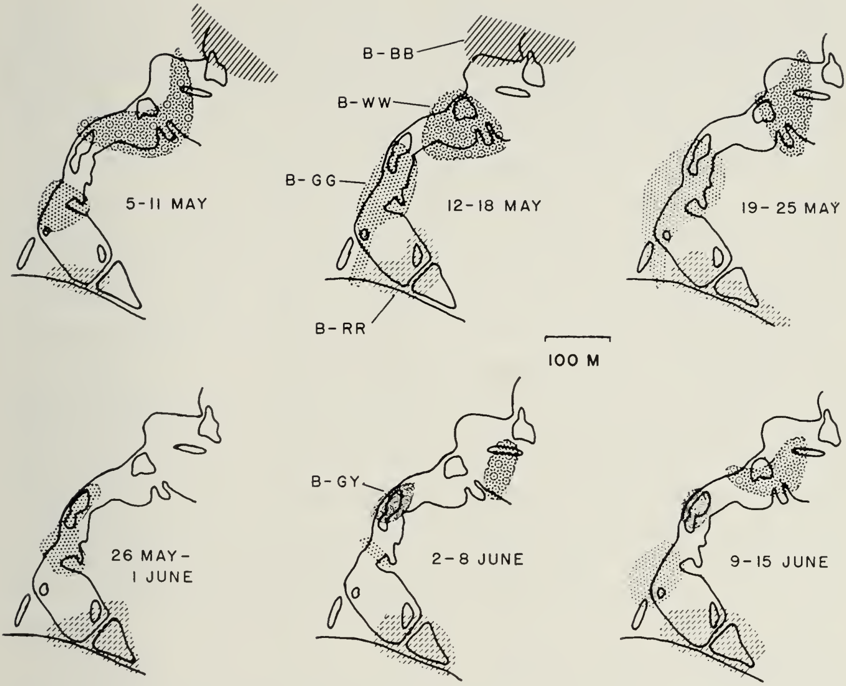

Fig. 6. Week by week "changes" in the mapped territories of Blue-winged Warblers at Island Lake in 1969. B-GY's activity on 31 May and 1 June is not included but was restricted to the area indicated for 2 to 15 June.

ing at each other while remaining relatively motionless to vigorous "supplanting," "flying past," or "fighting" (the terms are fairly descriptive and have been defined by Ficken and Ficken 1968a), and in associated vocalizations from chip notes to primary and secondary songs (either one or another or both) at different intensities (either muted or normal).

In order to demonstrate this diversity we describe below several of these encounters.

Between Blue-winged Warblers.—On 8 May 1969 at Island Lake B-BB was singing Type I songs when an unbanded Blue-winged Warbler sang Type II songs. B-BB gave chase with loud chips and buzz-chips almost landing on the other bird before being repulsed. Immediately both birds began foraging quietly.

On 20 May 1969 B-RR and B-GG engaged in a long encounter in an area that we have mapped as part of B-GG's territory. It began with B-RR chipping near a female Blue-winged Warbler. B-GG appeared without a sound, and the chase began, in circles and up and down through the trees with B-GG doing most of the chasing. Only chips were given by both birds until they disappeared. Then, B-GG reappeared and gave 3 muted primary songs with long intervals between. B-RR came back and was immediately chased by B-GG. Then, B-RR returned and gave 3 primary songs. We did not see B-GG, and the encounter ended.

Later, on 23 May these birds battled again. B-GG began singing Type II songs, which were answered by B-RR singing Type II songs. There followed a series of buzz-chips but the birds could not be seen. Finally B-GG disappeared, and B-RR started singing Type II songs again. (We mapped this spot as part of B-GG's territory because B-RR was seen here and in surrounding areas only rarely compared with B-GG.)

On 31 May 1969 at Island Lake we observed a new arrival (later banded B-GY) establish a territory in the northern portion of B-GG's territory. This encounter lasted over 45 min. It consisted of vigorous chasing and flying past with few direct supplanting attacks. Both birds sang and called continuously a mixture of muted Type I songs, Type II songs, and chips. Finally B-GG left the area, and B-GY took full possession, singing normal Type I songs. (At one time BGM was watching the encounter across a small clearing from G-YY, who was also watching the encounter, and incidentally was far outside his own territory.)

We observed a similar encounter on 9 June 1969 at Island Lake between B-RR and another intruder (later banded B-BG). We thought this encounter had the same result because B-BG was finally singing normal Type I songs without interruption by B-RR. We put up a net and caught B-BG, unfortunately when he was being chased by B-RR, who had apparently only taken a rest. B-BG disappeared, and B-RR continued singing muted Type I songs and Type II songs.

On 19 May 1970 at Burke Lake only Type I songs were heard in a singing duel between B-YG and another Blue-winged Warbler.

Between Golden-winged Warblers.—On 31 May 1970 at Burke Lake G-GR and G-RP engaged in a vocal duel at the boundary of their territories. For almost 12 min the 2 birds sang near each other, each singing muted and shortened (2 or 3 notes) Type I songs. There was no chase. Eventually they both moved off toward the centers of their territories, singing louder. As they moved apart G-RP attacked a male Cerulean Warbler (*Dendroica cerulea*).

On 27 May 1970 at Island Lake an incident occurred that involved G-RG, G-WR (which sang Blue-wing songs), certainly another but unidentified Golden-winged Warbler, and an unidentified Blue-winged Warbler. G-RG was singing Type I songs from within his territory but began chipping and chased a bird into the shrubbery. A Blue-winged Warbler appeared and departed. Then G-RG began singing Type I songs again. Another Golden-winged Warbler, not seen, began singing Type I songs. Both stopped. There followed a long bout of Type II songs, which ended with a chase, the second bird this time being G-WR outside his territory. Upon G-WR's departure, G-GR again began singing Type I songs.

Between Golden-winged Warblers and Blue-winged Warblers.—As reported by Ficken and Ficken (1968a) and by us elsewhere (Gill and Murray 1972b), male Golden-winged and Blue-winged warblers by and large ignore each other. We did observe, however, on several occasions aggressive interaction between these species, most of which were of short duration (a few seconds). All encounters involved the displays and vocalizations described above for intraspecific encounters. At least one male Golden-winged Warbler (G-GR at Burke Lake) was persistently and vigorously aggressive toward Blue-winged Warblers. A Blue-winged Warbler (B-YG) established a territory that was almost entirely overlapped by G-GR's (Fig. 5). Whenever B-YG sang Type I songs from the central portion of his territory he was attacked within a minute or so by G-GR. Eventually B-YG became quite inconspicuous, singing infrequently and only on occasion being detected by us.

Another Blue-winged Warbler (B-GR) became increasingly aggressive toward G-GR as the season progressed, but his territory was largely outside G-GR's (Fig. 5). On 17 May 1970 we observed B-GR sitting or foraging silently while nearby G-GR sang Type I songs for 15 min. As soon as G-GR moved away, B-GR began singing Type I songs. By 31 May B-GR was equally as aggressive as G-GR, and they could be seen almost any evening after that in aggressive encounters. Encounters in the morning were rare.

On another occasion a territorial Blue-winged Warbler (B-GP) remained silent while an unbanded Golden-winged Warbler sang from the former's usual singing perch.

In 1971 at Burke Lake, G-GR was challenged by 2 different Blue-winged Warblers. When he returned on 11 May a new Blue-winged Warbler had already established a territory that included G-GR's major 1970 singing perches. This area was disputed with G-GR subordinate but persistent until 14 May when he appeared to have established dominance, the Blue-winged Warbler moving to an adjacent area. On 20 May (BGM missed 2 days) B-GR had returned and was definitely dominant over G-GR. B-GR was singing loudly both song types without interference, and G-GR sang only occasionally. On 22 May, G-GR had re-established dominance in his territory, with B-GR moving slightly to the east, where he was apparently tolerated by G-GR. In 1970 B-GR would have been chased from this area by G-GR.

Of particular interest is a series of encounters between a Blue-winged Warbler (B-WW) and a bird (G-WR) with Golden-winged Warbler plumage (hybrid index 14) but Blue-winged Warbler Type I song and Golden-winged Warbler Type II song (see Table 1 and Fig. 3 in Gill and Murray 1972a). On 1 May 1970 B-WW established a territory in the area he held in 1969 (Figs. 3 and 4), and on 18 May G-WR arrived on B-WW's territory. Murray observed this bird (G-WR) and B-WW from 07:50 through 09:45. During this time G-WR sang from aspens and oaks bordering a swampy opening. Three times B-WW flew into G-WR's tree from a spot over 100 m away. B-WW flew from branch to branch within the tree, singing Type I songs all the while, for 5 to 15 min before leaving the tree. Within 30 min B-WW returned to the tree and repeated his previous performance. Evidently B-WW was responding to G-WR's Blue-wing-like song Type I but did not respond to G-WR's Golden-wing-like plumage. B-WW never seemed to locate the singer because he never approached G-WR closely. Instead he moved about within the tree, appearing to be searching for the singer, which normally would have a Blue-wing-like plumage. Normally, a response to Type I song leads to a "supplant" or "chase" of the intruder.

G-WR completely ignored B-WW's presence, at least there was no observable change in his behavior after B-WW arrived in the tree or after he departed from the tree.

When away from the tree B-WW was usually quiet and evidently nervous (before he discovered G-WR's presence Murray remarked in his field notes on B-WW's unusual behavior).

On 20 May Gill was observing B-WW foraging and chipping when G-WR began singing Type I songs nearby. B-WW immediately froze, into "study behavior," sitting motionless and only occasionally singing muted "*beee*" notes of the Type I song. G-WR left shortly, and B-WW moved off.

On 20 May Murray did see G-WR "chase" a Blue-winged Warbler, which probably had intruded G-WR's individual distance. As G-WR was foraging quietly in the top of a little oak, an unbanded and quiet Blue-winged Warbler (probably a female) moved upward through the tree with several short flights. It directly approached G-WR, who responded by "supplanting." The Blue-winged Warbler moved about 3 m and was again "supplanted" by G-WR, flying to the other side of the tree. It then flew away.

On 28 May Gill observed both G-WR and B-WW singing loud Type I songs within 10 m of each other for nearly 5 min. There was no interaction, both birds giving the appearance of coexistence without conflict.

The responses of both B-WW and G-WR to Blue-wing and Golden-wing Type I and Type II songs were tested experimentally with playbacks of tape-recorded songs (see Gill and Murray 1972b for details). B-WW did not respond to Golden-wing Type I but responded strongly to Blue-wing Type I and both Blue-wing and Golden-wing Type II songs. We interpreted this as indicating an ability to discriminate species by their Type I songs but not by their Type II songs (Gill and Murray 1972b).

The response of G-WR provided a surprise. On 18 May Gill's first playback was a Golden-wing Type I song, "heterospecific" to its own song type, to which G-WR responded strongly. A second test on 19 May presented the sequence: at 08:00, Blue-wing Type I followed by Golden-wing Type I; at 08:45, Blue-wing Type II followed by Golden-wing Type II. In each experiment G-WR did not respond in any way to Blue-winged Warbler songs and responded strongly to both types of Golden-winged Warbler songs.

On 21 May Gill played back to G-WR a recording of his own Type I song without response.

An experiment on 29 May had B-WW responding strongly to playback of Blue-winged Warbler Type I songs while ignoring, or not responding to, G-WR, which was singing Blue-wing Type I songs about 30 m away. This differential response of B-WW to Blue-wing Type I songs is consistent with his behavior of the previous day when both B-WW and G-WR were singing near each other without conflict.

Unfortunately we did not play back G-WR song to B-WW.

Encounters involving hybrid phenotypes.—On 10 June 1969 two birds were singing Type II songs near Burke Lake. Finally a Blue-winged Warbler flew away. The remaining bird was a Lawrence's Warbler.

On 12 May 1970 at Island Lake a Brewster's Warbler appeared in B-BB's territory, giving loud chips. B-BB responded by giving 2 muted Type I songs and chasing the Brewster's Warbler briefly. The Brewster's Warbler moved off, and B-BB sang a few more Type I songs.

On 27 May 1970 near Island Lake a Brewster's Warbler (Br-RR) was singing Blue-wing Type I songs from an exposed perch about 13 m above the ground. A Golden-winged Warbler (G-WW) that had been singing across a clearing came closer and eventually took a position 6 m directly above Br-RR, who took no notice of G-WW until the latter attacked by diving (Diving Attack of Meyerriecks and Baird 1968). Br-RR dropped straight downward into the brush with G-WW not far behind. No other activity or sound was noted for 15 min after the attack.

Aggression with other species.—Blue-winged and Golden-winged warblers engaged in brief encounters with individuals of a wide variety of other species. In almost all cases, the former were the aggressors. We saw male Blue-winged Warblers chase a female Cerulean Warbler, a Magnolia Warbler (*Dendroica magnolia*), and an American Goldfinch (*Spinus tristis*), which however did not move. Blue-winged Warblers were chased 3 times by goldfinches and supplanted once by an Indigo Bunting (*Passerina cyanea*).

Male Golden-winged Warblers attacked a Cerulean Warbler, Northern Parula (*Parula americana*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Yellowthroat (*Geothlypis trichas*), Indigo Bunting (both male and female), a goldfinch (without effect), Field Sparrow (*Spizella pusilla*), and Red-eyed Vireo (*Vireo olivaceus*). We saw none of these species or any other species chase Golden-winged Warblers.

Reproductive Behavior

The courtship sequence begins with a female Blue-winged or Golden-winged warbler approaching a singing male. Typically, the male is singing Type I songs from a perch in a tree, and the female is lower in the underbrush, often giving "*Buzz-chip*" notes (= *Tzip* of Ficken and Ficken 1967) that closely resemble the location and begging notes of fledglings. The male stops singing, stares intently downward at the female, and finally dives at and chases her. Subsequent interactions between the male and female are variable and include Bill Duelling, Gliding, and Moth Flight, as well as Soliciting and Copulation (see Baird 1967, Ficken and Ficken 1968b).

We observed what appeared to be ritualized Nest Site Prospecting in one pair of Blue-winged Warblers and one pair of Golden-winged Warblers. The male leads the female from one clump of vegetation to another. The male flies between clumps with a Moth Flight and after landing, pivots slowly around his perch like a mechanical toy with feathers fluffed (see Baird 1967) about 180° until facing the female, who is investigating the previous clump.

We did not observe courtship feeding, but BGM did see a male Golden-winged Warbler feed a female, who was sitting on a nest with recently hatched young, several times within one hour.

Nest Site Location

All 6 nests that we were able to find were located at the periphery of a male's territory rather than near the center (Figs. 3 and 4). Males rarely, if at all, sang in the vicinity of the nest once incubation was underway.

TABLE 3

RETURNS OF BANDED MALE *VERMIVORA* IN MICHIGAN

Island Lake	1969 Banded	1970 Returned
Blue-winged Warbler	10	5[a]
Golden-winged Warbler	5	3
Brewster's Warbler	1	1

Burke Lake	1969	1970		1971
	Banded	Returned	Banded	Returned
Blue-winged Warbler	0	—	5	1
Golden-winged Warbler	0	—	6	5[b]
Brewster's Warbler	1	0	1	1
Lawrence's Warbler	1	1	0	1

[a] Includes one bird rediscovered in 1970, 10 km from place of banding.
[b] Includes G-R, assumed to be G-RP.

Return Rates of Adults

The survival of adults from one year to the next is difficult to estimate. One male disappeared in 1969 only to be found nearby in 1970 when we expanded coverage into a new area. Even more surprising was the discovery of another male about 9.6 km distant from its 1969 territory. Considering only those birds in our intensively studied areas, the return rate was about 60% (Table 3), virtually the same as that reported by Mayfield (1960) for the Kirtland's Warbler (*Dendroica kirtlandii*). If we include the more distant returns, the survival rate of adults would be higher.

DISCUSSION

Basically our results confirm those of Ficken and Ficken (1968a) regarding the fact that male Blue-winged and Golden-winged warblers treat each other as distinct species and thus have largely overlapping territories where they occur together. We also agree that singing perches within mutually held territories tend to be separate though certainly not exclusive. Because we watched more birds than the Fickens did, we discovered that on occasion males do engage in persistent interspecific aggression, that is, some males of one species treat the males of the other species as if they were conspecific. This should not be too surprising inasmuch as we already know that the males and females of these hybridizing species sometimes respond to members of the other species as conspecifics.

In details our observations differ from those of Ficken and Ficken, who studied both species in central New York. These differences may reflect actual differences between geographically separate populations, or they may reflect the fact that our sample sizes are larger, our observations on some but certainly not all aspects were more intense, and we studied marked individuals.

For instance, Ficken and Ficken (1968a) state that "territories were roughly mapped by observing the positions of males for at least two days and usually over a period of several weeks," that the "Size of territories varied from less than one acre to almost two acres," and that "Both sexes confined all their activities to the territory from the time of arrival until the young were fledged." With our marked birds we found the territories of both the Blue-winged and Golden-winged warblers to vary between 1.3 and 4.9 ha (Table 2). We believe that had we not banded B-WW we could have easily considered his territory in 1969 to have been occupied by 2 males, one on either side of the wall of tamaracks and other trees that bisected his territory (Fig. 3). In another case, G-GG sang primarily in the southern portion of his territory and sporadically in the northern portion (Fig. 3). He certainly would have been considered 2 birds. Another Golden-winged Warbler (G-WR) had disjunct singing areas (Fig. 4), although we could have detected this because of his unique song.

As shown in Figures 3 and 4, some males at least were infrequent visitors to other males' territories, and surprisingly we saw B-RR courting a female building a nest in another male's territory, an event we could not have guessed by watching unmarked birds.

These and some other differences between the results of Ficken and Ficken and of ourselves cannot be resolved without further work with color-marked birds in other populations.

On the other hand some differences are undoubtedly real. Ficken and Ficken (1968a) state that "Song is usually absent during encounters and is only resumed after a few minutes, typically when one of the encountering birds has left the area." In Michigan aggressive encounters almost always included vocalizations. A particular encounter may have included one or more vocalizations, including normal Type I, muted Type I, Type II songs, and chips. In contrast to the situation in both New York and Michigan, Meyerriecks and Baird (1968) report that in Massachusetts "Singing was a predominant feature of the overall agonistic situation, but other vocalizations were remarkably infrequent" between a Brewster's Warbler and a Blue-winged Warbler.

The territories of Michigan Blue-winged and Golden-winged warblers are larger than those of other Blue-winged Warbler populations, which averaged 1.0 ha on Long Island (Gill, unpubl. data) and under 0.8 ha in central New York (Ficken and Ficken 1968a), as well as those of most other parulid species that have been studied (summarized by Mayfield 1960: Table 4). An exception is the Kirtland's Warbler, whose measured territories averaged 3.4 ha.

The pattern of territorial establishment by arriving males, such as we noticed in these warblers, has been observed in a variety of other species, including some parulids (Ficken and Ficken 1962). Generally it seems that early arriving individuals establish themselves on better quality territories. The basis for this conclusion is primarily the tendency for peripheral males to shift to central territories when opportunities arise and in the greater fluctuations in occupation of peripheral territories (Brown 1969), because suitable measures of territory quality are rarely achieved.

The occurrence of interspecific aggression in natural situations confirmed our experimental results on interspecific discrimination using tape-recorded playbacks—81% did not respond to heterospecific song (Gill and Murray 1972b)—assuring us that this technique, used earlier by Gill and Lanyon (1964) and Ficken and Ficken (1969) is justified, at least in these species.

Interspecific aggression between Blue-winged and Golden-winged warblers did not result in mutually exclusive territories. In one case B-YG reduced his singing and conspicuousness greatly as a result of G-GR's persistent aggression, and thus each was able to maintain largely overlapping territories (Fig. 5). In the other case, B-GR and G-GR had established territories that only partially overlapped (Fig. 5). These 2 birds were more aggressive toward each other than any other pair of *Vermivora* territory holders.

We are unable to confirm any pattern to the aggression between both *Vermivora* species and other species that was reported by Ficken and Ficken (1968a). These interspecific encounters are more complex than any theory suggesting similarities of color or pattern can predict. The very few encounters between male Blue-winged and Golden-winged warblers and hybrid phenotypes we observed also did not confirm the suggestion of Ficken and Ficken (1968a) that facial pattern more than song type determined who was aggressive toward whom.

Species discrimination and hybridization

The study of avian vocalizations has focused on the ontogeny of the sounds themselves (Lanyon 1960, Marler 1964, Konishi and Nottebohm 1969), on the effects of vocalizations on conspecific receivers (Marler 1956, Weeden and Falls 1959, Falls 1963, 1969), and on whether individuals of hybridizing species could distinguish heterospecific from conspecific song (Lanyon 1957, Gill and Lanyon 1964, Ficken and Ficken 1967, Gill and Murray 1972b, Kroodsma 1974, Emlen et al. 1975). We ask the question: How does an individual of species A develop species-specific responses to the vocalizations of species A rather than to those of species B, C, or D? Or, more specifically: why do some Blue-winged Warblers and Golden-winged Warblers respond only to conspecific song and others respond to both conspecific and heterospecific song?

The behavioral interactions of B-WW and G-WR are of special interest in this regard, as they constituted a kind of natural experiment in which a living bird (G-WR) combined the species-specific signals of 2 species.

G-WR was a Golden-winged Warbler in plumage and Type II song and a Blue-winged Warbler in his Type I song. It responded selectively to vocalizations usually associated with its plumage type but not at all to its own song Type I. This indicates that the ontogeny of its species-specific vocalization is independent of the ontogeny of species-specific *responses* to species-specific vocalizations. Whatever are the genetic and environmental variables that influence the acquisition of species-specific song, they are not the same genetic and environmental variables that influence the development of responses to those songs, unless these are acting during different critical periods.

The behavior of the Blue-winged Warbler B-WW is also enlightening. B-WW responded aggressively to the Blue-wing-like vocalizations of the Golden-winged Warbler G-WR by flying toward the singing G-WR from a great distance (over 100 m). But this aggressive behavior was never reinforced by the presence of an intruder with the appropriate, aggression-stimulating visual signal—Blue-wing-like plumage. Eventually B-WW ceased responding to G-WR's song, while still responding aggressively to playback of Blue-winged Warbler song.

Generalizing, we suggest that an individual bird may come to recognize "species"—that is, respond selectively to conspecific individuals—by the responses it generates in conspecific and heterospecific individuals. One example, of many imaginable examples, is the following: an inexperienced bird responds to a variety of similar stimuli in its environment, both appropriate and inappropriate. Response to appropriate (species-specific) stimuli results in a species-specific sequence of behavior, whereas response to inappropriate (not species-specific) stimuli does not because the inappropriate signaler does not respond to the signals given by the inexperienced bird. Because of this differential response from appropriate and inappropriate signalers, the inexperienced bird learns to respond only to appropriate (conspecific) signalers.

Such a notion is consistent with our interpretation of the difference in responsiveness of different Blue-winged Warbler populations to heterospecific songs (Gill and Murray 1972b). The Long Island population (Gill and Lanyon 1964) and Maryland population (Ficken and Ficken 1967) are more responsive to playback of Golden-wing song, where Golden-winged Warblers are rare, than are the Michigan populations (Gill and Murray 1972b), where Golden-winged Warblers are abundant. We suggested that Blue-winged Warblers are less responsive to playbacks of Golden-winged Warbler songs in Michigan than in areas of allopatry because, where sympatric, they have an opportunity to respond to acoustic signals which are similar to their own acoustic signals, but which usually do not lead to appropriate species-specific sequences of behavior (i.e., aggressive encounters) because of their distinctive plumages.

Nevertheless, species discrimination breaks down from time to time, even between species that seem sufficiently different to prevent mixed matings. A contributing factor may be the rarity of one species (Mayr 1963), especially as it expands its range into the range of another species. Mixed matings produce hybrids, if they produce any offspring, and these hybrids are intermediates, which may respond to either one of the parental species or to both. Hybrids, then, can provide noise in a system in that they might interfere with normal development of species-specific responses of progeny of matings between conspecifics. For instance, a Brewster's Warbler singing a Golden-wing song might combine a visual, aggression-stimulating cue of one species and an acoustic, aggression-stimulating cue of the other species, and it might respond aggressively toward either one or perhaps both of the parental types. An inexperienced progeny of conspecific parents could learn to respond to non-species-specific cues as a result of an interaction with a hybrid. Many combinations of events are imaginable, and this may explain the diversity of aggressive interactions we observed: a non-singing Brewster's Warbler was attacked by a singing Blue-winged Warbler; a Golden-winged Warbler attacked a Blue-wing-singing Brewster's Warbler, which in no way responded to the approaching Golden-winged Warbler until it fled from the direct attack; mutual aggression occurred between a Blue-winged Warbler and a Lawrence's Warbler, singing Blue-wing song; a Golden-winged Warbler was aggressive toward both Blue-winged and Golden-winged warblers; and the Blue-winged Warbler attacked by the Golden-winged Warbler became aggressive toward that Golden-winged Warbler.

As the rare species becomes commoner, the frequency of hybridization could decrease as birds have a greater opportunity to develop species-specific responses and to find conspecific mates, although when progeny of mixed matings are viable the initial noise in the system could persist for some time, if not indefinitely.

The hybridization of *Passerina* (Emlen et al. 1975) contrasts with that of *Vermivora.* Indigo Buntings (*P. cyanea*) and Lazuli Buntings (*P. amoena*) are not responsive to heterospecific song where allopatric, but they are where sympatric. And, whereas Blue-winged and Golden-winged warblers maintain overlapping territories with little conflict, the buntings and their hybrids maintain mutually exclusive territories. Nevertheless, Emlen et al. (1975:170) developed a model similar to ours: "that an individual bunting's behavior, upon hearing a heterospecific song, is determined by its prior behavioral experience with birds of the opposite species or song type." They also suggested (p 171) the possibility of "the existence of 2 separate processes in the ontogeny of bunting song: one associated with learning song *utterances* and another with song *recognition*" (emphases theirs).

Curiously, Emlen et al. (1975:172) concluded that response to heterospecific individuals, in places where the 2 species hybridize, is selected for because "we believe that this 'misidentification' is adaptive in promoting the establishment and maintenance of interspecific territories," contrary to the assumption of Murray (1971) that interspecific territoriality is most often misdirected intraspecific territoriality, resulting when 2 species share similar features that stimulate intraspecific territorial aggression, because of common ancestry, convergence, or accident. Interspecific territoriality between males of hybridizing populations seems most clearly to be the result of errors in the development of species-specific responses to both species-specific and non-species-specific stimuli.

We have generalized an observation into a model of the ontogeny of species discrimination. However, we also recognize that, just as the ontogeny of vocal development ranges from birds which develop species-specific vocalizations without hearing conspecifics, to birds which normally copy songs from conspecifics (Konishi and Nottebohm 1969), species discrimination may sometimes develop in birds without contacting either conspecifics or heterospecifics and may sometimes develop as a consequence of complex interactions between a bird and other individuals, conspecifics, heterospecifics, or both.

SUMMARY

We studied populations of color-marked Blue-winged, Golden-winged, Brewster's, and Lawrence's warblers at 2 places in south-central Michigan in 1969, 1970, and 1971. The birds arrived in late April or early May, but some individuals appeared on and competed for territories as late as early June. Arrival dates for the species broadly overlapped with only a few Blue-winged Warblers appearing before the earliest

Golden-winged Warblers. The territories of Blue-winged and Golden-winged warblers broadly overlapped in habitats occupied by both species. As expected from playback experiments most individuals discriminated, or at least did not respond to, the other species. Few birds were persistently interspecifically aggressive.

The intraspecific and interspecific aggressive behaviors of these warblers are described in some detail. They are characterized by their diversity in duration, intensity, and associated vocalizations. The interactions between a Blue-winged Warbler and a Golden-winged Warbler with Blue-wing Type I song proved of particular interest. We suggest the possibility that the development of species discrimination in males involves, in part, the kinds of responses the birds generate in other birds.

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LITERATURE CITED

Baird, J. 1967. Some courtship displays of the Golden-winged Warbler. Wilson Bull. 79:301–306.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293–329.

Emlen, S. T., J. D. Rising, and W. L. Thompson. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87:145–179.

Falls, J. B. 1963. Properties of bird song eliciting responses from territorial males. Proc. 13th Int. Ornithol. Congr., 259–271.

———. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207–232 *in* Bird Vocalizations (R. A. Hinde. ed.). Cambridge Univ. Press, London.

Ficken, M. S. and R. W. Ficken. 1962. The comparative ethology of the wood warblers: a review. Living Bird 1:103–122.

———. 1967. Singing behaviour of Blue-winged and Golden-winged warblers and their hybrids. Behaviour 28:149–181.

———. 1968a. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers and their hybrids. Wilson Bull. 80:442–451.

———. 1968b. Courtship of Blue-winged Warblers, Golden-winged Warblers, and their hybrids. Wilson Bull. 80:161–172.

———. 1969. Responses of Blue-winged Warblers and Golden-winged Warblers to their own and the other species' song. Wilson Bull. 81:69–74.

Gill, F. B. and W. E. Lanyon. 1964. Experiments on species discrimination in Blue-winged Warblers. Auk 81:53–64.

Gill, F. B., and B. G. Murray, Jr. 1972a. Song variation in sympatric Blue-winged and Golden-winged warblers. Auk 89:625–643.

——— and ———. 1972b. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. Evolution 26:282–293.

Konishi, M. and F. Nottebohm. 1969. Experimental studies in the ontogeny of avian vocalizations. Pp. 29–48 *in* Bird Vocalizations (R. A. Hinde, ed.), Cambridge Univ. Press, London.

KROODSMA, R. L. 1974. Species-recognition behavior of territorial male Rose-breasted and Black-headed grosbeaks (*Pheuticus*). Auk 91:54–64.

LACK, D. 1944. Ecological aspects of species-formation in passerine birds. Ibis 86:260–286.

———. 1971. Ecological Isolation in Birds. Harvard Univ. Press, Cambridge, Mass.

LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publ. Nuttall Ornithol. Club, no. 1.

———. 1960. The ontogeny of vocalizations in birds. Pp. 321–347 *in* Animal Sounds and Communication (W. E. Lanyon and W. W. Tavolga, eds.). AIBS, Washington.

MARLER, P. 1956. Behaviour of the Chaffinch, *Fringilla coelebs*. Behaviour, Suppl. 5.

———. 1964. Inheritance and learning in the development of animal vocalizations. Pp. 228–243 *in* Acoustic Behaviour of Animals (R. G. Busnel, ed.). Elsevier Publ. Co., Amsterdam.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Instit. Sci. Bull. no. 40.

MAYR, E. 1963. Animal Species and Evolution. Harvard Univ. Press, Cambridge, Mass.

———. 1970. Populations, species and evolution. Harvard Univ. Press, Cambridge, Mass.

MEYERRIECKS, A. J. AND J. BAIRD. 1968. Agonistic interactions between Blue-winged and "Brewster's" warblers. Wilson Bull. 80:150–160.

MURRAY, B. G., JR. 1971. The ecological consequences of interspecific territorial behavior in birds. Ecology 52:414–423.

NICE, M. M. 1941. The role of territory in bird life. Am. Midl. Nat. 26:441–487.

SHORT, L. L., JR. 1963. Hybridization in the wood warblers *Vermivora pinus* and *V. chrysoptera*. Proc. 13th Int. Ornithol. Congr., 147–160.

———. 1969. Taxonomic aspects of avian hybridization. Auk 86:94–105.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual selection and hybridization in birds. Condor 59:166–191.

WEEDEN, J. S. AND J. B. FALLS. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

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COMPARATIVE BREEDING ECOLOGY OF PHOEBES IN TRANS-PECOS TEXAS

Harry M. Ohlendorf

The Black Phoebe (*Sayornis nigricans*) and Say's Phoebe (*S. saya*) occur sympatrically in an area from western Texas and north-central Mexico to California. In addition, each of the species is found over a relatively wide range; Black Phoebes occur as far south as Argentina and Say's Phoebes nest in northern Alaska.

I conducted a field study to quantify the phoebes' use of resources in the area of overlapping occurrence. My approach was to consider the use of different resources, of the same resources at different places, and of the same resource in different ways. The objective was to determine which of these factors facilitate the sympatric occurrence of Black and Say's phoebes in the Trans-Pecos region.

METHODS AND STUDY AREA

Methods.—I conducted field work from June through August 1969 and May through August 1970, with supplemental observations in November 1970 and May 1971. I travelled throughout the Trans-Pecos area to determine the geographical and ecological distribution, nesting habits, and food consumption of the phoebes, as well as to study the habitat types of the area. Detailed studies were carried out at selected sites. Literature and museum locality records supplement my distributional data.

Phoebes were banded with colored plastic, and aluminum Fish and Wildlife Service, leg bands to learn about daily activities of individuals, including behavior toward other flycatchers. I caught adults with an insect net at their roost sites after dark; others were banded as nestlings.

Specimens for food analysis were shot. Food items were identified, counted, and then measured by volumetric displacement. The material contained in the stomach (proventriculus and ventriculus) of an individual bird is defined here as a sample. I also collected samples of food delivered to nestlings using the pipe-cleaner collar devised by Orians (1966) and Willson (1966).

Habitat data were analyzed by appropriate methods presented in Snedecor and Cochran (1967). Means and 95% confidence intervals were calculated for measurement data, and chi-square and t-test analyses were generally used to determine statistical significance. Additional details concerning methods have been described previously (Ohlendorf 1974).

Study area.—The Trans-Pecos, an area of some 83,000 km^2, encompasses a variety of habitat types, including the most arid and the highest areas of the state. It is situated west of the Pecos River, north of the Rio Grande, and south of New Mexico.

Most of the region is drained by the Rio Grande, the Pecos River, and their tributaries. Several perennial streams, although small, provide water at isolated spots throughout the region. Rainfall for the Trans-Pecos region averages 30.5 cm

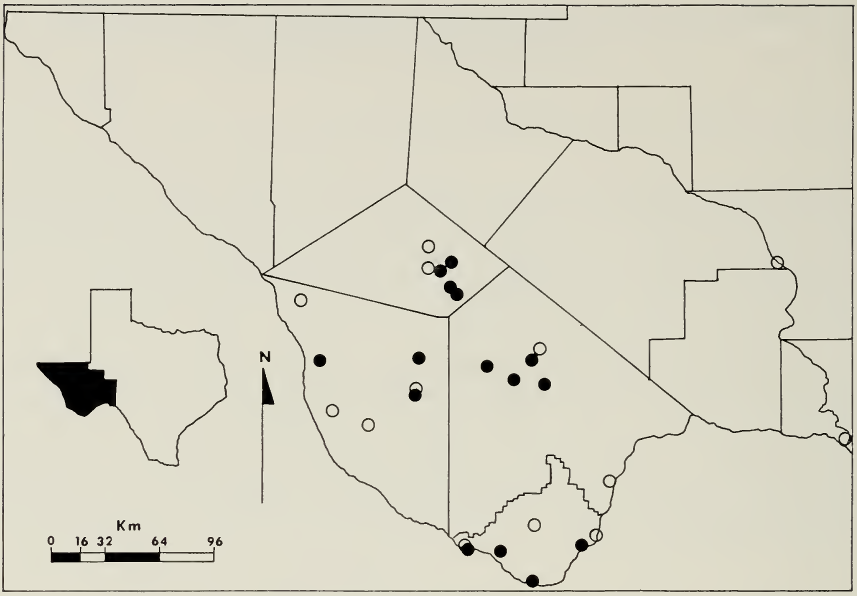

FIG. 1. Breeding distribution of Black Phoebes in the Trans-Pecos region. Filled circles represent nesting localities. Open circles represent locality records during the breeding season (10 April to 10 August) without observed nesting.

per year. Amounts are generally less at lower and greater at higher elevations, with a maximum of 45.7 cm in the Davis Mountains (Orton 1969).

The biota is typical of the Chihuahuan Desert (Blair 1950), and most of the area remains natural, but modified by grazing of livestock. Considerable vertical zonation exists in vegetative types. Desert shrub predominates up to 1200–1500 m; grassland and pine-oak-juniper types occur above this elevation. Cultivated areas are generally confined to irrigated valleys, e.g. at El Paso, Presidio, Balmorhea, and near Pecos.

DISTRIBUTION AND HABITAT

Both species of phoebes are near the margins of their distributions in the Trans-Pecos region. The area represents the northeastern limit for the Black and the eastern limit for Say's phoebe (A.O.U. 1957 and other sources). Farther north, the Eastern Phoebe (*S. phoebe*) occurs sympatrically with Say's Phoebe during the breeding season, but within my study area it occurs only as a winter resident (Wauer 1973).

The breeding distributions of the Black and Say's phoebes in the area were quite different (Figs. 1 and 2). Both species are resident, with individuals of the more northern populations (particularly Say's) also over-wintering in the Trans-Pecos region. Nest construction frequently

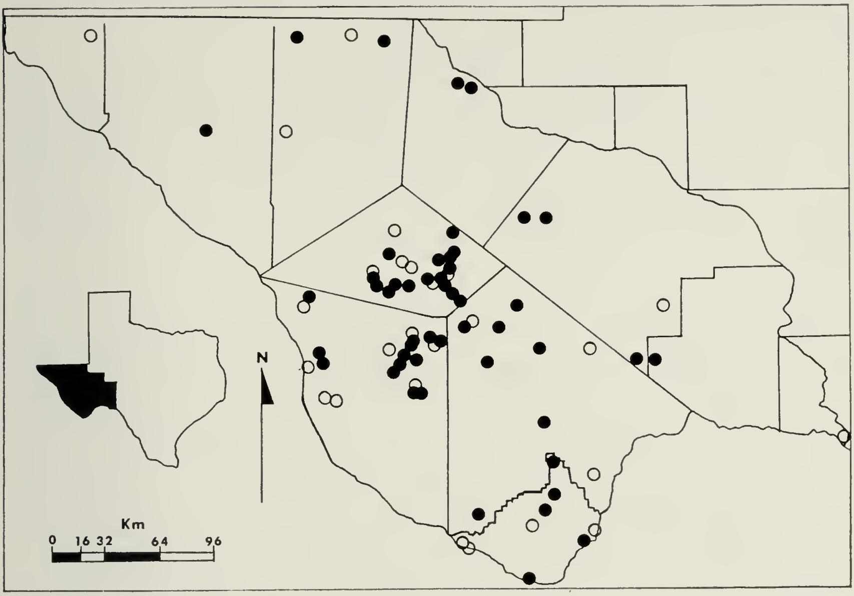

FIG. 2. Breeding distribution of Say's Phoebes in the Trans-Pecos region. Filled circles represent nesting localities. Open circles represent locality records during the breeding season (10 May to 10 August) without observed nesting.

begins in March, although it was observed at Fort Davis in February 1969 (Say's) by Pansy Espy (pers. comm.). Some migrant Black Phoebes are in the region until early April, and some Say's pass through until early May (Wauer 1973). Post-nesting dispersal from typical nesting situations occurs late in the summer, especially after early August. Therefore, I considered only localities at which the Black Phoebe was recorded from 10 April to 10 August, or at which Say's was recorded from 10 May to 10 August, as breeding localities. Nesting localities referred to in this paper are those at which nests, or fledglings incapable of extended flight, were found.

Nest data are based on the total number of nest constructions. Nests were frequently re-lined with fresh material and used for subsequent clutches, or new nests were sometimes constructed at a previously used locality. Counting each of these nest uses at a locality tends to reflect more nearly the relative importance of various habitat types than if the data were based merely on nesting localities.

Location of nests differed somewhat in respect to elevation, but the differences were not significant (χ^2, $P > 0.1$), based on 36 nestings of Black and 115 of Say's phoebes. The mean elevation for Black Phoebe nests was 1232 ± 86 m; Say's, 1297 ± 47 m.

Distributional differences in these species are due primarily to their differing habitat requirements, based on 35 nestings of Black Phoebes and 115 of Say's. The pine-oak-juniper and grassland types, in which 45.2% (52) of the Say's Phoebe nests occurred, were occupied primarily by this species. Distributional differences between the phoebes in the shared habitat types (i.e. desert shrub and riparian) are highly significant (χ^2, $P < 0.01$).

The Black Phoebe was restricted in nesting to areas with mud and suitable nesting substrate such as overhanging boulders, bridges, or culverts. The paucity of nesting records for this species reflects the scarcity of such habitat in the region. However, a nest may be constructed during one wet breeding season and then used again in subsequent dry ones. In one instance a pair of Black Phoebes began construction after a shower, but mud became too dry for completion. Construction resumed several days later when there was another shower, and the birds nested successfully.

One Jeff Davis Co. sight record for Black Phoebes was at 1737 m in the pine-oak-juniper type. Although nesting was not observed, I consider it probable that nesting does occur at these higher elevations where mud and nest substrate are available. The other breeding season locality in the county was in the riparian type flanked by grassland-oak. All of the nests recorded for the county were under bridges or in culverts in the grassland-oak type.

The occurrence of Say's Phoebe in all habitat types except farmland reflects its less restrictive requirements.

NESTING

Phoebes have benefited from man's construction of bridges, culverts, and buildings by having available an increased number of suitable nesting sites. I found many nests in habitat types that would otherwise have been unsuitable for phoebe nesting. Before man-made structures, both species probably nested only where there were vertical surfaces such as cliffs, rimrocks, steep creek banks, and caverns. Such substrates are rare over a great portion of the Trans-Pecos.

Black Phoebes build mud nests on vertical or near-vertical surfaces which are protected from rain. These sites must be within carrying distance of a source of mud. I did not find nests more than 15 m from mud. Say's Phoebes nest in holes, crevices, and on ledges and other protected horizontal surfaces of cliffs, rimrocks, steep creek banks, and caverns. They also use nests previously constructed by Cliff Swallows (*Petrochelidon pyrrhonota*),

Table 1

Nest Substrate Used by Phoebes

Substrate	Black	Say's
"NATURAL"	5 (13.9%)	9 (8.0%)
Boulder	3	1
Rimrock	1	1
Cavern	1	–
Gravel bank	–	6
Cliff	–	1
MAN-MADE STRUCTURES	31 (86.1%)	103 (92.0%)
Bridges	24	42
Structural	24	21
Cliff Swallow nests	–	18
Black Phoebe nests	–	3
Culverts	2	30
Structural	2	–
Cliff Swallow nests	–	22
Barn Swallow nests	–	5
Black Phoebe nests	–	3
Buildings	4	31
Unoccupied	4	25
Occupied	–	6
Well	1	–
TOTAL	36 (100.0%)	112 (100.0%)

Barn Swallows (*Hirundo rustica*) and Black Phoebes. Only when the Cliff Swallow nests had been broken into the form of a shelf were they used by Say's Phoebes. I do not know whether these nests were appropriated by the phoebes while still in use by the swallows. In this study I found 3 instances of nest reclamation by Cliff Swallows and Barn Swallows after use by Say's Phoebes. In each case the phoebes nested again in a similar nest at the same locality. In 2 cases, nests known to have been abandoned by Black Phoebes (but for unknown reasons) were used by Say's Phoebes.

Only 5 of 36 Black Phoebe nestings (13.9%) and 9 of 112 Say's Phoebe nestings (8.0%) occurred on "natural" substrates (Table 1). Nests of Black Phoebes on bridges and culverts were on vertical surfaces of structural elements. Those of Say's Phoebes were on guard rail supports or on other horizontal surfaces such as pillars and beams under the bridges. Culverts were composed of smooth vertical and horizontal surfaces devoid of structural features suitable for Say's nesting.

The relative use of natural, bridge, culvert, and building nest sites by the 2 species was significantly different (χ^2, $P < 0.01$).

Nests of both species were re-used for successive clutches in the same year, and in subsequent years. Many nest sites used in 1969 were also used in 1970, sometimes by the same birds. One Black Phoebe banded at Capote Canyon, northeast of Candelaria, in 1969 laid 2 clutches of eggs in that year and nested there again (same nest) in 1970. A similar observation was made in the case of Say's Phoebe at Plata.

Other data indicate a rapid replacement of birds at favored nest sites. Such replacement occurred in the case of a Black Phoebe at Plata after it was injured in a mist net. A nest in Capote Canyon that was used by Say's Phoebes in 1967 was used again in 1969 and 1970. Both adults of the pair were collected on 12 June 1969. Another pair of Say's was feeding nestlings in the same nest on 21 July. Southeast of Fort Davis, I collected an adult female and single nestling on 15 June 1969. An adult was carrying nesting material on 18 June and "improving" the same nest. On 22 June an adult was incubating 3 eggs and on 27 and 28 June 4 eggs were in the nest.

A pair of Say's Phoebes began construction about 6 March 1971 at a ranch house where nesting was recorded during previous seasons (Pansy Espy, pers. comm.). Eggs were laid from 20–24 March and the young were fledged on 29–30 April. At least one individual of this pair was replaced and 5 eggs had been laid in the same nest by 23 May. The replacement individual had been banded at this locality on 29 November 1970.

The mean height of Black Phoebe nests above ground or water (3.1 ± 0.7 m, range 0.3–10.7 m) was not significantly different from that of Say's (2.8 ± 0.3 m, range 1.2–12.2 m).

Nests of Black Phoebes were generally so widely separated that measurement was not meaningful, but in one case nests were separated by only 160 m. These 2 nests were under bridges located northeast of Fort Davis.

I recorded separation of Say's Phoebe nests by as little as 410 m at Capote Canyon. In 2 instances they were as near as 480 m at localities northeast of Fort Davis and north of Plata.

Only one nest of a particular species was ever located under a bridge or culvert, or at an isolated locality such as Plata, but there were 7 instances where the 2 species occurred relatively close to each other. At Capote Canyon, nests of Say's and Black phoebes were located as near as 390 m during both breeding seasons. The phoebes also nested close to each other at Plata (76 m), and under bridges north of Plata (56 and 61 m) and northeast of Fort Davis (23, 27, and 38 m). The species have nested within 15 m of each other in an abandoned building (Wauer 1973).

Table 2

Fate of 66 Phoebe Clutches

	Black	Say's
Number of clutches[1]	21	45
Eggs laid	75	169
Eggs per nest	3.57	3.76
Eggs hatched	69 (92.0%)	124 (73.4%)
Eggs hatched per nest	3.29	2.76
Eggs infertile	1 (1.3%)	12 (7.1%)
Eggs lost	5 (6.7%)	33 (19.5%)
Young fledged	53	96
Fledged per nest	2.52	2.13
Fledged of eggs laid	53/75 (70.7%)	96/169 (56.8%)
Fledged of eggs hatched	53/69 (76.8%)	96/124 (77.4%)
Young lost before fledging	16 (23.2%)	28 (22.6%)
Successful nestings[2]	15 (71.4%)	30 (66.7%)

[1] Excluding abandoned nests.
[2] At least one young fledged.

Young-of-the-year Black Phoebes that had attained adult size were observed at Plata on 11 May 1970; this indicates hatching about 19–20 April. A brood of Say's Phoebes at Plata fledged on 11 May, indicating hatching about 24–25 April. A pair of Say's Phoebes at Fort Davis hatched its first clutch of eggs 12 April 1969; nest construction had begun in February (Pansy Espy, pers. comm.). The latest recorded dates of hatching were 10 July for Black Phoebes and 27 July for Say's.

Clutch size ranged from 1 to 4 (mean = 3.42 ± 0.30) for 26 clutches of Black Phoebe and from 1 to 6 (mean = 3.77 ± 0.30) for 69 clutches of Say's. I was able to determine the fate of 21 Black (mean clutch size 3.57 ± 0.23) and 45 Say's (3.76 ± 0.29) clutches (Table 2). The primary differences noted were in the number of infertile eggs (1.3% for *S. nigricans*, 7.1% for *S. saya*) and eggs lost prior to hatching (6.7% for *S. nigricans*, 19.5% for *S. saya*). I attributed almost half (44.7%) of the egg loss before hatching to human destruction of nests located under culverts and bridges. Heavy infestation by argasid tick larvae (*Argas cooleyi*) and dermanyssid mites (*Ornithonyssus sylviarum*) resulted in loss of 6 Black and 5 Say's nestlings. All of the Black and 3 of the Say's lost to these ectoparasites were in nests constructed above or within a few meters of Cliff Swallow nests. The other 2 Say's were in a nest constructed over one used previously that season by a House Finch (*Carpodacus mexicanus*). Eggs of Brown-headed Cowbirds (*Molothrus ater*) were never found in phoebe nests, although cowbirds do occur in the area.

Ten broods of Black Phoebes were raised near 8 broods of Say's. The average clutch size for such nests (3.7 and 3.5) was not significantly different (t-test, $P > 0.75$) from those for other nestings.

An insufficient number of adult birds was banded to determine the number of clutches laid per pair. At least 2 pairs of Black Phoebes still fed earlier broods of young while the female of each pair began laying the second clutch and sat on the eggs at night. One Say's Phoebe nest used in 1969 was used again for 3 clutches in 1970. Another nest in which well-feathered young were banded on 10 May 1970 had been used for 3 broods in 1968 (Roland Wauer, pers. comm.). There is an indication that 3 broods are produced by some birds, but 2 are clearly more frequent. Furthermore, when 3 broods are produced in some nests, they may be progeny of different adults.

FEEDING

An analysis of 14 Black and 23 Say's phoebe stomach samples taken during the study illustrates similarities and differences in the diets of the birds.

Most food items could be identified to family. Percent occurrence, percent individuals, and percent volume were considered in analyzing the samples. For each prey taxon of each phoebe species, the "% occurrence" represents its frequency in the occurrence of different prey taxa in the diet; "% individuals" represents its frequency in the total number of individual prey items; and "% volume" is its portion of the volume for all food. The relative importance of these parameters was described previously (Ohlendorf 1974).

Both phoebes fed primarily on insects (96.4% in Black, 98.1% in Say's). Spiders (Arachnida) were taken by both species, and Black Phoebes consumed fruits of buckthorn (Rhamnaceae) on one occasion. Black had a mean of 3.93 ± 1.43 prey taxa per sample and Say's a mean of 4.78 ± 0.33. This difference is not significant (t-test, $P > 0.2$).

The relative occurrence of various food types is different in the 2 species (Fig. 3). Extent of overlap (see Ohlendorf 1974) in diet is 77.7% on the basis of major food types (Fig. 3), but only 42.9% when based on families. Although many of the food items for both species were beetles (Coleoptera), the diets were still quite different because of the families that were represented.

The great number of termites (Isoptera) which had been consumed by 2 of the Black Phoebes was among the factors contributing to differences in the consumption of individual prey items (Fig. 4). I noted, however, that more swarming termites were seen in the habitat types in which

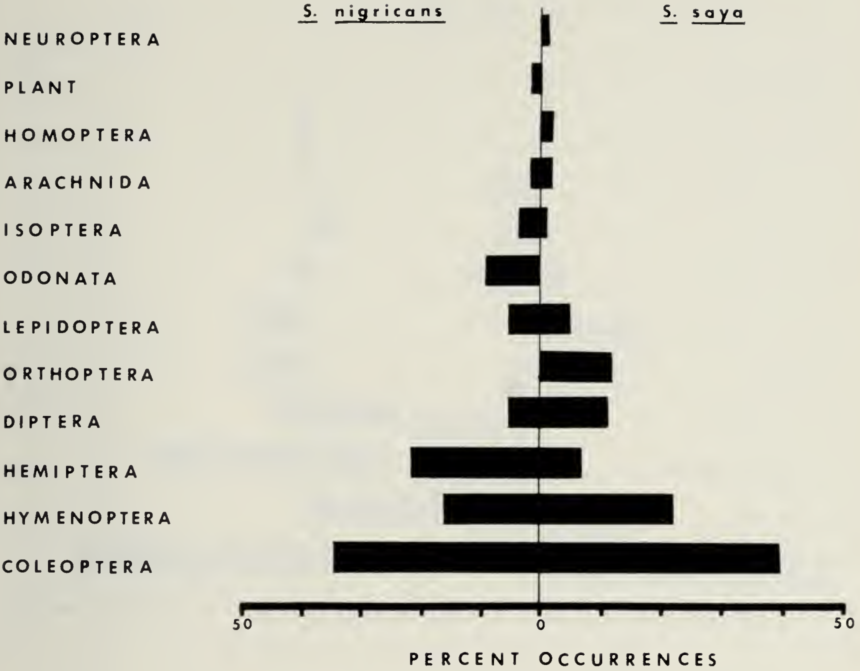

FIG. 3. Relative frequency, expressed as percent total taxon occurrences, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

Black Phoebes occurred than in the more xeric types where Say's Phoebe predominated. Thus, Black Phoebes were more likely to capitalize on this resource when it became available.

Some prey taxa are of greater importance in the diet because of their larger size (Fig. 5). Dragonflies and damselflies (Odonata) seem to be most important for Black Phoebes, whereas grasshoppers (Orthoptera) seem to be most important for Say's. There was no overlap in the occurrence of these taxa in the samples.

Although they do not represent a large portion of the diet, other water-related insects (i.e. Corixidae, Notonectidae, Naucoridae, Omophronidae, and Hydrophilidae) were taken exclusively or more frequently by Black Phoebes. Other beetles, flies (Diptera), and bees (Apoidea; Hymenoptera) were taken principally by Say's.

Differences in composition of diets are illustrated by 2 groups of specimens. At Capote Canyon, I collected 5 Black Phoebes on 11 June 1969,

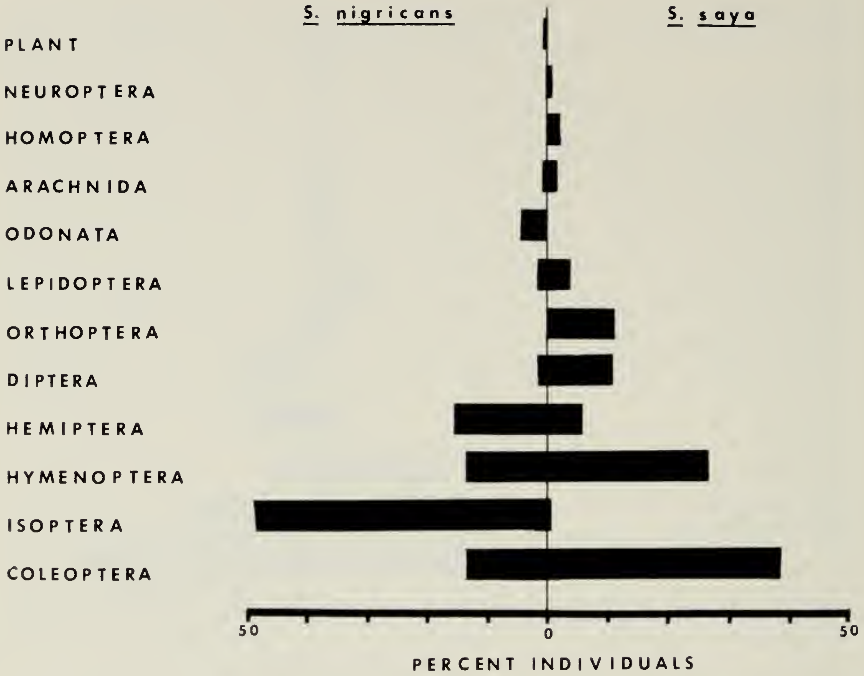

Fig. 4. Relative number of individuals, expressed as percent total individuals, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

and 3 Say's Phoebes on the following day. The prey taxa in Black Phoebe samples consisted entirely of damselflies, termites, assassin bugs (Reduviidae), stink bugs (Pentatomidae), tiger beetles (Cicindelidae), round sand beetles (Omophronidae), water scavenger beetles (Hydrophilidae), and wasps (Vespidae). Prey in Say's Phoebe samples were grasshoppers (Acrididae), bugs (Lygaeidae), and bees.

A Black Phoebe sample from south of Marfa contained damselflies, assassin bugs, creeping water bugs (Naucoridae), leaf beetles (Chrysomelidae), and spiders (Lycosidae), whereas a Say's Phoebe sample from near this location on the same day had grasshoppers and robber flies (Asilidae). The Black Phoebe had been feeding in the riparian habitat type and the Say's was in the nearby desert shrub, similar to their typical occurrence in the region.

The intimate association of the Black Phoebe with water is demonstrated in its feeding behavior. Aquatic insects are sometimes picked from the water as the bird hovers near the surface. I never saw this species feeding

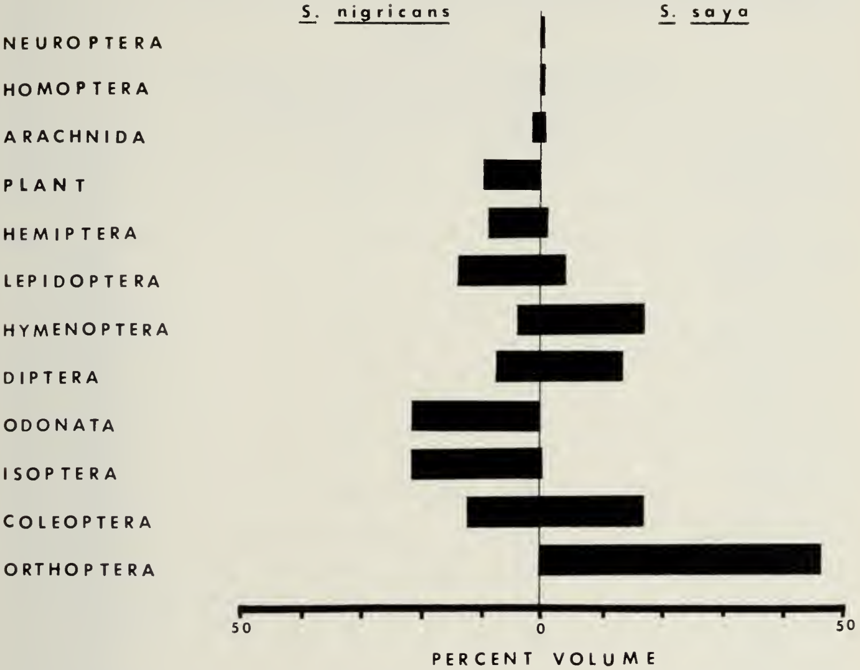

FIG. 5. Relative importance, expressed as percent total volume, of major prey types in Black (n = 14) and Say's phoebe (n = 23) samples. Asymmetry indicates different diets of these birds.

more than a few meters from water. On the other hand, I never saw Say's Phoebe feeding in such a manner, and aquatic insects were absent in the samples. Both species took spiders from the ground.

The perches used by Black Phoebes were shaded lower branches (less than 2 m) of willows (*Salix* spp.) and baccharis (*Baccharis* spp.). Mesquite (*Prosopis* sp.) was also used at Plata where it bordered the marshy sedge (*Eleochris* sp.) field in which the birds fed. Say's fed from perches exposed to full sunlight; these were generally using the tops of mesquite, acacias (*Acacia* spp.), yuccas (*Yucca* spp.), and fences. Differences in coloration of these 2 birds may be adaptations to this difference in feeding perches. The back of Black Phoebes is black; it is predominately pale gray in Say's.

In addition to items found in the samples, Black Phoebes caught other dragonflies, moths (Lepidoptera), and butterflies (Nymphalidae). Items of food recovered from 3 nestlings by use of pipe-cleaner collars were a

TABLE 3

FOOD ITEMS CARRIED BY SAY'S PHOEBES TO NESTLINGS AT DAVIS MOUNTAINS STATE PARK[1]

Prey taxa	Number	Percent
ORTHOPTERA	**14**	**35.0**
Acrididae	14	35.0
COLEOPTERA	**1**	**2.5**
Cicindelidae	1	2.5
LEPIDOPTERA	**7**	**17.5**
Papilionoidea	3	7.5
Lycaenidae	1	2.5
Hesperiidae	3	7.5
DIPTERA	**4**	**10.0**
Tabanidae	1	2.5
Asilidae	2	5.0
Undetermined	1	2.5
HYMENOPTERA	**3**	**7.5**
Formicidae	1	2.5
Apoidea	2	5.0
CHILOPODA	**1**	**2.5**
UNDETERMINED	**10**	**25.0**
TOTAL	**40**	**100.0**

[1] Observations made at one nest.

dragonfly nymph, cicada (Cicadidae), long-horned wood borer (Cerambycidae), skipper (Hesperiidae), and soldier fly (Stratiomyidae).

More extensive sampling of Say's Phoebe nestling food was possible. At a nest in Davis Mountains State Park, I made intermittent observations during the last 3 days before the young fledged. It was usually possible (30 of the 40 items) to determine what the adults were carrying as they made their final pre-nest stop (Table 3).

I used pipe cleaners to prevent other Say's nestlings from swallowing food, and obtained 57 items from 17 July to 6 August 1970, near Fort Davis. Such sampling involved 9 nestlings in 5 nests (Table 4). Some smaller food items may have been swallowed in spite of the collars. Nevertheless, the items give a representation of nestling food which indicates that the diet of nestlings is similar (73.7% overlap) to that of the adults. Most interesting was the large size of grasshoppers (up to 0.9 ml displacement) given to nestlings weighing as little as 14 g.

Table 4

Composition of Say's Phoebe Nestling Food (9 Nestlings in 5 Nests) Near Fort Davis

Prey taxa	% Individuals (n = 57)	% Volume[1] (12.625 ml)
ISOPODA	**1.7**	**0.6**
ORTHOPTERA	**35.1**	**60.8**
Acrididae	(35.1)	(60.8)
Acridinae	3.5	4.6
Oedipodinae	31.6	56.2
HEMIPTERA	**1.7**	**0.6**
Reduviidae	1.7	0.6
HOMOPTERA	**3.5**	**5.5**
Cicadidae	3.5	5.5
COLEOPTERA	**14.0**	**9.2**
Cicindelidae	5.3	1.4
Meloidae	3.5	4.4
Tenebrionidae	3.5	2.2
Scarabaeidae (Cetoniinae)	1.7	1.2
LEPIDOPTERA	**13.9**	**9.2**
Pieridae	1.7	0.8
Hesperiidae	3.5	3.2
Noctuidae	7.0	3.2
Aegeriidae	1.7	2.0
DIPTERA	**19.5**	**11.5**
Asilidae	12.5	6.3
Bombyliidae	3.5	2.8
Tachinidae	3.5	2.4
HYMENOPTERA	**3.5**	**T**
Formicidae	3.5	T
TOTAL INSECTA	**92.7**	**97.4**
ARACHNIDA	**7.0**	**2.8**
Lycosidae	5.3	2.4
Oxyopidae	1.7	0.4
TOTAL	**99.7**	**100.2**

[1] T — Indicates trace value, less than 0.4 percent.

AGONISTIC BEHAVIOR

A Black Phoebe was seen on 24 April 1970, by Charles Crabtree (pers. comm.) as it apparently defended its territory repeatedly and successfully against a Say's Phoebe at a small pond. This indicates that early in the breeding season there is some interspecific territoriality in this species pair, but I never observed such aggression later in the breeding season. On one occasion both species fed from perches in the same tree at Capote Canyon. The adult Black there also passed with its 4 fledglings within 10 m of a Say's and its nest without either bird reacting.

This same Black Phoebe chased an Ash-throated Flycatcher (*Myiarchus cinerascens*) which entered its feeding territory, but the phoebe was in turn chased away by a Pyrrhuloxia (*Pyrrhuloxia sinuata*) a few minutes later.

I saw a Cassin's Kingbird (*Tyrannus vociferans*) and a Black Phoebe feeding about 40 m from the phoebe's nest. There was no aggression in this instance.

Where Vermilion Flycatchers (*Pyrocephalus rubinus*) were feeding over dried mud and Black Phoebes were feeding over the mud and water, the phoebes defended their feeding perches intraspecifically without responding to the Vermilions.

An Ash-throated Flycatcher was sitting quietly within 3 m of a pair of Say's Phoebes whose nest (with nestlings) was only 5 m away. Likewise, at another Say's nest site an Ash-throated Flycatcher and the phoebe were perched in the same shrub about 11 m from the phoebe's nest.

When one of the banded Say's Phoebes (thought to have been the female) at Plata disappeared, 2 unbanded birds entered the area. One of these subsequently nested there with the remaining banded bird, but only after a period of intense aggression (chasing) between the banded resident and one of the unbanded birds.

I banded one brood of Say's Phoebes that was near fledging. When I returned the birds to their nest, some of them flew a short distance and were attacked by a pair of Cassin's Kingbirds, but the attack did not persist.

COMPARISONS BETWEEN PHOEBES AND KINGBIRDS

In addition to the observations that are reported in this paper, I studied the Western Kingbird (*Tyrannus verticalis*) and Cassin's Kingbird (Ohlendorf 1974). There were considerable differences in the 2 pairs of species.

There was distinct altitudinal segregation (and consequently also in habitat type) of the kingbirds throughout most of the region. This was not the case with the phoebes, but they did differ in respect to habitat type.

Although there was no indication of interspecific defense of feeding areas in either pair of species, such behavior was exhibited by kingbirds in relation to nesting sites. For kingbirds, I considered nesting sites to be the resource most limited in supply and therefore worthy of interspecific defense. Wherever substrate suitable for phoebe nesting occurred it was almost invariably used, but in several instances pairs of opposite species nested close together without apparent interaction. Interspecific phoebe nesting compatibility may be related to their dietary differences, which are much greater than I observed in the kingbirds.

On one occasion a Say's Phoebe began nesting within a few days after nesting substrate was provided. The rapid replacement of lost nesting birds, particularly evident in Say's Phoebe but also observed in Black Phoebes, is also an indication of the shortage of suitable nesting substrate.

I found great differences in selection of nest sites and food, as well as in feeding behavior, between the genera. The kingbirds are principally tree-nesting species, but the phoebes nest in sheltered locations on cliffs, bridges, culverts, and buildings. Differences in food and feeding behavior are particularly evident in comparing Black Phoebes with the other 3 species. As a result, there was considerably less overlap in the diets of the 2 phoebes than there was in the diets of the 2 kingbirds.

These 4 species of flycatchers occurred together only at Plata, where the presence of kingbirds apparently had no effect on phoebes, and the converse was also true. Only one pair of each phoebe species nested there. This limitation in phoebe numbers was not caused by the presence of kingbirds, but rather was the result of intraspecific territoriality of the phoebes and the scarcity of nesting substrate for them. Three pairs of Western Kingbirds and 2 pairs of Cassin's Kingbirds remained there with such intense intraspecific aggression in the Western Kingbirds that nesting by one pair was prevented. I attributed the nesting failure of the Cassin's Kingbirds to other environmental factors.

Essentially, the kingbird species occupied different habitat types but exploited the resources in a similar manner and seldom occurred together. The phoebe species were frequently found together but were dependent on different resources. Hence, different strategies may serve to reduce competition in the 2 species pairs.

DISCUSSION AND CONCLUSIONS

Ecologically diverse areas favor sympatry and less interspecific territoriality than do uniform areas (Orians and Willson 1964). The selective pressure for ecological divergence in areas of sympatry favors selection of different habitats, different ways of exploiting the same habitat, and reduction of the area of interspecific aggression. Orians and Willson consider the main function of territorial behavior to be to allow more effective exploitation of food resources.

One instance of interspecific (i.e. Black and Say's phoebes) aggression was reported to me, but the cause for this behavior was unknown. It appears unlikely that it was related to a feeding territory, for the diets of these birds are quite different.

Effects on reproductive success may be an indication of competition (Elton and Miller 1954), but I observed no effect of this nature during my study. There were instances of both phoebe species nesting at the same locality and the success of these pairs was not different from the success of those nesting away from each other.

Location of nests by the 2 species was not significantly different in respect to elevation, but the species differed in respect to habitat type. The presence of mud plus suitable substrate was required for the presence of Black Phoebes. Such conditions are not widespread in the region; consequently the less restricted tolerances of Say's Phoebe contribute to greater relative abundance and more widespread distribution.

Both species have responded favorably to man's construction of buildings, bridges, and culverts by nesting on them in habitat types that were otherwise favorable, but lacked nesting substrate. The presence of only one pair of either species is an indication of their intraspecific exclusion. However, interspecific tolerance is indicated by the presence of pairs of both species in several instances. Separation of the nesting pairs of any one species was always greater than their separation from nesting pairs of the other species.

The overlap in diets of phoebes was 77.7% on the basis of major taxa (i.e. insect orders) and 42.9% when minor taxa (families) were compared. The use of damselflies and dragonflies by the Black Phoebe as a major food resource and of grasshoppers by Say's Phoebe contributes to their ecological compatibility.

SUMMARY

Some aspects of the breeding ecology of Black and Say's phoebes were studied in the Trans-Pecos region of Texas. The geographical and ecological distribution, nesting habits, food composition, and behavioral interactions were determined for each species.

There was no apparent elevational difference between the phoebes, but differences were noted in habitat types. Black Phoebes nested only where mud was available in the immediate vicinity of suitable nest substrate, i.e. a vertical surface protected from rain. Nesting requirements of Say's Phoebes were less restrictive and account for that species' wider distribution within the study area. Rapid replacement of lost breeding birds indicated a shortage of nesting sites. On several occasions the birds were not separated interspecifically, but intraspecific separation was maintained. The clutch size for nests in close proximity (interspecifically) was similar to that of the species means for other nests in the area.

Differences in feeding behavior of the phoebes were reflected in the composition of the diets.

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LITERATURE CITED

American Ornithologists' Union. 1957. Checklist of North American birds. Am. Ornithol. Union, Baltimore.

Blair, W. F. 1950. The biotic provinces of Texas. Tex. J. Sci. 2:93–117.

Elton, C. S. and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J. Ecol. 42:460–496.

Ohlendorf, H. M. 1974. Competitive relationships among kingbirds (*Tyrannus*) in Trans-Pecos Texas. Wilson Bull. 86:357–373.

Orians, G. H. 1966. Food of nestling Yellow-headed Blackbirds, Cariboo Parklands, British Columbia. Condor 68:321–337.

——— and M. F. Willson. 1964. Interspecific territories of birds. Ecology 45:736–745.

Orton, R. B. 1969. Climates of the states: Texas. Climatography of the United States. U.S. Dep. Commer.. Washington.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames.

Wauer, R. H. 1973. Birds of Big Bend National Park and vicinity. Univ. of Texas Press, Austin.

Willson, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51–77.

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FALL RESOURCE DIVISION IN SANTA CRUZ ISLAND HUMMINGBIRDS

Richard I. Yeaton and Lyndall Laughrin

Six species of hummingbird breed in mainland California, but only the Anna's Hummingbird (*Calypte anna*) remains year-round in the vicinity of its breeding habitat. However, on some of the Channel Islands, particularly Santa Cruz and Santa Catalina, and on the island-like Palos Verdes Peninsula, Anna's and the insular race of the Allen's Hummingbird (*Selasphorus sasin sedentarius*) are both resident year-round. Temperate zone hummingbirds, when not separated by habitat differences, generally defend territories between, as well as within, species (Pitelka 1951, Legg and Pitelka 1956, Cody 1968), presumably the result of their specialized and relatively similar feeding behavior. Grant (1966) has suggested that ecologically similar species do not generally occur together in insular situations. On the large, habitat-diverse islands of the West Indies, Lack (1971) reported that hummingbirds were separated most frequently by habitat. Whenever Lack found 2 species of hummingbirds using the same habitat, they were different in body size (as measured by wing and/or culmen length), indicating to him that the species were occupying different ecological niches. For example, the larger member of a sympatric pair of hummingbirds had on the average 1.55 times longer wings and 2.08 times longer culmen than the smaller member (Lack 1971: 230). It is therefore interesting that 2 relatively similarly-sized species of hummingbird (Anna's Hummingbird has 1.22 times longer wings and 1.05 times smaller culmen than the resident race of Allen's Hummingbird) should be resident year-round on the Channel Islands.

This paper examines the resource use of Anna and Allen hummingbirds on Santa Cruz Island, to determine how these species coexist between September and early November. This period is deemed critical for the continued existence of the 2 hummingbirds because only 2 native plants, California fuchsia species *Zauschneria californica* and *Z. cana*, are flowering on the island. These food plants are not abundant and are found only infrequently in dense concentrations, so both species of hummingbirds aggregate in the bottoms of canyons and washes to feed on *Zauschneria* nectar. Also during this period of the year on Santa Cruz Island, insect availability reaches its lowest level (Yeaton 1972), presumably due to the previous 3 months in which there is no rain. During the remainder of the year the hummingbirds are separated by habitat on Santa Cruz Island. Allen's are found in the denser and taller chaparral of the north-facing slopes and in riparian woodlands, while Anna's occupy more open chaparral of south-facing slopes, pine forests, and oak woodlands (Yeaton, pers. obs.). During this time, from December through August, on Santa Cruz Island many food plants and insects are available for hummingbirds.

STUDY AREAS AND METHODS

Santa Cruz Island (N 34° W 119°), a member of the northern Channel Islands group, is 30 km offshore from Santa Barbara, California. It is 250 km^2 in area and contains many habitat types of which grassland, chaparral, and pine forest are most abundant. The avifauna of Santa Cruz Island, as well as the other Channel Islands, is well known (Johnson 1972, Yeaton 1972).

We studied hummingbirds at 3 sites containing *Zauschneria* spp. during October, 1972. A chaparral situation with a varying degree of canopy cover on north- and south-facing slopes was observed in Canada d'Islay which opens into the central valley of the island. North-facing slopes were densely vegetated while south-facing slopes were grassy with scattered shrubs. In addition to *Zauschneria*, *Eucalyptus* was present near the mouth of the canyon. Along the moist canyon floor of an unnamed tributary of Water Canyon on the north side of the island, a second site composed of the vegetation type coastal sage, intermingled with some chaparral elements, was observed. Surrounding the general area of this site were grasslands and scattered oaks. The third site observed consisted of a chaparral-oak woodland transition type of vegetation in Canada de las Sauces de l'Oeste in the southwestern part of the island.

Birds at the 3 sites were censused by walking slowly in the bottoms of the canyons, recording the species of the individuals holding feeding territories, and mapping the extent of these feeding territories. We define feeding territory as being 2 or more flowering clumps of *Zauschneria* spp. defended by an individual against other hummingbirds. The shape and size of feeding territories varied with the topography of the canyon sides. Most territories were elongate, centered in the bottom of the canyon and extending up the sides of the canyon. Hummingbirds holding adjacent feeding territories in the bottom of each canyon were studied, and the number and distribution of flower clumps within an individual's feeding territory were determined. In addition, for each territory the distance between the flower clumps farthest apart was measured. This distance represents the maximum distance within the territory which a hummingbird had to fly to feed.

In Canada d'Islay and Water Canyon the sizes of flower clumps were compared. Since each flower clump was roughly spherical in shape, average diameter gave us a relative measure of clump size. Flowers are distributed over the surface of the clumps. Assuming that a constant proportion of flowers on each bush is producing nectar suitable for hummingbird use, larger bushes have more flowers producing nectar than smaller bushes.

We observed the behavior of 2 Anna's Hummingbirds in Canada d'Islay for a total of 9.75 activity hours and 3 Allen's Hummingbirds in Water Canyon for a total of 7.75 activity hours. We quantified the flower clump use of each species by mapping the location of bushes within an individual's feeding territory and then noting the feeding pattern of that individual on these flower clumps. Also we recorded the length of the feeding bouts and the time between bouts for a territorial individual, and the use of a territorial individual's flower clumps by other hummingbirds. These feeding observations were made between 31 October and 3 November 1972 from 09:00 to 13:00 under sunny and cloudless weather conditions.

Histograms showing the pattern of occurrence and duration of feeding bouts were

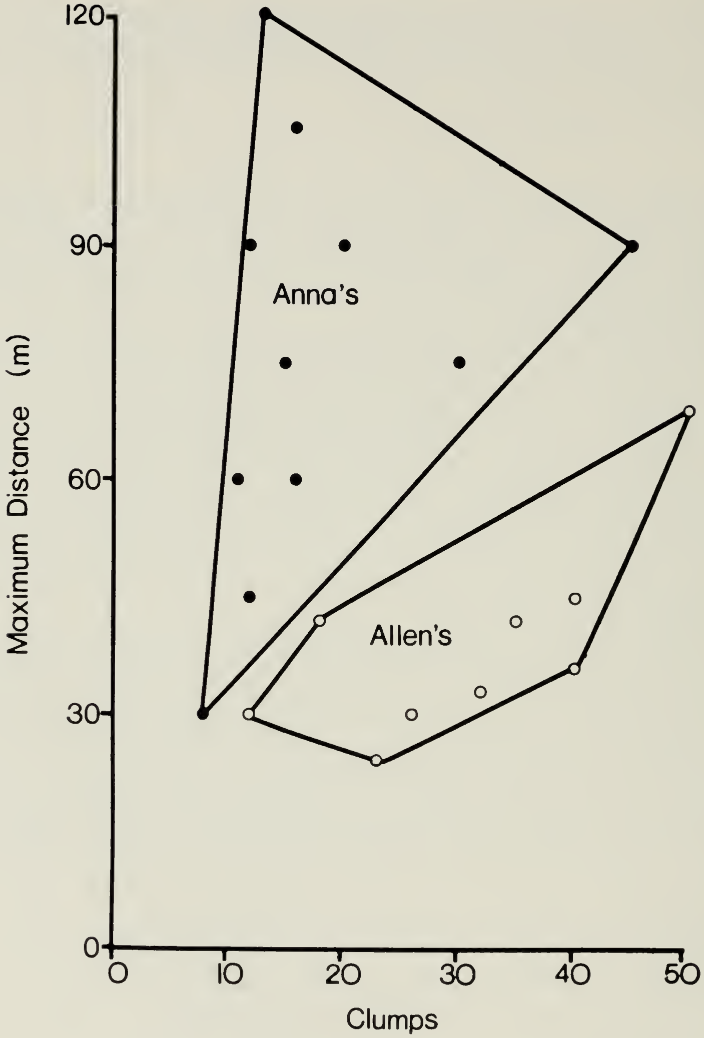

FIG. 1. Comparison of feeding territories of Allen and Anna hummingbirds with reference to number of *Zauschneria* clumps and maximum distance between defended clumps.

drawn. The average duration of a feeding bout (defined as a period of feeding by an individual separated by at least 5 min from the next onset of feeding) and the average time between bouts were then obtained from these histograms. When an individual had not fed on flower clumps for 60 min, we ceased observations and the time between feeding bouts was considered to be 60 min. The mean duration of a feeding bout was obtained by dividing the total number of seconds spent feeding by the number of feeding bouts.

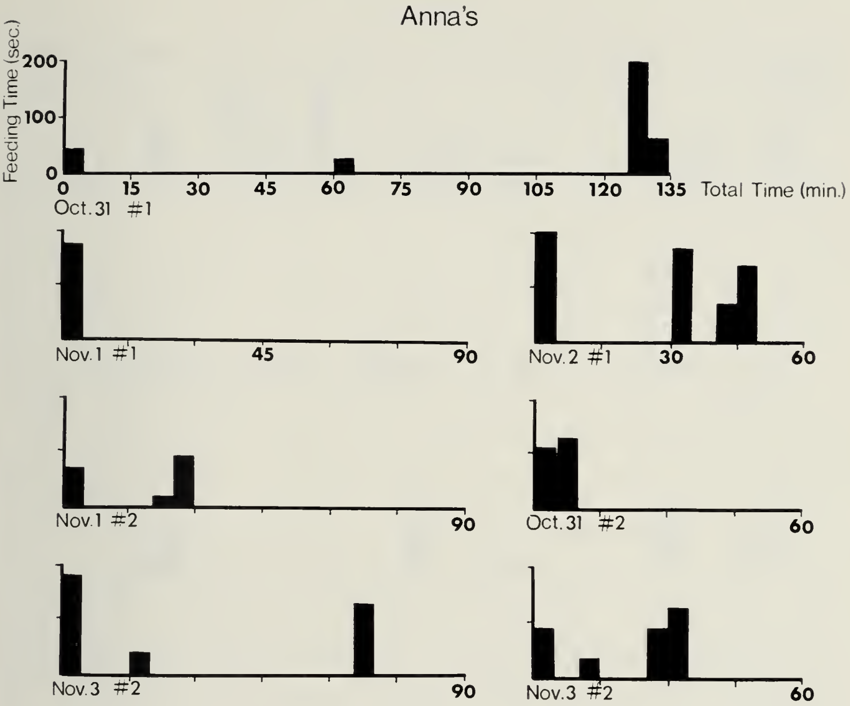

Fig. 2. Anna Hummingbird feeding bouts on Santa Cruz Island between 09:00 and 13:00; # represents bird watched. The horizontal axis represents the total time in min spent watching an Anna Hummingbird, starting with the first feeding bout observed and continuing until observations on that individual ceased.

RESULTS

In Canada d'Islay there were 7 Anna feeding territories, in Sauces 4 Anna feeding territories and 1 Allen, and in Water Canyon 3 Anna and 15 Allen feeding territories. The major differences in the feeding territories of the 2 species seemed to be the abundance of and maximum distance between *Zauschneria* plants (Fig. 1). Allen Hummingbirds had smaller feeding territories containing a high density of clumps of *Zauschneria.* The feeding territories of Anna Hummingbirds were larger and contained fewer food plants.

Analysis of the feeding behavior of the 2 species indicated differences in the method of harvesting nectar from the flowers (Figs. 2 and 3). Allen Hummingbirds fed more frequently and for shorter periods of time than did Annas. Allens fed every 16.9 min (S.E. = 3.5 min) on the average for

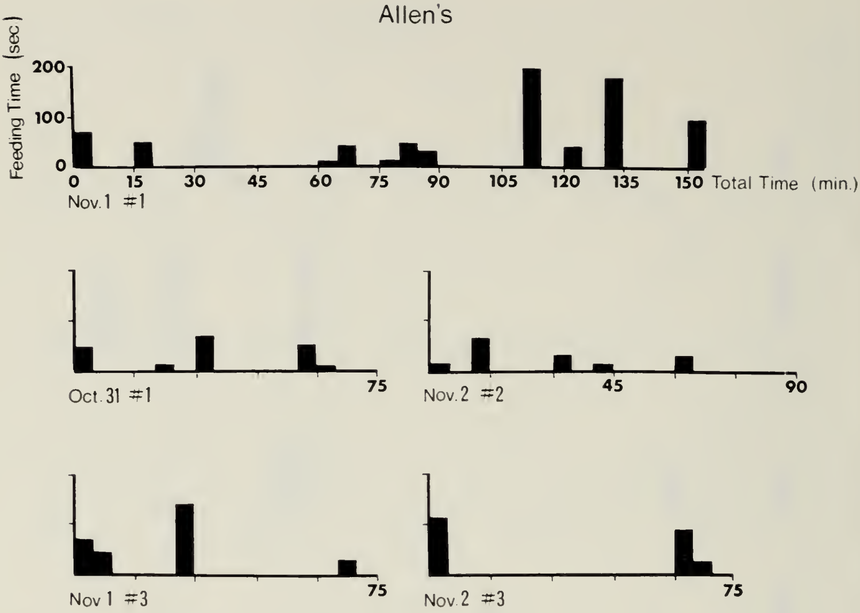

FIG. 3. Allen Hummingbird feeding bouts on Santa Cruz Island between 09:00 and 13:00; # represents bird watched. The horizontal axis represents the total time in min spent watching an Allen Hummingbird, starting with the first feeding bout observed and continuing until observations on that individual ceased.

a mean duration of 1.7 min (S.E. = 0.2 min) whereas Annas averaged 31.8 min (S.E. = 7.3 min) between bouts which lasted an average of 2.8 min (S.E. = 0.3 min). The average distance flown during a feeding bout was 16.4 m ($S_{\bar{x}}$ = 6.3 m) for Allens and 31.1 m ($S_{\bar{x}}$ = 8.2 m) for Annas. Although Allen Hummingbirds visited only 3.1 flower clumps per bout (S.E. = 0.4) while Annas visited 4.2 flower clumps (S.E. = 0.5), when corrected for the size differences of flower clumps in Allens (mean = 105.6 cm, S.E. = 14.6 cm diameter) and Annas (mean = 77.6 cm, S.E. = 10.5 cm diameter) feeding territories, the number of flowers visited during a feeding bout by Allens was potentially greater assuming at least equal numbers of nectar producing flowers per average size flower clump in each species' feeding territory.

Our observations also indicated that within an individual Allen feeding territory, 38% of the flower clump feeding time was used by an individual other than the territory owner. The comparable figure for Anna Hummingbirds was 8%.

DISCUSSION

The distribution patterns of Allen and Anna hummingbirds during the fall in the 3 canyons seemed to be affected by the abundance and spacing of *Zauschneria.* Canada d'Islay contained only Annas whereas both species were found in Sauces and Water canyons. We have shown that the hummingbirds divide the *Zauschneria* resource on the basis of its density. In Canada d'Islay where only Annas were found, *Zauschneria* plants were sparsely distributed. In Sauces and Water canyons a similar sparse distribution existed and Annas were present. But in addition many portions of these latter canyons had a large number of *Zauschneria* plants located close together, due in part to the presence of permanent streams. In these latter areas Allen Hummingbirds established their feeding territories.

What are the differences between the species that enable or require one to use a concentrated and the other a sparse resource? Intuitively the best kind of feeding territory would seem to be one in which food plants are abundant and close together, minimizing the energy expenditure for maintenance and defense of the territory. Alternatively a dense nectar source might also be attractive to many other individuals and lead to increased energy costs for defense of a feeding territory (Gill and Wolf 1975). Allen Hummingbirds crowded into areas with high densities of *Zauschneria* clumps. While these areas might be favorable in terms of nectar availability they are also areas which are attractive to other individuals. The 38% of time (as opposed to 8% for Annas) in which individuals other than the territory holder used the feeding territory in areas of high *Zauschneria* availability may be indicative of the extra pressure placed on these high density areas. Why then were Allens only found in such areas? Allen Hummingbirds weigh about 1.18 times less than Annas (Stiles 1974). Smaller hummingbirds have less storage capacity in their crops relative to their metabolic rates per gram than do larger hummingbirds (Hainsworth and Wolf 1972). A smaller crop means less nectar can be gathered and stored per feeding flight and hence for an Allen Hummingbird to maintain itself, it must feed at shorter intervals than do the larger Anna Hummingbirds. Allen Hummingbirds fed twice as often as did Annas. In conjunction with the increased rate of feeding in Allen Hummingbirds is the problem of nectar renewal in the *Zauschneria* plants. Shorter return times to a given plant meant that there was less time for nectar levels to renew themselves and so Allen Hummingbirds by feeding more frequently actually may have harvested less nectar per flower visit. In addition individuals attempting to steal nectar were likely doing it at a reduced efficiency since they were not familiar with which *Zauschneria* bushes had been harvested last by the territory holder. As a result of the combination of small crop size, necessitating shorter intervals between feeding bouts. and the relatively slow renewal rates of the flowers, Allen Hummingbirds were obligated to establish feeding territories in areas of dense *Zauschneria* concentrations in order to optimize energy expenditures.

Anna Hummingbirds, by waiting longer, allow the nectar more time to renew and increase the amount of nectar harvested per feeding flight. Longer waiting times alone would allow Annas to use a feeding territory containing a sparser resource. Contributing also to use of a sparser resource is a possible reduction in defense costs due to the reduced attractiveness of areas with lower densities of food plants. Of course defense costs are compromised somewhat by the necessity to protect the few but rich nectar sources available to a territorial individual from the possible raid of a neighboring individual. The choice of perches by Anna Hummingbirds which allowed observation of all of an individual's food plants and the relatively low percentage of time spent feeding on the food plants lost to intruders (8%) would seem to indicate a more effective territorial defense by Annas of their sparse food plants than by Allens in their density *Zauschneria* feeding territory.

We did not observe the mechanism by which the slightly smaller Allen Hummingbirds excluded Annas from the high density *Zauschneria* areas. Stiles (1973) recorded the displacement of Anna Hummingbirds at a rich nectar source on the mainland by the smaller, migratory Allen Hummingbird (*Selasphorus s. sasin*). In that study the great number of migrants produced a "swamping" effect, forcing Annas to spend such a large proportion of time in defense of food bushes that Annas abandoned the area. A similar mechanism might be invoked for territory establishment by Allen Hummingbirds on Santa Cruz Island.

Why Allen Hummingbirds are not resident on the adjacent mainland (other than on the insular Palos Verdes Peninsular) is unknown. Our preliminary observations from the Santa Monica Mountains indicate that *Zauschneria* is sparsely distributed and does not attain the compact distribution necessary for establishment of feeding territories by Allens. The mainland distribution of *Zauschneria* may be the result of fire disturbance which is relatively common on the mainland compared with the island. An additional factor preventing Allens from being a resident species on the mainland may be increased competition from other hummingbird species migrating south in the fall. Few, if any, hummingbirds have been recorded in migration on the Channel Islands (Grinnell and Miller 1944).

SUMMARY

The sympatry of 2 hummingbird species, Anna's (*Calypte anna*) and Allen's (*Selasphorus sasin sedentarius*), on Santa Cruz Island, California, was examined during the fall when there is only one abundant food resource, *Zauschneria* sp. nectar. A study of the subdivision of this resource by the species revealed 2 strategies. Allen establishes small

feeding territories containing a high density of flowering *Zauschneria* and Anna uses large feeding territories with a low density of food plants. Analysis of feeding behavior indicated that Allen feeds more frequently and for shorter periods of time than does Anna. These differences in feeding strategy and choice of feeding territory are likely the results of differences in crop size and variable nectar renewal rates.

LITERATURE CITED

CODY, M. L. 1968. Interspecific territoriality among hummingbird species. Condor 70: 270–271.

GILL, F. B. AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333–345.

GRANT, P. R. 1966. Ecological compatibility of bird species on islands. Am. Nat. 100: 451–462.

GRINNELL, J. AND A. H. MILLER. 1944. The distribution of the birds of California. Pac. Coast Avif. 27:1–608.

HAINSWORTH, F. R. AND L. L. WOLF. 1972. Crop volume, nectar concentration and hummingbird energetics. Comp. Biochem. Physiol. 42A:359–366.

JOHNSON, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. Condor 74:295–315.

LACK, D. 1971. Ecological isolation in birds. Blackwell Scientific Publ., London.

LEGG, K. AND F. A. PITELKA. 1956. Ecological overlap of Allen and Anna hummingbirds nesting at Santa Cruz, California. Condor 58:393–405.

PITELKA, F. A. 1951. Ecological overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology 32:641–661.

STILES, F. G. 1971. On the identification of California hummingbirds. Calif. Birds 2: 41–54.

———. 1973. Food supply and annual cycle of the Anna Hummingbird. Univ. Calif. Publ. Zool. 97:1–110.

YEATON, R. I. 1972. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ph.D. thesis, Univ. of California, Los Angeles.

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A MONTANE HUMMINGBIRD TERRITORIAL SYSTEM IN OAXACA, MEXICO

David L. Lyon

Where common resources are exploited by 2 or more related species the concept of resource partitioning suggests that those conspecifics which compete least intensely with individuals of other species will be favored, thus the tendency is for initially competing species to diverge functionally in environmental use (MacArthur 1958). Many investigators, especially Lack (1954, 1966) and Mayr (1963), have regarded food as the critical resource and thus the one most likely to engender these changes; under certain conditions the protection of this potentially scarce resource is given selective advantage because the ratio of energy saved to energy expended is increased by excluding conspecifics (Brown 1964), and occasionally, seemingly contrary to the MacArthur prediction, other species as well (Orians and Willson 1964).

Wolf (1960) and Stiles and Wolf (1970) have reported on intraspecific and interspecific interactions in some Central American hummingbirds. Among the concepts advanced are: (1) distribution of the nectar resource in space and time will affect the outcome of territorial encounters, (2) length of the blooming season, and richness and degree of localization of nectar relative to alternative nectar sources will affect the formation, longevity, and rigidity of the territorial system, and (3) territoriality, both intra- and interspecific, is useful when alternative food sources are limited or widely scattered, but energy expensive when intra- and interspecific competitors are abundant. The purpose of this paper is to relate the above concepts of interspecific territoriality, system rigidity and longevity, and nectar distribution and partitioning to a montane hummingbird territorial system in the state of Oaxaca, Mexico.

STUDY AREA AND METHODS

The study was carried out during the summers (early June to early September) of 1967, 1968, and 1969 on Cerro San Felipe at 2500–3000 m in pine forest in the Sierra de Oaxaca north of the city of Oaxaca, Mexico. The area is classified as Montane Wet Forest according to the Holdridge (1947) scheme. This zone is characterized by summer wet and winter dry seasons, but the distinction between them is less well marked than at lower elevations. During the summer heavy thundershowers occur almost daily and lighter all-day rains are frequent. Temperatures range from 13–24°C during the day to 1–13°C at night. Near the summit (2800–2900 m) are well defined small meadows, most less than 2 ha, some slightly enlarged by lumbering and supporting dense stands of flowering plants during the summer and fall. Large numbers of hummingbirds were

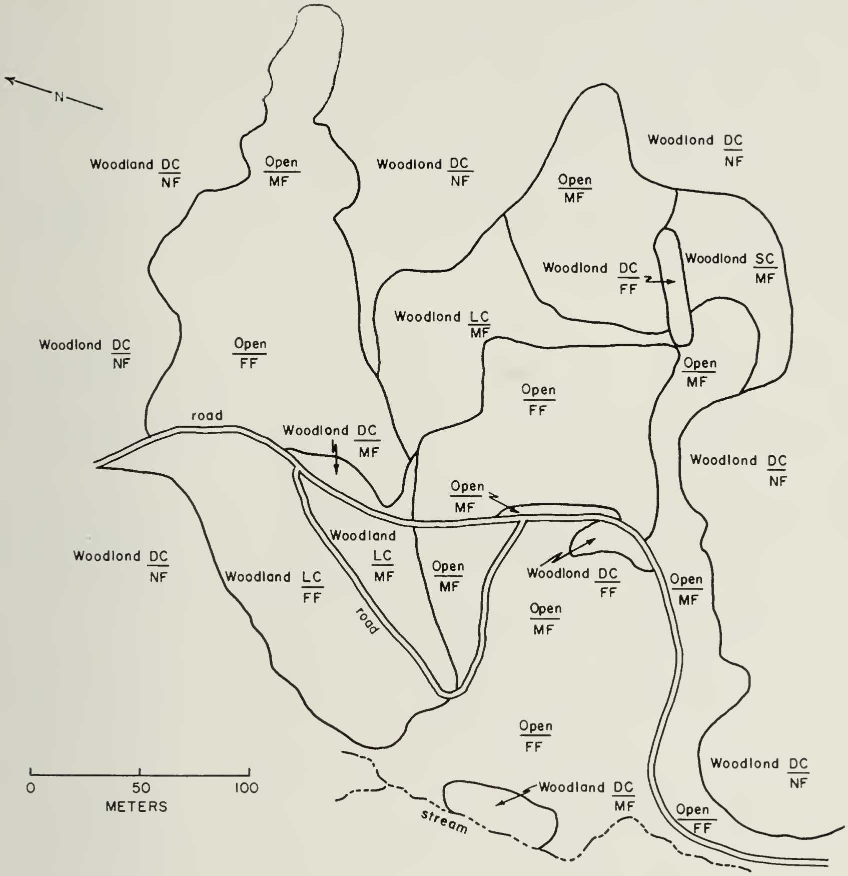

FIG. 1. Map of main meadow of study area indicating general vegetation pattern and flower abundance. LC = light canopy; DC = dense canopy. MF = many flowers; FF = few flowers; NF = no flowers.

attracted by the rich floral food source and it was in these meadows that most observations were made (Fig. 1).

In most meadows, trees were absent or widely scattered, but others resembled open parkland dominated by 20–25 m pines (*Pinus montezumae*, *P. pseudostrobus*, and *P. rudis*) and with a sparse understory of alder (*Alnus* sp.), oak (*Quercus* spp.) and madrone (*Arbutus* spp.). Small streams were present in some meadows, and willows (*Salix* sp.) and elderberry (*Sambucus* sp.) occurred along them locally. Border between meadow and dense forest was usually abrupt. Hummingbirds of all species were occasionally encountered within forest, but with the exception of White-ears (*Hylocharis leucotis*) most species were primarily restricted to meadows or meadow-forest ecotone.

Birds were captured for marking in 10 m, 4-shelf, nylon mist nets. In 1967 4 nets and in 1968 and 1969 8 nets were in continual operation. Nets were placed around meadow edges where territorial chases were especially frequent. Locations were usually changed twice weekly. Various colors of "Pla" enamel chosen for high visibility were used to mark individual birds. Unmarked individuals were identified by distinctive physical or behavioral features, but near the end of the study period in all years most territorial birds were marked. Territory boundaries were determined by noting consistency of perch occupancy, and the frequency and location of chases and displays. Area of territories was determined by planimeter measurement from hand-drawn scale maps. During periods of observation of feeding activity various measurements of movement, location, and positioning of birds at plants and blossoms were obtained with a stopwatch and recorded on a tape recorder.

RESULTS AND DISCUSSION

Hummingbirds in the territorial system.—Six species of hummingbirds were important in the territorial system on Cerro San Felipe: Blue-throated (*Lampornis clemenciae*), Amethyst-throated (*L. amethystinus*), Rivoli's (*Eugenes fulgens*), White-eared, Violet-eared (*Colibri thalassinus*), and Bumblebee (*Atthis heloisa*) (Table 1). White-ears were probably the only abundant year-round residents in the study area judged by the general scarcity in early June of other species prior to the flowering season, although Blue-throats and Bumblebees may have been resident in small numbers. With the exception of Bumblebees which were relatively abundant in early June but rare the rest of the summer, other species were first observed in the study area in late May to mid-June and increased steadily in number until populations stabilized in July–August. Blue-throats and White-ears were the most abundant species in meadow areas as determined by general observation and the number captured in mist nets over the 3-summer period (Table 1). All species were observed in about the same proportions each year with the exception of Rivoli's which was common in 1967 and 1968, but uncommon in 1969.

Nectar resource.—Meadows on Cerro San Felipe supported a profusion of flowering plants during June–September, a large proportion of which were hummingbird-pollinated plants. *Penstemon kunthii* (Scrophulariaceae) and *Rigidella orthantha* (Iridaceae) (Fig. 2) were the most abundant and the major sources of nectar for most hummingbirds. *Rigidella* occurred in dense but scattered stands throughout the meadows, often near streams, but sometimes on drier sites along the meadow edge or under open stands of pine. During the major blooming period, May through June, recruitment of blossoms was rapid and stands showed little variation in blossom number from day to day. After mid-June, stands were in blossom only infrequently for short periods and often out of phase with each other. *Penstemon* began to bloom sporadically in late May, reached peak blossoming in early August and maintained this level from August (Fig. 2) into October (Rowley, pers. comm.). It thus was the most stable and dependable nectar source during my study

Table 1

Number and Weights of Captured Hummingbirds, 1967–1969

Species	Males n	Males Recaptures	Wt. (g) x ± SD*	Females n	Females Recaptures	Wt. (g) x ± SD*
Bumblebee	2	0	2.7 ± 0.0	0	—	—
Violet-eared	31	3	6.3 ± 0.2	11	0	6.0 ± 0.3
Rivoli	119	38	7.7 ± 0.4	24	8	6.4 ± 0.5
White-eared	158	34	3.6 ± 0.3	51	9	3.2 ± 0.2
Amethyst-throated	21	1	6.8 ± 0.8	5	0	6.6 ± 1.3
Blue-throated	190	43	8.4 ± 0.4	62	12	6.8 ± 0.4
Totals	521	119		153	29	

*Includes recaptures.

and the primary factor in conferring stability to the territorial system. Like *Rigidella, Penstemon* was largely restricted to open situations, but was less clumped and more widely distributed.

Eleven other species of flowering plants were used by hummingbirds (Fig. 2), but only cuphea (*Cuphea jorullensis*) was sufficiently abundant to encourage territoriality. This plant sometimes occurred in scattered small stands throughout the larger meadows, but was most abundant at meadow edges or in small openings within forest. Average blossom size was small (ca. 2 cm long) and also presumably was nectar production—only White-ears and Bumblebees used it frequently and Violet-ears occasionally. The 2 most abundant plants in the meadows, *Penstemon perfoliatus* and *P. gentianoides*, were typical bee-pollinated species. Blossoms were seldom used by hummingbirds, apparently because nectar production was low relative to hummingbird-visited species. The Bumblebee Hummingbird was the most frequent user followed by White-ears. Blue-throats, and Rivolis were never seen to use these species.

The peak of nesting on the study area apparently occurred in late summer and early fall. Rowley (pers. comm.), during extensive monthly nest searches throughout the state of Oaxaca, recorded fewer nests in July and August at all elevations than at any other time of year, but above 2500 m the largest number was recorded in September and October after the rainy season was well under way. On Cerro San Felipe this period coincided with maximum flower abundance.

General aspects of territoriality and behavior.—The territorial system was dominated by males, an observation made frequently for other hummingbirds

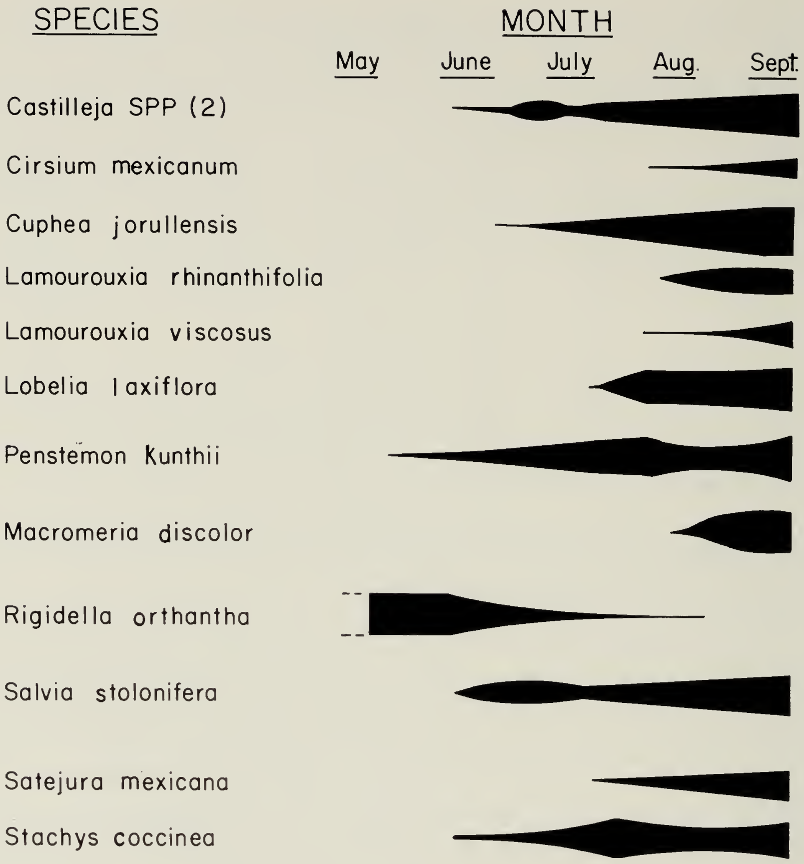

FIG. 2. Phenology of flowering of hummingbird-pollinated plants in meadows and adjacent areas of Cerro San Felipe, 2500–3000 m. Data on phenology determined from 25 10 × 20 m randomly selected plots in and contiguous to meadows supplemented by general observations from surrounding areas. Width of bars in figure proportional to density only within each species.

(Bent 1940, and others). A notable exception is the Fiery-throated Hummingbird (*Panterpe insignis*), a tropical montane species in Costa Rica and Panama in which female territoriality is well developed (Wolf 1969). I recorded female territoriality infrequently in Blue-throats, White-ears, and Rivolis, but in all cases territories were more temporary and usually smaller than those of males and the areas held frequently were deserted and reoccupied, usually by other female conspecifics. Except for Violet-ears and Amethyst-throats females were abundant in the meadows though never as numerous as males

(Table 1). Some seemed to be resident in the general area, but like non-territorial males, most were apparently transient and once netted and marked were not reobserved.

Dominance was directly proportional to body size. Territorial Blue-throats and Rivolis successfully invaded territories of other hummingbirds except conspecifics. Violet-ears and Amethyst-throats were dominant over White-ears and Bumblebees, and White-ears were dominant only over Bumblebees. Though Moore (1939) reported that in Sonora an individual White-ear was successful in repeatedly ejecting larger hummingbirds from its territory, including Blue-throats and Rivolis, I never observed this; White-ears were always subordinate to Blue-throats and Rivolis. In June, when *Penstemon* was beginning to bloom and the only important nectar source was *Rigidella*, all species except Bumblebees successfully invaded White-ear territories in *Rigidella.* Initially, territorial White-ears always attacked invaders regardless of size, but when the larger species persisted, White-ear aggression ceased and only conspecifics and Bumblebees continued to be harassed. Bumblebee Hummingbirds appeared to be neither inter- nor intraspecifically aggressive. Two or more individuals sometimes fed within a short distance of each other without aggression, but such occasions usually occurred within White-ear territories and this may have influenced behavior. I recorded no territories of Bumblebees during the 3 years of the study. Though Violet-ears and Amethyst-throats were intermediate in size and dominance, Violet-ears were much more persistent than Amethyst-throats in reentering territories of Blue-throats and Rivolis to feed. Amethyst-throats, when chased from a territory, seldom returned to attempt feeding immediately, but flew a short distance to a contiguous territory or unprotected area to forage. Some Violet-ears attempted to establish territories and were successful for short periods, but always eventually were displaced and the area incorporated in a new or already established Blue-throat or Rivoli territory. Unlike Violet-ears, Amethyst-throats did not attempt to establish territories. Both Amethyst-throats and Violet-ears, however, were dominant over White-ears and Bumblebees, invading the former's territories and frequently chasing both species from unprotected feeding areas.

The Blue-throated was the most successful territorial species in the meadow over the 3-year period judged by the number and size of territories maintained and the amount of *Penstemon* dominated (Table 2). This species gave both vocal and visual displays. While feeding in the territory it constantly gave a sharp "wheep" call at intervals of 2–3 sec and the tail flicked and spread outward at the same time exposing the white corner edgings of outer rectrices. Presumably these vocal and visual effects constituted an intimidation display. It was given most frequently by feeding territorial individuals, less often by

TABLE 2

TERRITORY SIZE BY SPECIES AND SEX, 1967–1969*

Species		Males	Females
Violet-eared	No. Territories	4	0
	Mean Size (m^2) ± SD	232.4 ± 229.6	—
Rivoli	No. Territories	16	5
	Mean Size (m^2) ± SD	722.6 ± 265.4	683.7 ± 158.8
White-eared	No. Territories	41	1
	Mean Size (m^2) ± SD	431.6 ± 88.5	70.8
Blue-throated	No. Territories	58	5
	Mean Size (m^2) ± SD	777.5 ± 442.2	444.8 ± 108.7

* For territories established after 1 June for White-ears, after 1 July for Violet-ears, and after 15 July for Rivolis, and Blue-throats. No territories of Bumblebees, Amethyst-throated, or female Violet-ears were recorded during the three years.

birds feeding in neutral areas with other hummingbirds, and seldom when feeding alone in these same areas (Table 3). This same call was also given by perched territorial birds, the frequency of the call usually increasing as a bird from an adjacent territory approached the territory boundary. All other territorial species demonstrated no obvious visual or vocal displays when their territories were invaded other than direct pursuit sometimes accompanied by rapid high-frequency "chittering," varying somewhat by species.

Territory stability varied by species due mainly to the persistence in blossoming of the flower resource controlled. Because *Penstemon* flowered from mid-June through August and Blue-throats and Rivolis controlled all large important stands, territories of these species tended to be held for as long as 12 weeks. Conversely, White-ear territories in *Rigidella* were much less stable, persisting for no more than 3–4 weeks. During early June when *Rigidella* was at peak blooming, territories appeared stable and were con-

TABLE 3

COMPARISON OF "TAIL-FLICKING" PER 200 TEN-SECOND OBSERVATION UNITS OF MALE BLUE-THROATS IN 3 FORAGING SITUATIONS

Situation	Foraging alone within territories	Foraging with others in neutral areas	Foraging alone in neutral areas
Number "flicks"	176	83	19*
n	134	128	52

* $\chi^2 = 102.8$; $P < .005$.

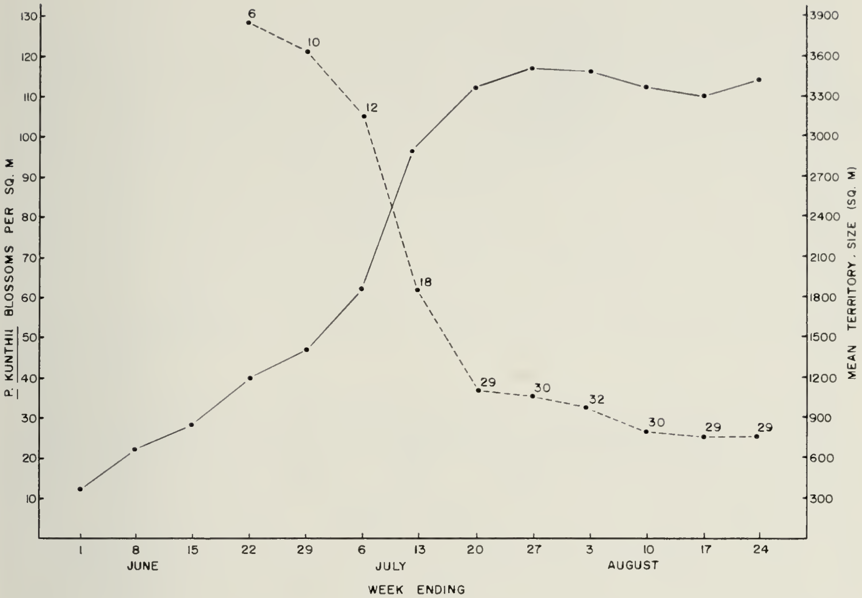

FIG. 3. Relation of territory size of Blue-throats to phenology of *Penstemon* blossoming, 1969. Solid line = blossom number; broken line = territory size. Numbers at points on broken line represent number of territories. Data on blossom density recorded from 25 2 × 2 m randomly selected plots in main meadow.

sistently held by the same individuals. In late June, however, the number of flowering plants decreased rapidly; blossoms might be abundant one day and almost absent the next, thus territories also fluctuated, disappearing and reforming with each major blooming pulse until blooming ceased in late July. Territory boundaries and control of areas by specific individuals changed daily as blooming resurgencies continued sporadically but at different locations within each *Rigidella* stand.

Violet-ears and Rivolis were present in the meadows only sporadically through June (Fig. 4) and thus missed the major blooming period of *Rigidella.* As blossom number declined only a few individuals made attempts to establish territories in *Rigidella*, but these were never defended for more than a day and the birds spent long periods away from the territory. Blue-throats, though present in relatively large numbers by mid-June, never established territories in *Rigidella.* Why this potential source of nectar was not used is not clear. Nectar quantity per blossom may have been low or extraction may have been more difficult for the larger species (Wolf et al. 1972). In addition, *Rigidella* seemed also to be best adapted to pollination by small,

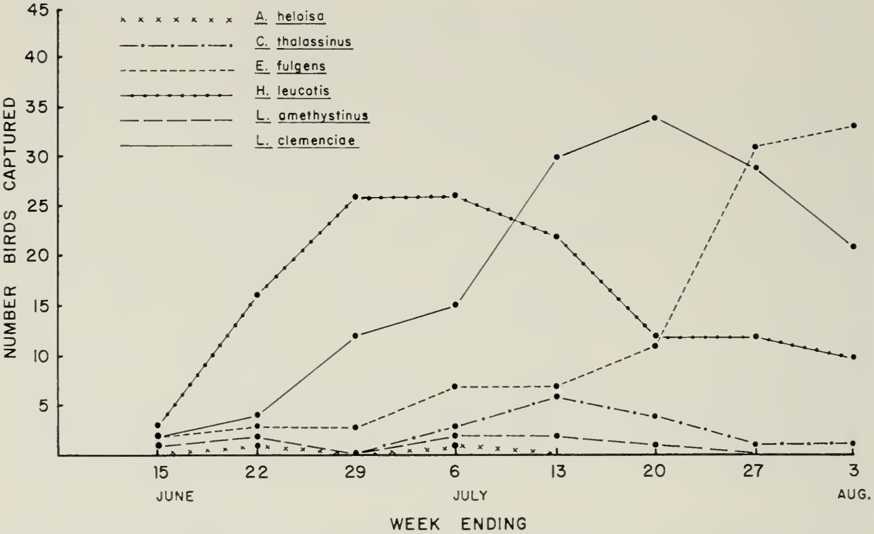

FIG. 4. Number of individuals of each species captured per week, 1968.

more mobile hummingbirds and the larger species had difficulty in maintaining feeding position while probing blossoms. These combined effects may have prevented Blue-throats and Rivolis from securing enough nectar to make more long-term territoriality energetically worthwhile.

Interspecific territoriality.—Territorial interaction in birds appears mainly to be restricted to conspecifics. It thus might be argued *a priori* that interspecific territoriality, if adaptive, should tend to be less well developed than intraspecific territoriality because competition for common resources among conspecifics would be more intense than between individuals of closely related species with similar ecological requirements. If interspecific territoriality was poorly developed, then in the present system in which the most important food source (nectar) is the focus of competition, birds of subdominant species should have an advantage over conspecifics of the larger dominant species because they could more easily invade territories of these species and satisfy a significant portion of their total nectar requirements from that source. For example, Violet-ears and White-ears could be less persistently expelled from Blue-throat and Rivoli territories than conspecifics and thus a degree of species coexistence could prevail despite the presence of a general interspecific aggressiveness on the part of all species.

I established criteria to attempt to differentiate among degrees of response to territorial invasion. The longer the invading bird was allowed to feed before attacked, the more nectar that potentially could be consumed, and the less distant the chase, the less energy expended and the more quickly the invading bird could return to feeding. Judged by these criteria, territorial defense against conspecifics and others appeared equally well developed. No statistically significant differences in response of territorial individuals to invasion of territories were detected among species except for White-ears against conspecifics and Bumblebees (Table 4). White-ears seemed slightly more quick to respond to territory invasion by conspecifics, less quick in reacting to invasion by Bumblebees, and not so persistent in the chase. Thus except for the White-ear–Bumblebee interaction the nectar resource within territories appeared to be protected equally well against invading individuals of all species.

Despite domination of the large continuous stands of *Penstemon* by Blue-throats and Rivolis, numerous small stands of *Penstemon* existed in isolated and widely dispersed clumps throughout meadows and along forest-meadow edge. The largest of these were controlled by White-ears. Occasionally Violet-ears displaced White-ears, but did not return to the territory the following day. Blue-throats and Rivolis never attempted to control these stands. This suggests that nectar production was inadequate for the larger species, marginal for Violet-ears, but sufficient to encourage the establishment of territories by the smaller White-ear. The many remaining smaller, scattered, uncontrolled stands constituted undefended feeding areas in which hummingbirds of all species fed in close proximity with minimum conflict. These latter groupings of *Penstemon* appeared too widely scattered to permit effective defense, yet they provided an important source of nectar for nonterritorial birds.

Since many species of hummingbirds compete for the nectar resource, on the basis of MacArthur's (1958) prediction it would be expected that the most efficient use of flowers, especially the unprotected *Penstemon* stands, would occur through the evolution of species-specific feeding patterns and related behaviors. Potentially a minimum of 2 distinctive patterns of feeding seemed possible in the Oaxaca system and specialization in either could allow some measure of sharing of the food resource by various species of hummingbirds. In clumps of flowers some species could (1) feed on perimeter blossoms, others on interior blossoms, or (2) certain species could feed at upper levels of a stand, others at lower levels. The first of these possibilities seemed unlikely. Most individual plants were not sufficiently dense so that "interior" blossoms could be considered present. The second possibility was tested by recording the time in seconds each species spent feeding at upper, middle, low, and very low levels in *Penstemon* stands. Height classifications were visually estimated and relative between stands; some stands were taller than others and therefore intervals were somewhat larger than in shorter stands.

TABLE 4

COMPARISON OF INTRASPECIFIC AND INTERSPECIFIC TERRITORIALITY AS DETERMINED BY TIME LAPSE RESPONSES OF TERRITORIAL TO TRESPASSING BIRDS AND DISTANCE OF CHASE

Territorial Bird	Trespassing Bird	Time Lapse Between Sighting & Chase (sec.)					Distance of Chase (m)			
		n	< 2	2–6	> 6	no chase	n	0–10	11–50	> 50
LC ---→	LC	866	617	236	6	7	859	116	174	569
LC ---→	EF	441	324	113	2	2	439	48	95	296
LC ---→	LA	45	33	11	1	0	45	8	10	27
LC ---→	CT	37	25	11	0	1	36	4	9	23
LC ---→	HL	1023	708	296	8	11	1009	121	198	690
$\chi^2 = 9.34$; $P > .80$							$\chi^2 = 7.96$; $P > .60$			
EF ---→	EF	292	230	61	0	1	289	33	68	188
EF ---→	LC	410	305	95	7	3	397	46	77	274
EF ---→	LA	24	15	9	0	0	24	3	5	16
EF ---→	CT	30	22	6	1	1	29	4	6	19
EF ---→	HL	483	323	156	3	1	477	48	89	340
$\chi^2 = 17.80$; $P > .25$							$\chi^2 = 13.50$; $P > .25$			
HL ---→	HL	249	200	48	1	0	244	41	57	146
HL ---→	AH	62	26	24	4	8	54	20	18	16
$\chi^2 = 80.23$; $P < .001$*							$\chi^2 = 23.66$; $P < .001$*			

AH = *A. heloisa*; CT = *C. thalassinus*; EF = *E. fulgens*; HL = *H. leucotis*; LA = *L. amethystinus*; LC = *L. clemenciae*. *Denotes significance.

However, since difference in total stand height between the tallest and shortest stands averaged no more than about 0.3 m. difference in interval size among stands was judged too slight to be important. I noted no significant differences in feeding levels either among species or by location except for White-ears (Table 5). The White-ear was also the only species that foraged in proportion to the numbers of flowers at the 3 levels. This was apparently due to its small size and ability to feed at lower-positioned blossoms than could the larger species. Further, White-ears showed a higher rate of blossom use at low levels when feeding within territories of Blue-throats and Rivolis than when feeding within its own territories or in unprotected areas (Table 5). This appeared to be a learned response to harassment by the 2 larger species when White-ears invaded territories to feed. The behavior was functional in that birds practicing it were able to feed for longer periods before discovery. Depending on the topography, density of the stand and associated vegetation, and the size of the invaded territory, some White-ears became adept at approaching and feeding within particular Blue-throat or Rivoli

TABLE 5

PROPORTION OF TIME (SEC) HUMMINGBIRDS SPENT NECTAR FORAGING AT 4 HEIGHT CATEGORIES* IN *P. KUNTHII* STANDS[1]

Species	Situation	Time (sec)/Height Category				
		VL[2]	L	M	H	Total
Blue-throated	Within territory					
n	323	86.2	367.8	2023.8	2299.0	4776.8
%		1.8	7.7	42.4	48.1	100.0
Rivoli	Within territory					
n	158	8.8	205.6	1091.2	1550.8	2856.4
%		0.3	7.2	42.4	48.1	100.0
White-eared	Within territory					
n	41	36.2	72.4	295.5	199.0	603.1
%		6.0	12.0	49.0	33.0	100.0
White-eared	In neutral feeding areas					
n	55	45.8	164.9	448.8	247.3	906.8
%		5.1	18.2	49.5	27.3	100.1
White-eared	In *L. clemenciae* or *E. fulgens* territories					
n	104	338.6	658.4	733.6	169.3	1899.9
%		17.8	34.7	38.6	8.9	100.0
Mean number of useable blossoms in each category		572	1050	5387	3341	10350
%		5.5	10.2	52.1	32.3	100.1

[1] Because time units were not independent (the feeding location in a given time might be influenced by its activity in the preceding time unit) the length of time spent foraging in the 4 height categories was not treated statistically.

[2] VL = very low; L = low; M = middle; H = high.

territories for various periods. During the 3 summers, I noted 9 such territories. In each case White-ears defended the area from a perch usually immediately outside the territory boundaries in an unprotected area. The most unusual example involved a marked individual which maintained a territory within a Blue-throat territory and defended it from a small tree approximately 50 m away. Though these territories-within-territories were uncommon and therefore of little importance in greatly increasing the total nectar supply available to White-ears as a species, raiding facilitated by low approach and feeding was frequent and undoubtedly permitted a higher consumption of nectar than would have otherwise been possible. Thus the White-ear has evolved a flexible feeding behavior repertoire which under the conditions on Cerro San Felipe may be as close to a species-specific feeding pattern as could be expected to develop. Indeed, such flexibility in behavior may be the only possible way in which any significant ecological divergence in feeding can occur and probably is an important factor in the success of the White-ear in montane Mexico as judged by its reported wide geographical and elevational range and habitat tolerance.

Dynamics of territoriality in relation to habitat and phenology of flowering.—If territoriality is an adaptive behavior, it cannot be divorced from the range of evolutionary and extant environmental events which affected its development and presently work to maintain it. In hummingbirds, especially at times of the year when nectar is the major food, the phenology of flowering, particularly in nectar-rich hummingbird pollinated species of plants, is the major factor controlling the dynamics of territoriality. Not only the quantity of the nectar, the distribution and period of flowering, and richness in relation to alternative food sources (Wolf 1969, 1970, Wolf and Hainsworth 1971, Stiles and Wolf 1970), but also its "packaging" in blossoms of various shapes and sizes, and rate of production and decline of flowering are important in controlling the stability of the territorial system. In turn the territorial system is related to the pollination system involving both flowers and birds, and cannot be thoroughly understood without recognizing some of the details of operation of the pollination system. During the course of my study, the timing and extent of the major blooming periods of hummingbird flowers, and the phenology of territorial events in relation to them, made clear the degree of interaction and interdependencies in the 2 systems.

White-ears were present on Cerro San Felipe year-round, but because freezing temperatures commonly occur above 2500 m from late December through March, flowers were absent in the meadows during this period (Rowley, pers. comm.). White-ears must have been primarily insectivorus during this period or migrated to lower elevations where some plants may have continued to blossom through the winter. *Rigidella* was the first hummingbird plant to bloom in the spring. Flowering began in early May and the number of White-ears increased rapidly in the meadows. Territoriality was well developed by mid-May and continued into early June, but became temporary and sporadic in late June when the number and regularity of *Rigidella* in flower declined. During this same period the Bumblebee population was maximum and birds of this species were observed daily in *Rigidella* beds attempting to forage, but were under constant harassment by White-ears. Its small size, bee-like (*Bombus*) flight and buzz while hovering appeared to confuse territorial White-ears and allowed some Bumblebees to feed for relatively long periods before being discovered and chased. Occasional smaller isolated unprotected stands and clumps of *Rigidella* were heavily used by Bumblebees. As *Rigidella* blossoming declined, Bumblebees disappeared from

TABLE 6

CULMEN LENGTH OF *E. FULGENS* AND *L. CLEMENCIAE*

Species	Females		n	Males		n
E. fulgens	26.5	2.8	20	22.1	1.9	58
L. clemenciae	29.6	3.5	16	26.4	2.1	27

the meadows and surrounding areas and were observed only infrequently thereafter. Since Bumblebees were most abundant during the period of major White-ear territoriality in *Rigidella*, and its decline in numbers coincided closely with decrease in *Rigidella* flowering but was before the peak blooming of *Penstemon* and *Cuphea*, it is unlikely that White-ear, Blue-throat, or Rivoli territoriality was the main cause of its disappearance, although it may have been a contributing factor.

By early June *Penstemon* had begun to flower and the first Blue-throats arrived in the meadows and by mid-June had established territories. Most territories were large (1566 m^2 mean size prior to June 15, $n = 24$) yet were efficiently defended against all species except White-ears. This period coincided with flowering decline in *Rigidella*. The shift in White-ear foraging from *Rigidella* to *Penstemon* greatly increased the use of *Penstemon* as a nectar resource and resulted in an increased frequency of Blue-throat–White-ear chases. As territorial Blue-throats ejected and chased one White-ear, others invaded and fed in the unguarded territory. Thus though Blue-throat territoriality was already well developed and effective in controlling trespass of all other hummingbirds in this early June period, it was ineffective against White-ears. The effect of the rapid decline of *Rigidella* on White-ears was thereby minimized by increased blossoming of *Penstemon* despite attempts by Blue-throats to control it. However, by early to mid-July the steady influx of Blue-throats and increasing numbers of *Penstemon* in flower resulted in an increase in the number and a decrease in the size of Blue-throat territories (Figs. 3, 4). Trespassing in territories increased with increase in flowering, and the large territories established and successfully defended earlier when numbers of flowers were low could not be controlled when numbers of flowers were much higher. This resulted in the displacement of the territorial bird from part of the territory and the establishment of 2 or more new territories within the original. In all such cases the resident remained in and defended a smaller portion of the original territory; total displacement of the original tenant was never observed. In all situations involving the complete takeover of Blue-throat territories by conspecifics, the original bird had been absent

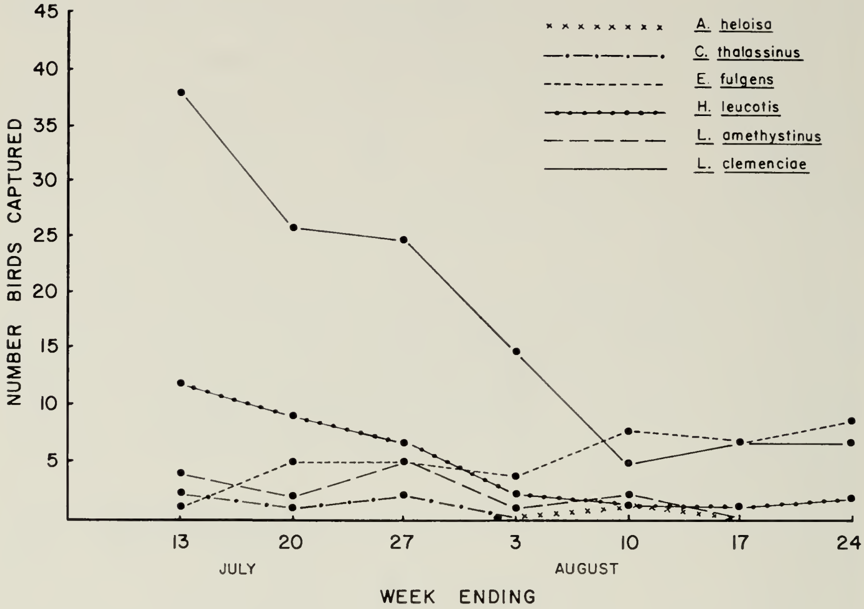

FIG. 5. Number of individuals of each species captured per week, 1969.

from the territory for at least one day and was unable to reclaim the territory upon returning, thus replacement appeared to be by default, not by expulsion. The reduction in territory size increased the effectiveness of exclusion of White-ears by Blue-throats. Thus the increase in numbers of *Penstemon* in flower, rather than alleviating the nectar shortage for White-ears, aggravated it because of the shrinkage in Blue-throat mean territory size.

During the same period in 1968 (early to mid-June) Rivolis were netted with increasing frequency (Fig. 4) and territorial confrontations between Blue-throats and Rivolis became more frequent. By mid-July all important stands were effectively controlled by Blue-throats and there was no further increase in the number of Blue-throat territories. Prior to this time Rivolis had been unable to establish territories, but on 17 July began the start of a 2 week period during which established territorial Blue-throats were replaced by Rivolis. Unlike the situation in which conspecifics were unable to completely displace territorial Blue-throats, displacement was total and Rivolis confiscated territories intact with no noticeable alteration in boundaries (Fig. 6). The actual event of displacement was not observed directly. Like other hummingbirds, Rivolis raided in Blue-throat territories and were consistently ejected. Often, upon return of the Blue-throat resident, a Rivoli was perched or feeding in the territory and a second chase ensued. During some very active periods of raiding, certain territorial Blue-throats were in almost constant pursuit of thieving Violet-ears, White-ears, Amethyst-throats, and Blue-throats as well as Rivolis. None except Rivolis, however, attempted to perch at favorite perches of the Blue-throat resident. At the end of this 2 week period of intense interaction, 13 Rivolis had replaced Blue-throats and were feeding exclusively within the territories and defending them. Displaced Blue-throats usually were not observed or netted again; a few were present in the meadows for a few days and became part of the raiding population but then disappeared. None were able to displace territorial conspecifics or Rivolis. Twice, a newly territorial Rivoli was displaced by a conspecific but in each case this occurred within 2 days of displacement of the original Blue-throat resident. Once securely established, Rivoli territories remained stable and unchanged through the remainder of my study.

In 1969 displacement of Blue-throats by Rivolis did not occur. Although Rivolis were present and foraged in Blue-throat territories, the Rivoli population did not reach 1968 levels (Fig. 4). Thus there appeared to be a relationship between numbers of Rivolis and their ability to displace territorial Blue-throats, but the precise nature of the interaction is not clear. A minimum number of Rivolis was perhaps necessary to effect an increased frequency of chases and to allow some conspecifics to invade and temporarily occupy territories when resident Blue-throats were occupied in ejecting others.

In 1968 displacement by Rivolis by the end of July resulted in a distinct patterning of Blue-throat and Rivolis territories (Fig. 6). Blue-throats were restricted primarily to the edges of the meadows or open forest and Rivolis occupied all open areas that had suitable *Penstemon* densities. Why Rivolis were successful in displacing Blue-throats in open areas but not in others is not well understood, but it is clear that an ability to discern and discriminate subtle differences in habitat is present in one or both species. It also indicates the need to be cautious in making statements about dominance relationships in hummingbirds. Rising (1965) and others have commented on the consistent dominance of Blue-throats over Rivolis at feeders. My own observations in the Chiricahua and Huachuca Mountains in Arizona support these reports. Further, on Cerro San Felipe, Blue-throats were usually dominant over Rivolis in "neutral" undefended feeding areas. However, the interaction resulting in the displacement of Blue-throats by Rivolis suggests that observations made at feeders and other "neutral" sites may result in oversimplification of interspecies behavioral relationships and can be misleading.

By the end of July 1968 the territorial system had once again stabilized and remained unchanged to the end of the study period. Territorial Rivolis were as efficient as Blue-throats in defending against conspecifics and other

FIG. 6. Blue-throat and Rivoli territories in main meadow, late July 1968. In early July all territories shown here were already present but held only by Blue-throats. Compare territory placement of each species with vegetation pattern in Fig. 1. LM = Blue-throat male; LF = Blue-throat female; EM = Rivoli male; EF = Rivoli female.

species, and thus the final effect was a substitution of a portion of the territorial Blue-throat population by Rivolis but no additional pressure on the *Penstemon* resource. In 1968 the combined maximum number of Blue-throat and Rivoli territories was only 2 fewer than the maximum number of Blue-throat territories (30) in 1969 when no displacement of Blue-throats by Rivolis took place. This tends to further substantiate that Rivolis effectively substitute for Blue-throats and suggests that there exists a saturation level in numbers of territories of these species that the meadows will support, whether all of one species or a mix of each, and that this level is determined primarily by the abundance of *Penstemon.*

The well-developed territoriality of Blue-throats and Rivolis also appeared effective in limiting the number of hummingbirds of all species which could feed in the meadows. With the exception of the multispecies territorial populations and a few nonterritorial frequently netted Blue-throats, Rivolis, and White-ears which were seen in the meadows daily, few marked individuals of any species were reobserved for more than 1 or 2 days after having been marked. Further, only 11% of the marked nonterritorial individuals in 1968 and 12% in 1969, were recaptured. Since birds were captured in large numbers throughout June and July in all years, a rapid turnover in the nonterritorial population must have occurred. Thus when the total number of birds using the meadows during the entire summer is considered, most were transients, though on any single day territorial birds constituted a large proportion of the population.

Toward the end of the summer study period, particularly in 1969, the number of birds captured of all species other than Rivolis declined rapidly (Figs. 4, 5). An additional indication of decline in total numbers was the distinct decrease in territorial chases during this period except during brief flurries of feeding activity immediately prior to sunrise and following sunset. Since the number of territorial individuals remained relatively constant during this same period, the decrease reflected a decline in numbers of transients, a reduction possibly initiated by the increase in blooming of other species of hummingbird-pollinated plants in areas outside meadows. Many of these bird flowers began blooming as early as *Penstemon* but did not reach peak blooming until late July. Still others did not begin to bloom until early August (Fig. 2). One of these, *Cuphea*, appeared to take up much of the slack for White-ears, but probably because of its small size was not used by the larger species. *Cuphea* was present early in small numbers scattered throughout Blue-throat and Rivoli territories and in undefended feeding areas, but it was most concentrated later in small openings within forest, and White-ears established territories in these areas. Some of these birds were marked and several had been territorial earlier in *Rigidella.* The other later-developing hummingbird-pollinated species were more dispersed and though used frequently by hummers seemed insufficiently clumped or abundant to encourage the establishment of territories. Most of these grew in isolated clumps or singly in light shade or, like *Cuphea*, in small forest openings. Marked nonterritorial Blue-throats, Rivolis, Violet-ears, and Amethyst-throats were observed occasionally at freshly blooming plants of these species, but because they were widely dispersed it was not possible to spend the long periods of observation necessary to determine the full extent of use by birds.

However, frequent examination of other locations indicated that flowering of these species was general throughout the Sierra de Oaxaca at this elevation and thus must have provided an increased nectar supply for nonterritorial birds.

SUMMARY

A study of an interspecific territorial system involving 6 species of hummingbirds (Bumblebee, *Atthis heloisa*; Violet-eared, *Colibri thalassinus*; Rivoli, *Eugenes fulgens*; White-eared, *Hylocharis leucotis*; Amethyst-throated, *Lampornis amethystinus*; Blue-throated, *Lampornis clemenciae*) was carried out between 2500 and 3000 m on Cerro San Felipe in the Sierra de Oaxaca north of the city of Oaxaca, Mexico. The basis of the system was a complex of 12 hummingbird-pollinated plants, the most important of which were *Rigidella orthantha* (Iridaceae) and *Penstemon kunthii* (Scrophulariaceae).

Blue-throats, Rivolis, Violet-ears, and White-ears were both intra- and interspecifically territorial, but Bumblebees, the smallest in the system, and Amethyst-throats, were nonterritorial. Interspecific territoriality, as judged by the response of territorial individuals to thieving birds, appeared as well developed as intraspecific territoriality. Species' success in establishing and maintaining territories was directly proportional to body size. The 2 largest species and nearly equal in size, Blue-throats and Rivolis, dominated the richest nectar sources, but partitioned these sources on the basis of habitat. Initially, early in the season all significant *Penstemon* stands were held by territorial Blue-throats, but by mid-July in 1968 Rivolis had displaced territorial Blue-throats in all open meadow situations, yet were unable to do so in meadow-forest edge or open forest areas. In 1969 no displacement of Blue-throats by Rivolis occurred and this lack was associated with a much smaller population build-up of Rivolis compared to 1968. When it occurred, displacement was total, with Rivolis confiscating entire territories and with no noticeable alteration in boundaries.

The interspecific territoriality of Blue-throats and Rivolis also appeared effective in limiting the number of hummingbirds which could feed in the meadows. Most marked birds were seen for only short periods following their initial capture and few marked nonterritorial individuals were recaptured, indicating a rapid turnover in the nonterritorial population.

White-ears demonstrated the most flexible feeding behavior of any species in the system. They not only were able to use a wide range of blossom sizes, but also showed a functional and presumably learned raiding pattern involving secretive low approaches to *Penstemon* stands located within territories held by Blue-throats and Rivolis. Bumblebees were nonterritorial but their small size allowed them to subsist on the blossoms of unprotected plants located outside territories. Also, their peculiar bee-like flight appeared to permit them to feed for long periods in stands of *Rigidella* within White-ear territories without being evicted.

The phenology of flowering was the main factor controlling the behavioral events and interactions among species of hummingbirds. In May and early June *Rigidella* was the most important nectar source for White-ears, but as flowering waned, White-ears were forced to feed increasingly on early blooming plants of *Penstemon* even though these stands were defended by territorial Blue-throats. However, because *Penstemon* blossoms were widely dispersed at this time, territories were necessarily large and defense, though efficient against most species, was inefficient against the raiding strategy of White-ears. As flowering continued with season, blossom density of *Penstemon* increased and was

accompanied by the expropriation of parts of Blue-throat territories by conspecifics. Mean territory size therefore decreased and this increased the efficiency of territorial defense. By mid-July defense was so efficient that White-ears were effectively excluded from all significant stands of *Penstemon* and became dependent on other more scattered or smaller-flowered hummingbird plants, particularly *Cuphea.*

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LITERATURE CITED

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull. 176.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367–368.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

———. 1966. Population studies of birds. Clarendon Press, Oxford.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

Mayr, E. 1963. Animal species and evolution. Belknap Press of Harvard Univ. Press, Cambridge, Mass.

Moore, R. T. 1939. Habits of White-eared Hummingbirds in northeastern Mexico. Auk 56:442–446.

Orians, G. H. and M. F. Willson. 1964. Interspecific territories in birds. Ecology 45: 736–745.

Rising, J. D. 1965. Notes on behavioral responses in the Blue-throated Hummingbird. Condor 67:352–354.

Stiles, F. G. and L. L. Wolf. 1970. Hummingbird territoriality at a flowering tropical tree. Auk 87:467–491.

Wolf, L. L. 1969. Female territoriality in a tropical hummingbird. Auk 86:490–504.

———. 1970. The impact of seasonal flowering on the biology of tropical hummingbirds. Condor 72:1–14.

——— and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980–988.

———, F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176:1351–1352.

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GANNETS IN NORTH AMERICA: PRESENT NUMBERS AND RECENT POPULATION CHANGES

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Gannets (*Morus bassanus*) are common in spring, summer, and fall on the Atlantic coast of Canada. While their present breeding sites have long been known, existing data on populations and history are fragmentary and incomplete, as these colonies are in generally remote and inaccessible areas (Fig. 1). However, the sparse information on populations is sufficient to indicate that Gannet numbers and distribution have fluctuated considerably during the period of historical record, views which have been extensively documented and published (Bent 1922, Fisher and Vevers 1943, 1944, Fisher and Lockley 1954, Palmer 1962). It is my purpose to present here the results of 1972 and 1973 surveys of 6 North American gannetries and briefly review and summarize other recent census data.

CENSUS METHODS

Procedures used to census North American Gannet colonies in the past have varied widely, ranging from simple visual impressions of bird numbers to ground counts of nests. In some cases, such as at Funk Island, methods used to count breeding pairs have been reasonably consistent since the early 1950's as they were performed largely by the same investigator (Dr. L. M. Tuck). Most counts at other colonies, however, were not performed by the same observer in different years nor were similar census techniques always used. Clearly this variation in census reliability and accuracy has made it very difficult, if not impossible, to make precise comparisons of population numbers either within or between colonies. To avoid similar difficulties in the collection and interpretation of data in the future, it seemed evident that a standardized census method was required, one which would be sufficiently rigid to reduce individual observer bias to a minimum and provide a permanent and precise record of the distribution and numbers of nesting birds at individual colonies. Consequently, I developed a technique of population analysis from aerial photography, similar to those used to count Gannets elsewhere (Salmon and Lockley 1933, Barrett and Harris 1965).

The method used at each colony in 1972 and 1973 was basically the same. A series of over-lapping aerial photographs was taken during the incubation period in June or July (see Tables 1 and 2 for details) from a light fixed-wing aircraft using either a 35 mm (Baccalieu Island), 70 mm (Anticosti Island, Bird Rocks, Bonaventure Island, Cape St. Mary's), or K-24 aerial reconnaissance camera (Funk Island) with standard lenses (135 mm, 100 mm, 177 mm, respectively) and Kodak Plus-X or Double-X black and white film. The usual distance from the colony was about 550–610 m, although Funk Island was photographed at a vertical overhead distance of about 1220 m.

The disturbance of nesting birds by the aircraft was slight, and no movement from nest territories was detected. Nesting areas were easily delimited on the photos

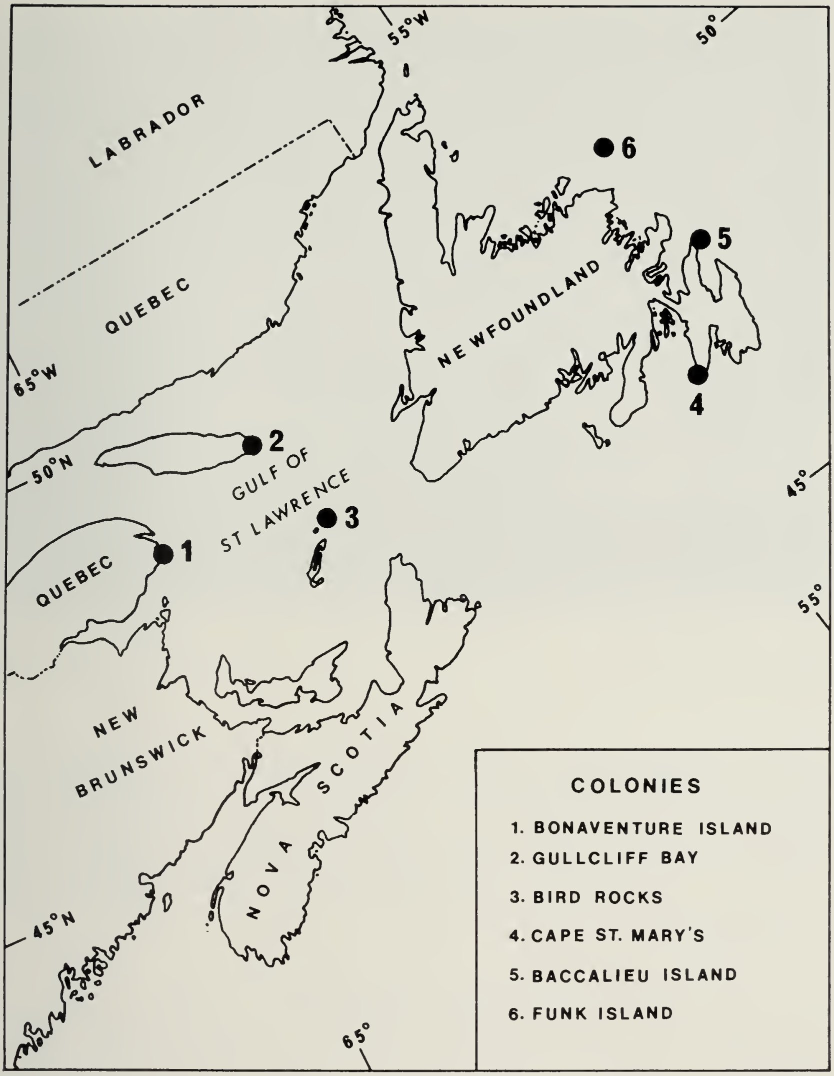

FIG. 1. Approximate locations of Gannet colonies in North America.

(18 × 25 cm or 23 × 32 cm glossy enlargements) by the extremely regular spacing of white dots (see Barrett and Harris 1965). Individual attended nests were counted under a hand lens (8×) using a plastic grid overlay (1 cm × 1 cm quadrats) and following procedures similar to those outlined by Barrett and Harris (1965). Photo quality not only allowed individual nests to be counted, but often made it possible to determine whether 1 or 2 birds were associated with each nest. The single source of

FIG. 2. Aerial view of a portion of the Gannet colony on Bonaventure Island, Quebec, 7 July 1973, showing the 2 principal nesting habitats: cliff ledges and flattish ground above the cliff top.

error is in the demarcation of nesting areas on the prints, but this has been estimated by Barrett and Harris (1965) to be less than 2%. Since only attended nests were counted, and the status of each nest was unknown, this assessment of breeding population represents the number of "nest-site holders" rather than the number of "true breeders" (i.e., pairs that built a nest and laid 1 egg). Number estimates given in the tables and text are those actually calculated even though their "exactness" may be a bit spurious.

DESCRIPTION OF COLONIES

Bonaventure Island, Quebec.—Bonaventure Island, at 48°30'N × 64°09'W, is approximately 2.7 km long and 2.6 km broad at its widest point and is roughly circular in shape with an area of about 460 ha. The cliffs are made up of a conglomerate-red sandstone mixture that reaches a height of 91 m on the southeastern coast where the Gannets nest (Fig. 2).

Gullcliff Bay, Anticosti Island, Quebec.—Anticosti Island, at 49°09'N × 61°42'W, is situated in the western entrance to the Gulf of St. Lawrence and measures 225 km long and 48 km wide. The Gannet colony on the southeastern tip of the island in Gullcliff Bay, consists of several small nesting groups (2 to 37 pairs per group) scattered along about 1.69 km of highly fractured and crumbly 46–61 m high cliffs (Fig. 3).

FIG. 3. Aerial view of a portion of the Gannet colony in Gullcliff Bay, Anticosti Island, Quebec, 12 June 1972.

Bird Rocks, Magdalen Islands, Quebec.—The Bird Rocks, at 47°50′N × 61°09′W, are the northernmost islands of the Magdalen Islands Archipelago in the Gulf of St. Lawrence. There are 2 islands in the Bird Rocks group, Great Bird and North Bird (= Little Bird), both of which have nesting Gannets. Great Bird is somewhat circular in shape (0.4 km diameter) with a grassy-turf top and 30 m precipitous limestone cliffs on which the Gannets nest; North Bird, immediately northwest of Great Bird, is much smaller and highly eroded (Fig. 4).

Cape St. Mary's, Newfoundland.—Cape St. Mary's, at 46°50′N × 54°12′W, is the southwestern extremity of the Avalon Peninsula. It appears as a high tableland when viewed from a distance. The Gannet colony is on Bird Rock, a large 152 m high rock stack, only slightly separated from the adjacent mainland cliffs (Fig. 5). Nests cover the seaward-facing, sloped, cliff face from about 30 to 46 m above the sea to the top of the stack.

Baccalieu Island, Newfoundland.—Baccalieu Island, at 48°07′N × 52°47′W, is situated at the northeast tip of the Avalon Peninsula, about 2.4 km eastward of Split Point. It is about 6.1 km long and 1.3 km broad at its widest point and runs north-south along the greater dimension. The gannets nest on high, almost inaccessible, precipitous rock cliffs towards the mid-point of the east, seaward-facing coast (Fig. 6).

Funk Island, Newfoundland.—Funk Island, at 49°46′N × 53°11′W, is a flat-topped oblong granite rock situated about 56 km north-northeast of the east coast of Newfoundland (Cape Freels). It is 0.8 km long, 0.4 km wide, and approximately 14 m high at its highest point. The Gannet colony is towards the west end of the island on level ground, ringed by breeding murres, principally *Uria aalge* (Fig. 7).

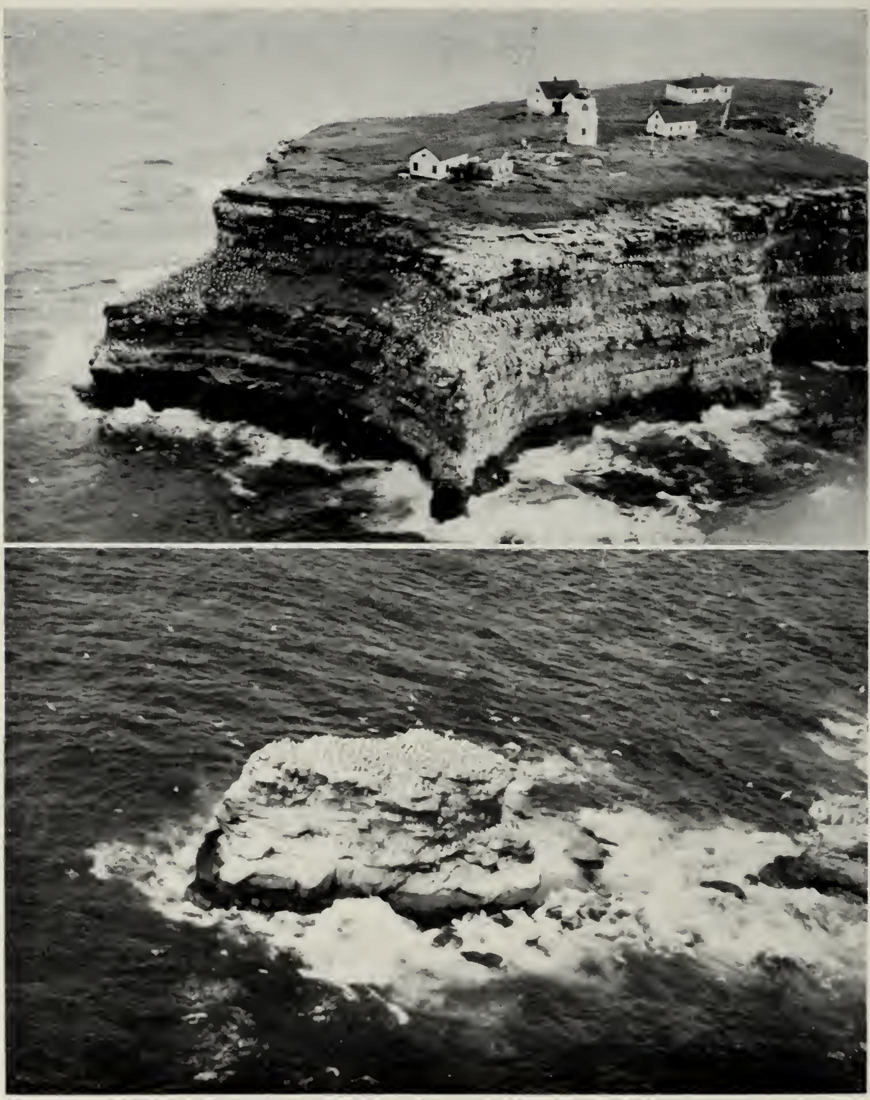

FIG. 4. Aerial view of the Bird Rocks: Great Bird (above) and North Bird (below), Magdalen Islands, Quebec, 7 July 1973.

RESULTS AND DISCUSSION

Present Breeding Population Size

The results of the 1972 and 1973 censuses are summarized in Table 1. On the basis of my surveys, I estimate that there were 32,731 pairs of Gan-

FIG. 5. Aerial view of Bird Rock, Cape St. Mary's, Newfoundland, 18 June 1972.

nets breeding in eastern North America. Of this total, 22,747 pairs (69.5%) nest in the Gulf of St. Lawrence and 9984 pairs (30.5%) on the Atlantic coast of Newfoundland.

Recent Population Changes

Data from counts made before 1972 at the various colonies are fragmentary and often incomplete. In general, though they lack the standardization necessary to allow precise comparisons of population estimates, they appear adequate to detect major numerical changes and population trends, especially in the Gulf of St. Lawrence where photography has been used to estimate numbers of breeding pairs since 1961. Table 2 summarizes the estimates of population sizes at the 6 colonies between 1959 and 1973.

Bonaventure Island, Quebec.—It appears that the breeding population peaked close to 1966, followed by an abrupt decline of roughly 16% between 1969 and 1973. While the difference between the 1966 and 1969 estimates may be due to different methods of counting and estimating the colony, the decrease in numbers from 20,511 pairs in 1969 to 17,281

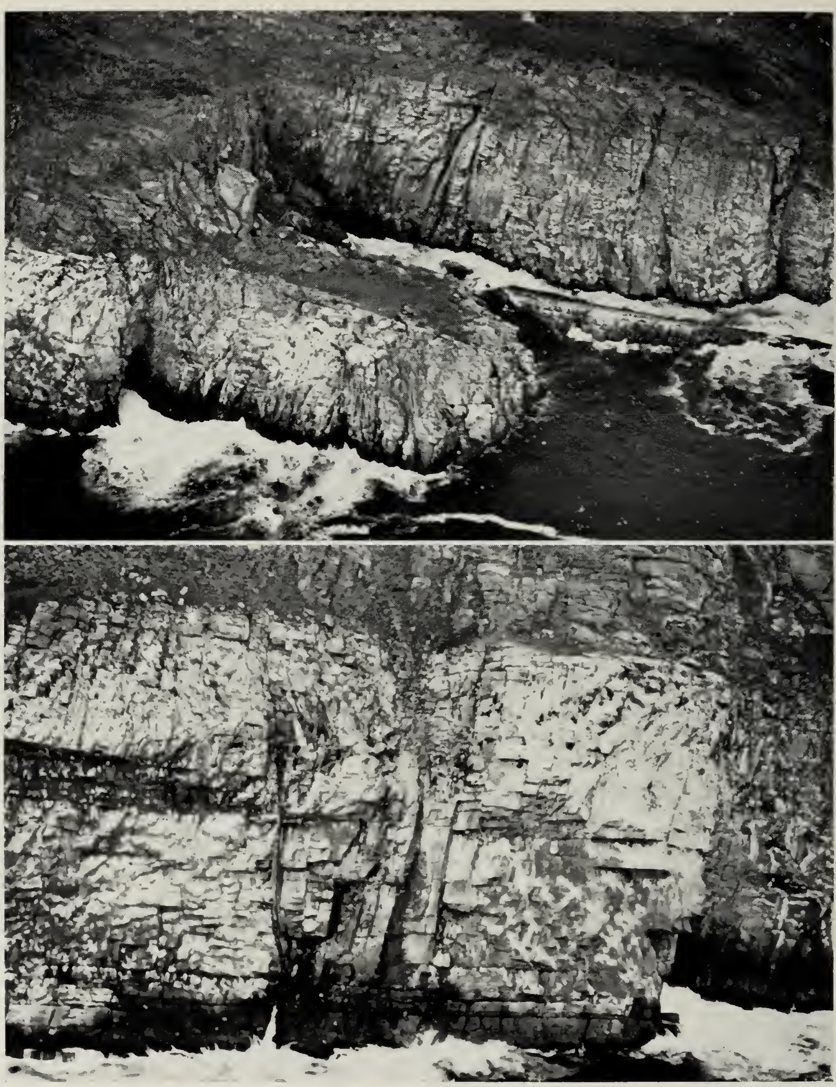

FIG. 6. Aerial views of the Gannet colony on Baccalieu Island, Newfoundland, 21 June 1973: most of the colony (above) and a close-up of a portion of the cliffs (below).

pairs in 1973 appears to be real as the census procedures and method of analysis were virtually identical.

Much of the 1969 to 1973 decrease seems to have occurred among birds breeding on ledges on the cliffs. In 1969, the population comprised

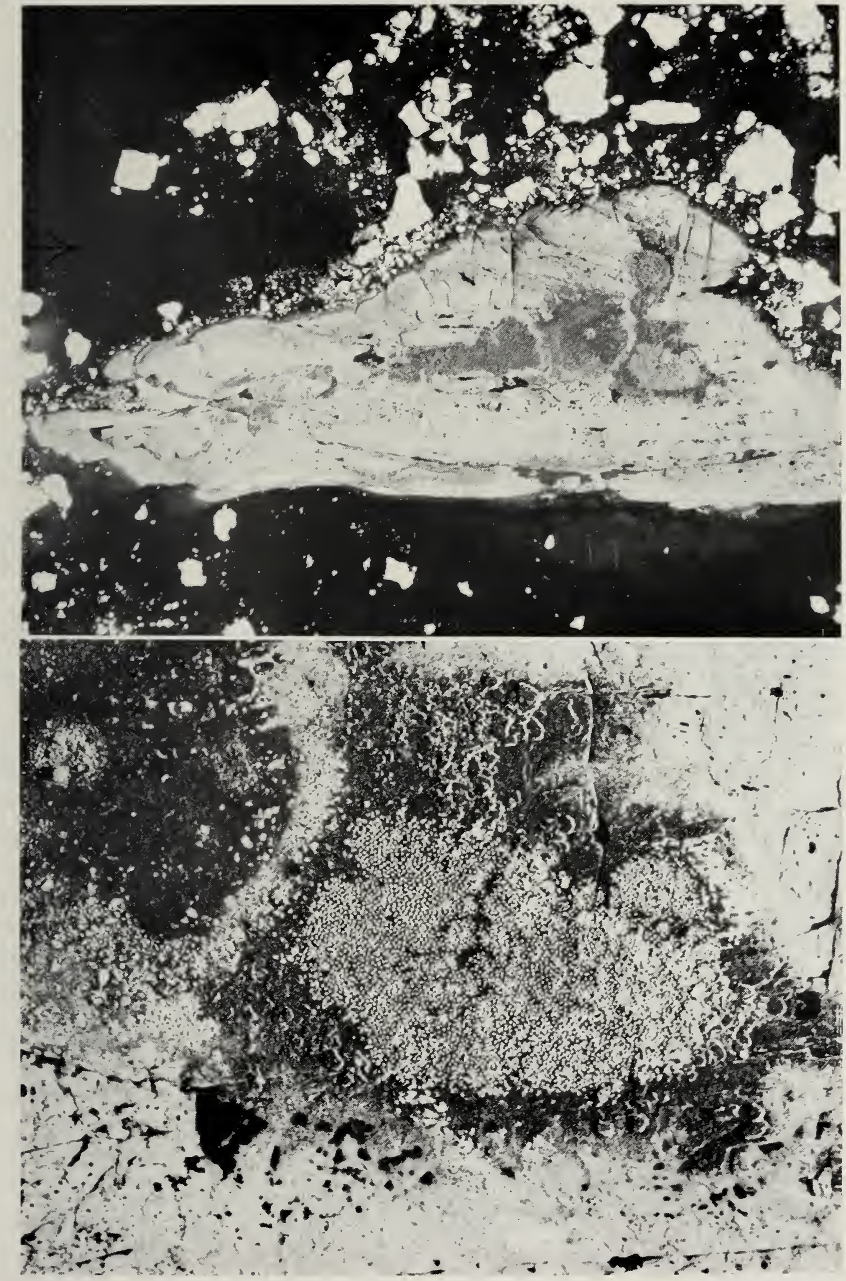

Fig. 7. Aerial view of Funk Island, Newfoundland, showing the total island (above) and a close-up of the Gannet colony (below), 19 June 1972.

TABLE 1

PRESENT NUMBER OF PAIRS OF GANNETS IN NORTH AMERICA, 1972–73

	Number of pairs*	
Colony	1972	1973
Gulf of St. Lawrence:		
Bonaventure Island	–	17,281
Gullcliff Bay, Anticosti Island	135	–
Bird Rocks, Magdalen Islands		
Great Bird	–	4527
North Bird	–	804
Total	22,747	
Eastern Newfoundland:		
Cape St. Mary's	5260	–
Baccalieu Island	–	673
Funk Island	4051	–
Total	9984	

* Represents the number of "nest-site holders."

8657 cliff-top pairs (nests on flattish ground on top of the cliff) and 11,854 cliff-ledge pairs (nests on ledges on the cliff face), whereas in 1973 there were 8007 and 9274 pairs, respectively.

Gullcliff Bay, Anticosti Island, Quebec.—Counts of birds at this colony indicate a decline in numbers in recent years of approximately 19% (Table 2). At least 200 pairs, and probably up to 250 pairs, bred there in 1963 (Dr. H. Ouellet, pers. comm.; Ouellet 1969). By 1969 there were only 167 pairs, and in 1972 numbers had dropped to 135 pairs.

Bird Rocks, Magdalen Islands, Quebec.—A comparison of the census figures for 1969 and 1973 indicates a relatively stable population (Table 2). The slightly higher number estimate on Great Bird in 1973 does not suggest an increase as a small portion of the cliff (ca. 5% of total) was not photographed in 1969. If the some 170 nests which were likely missed in 1969 are added to the total counted from the photographs (4397 pairs), colony size appears to be very similar (4567 pairs) to the 1973 estimate (4527 pairs).

It is more difficult to assess the results from 1967 as they were collected and analyzed using different procedures. All that can be said is that there may have been a shift of birds from North Bird to Great Bird between 1967 and 1969, perhaps due to cliff erosion. However, it does appear that no recent major changes in numbers of Gannets have occurred at the Bird Rocks.

TABLE 2

ESTIMATES OF GANNETS NESTING IN NORTH AMERICA BETWEEN 1959 AND 1973

Colony	Census date	Number of pairs*	Census method**	Authority
Bonaventure Island	10–13 July 1961	13250	GC-BP	Peakall (1962)
	July 1966	21215	AP-BC-GC	Poulin (1968), J. Poulin & G. Moisan (pers. comm.)
	13 July 1969	20511	AP	J. A. Keith & D. N. Nettleship
	7 July 1973	17281	AP	D. N. Nettleship
Gullcliff Bay, Anticosti Island	9 August 1963	ca.200	BC	Ouellet (1969), & pers. comm.
	13 July 1969	167	AP	J. A. Keith & D. N. Nettleship
	12 June 1972	135	AP	D. N.Nettleship
Bird Rocks, Magdalen Islands				
Great Bird	27 June 1967	3750	AP	R. W. Fyfe
	25 July 1969	4397	AP	D. N. Nettleship & S. M. Teeple
	7 July 1973	4527	AP	D. N. Nettleship
North Bird	27 June 1967	1250	AP	R. W. Fyfe
	25 July 1969	807	AP	D. N. Nettleship & S. M. Teeple
	7 July 1973	804	AP	D. N. Nettleship
Cape St. Mary's	17 July & 17 August 1969	(ca.3000) +	GC	L.M. Tuck & S. Temple
	18 June 1972	5260	AP	D. N. Nettleship
Baccalieu Island	20–21 July 1960	ca.900	BC-GC	L. M. Tuck
	21 July 1969	(351) +	GC	W. J. Learning
	21 June 1973	673	AP	D. N. Nettleship
Funk Island	14 July 1959	2768	GC	L. M. Tuck & J. Fisher
	10 July 1967	2900	GC	L. M. Tuck & H. J. Boyd
	18 July 1969	2786	GC	W. J. Learning
	9 July 1970	2760	GC	L. M. Tuck & R. Long
	11 July 1971	2987	GC	L. M. Tuck & W. J. Learning
	19 June 1972	4051	AP	D. N. Nettleship

* Represents the number of "nest-site holders".

** Census methods: AP = aerial photography, BC = boat count, BP = boat photography, GC = ground count; hyphen indicates combined use of methods.

\+ Count based on incomplete survey (see text).

Cape St. Mary's, Newfoundland.—This colony is not easy to census from a ground location or by boat because neither provides full colony coverage, either separately or when combined. In 1969, the total population was estimated to be about 3000 pairs, though the actual count did not include all parts of the colony (Table 2). However, more important than the reliability of the absolute number estimate is the fact that according to Dr. L. M. Tuck (pers. comm.) numbers of Gannets did not fluctuate significantly between 1959 and 1969.

In 1972 the number of nest-site holders was 5260 pairs. It is impossible to know whether the 1969 estimate was low or the colony has undergone a recent substantial increase, but the available evidence seems to indicate that at least part of the difference is due to a low estimate of occupied nests in 1969.

Baccalieu Island, Newfoundland.—This colony is difficult to census accurately from the ground because only the sloping top of the colony is visible. The view is better from the sea, though the complexity of the cliff face still makes a precise count difficult.

On 20-21 July 1960 Dr. L. M. Tuck (pers. comm.) examined the colony from the land and sea (Table 2), and calculated that there were about 900 occupied nests. In 1969 the population was estimated to be 351 pairs, but it seems quite likely that 2 of the 3 occupied cliff areas that comprise the colony were not examined (W. J. Learning, pers. comm.). From aerial photography, the total count of nests in 1973 was 673.

Funk Island, Newfoundland.—This population is perhaps the best known colony in North America. Counts have been made fairly regularly since its re-establishment was reported by Gilliard (1937), especially from 1951 onwards. While there was a major increase in numbers in the 1950's (see Palmer 1962), the total population did not change appreciably between 1959 and 1971 (Table 2). The nature of the apparent increase in population size from 2987 pairs in 1971 to 4051 pairs in 1972 is hard to assess. If the number difference between the 1971 and 1972 estimates is not real, but due to changes in census technique, there seem 2 main factors capable of explaining the difference: (1) ground counts at Funk Island regularly produced an underestimate of nesting pairs due to the short time period available (usually 4 to 6 hours) to census the colony during any single day visit, and (2) a substantial number of non-breeding birds was included in the analysis of the 1972 aerial photographs. The shortage of time may have limited the completeness of the ground counts in 1967, 1969, and 1971, but any error underestimate is believed to be less than 10% (H. J. Boyd and W. J. Learning, pers. comm.). The absence of ground control data for 1972 prevents an estimation of possible error associated with the population analysis from photography. However, from tests performed elsewhere (Barrett and Harris 1965), it seems unlikely that the error would be greater than 5%, and probably closer to 2%. Therefore, the interim conclusion is that at least part of the number difference between 1971 and 1972 is real and not due to a change in methodology alone.

CONCLUSIONS

Total numbers of Gannets in the Gulf of St. Lawrence increased rapidly to a peak by 1966, and have since experienced a slight decline (Table 2). Most of the fluctuations in numbers have been due to changes at Bonaventure Island, where the number of pairs breeding increased from 13,250 in 1961 to a known high of 21,215 in 1966, and then declined to a recent low of 17,281 in 1973. Changes in numbers at the other 2 Gulf colonies during the same time period are uncertain, although it appears that since 1969 the Anticosti Island colony has decreased by about 19% while total bird numbers at the Bird Rocks have remained the same; a slight shift of birds from North Bird to Great Bird may have occurred.

Changes in numbers at the Newfoundland colonies are more difficult to assess (Table 2). Qualitative evidence indicates that the Cape St. Mary's population remained somewhat stable between 1959 and 1969, but a precise estimate of numbers was not made. It is impossible to determine if the 1972 estimate is representative of the number of birds present through the 1960's or includes a recent increase. Unlike Cape St. Mary's, the Baccalieu Island colony is believed to have declined since the early 1960's, although the decrease between 1960 and 1969 (900 to 351 pairs) and the subsequent increase (351 to 637 pairs) are likely not to be real, but due to an incomplete count in 1969 (Table 2). Moreover, it is also possible that the population has not fluctuated significantly between 1960 and 1973, the small number difference being merely an artifact of differing census procedures. Funk Island Gannets increased rapidly in the early 1950's (Palmer 1962), reaching a peak in 1959, with no appreciable change in numbers since 1959 and 1971. The colony has apparently increased since 1971, the absolute value of which is unknown.

The reasons for the decreases in the Gulf of St. Lawrence populations are unclear and require further investigation. What is clear, however, is that environmental contamination by toxic chemicals (chlorinated hydrocarbons and heavy metals) is greater in the Gulf than along the Atlantic coast of Newfoundland. In addition, Gannet breeding success is lower in the Gulf (Bonaventure Island) where toxic chemical levels (DDE) in Gannets (mean ppm wet weight brain tissue) are significantly higher than those at Funk Island in Labrador Current waters (Pearce et al. 1973).

Furthermore, egg-shell thinning was detected among Bonaventure Island birds in 1969 to an extent (ca. 17% thinner than pre-1915 eggs) that has been associated with reproductive failure in other birds (Pearce et al. 1973, Keith and Gruchy 1972). This combined with the fact that both colonies which have decreased (Anticosti and Bonaventure) are situated in the Gulf where contamination is most concentrated (i.e., towards St. Lawrence estuary) suggests that toxic chemicals may be the major contributing factor to the observed declines. Less obvious causes such as changes in mackerel numbers and distribution (the main summer food of Gannets in the Gulf) or an increased emigration of Gulf-reared birds to east Newfoundland colonies at time of first breeding may also be operative (see Nettleship 1975).

SUMMARY

The results of 1972 and 1973 surveys indicate a total North American Gannet population of about 32,731 pairs, of which 22,747 (69.5%) nest in the Gulf of St. Lawrence and 9984 (30.5%) on the Atlantic coast of Newfoundland. A considerable decrease in Gannet numbers has taken place at 2 of the 3 colonies (Bonaventure and Gullcliff Bay) in the Gulf since 1969. Reasons for these declines are obscure, though contamination by toxic chemicals seems a likely prime cause. Colonies in Newfoundland appear to have remained somewhat stable (Cape St. Mary's and Baccalieu) or undergone a slight increase (Funk) in recent times.

ACKNOWLEDGMENTS

I am grateful to the following persons for their excellent assistance in collecting the photographic materials necessary for the Gannet project: J. Bouzane (Cape St. Mary's, Funk Island), Dr. A. R. Lock (Anticosti Island, Bonaventure Island, Bird Rocks), and R. D. Montgomerie (Baccalieu Island). Thanks are also due to J. A. Keith and S. M. Teeple for providing me with their Gannet photographs taken in 1969, and Dr. L. M. Tuck for counts of Newfoundland colonies made prior to 1972. My special thanks to M. Channing for his careful analysis of all the 1969, 1972, and 1973 photographs, and to H. J. Boyd and Dr. R. G. B. Brown for their critical review of the manuscript.

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LITERATURE CITED

Barrett, J. H. and M. P. Harris. 1965. A count of the Gannets on Grassholm in 1964. Br. Birds 58:201–203.

Bent, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. No. 121.

Fisher, J. and H. G. Vevers. 1943–1944. The breeding distribution, history and population of the North Atlantic Gannet (*Sula bassana*). J. Anim. Ecol. 12:173–213, 13:49–62.

Fisher, J. and R. M. Lockley. 1954. Sea-birds. Collins, London.

Gilliard, E. T. 1937. The Gannets of Funk Island. Auk 54:379–381.

Keith, J. A. and I. M. Gruchy. 1972. Residue levels of chemical pollutants in North American birdlife. Proc. XVth Int. Ornithol. Congr., The Hague, 1970: 437–454.

Nettleship, D. N. 1975. A recent decline of Gannets *Morus bassanus* on Bonaventure Island, Quebec. Can. Field Nat. 89:125–133.

Ouellet, H. 1969. Les oiseaux de l'ile Anticosti, Province de Quebec, Canada. Natl. Mus. Nat. Sci. Publ. Zool. No. 1. Ottawa.

Palmer, R. S. 1962. Handbook of North American birds. Yale Univ. Press, New Haven.

Peakall, D. 1962. Gannet population of Bonaventure Island. Can. Field Nat. 76:179–180.

Pearce, P. A., I. M. Gruchy, and J. A. Keith. 1973. Toxic chemicals in living things in the Gulf of St. Lawrence. Proceedings of the Canadian Society of Fisheries and Wildlife Biologists, Canadian Society of Zoologists Symposium: Renewable resource management of the Gulf of St. Lawrence, 5 January 1973, Halifax, Nova Scotia.

Poulin, J. -M. 1968. Reproduction du Fou de Bassan (*Sula bassana*) Ile Bonaventure (Quebec). M.Sc. thesis, L'Universite Laval, Province de Quebec.

Salmon, H. M. and R. M. Lockley. 1933. The Grassholm Gannets: a survey and census. Br. Birds 27:142–152.

CANADIAN WILDLIFE SERVICE, ENVIRONMENT CANADA, 2721 HIGHWAY 31, OTTAWA, ONTARIO, CANADA. ACCEPTED 18 MAR. 1975.

REQUEST FOR ASSISTANCE

Black and Turkey Vultures. As part of a study of their ecology, Black and Turkey vultures are being marked with white plastic wing tags. These tags are fastened around the humerus and are visible from above or below. Each tag has a combination of a letter and a 2-digit number painted on it. All birds are being marked in east Mississippi. If marked vultures are observed, please send details of the observation to: Jerome A. Jackson, Department of Zoology, Mississippi State University, Mississippi State, MS 39762.

FEEDING BEHAVIOR AND DIET OF THE LONG-BILLED CURLEW AND WILLET

Lynne E. Stenzel, Harriet R. Huber, and Gary W. Page

To study shorebird feeding ecology, most people collect birds and examine stomach contents although in a few instances regurgitated pellets (Hibbert-Ware and Ruttledge 1944, Swennen 1971) or observations of feeding birds (Baker and Baker 1973) have been used. In this study we used both observations and regurgitated pellets to examine the feeding behavior and the diet of the Long-billed Curlew (*Numenius americanus*) and the Willet (*Catoptrophorus semipalmatus*) on Bolinas Lagoon, in California. Our objective was to find a suitable method for studying shorebird diets without sacrificing the birds. In the literature we found little information on the diet of the Long-billed Curlew, and data on the Willet in California that we found are limited to the examination of 21 stomachs (Reeder 1951, Recher 1966, Anderson 1970). There is little information on the feeding behavior of either species. We felt, therefore, that any information we could add on the feeding behavior and diet of these shorebirds would be useful.

METHODS

Bolinas Lagoon is a shallow 570-ha estuary 24 km northwest of San Francisco, California. High hills, marshy pastures, and the Seadrift sand spit surround this wedge-shaped estuary except for a narrow opening to the ocean on the southwest side (Fig. 1). Pine Gulch Creek drains into the estuary year round and is the main source of the estuary's fresh water. Kent Island is a 40-ha island within the estuary. A large part of Kent Island and the Pine Gulch Creek delta are salt marsh where the chief plant species are *Salicornia virginica* and *Spartina foliosa.* At mean low water about 70% of the estuary comprises tidal flats which are divided by several channels (Ritter 1969).

This study was conducted from June 1973 to February 1974 and divided into a fall period (July through October) corresponding with a warm dry season, and a winter period (November through February) corresponding with most of the rainy season at Bolinas.

We made a census of all shorebirds on the estuary during every 5-day period from 31 May to 7 October and with one exception during every 10-day period from 8 October to 1 March. All but 2 censuses were taken on flood tides 1.1-1.7 m above mean low water. During the census the estuary was divided into 3 areas and an observer in each area counted or estimated all shorebirds in that area. The counts in the areas were made simultaneously.

Additional censuses of specific areas on or near the estuary were also made to find out which were most used by the birds. We censused shorebirds in the salt marsh on Kent Island at low and moderate tides several times a month, and on

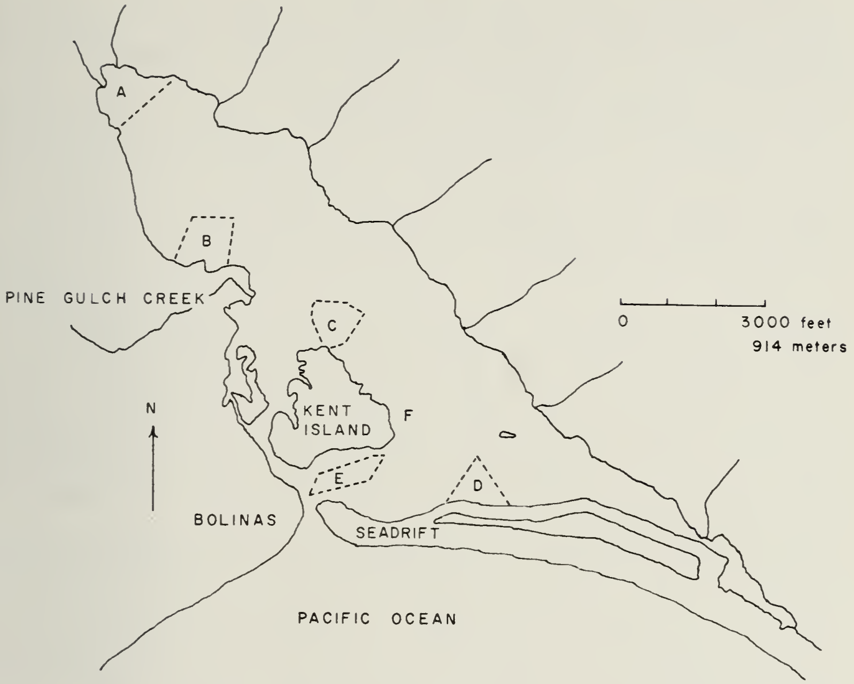

FIG. 1. Map of Bolinas Lagoon showing 5 areas of intensive study. Area A is approximately 12.6 ha; B, 9.8 ha; C, 8.0 ha; D, 7.0 ha; and E, 8.4 ha.

8.5 km of open coast (comprising sand to pebble beaches and soft shale reefs) adjacent to and north of Bolinas Lagoon 3 times a month.

We selected 5 areas within the tidal flat of the estuary (Fig. 1) for the most intensive study. The substrate of area A was a very poorly sorted, very fine sand (Ritter 1969) containing considerable organic debris such as twigs and leaves. Much of the high-water zone of this area was covered by a layer of sediment, dried and cracked into leathery plates. The high-water zone abutted a small salt marsh through which a fresh-water stream ran year round; the low-water zone bordered a basin. Area B was similar to area A except that a fresh-water stream ran into it only during periods of heavy rain and that the substrate ranged from fine to medium sand (Ritter 1969). The substrate of area C was a well to moderately sorted, fine sand (Ritter 1969) and lacked the organic debris of areas A and B. Unlike areas A and B the high-water zone of area C was pock-marked with the burrow openings of the ghost shrimp (*Callianassa californiensis*) and was not covered by hard, dried plates of sediment. The high-water zone of area C abutted the Kent Island salt marsh on one side and a channel on the other; the low-water zone bordered a small basin. Area D had a substrate of moderately sorted, fine sand (Ritter 1969), and was bordered on 2 sides by channels and on a third side by a basin. The high-water zone in the center was less burrowed than area C. Area E differed markedly from the other areas. It comprised sediment ranging from medium sand through pebble. The pebble fraction contained numerous shell fragments and was largely in the low-water zone. The high-water zone was separated from the Kent Island sand beach by a shallow channel; the low-water zone bordered a main channel.

To find out where shorebirds fed on the tidal flat, 10 censuses, in which feeding and non-feeding birds were counted separately, were made in each of the 5 areas every month of the study. Each month we tried to census on all combinations of high, moderate, and low water with an ebb tide, a flood tide, and slack water. We tried to take censuses for a particular tidal condition in all areas on the same day.

We further divided each of the 5 areas into microhabitats, defined by elevation in the tidal zone and the water level in relation to the substrate surface. We defined the high-water zone of each area as the highest third of the area, the low-water zone as the lowest third, and the mid-water zone as the area between. In each zone, surface irregularities on the tidal flat such as pools and channels created emerged, edge (substrate holding a surface film of water), and submerged substrate, giving a total of 9 microhabitats. Recher (1966) and Baker and Baker (1973) also used the water level in relation to the substrate surface to describe tidal flat microhabitats. During the study, we censused at low tide in each area, counting the number of individuals of each species feeding in each of the microhabitats. Birds feeding in algae were counted separately.

Substrate cores were taken at low tide from each area to measure the relative abundance of small invertebrates, and from an invertebrate study plot to measure the seasonal abundance of some invertebrates. The cores, 9.8 cm deep and 6.6 cm in diameter, were washed through sieves with 1 mm openings and the organisms retained were identified and tallied. Nine cores were taken from each microhabitat (with the exception of a few very limited microhabitats) from all areas in June and from areas A, D, and E in December. The invertebrate study plot (280 × 20 m) lay along the southern border of area C and ran from the edge of the salt marsh to a basin in the low-water zone. Every month 2 cores were taken at random from each of 28 stations (10 × 20 m) along the length of the plot. Each month we estimated the algal coverage in each station.

As an estimate of the availability of the tidal flat to shorebirds, we calculated the number of daylight hours during which the tidal level was less than 1.4 m above mean low water. This calculation was made for one day of every 3-day period of the study; we used the tidal charts to estimate the rate at which the water ebbed or flooded and the time at which the water level reached 1.4 m above mean low water.

We watched individual Long-billed Curlews and Willets to determine their feeding rates, methods of searching for and capturing prey, use of microhabitats, and the type of prey they captured. We observed birds through 20-× spotting scopes and tape-recorded data. The type, success, and microhabitat location of each prey-capture attempt were recorded as well as interactions between the bird under observation and other birds. Prey-capture attempts were defined as follows. A *peck* was a single movement of the bill usually to the surface of the mud but occasionally at flying insects or organisms on snags or rocks. A *multiple peck* was a series of 2 or more consecutive movements of the bill to the surface of the substrate without lifting the bill back to the horizontal position. *Probes* were single movements of the bill into and out of the substrate, that appeared to penetrate the substrate at least 1 cm. *Multiple probes* consisted of 2 or more vertical motions of the bill during which it was not withdrawn from the substrate. All pecks and probes were considered prey-capture attempts although a few may have been search tactics. An observation was terminated when the bird stopped feeding and only observations of 4 min or longer were analyzed. Observations of Long-billed Curlews were taken at many locations on the estuary but those of Willets only in areas A, C, D, and E. In the fall period we made 46 Long-billed Curlew observations totaling 744 min and 28 Willet observations totaling 164 min; in the winter period, 22 Long-billed Curlew observations totaled 272 min and 67 Willet observations totaled 499.5 min. The average distance of the observer from the bird was 50 m for the Long-billed Curlew and 30 m for the Willet. In the Willet feeding observations, differences among areas are taken from winter observations only and differences between seasons from observations in areas A and C only because we did not collect an adequate sample of Willet observations in all areas for both seasons.

We analyzed regurgitated pellets of Long-billed Curlews and Willets to identify their prey. Most pellets were collected from locations where a group of roosting birds of a single species had just been flushed, but a few were collected from individuals after pellet regurgitation had been observed. Only moist, fresh pellets were collected; they were preserved in alcohol for later analysis. In the fall period 30 Long-billed Curlew pellets were collected on high tides in the salt marshes of the Pine Gulch Creek delta and Kent Island where most of the curlews on the estuary roosted. No curlew pellets were obtained during the winter period. Willet pellets were obtained from birds that fed in areas A, C, D, and E and roosted in the high-water zone of these areas during flood tides and from area F (Fig. 1) where many Willets that fed over a large portion of the estuary roosted. In the fall period we collected 19 Willet pellets from area A, 14 from C, 10 from D, and 15 from F; in the winter period, 2 from A, 7 from C, 4 from D, 2 from E, and 9 from F. We also obtained 6 stomachs from Willets that had been eaten by raptors and used 2 additional stomachs obtained in previous years from raptor kills. The contents of the pellets and stomach samples were examined under a 30-× dissecting microscope and the prey identified from characteristic fragments.

Two statistical procedures were used to test the similarity of one result against another: the test for the equality of 2 percentages (Sokal and Rohlf 1969:607–608) and Student's *t*-test for the difference between means (Steel and Torrie 1960:73–75).

In this paper mud crab is used synonymously with *Hemigrapsus oregonensis*, ghost shrimp with *Callianassa californiensis*, and mud shrimp with *Upogebia pugettensis*.

RESULTS

Long-billed Curlew

Distribution.—During this study the number of Long-billed Curlews on Bolinas Lagoon consistently averaged 40. At nearby estuaries such as Limantour Estero, Tomales Bay, and Drake's Estero, 1 or 2 curlews were all that could be found on any date. On Bolinas Lagoon the curlews were scattered at low tide over the tidal flat, feeding primarily in emerged and submerged microhabitats; when the flats were covered at high tide the birds roosted in the salt marsh. Curlews were not seen feeding on the coast or in pastureland but occasionally one or two were seen feeding in the salt marsh.

TABLE 1

MEAN FEEDING RATES OF THE LONG-BILLED CURLEW FOR 2 FEEDING METHODS AND 2 SEASONS ON BOLINAS LAGOON

	Combined Seasons			Combined Methods		
	"Pause-probe"		"Burrow-probe"	Fall Period		Winter Period
PCA[a]/Min.	5.6	*[b]	9.4	8.5	*	11.1
Prey/PCA (%)	8.5	*	4.9	4.9		4.8
Prey/Min.	0.4		0.4	0.3	*	0.5

[a] PCA is prey-capture attempts.
[b] An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Feeding behavior.—Long-billed Curlews used 3 methods to obtain prey. In the "burrow-probe" method, used primarily in the emerged areas, the curlews probed into burrows until prey was sensed, then probed rapidly in a burrow until the prey was seized. In the "pause-probe" method, used only in submerged areas, the curlews stood in 5–10 cm of water with their bills partly under water and slightly ajar. They remained motionless in this position for 5–10 sec, presumably until detecting some movement in a burrow below. The bill was then moved slowly down until, with a sudden lurch, the prey was captured. If this attempt was unsuccessful the movement was often repeated. The burrow-probe and the pause-probe methods were used by the curlews to obtain all of their major prey species. The third capture technique, the "peck," was used much less often than the other methods and only to obtain prey on the substrate surface. The curlews were not observed to obtain any small prey by this method and only a few small, surface-dwelling prey were detected in the pellets. However, the curlews did obtain the mud crab with this technique. When a crab was sighted the curlew ran swiftly toward it. If the crab escaped to a burrow, the curlew often ignored the burrow entrance and probed directly through the mud to capture the crab. The curlews often switched among the 3 feeding methods.

Birds using the burrow-probe method made significantly ($P < .05$) more attempts per minute but were successful less often than birds using the pause-probe method (Table 1). There was no significant difference ($P > 0.05$) between the methods in the number of prey obtained per minute and no apparent difference in the size of the prey taken. In the winter period more attempts were made and more prey obtained per minute ($P < 0.05$) than in the fall (Table 1). However, the number of prey captured per attempt was nearly the same for both seasons ($P > 0.05$).

Although many prey were eaten whole, prey that were particularly large or lively were not. The bird first removed some or all of the legs from such a prey by biting them off or by holding the prey by a leg and shaking it vigorously. The body was eaten first, then the legs. Claws of large male ghost shrimps were sometimes left uneaten. The curlews often washed muddy prey before eating them.

Willets and Ring-billed Gulls (*Larus delawarensis*) sometimes attempted to steal prey from Long-billed Curlews. In 9 attempts during feeding observations Willets were successful twice and in 10 attempts the Ring-billed Gulls successfully usurped a curlew's prey 3 times.

Diet of Long-billed Curlews.—Of the 30 pellets collected during the fall period 97% contained the remains of mud crabs, 77% of ghost shrimps, and 47% of mud shrimps. Of the 370 large invertebrates found in the pellets 59% were mud crabs, 34% ghost shrimps, 6% mud shrimps, and 1% unidentified decapods. In addition to the large prey, in the pellets were also remains from 9 insect pupae, 6 *Gemma gemma*, 3 seeds, 3 *Cryptomya californica*, 1 worm (Nereidae), and 1 *Littorina scutulata.* Fragments from several amphipods (Talitridae) were found in 2 pellets and traces of adult insects in 7 pellets.

From direct observations of 205 prey items observed being taken by curlews during the fall period, 55% were mud crabs, 24% ghost shrimps, 15% mud shrimps, and 7% were unidentified. During the winter period the direct observations on type of prey eaten were similar to those of the fall period: of 134 prey, 63% were mud crabs, 20% ghost shrimps, 7% mud shrimps, and 9% were unidentified. Occasionally during winter censuses on Bolinas Lagoon, but not during feeding observations, we saw Long-billed Curlews catch and eat small fish in submerged areas. No pellets were found during the winter period, perhaps because the curlews spent more time feeding and less time in the roosting areas than in the fall.

Willet

Distribution.—Willets were the most abundant large shorebirds both on Bolinas Lagoon (averaging 560 birds during the fall and 385 in the winter period) and also on the adjacent coast (averaging 58 birds during the fall and 76 in the winter period). On Bolinas Lagoon, at low tide, most Willets fed on the tidal flats; however, as the tide rose, the number of Willets in the salt marsh increased until, at high tide, many Willets were either feeding or roosting there. When high tides and rain coincided during the winter, flooding the intertidal areas, Willets fed in the water-soaked pastures adjacent to the estuary. During all periods Willets often flew

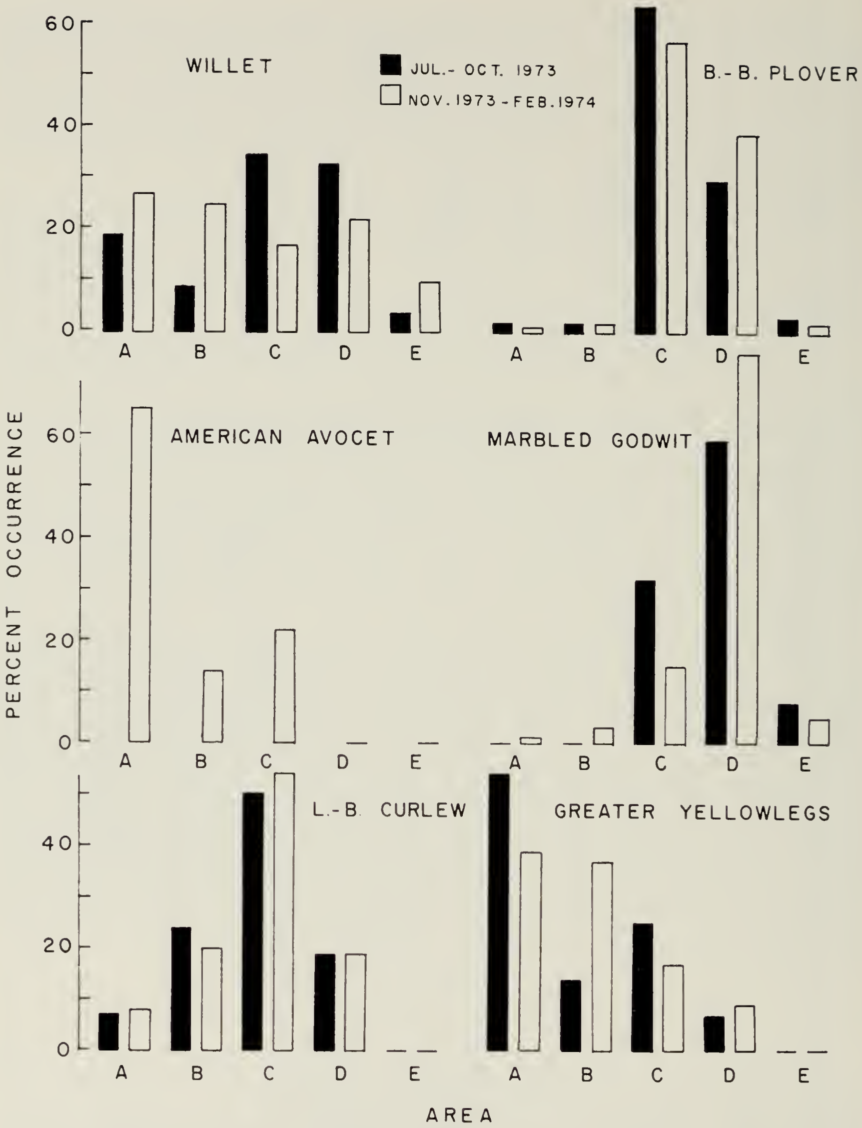

FIG. 2. Distribution of large shorebirds among 5 areas on Bolinas Lagoon. In the calculation of percent occurrence, equal weight was given to each month.

between the estuary and the adjacent coast indicating that both habitats were used by some of the birds.

Willets fed over all of the tidal flat on Bolinas Lagoon and were more equally distributed among the different areas (Fig. 2) and microhabitats

Fig. 3. Distribution of feeding shorebirds in 3 microhabitats on Bolinas Lagoon. EM is emerged; ED, edge; and S, submerged microhabitat. Sample sizes are under the species' names with the high-tide sample sizes in parentheses.

(Fig. 3) than were the other common large shorebirds: Long-billed Curlew, Black-bellied Plover (*Pluvialis squatarola*), American Avocet (*Recurvirostra americana*), Marbled Godwit (*Limosa fedoa*), and Greater Yellowlegs (*Tringa melanoleuca*). When algae, *Enteromorpha* sp. and *Ulva* sp., covered areas of the tidal flat, Willets fed heavily on invertebrates in the algal beds. They were the only large shorebirds that fed extensively in the salt marsh.

Feeding behavior.—Willets most commonly searched visually for prey while walking. Another important search technique was lifting or flipping algae, rocks, debris, or dried, cracked mud with the bill. Less commonly, Willets in water up to their tibio-tarsi ran erratically and pecked in the water. By this method Willets obtained small unidentified prey and occasionally fish.

We distinguished 5 methods of capturing prey used by Willets: peck, multiple peck, probe, multiple probe, and theft from Long-billed Curlews. In all areas studied Willets captured 93% or more of their prey with pecks and multiple pecks.

Capture of small prey was detected indirectly by movements of the head and swallowing motions but capture of large prey was easily seen and large organisms were often identified. Large prey such as fish or pelecypods were swallowed whole; decapods were often shaken apart, the appendages then being eaten before the carapace. When large organisms were covered with mud, Willets often washed them before eating them. We saw Willets reject some prey: a few large cockles and crabs that the birds first struggled to swallow and then rejected (probably because they were too large) and large snails which the birds merely investigated. Willets sometimes lost large quarry to Ring-billed Gulls and Western Gulls (*Larus occidentalis*).

Diet of the Willets.—Pellets from Willets contained small organisms from the tidal flats such as the surface-dwelling gastropod *Cerithidea californica*, the pelecypods *Gemma gemma* and *Transenella tantilla*, and tube-dwelling amphipods (*Corophium* spp.). The amphipods *Allorchestes angustus* and *Ampithoe* spp., the gastropod *Lacuna* sp., and most of the mussels (*Mytilus* sp.) were taken from algae. The gastropod *Littorina scutulata* and some of the mussels (*Mytilus* sp.) found in the pellets were probably taken from tires, rocks, and snags; adult insects (mostly Coleoptera and Diptera) and talitrid amphipods (mostly or entirely *Orchestia traskiana*) were probably taken in the salt marsh. Remains of large prey in the pellets included the pelecypods *Protothaca staminea* and *Macoma* spp., the brachyurans *Hemigrapsus oregonensis* and *Cancer antennarius*, and the anomurans *Callianassa californiensis*, *Upogebia pugettensis*, and *Pagurus* sp. Other prey, occurring infrequently in the pellets, included the polychaetes *Capitella capitata*, *Lumbrineris zonata*, and an unidentified nereid, ostracods, the cheliferan *Leptochelia dubia*, the amphipod *Grandidierella japonica*, the brachyurans *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Cancer magister*, larval and pupal dipterans, and the pelecypod *Clinocardium nuttallii*.

We detected additional tidal flat prey from feeding observations. While Willets took only one fish in 164 min of observation in the fall period, they captured 11 during 499.5 min of winter observation, mostly from areas D and E. During the winter period some Willets, feeding in the mid- and high-water zones of area A during rising tides, captured up to 19.7 worms per minute. Since several species of Spionidae constituted 85% of the worms in our samples from area A during the winter period, 1 or more of these were probably the worms that the Willets ate.

Cooper's Hawks (*Accipiter cooperii*), Red-shouldered Hawks (*Buteo lineatus*), and Marsh Hawks (*Circus cyaneus*) often hunted Willets in the salt marsh and sometimes left the entrails and flight feathers of Willets they had eaten there or under the pines on Kent Island. In the 8 stomachs left with such remains we found *Orchestia traskiana* in all, adult Coleoptera in 6, unidentified seeds in 6, *Littorina scutulata* in 4, the small gastropod

TABLE 2

MEAN FEEDING RATES OF THE WILLET DURING WINTER IN 4 AREAS ON BOLINAS LAGOON

Area	PCA[a]/Min.	Prey/PCA (%)	Prey/Min.	% Large Prey[b]	Sample Size[c]
A	30.0	39.2	13.1	2.0	12
C	27.3	31.7	9.1	2.5	14
		*[d]	*		
D	26.3	16.4	3.8	4.3	26
		*	*	*	
E	23.1	8.2	1.8	20.1	15

[a] PCA is prey-capture attempts.
[b] Large prey includes decapods, pelecypods greater than 3 cm long, and fish.
[c] Sample size is the number of feeding observations used to calculate the means.
[d] An asterisk indicates a significant difference ($P < 0.05$) between adjacent means.

Phytia setifer in 3, *Lacuna* sp. in 2, *Hemigrapsus oregonensis* in 2, *Gemma gemma* in 1, and *Mytilus* sp. in 1.

Inter-area variation.—The Willets' feeding success varied among different areas of the tidal flat. Although the number of prey-capture attempts per minute did not differ significantly between any of the areas (for all possible pairs of data, $P > 0.05$), the success rate (prey per prey-capture attempt) differed significantly ($P < 0.05$) between some areas and resulted in different rates of prey intake between areas (Table 2). A trend for the number of prey per minute to decrease from areas A to E may have been partially offset by a tendency for large prey to make up an increasing percentage of the diet from areas A to E (Table 2). Among areas there was also considerable variation among the microhabitats in which Willets fed (Table 3).

As expected, variations among different areas in the abundance of the

TABLE 3

USE OF DIFFERENT MICROHABITATS BY WILLETS DURING WINTER IN 4 AREAS ON BOLINAS LAGOON

Area	Percent of PCA[a]			Sample Size	Percent of Prey Taken			Sample Size
	Em[b]	Ed	S		Em	Ed	S	
A	0.2	55.9	43.9	2273	0.1	68.0	31.9	1025
C	1.0	5.8	93.1	2477	1.6	4.2	94.2	738
D	8.8	15.2	76.0	4731	12.1	19.4	68.5	660
E	38.0	2.9	59.1	2141	49.7	2.5	47.8	157

[a] PCA is prey-capture attempts.
[b] Em is emerged, Ed is edge, and S is submerged.

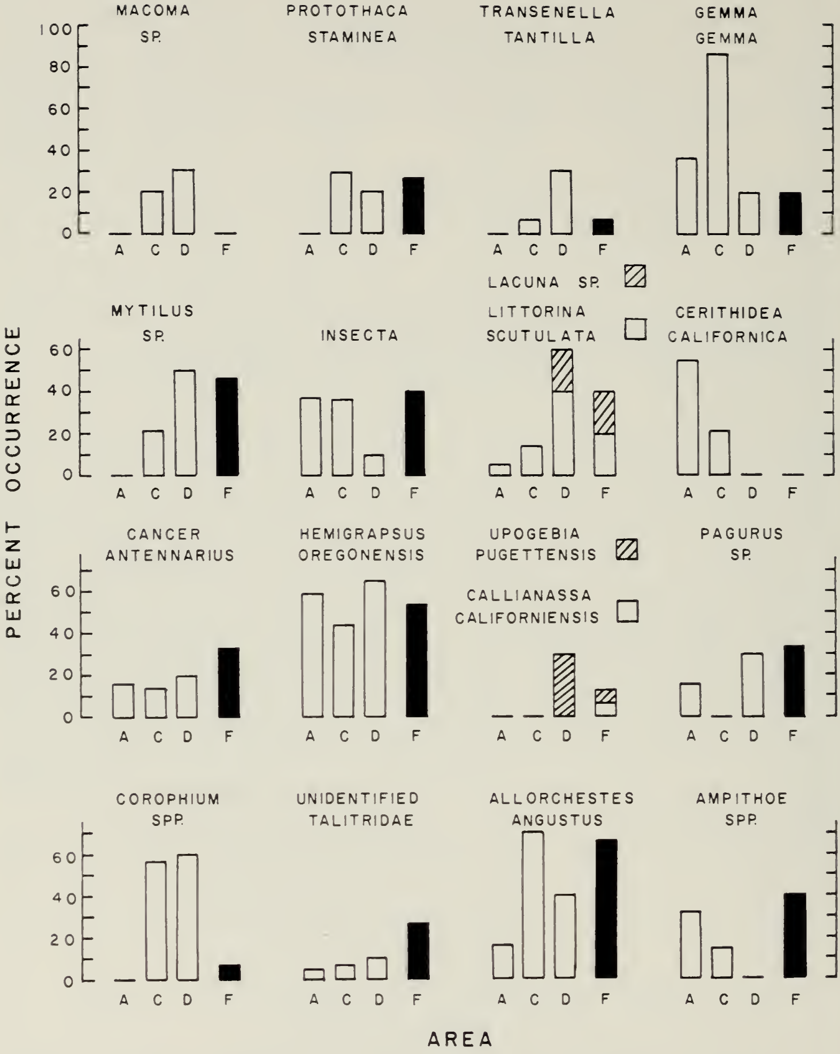

FIG. 4. Percent occurrence of prey in Willet pellets collected from 4 areas of Bolinas Lagoon from July to October 1973. Pellets collected in areas A, C, and D were from birds feeding in or in the vicinity of those areas; pellets from area F were from birds feeding over a large area of the estuary. Sample size for A is 19; C, 14; D, 10; F, 15. Two additional pellets from area E contained a total of 4 *Pagurus* sp., 5 *Pachygrapsus crassipes*, and 3 *Hemigrapsus oregonensis*.

Table 4

Relative Abundance of Selected Invertebrates in 4 Areas on Bolinas Lagoon in June 1973

Species	Mean Number per Core in Area[a]			
	A	C	D	E
Cerithidea californica	0.1	0.1	0.0	0.0
Gemma gemma	152.6	28.0	4.6	0.0
Transenella tantilla	0.0	0.1	12.1	0.0
Corophium spp.	21.7	41.0	56.9	45.4
Number of cores	9	9	9	9

[a] Means are from microhabitats with the highest abundance of the organism in each area.

tidal flat invertebrates were sometimes reflected in the pellets. There was an increase in the abundance of *Transenella tantilla* in the substrate (Table 4) and pellets (Fig. 4) from area A to C to D. *Gemma gemma* and *Cerithidea californica* were less abundant in the substrate (Table 4) and pellets (Fig. 4) of area D than areas A and C, and *Corophium* spp. were found only in pellets (Fig. 4) from the areas in which these amphipods occurred most abundantly (Table 4). The relative abundance of prey in pellets from different areas did not always occur in direct proportion to the relative abundance of invertebrates in the substrate. For example, *Gemma gemma*, which occurred most frequently in pellets from area C, occurred most abundantly in the substrate of area A. The abundance of prey in each area, such as *Littorina scutulata* on rocks and snags or *Ampithoe* spp., *Allorchestes angustus*, *Lacuna* sp., and *Mytilus* sp. which occurred primarily on algae, depended on properties that we did not measure. We did not sample for the abundance of the large invertebrates.

Seasonal variation.—There were several environmental changes that affected the availability of prey to the Willets on the tidal flats from the fall to the winter period. The number of daylight hours that were available for feeding on all but the highest portion of the tidal flat decreased from a mean of 10.1 h in the fall to 7.8 h in the winter period. Prolonged rain during the winter period sometimes flooded the estuary for several days and further reduced the number of daylight hours that the tidal flats were available.

There was a decrease in the abundance of some of the Willets' prey from the fall to the winter period. Numbers of substrate-dwelling invertebrates *Gemma gemma* and *Corophium* spp. and alga-dwelling invertebrates *Allorchestes angustus* and *Ampithoe* spp. all declined from the fall to the winter period (Table 5). The decline in alga-dwelling amphipods was probably

TABLE 5

SEASONAL ABUNDANCE OF SOME OF THE WILLETS' PREY ON BOLINAS LAGOON

Species	Location[a]	Mean Number per Core in: Fall Period		Winter Period
Gemma gemma	Area A	152.6	*[b]	14.7
	I.S.P.	4.9	*	2.3
Corophium spp.	I.S.P.	20.1	*	4.0
	Area D	56.9	*	10.6
Transenella tantilla	Area D	12.1		4.9
Allorchestes angustus	I.S.P.	6.1	*	0.1
Ampithoe spp.	I.S.P.	0.2	*	0.0

[a] Data from areas A and D taken from 9 cores from the microhabitat in each area in which each organism occurred most abundantly. Data from the invertebrate study plot (I.S.P.) taken from 56 cores per month during each period.

[b] An asterisk indicates a significant difference ($P < 0.05$) between fall and winter period means.

related to a decline in the extent of the algal beds on the estuary. In July algae (primarily *Enteromorpha* sp.) covered 57% of the invertebrate study plot, in August 41%, in September 20%, in October 3%; from November to February only an insignificant area was covered. *Ulva* sp., another green alga, covered 2.1% of the invertebrate study plot in the fall period and only 0.4% in the winter.

The success of Willets' feeding attempts (prey per prey-capture attempt) decreased ($P < 0.05$) from 70.7% in 22 fall observations to 35.2% in 26 winter observations. In censuses of birds in the different areas the proportion of Willets feeding at any time increased ($P < 0.05$) from a mean of 84.0% of the total birds censused in fall to 92.1% in winter. This was probably due to increased pressure on the birds to use more of the available feeding time in the winter than in the fall period. There were also seasonal changes in the Willets' use of different feeding areas within and near the estuary. During fall 26.1% of 890 Willets censused in areas A, B, C, and D were feeding in algae but during the winter period only 6.7% of 878 birds were feeding in the much depleted algal beds. The number of Willets feeding in the Kent Island salt marsh at low and moderate tides increased ($P < 0.05$) from 5.0% of the estuary's Willets in fall to 17.5% in winter. The number of Willets found on the open coast also increased ($P < 0.05$) from 9.2% of the combined estuary and open coast Willet population in the fall to 17.3% in the winter period. It appears that the decreased availability of the tidal flat and the decline in abundance of some tidal flat invertebrates resulted in increased daytime use of feeding areas other than the tidal flat from the fall to winter period for the Willets. We found Willets feeding

TABLE 6

SEASONAL DIFFERENCES IN WILLETS' PREY FROM PELLETS[a] COLLECTED FROM AREAS C AND F ON BOLINAS LAGOON

Prey of Willet	% of Pellets in which Prey Occurred		
	Fall Period		Winter Period
Pagurus sp.	17	*	0
Gemma gemma	52	*	12
Corophium spp.	31	*	0
Ampithoe spp.	28	*	0
Allorchestes angustus	69	*	6
Mytilus sp.	34	*	6
Cancer antennarius	24		6
Lacuna sp.	10		12
Cerithidea californica	10		12
Littorina scutulata	17		19
Macoma spp.	10		12
Protothaca staminea	28		38
Transenella tantilla	7		12
Callianassa californiensis	3		12
Upogebia pugettensis	3		19
Hemigrapsus oregonensis	48	*	94
adult Insecta	38	*	69
Talitridae[b]	17	*	50
sample size	29		16

[a] Significant seasonal differences ($P < 0.05$, test for equality of 2 percentages) are indicated by an asterisk.

[b] Talitridae are mostly or entirely *Orchestia traskiana*.

on the tidal flats at night during the winter, but during the fall our observations suggest that most Willets leave the estuary at or shortly after dusk. There may be a greater tendency for Willets to feed at night during the winter than during the fall period.

A change in the diet from the fall to the winter period was detected in the pellets (Table 6). *Allorchestes angustus*, *Ampithoe* spp., and *Corophium* spp. were major prey in the fall but nearly absent from the winter pellets. The presence of *Gemma gemma* in the pellets decreased from the fall to the winter period. As already described, our substrate samples also showed a decline in these species during winter (Table 5). *Mytilus* sp. and *Pagurus* sp. decreased from the fall to the winter period in the pellets but we have no information on their seasonal abundance. The increase during the winter period of some amphipods (Talitridae) and insects (mostly Coleoptera) in the pellets is probably a reflection of the increased use of the salt marsh by the Willets during this period.

DISCUSSION

On Bolinas Lagoon the Long-billed Curlew is a hunter of large burrow-dwelling prey and its exotic morphological features are in harmony with this pursuit. Its major prey species live in different habitats but all have curved burrows. Mud shrimps live at low tide levels in U-shaped burrows that extend about 45 cm into the substrate (MacGinitie and MacGinitie 1968). Ghost shrimps live in a higher tidal zone than mud shrimps, in many-branched burrows that extend vertically into the substrate (MacGinitie 1934). Both organisms feed near the entrance of their burrows. Mud crabs live throughout most of the estuary in horizontal burrows or under algae and debris. The curlew is well adapted to obtain these prey as the length of its bill (average 16.5 cm, Dawson 1923) allows it to probe deeply into the substrate and the bill's curve fits nicely into the burrows. Curlews often twist their heads as much as 180°, apparently to follow the curve of a burrow with their bills.

The diet of the Long-billed Curlew on Bolinas Lagoon is not representative of the species in California since in California Long-billed Curlews are more abundant inland than along the coast (Jurek 1973). Curlews that live inland must rely on terrestrial and fresh-water organisms for their food. Such a diet is indicated from the limited information in the literature which gives insects of several families, spiders, berries, crayfish, snails, fiddler crabs, amphipods, and occasionally nestling birds as food of the Long-billed Curlew (Wickersham 1902, McLean 1928, Sugden 1933, Palmer 1967, Timken 1969). Comprehensive studies of curlews feeding in various inland habitats are necessary for a more representative picture of this bird's diet in California.

In contrast to the curlew, the Willet occurs primarily along the coast when not on the breeding grounds (Jurek 1973). At Bolinas Lagoon the Willet was much more opportunistic in obtaining prey than was the Long-billed Curlew. Willet pellets contained at least 30 different prey from a wide variety of habitats but curlew pellets contained primarily 3 burrow-dwelling decapods and only small numbers of other invertebrates. Seasonal changes in the diet were prominent for the Willet but not the Long-billed Curlew. Other people studying shorebirds along the California coast found the Willet eating different organisms than at Bolinas Lagoon. Reeder (1951) found *Hemigrapsus oregonensis* present in 2 and cirratulid worms present in 1 of 2 Willet stomachs collected in May from Orange Co. Recher (1966) collected 16 Willets at one location on San Francisco Bay from September through May and found in decreasing order of abundance in the stomachs *Gemma gemma, Ilyanassa obsoleta, Nereis succinea, Mya arenaria, Macoma inconspicua, Hemigrapsus oregonensis,* and

TABLE 7

PREY OF WILLETS COLLECTED IN THE SAN FRANCISCO BAY AREA

	Number of Stomachs in which Each Prey Occurred		
		San Francisco Bay	
	San Pablo Bay[a]	Bay Tidal Flats[a]	Leslie Salt Ponds[b]
Annelida	1	6	
Decapoda	1	1	
Isopoda		1	
Ephydra cinerea larva			3
Ephydra cinerea pupa			1
Ephydridae larva		2	
Ephydridae pupa		2	
Ephydridae adult		1	
Corixidae		1	
Insecta		1	
Arachnida	1		
Macoma inconspicua	5	3	
Protothaca semidecussata		1	
Gemma gemma		4	
Mytilus sp.		6	
Pelecypoda		2	1
Ilyanassa obsoleta	3	4	
Gastropoda		4	2
Cottus sp.		4	
Pisces	1		
empty stomachs	3	1	
total number of stomachs	9	11	3

[a] Unpublished data from California Department of Fish and Game.
[b] Data from Anderson 1970.

Volsella demissa. Additional information on the diet of the Willet, collected by the California Department of Fish and Game, is summarized in Table 7. Because the Willet's diet is so varied it is apparent that studies from many coastal habitats are necessary before a representative diet for the Willet on the California coast will be adequately documented.

If we had obtained stomachs instead of pellets in this study it would have been equivalent to removing 75% of the Long-billed Curlews and 21% of the Willets on Bolinas Lagoon during the winter period. Consequently, we needed an alternative to collecting the birds in order to study their diet and an important consideration of the study was to determine the usefulness of feeding observations and pellets to meet this end. The Long-billed Curlews' 3 major prey were easily identified in feeding observations because of their large size and in pellets because of their digestion-resistant claws. The relative frequency with which the 3 prey species were taken by Long-billed Curlews on Bolinas Lagoon could not be measured from feeding observations because the observations were not taken with regard to the distribution of the curlews on the estuary, or from pellets because pellets were collected at high tide and consequently emphasized the prey taken on a rising tide. Most of the Willets' prey were too small to be identified in feeding observations and too broken down in the pellets for us to tally the number of individuals making up the remains. Swanson and Bartonek (1970) for waterfowl and Tuck (1972) for shorebirds reported that wide variation occurs in the digestibility rates of different prey. Considerable variation in the digestibility rates of the Willets' many prey certainly must have occurred and further hindered interpretation of the results. Hartley (1948) has discussed in detail the problems in analyzing stomach contents posed by variation in digestibility rates of different prey. Many of the problems are similar for the analysis of stomach contents and pellets, but our lack of knowledge of the factors causing pellet regurgitation in shorebirds and our inability to collect pellets under all tidal conditions are specific problems related to pellets. Because the shortcomings of analyzing stomach contents and pellets are similar in many ways, we feel that shorebird pellets and stomach contents in many instances can provide comparable information on the birds' diet. Observations of feeding birds can be very useful in extending the information on diet drawn from the examination of pellets or stomach contents.

SUMMARY

Visual observations and regurgitated pellets were used to study the feeding behavior and the diet of the Long-billed Curlew and Willet on Bolinas Lagoon from July 1973 through February 1974. Samples of the invertebrates in the tidal flats were collected at different locations and at different times to obtain information on their spatial and temporal distribution for comparison with the shorebirds' diets. The Long-billed Curlews' major prey were 3 large, burrow-dwelling decapods that the curlews obtained primarily by probing into burrows. No seasonal change was detected in the curlews' diet. Most of the Willets' prey were too small to identify in visual observations and too finely divided in the pellets to permit determination of the number of individual prey in each pellet. Therefore, the percentage of the pellets in which each prey occurred was used to compare the abundance of each prey species in the Willets' diet. The Willets' feeding behavior and diet were much more variable than the curlews'. The Willets' diet and feeding success varied among different areas in the estuary and between a fall and winter period.

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LITERATURE CITED

ANDERSON, W. 1970. A preliminary study of the relationship of saltponds and wildlife—South San Francisco Bay. Calif. Fish Game 56:240–252.

BAKER, M. C. AND A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43:193–212.

DAWSON, W. L. 1923. The birds of California, vol. 2. So. Moulton Co., San Diego.

HARTLEY, P. H. T. 1948. The assessment of the food of birds. Ibis 90:361–381.

HIBBERT-WARE, A. AND R. F. RUTTLEDGE. 1944. A study of the inland food habits of the Common Curlew. Br. Birds 38:22–27.

JUREK, R. M. 1973. California shorebird study. Final report. Accelerated research program for shore and upland migratory game birds. California Department of Fish and Game. (A copy of this report is available in the Van Tyne Library—ed.)

MACGINITIE, G. E. 1934. The natural history of *Callianassa californiensis* Dana. Am. Midl. Nat. 15:166–177.

——— AND N. MACGINITIE. 1968. Natural history of marine animals, 2nd ed. McGraw-Hill, N.Y.

MCLEAN, D. D. 1928. A note on the food of the Long-billed Curlew. Calif. Fish Game 14:173.

PALMER, R. S. 1967. (Species accounts). *In* The shorebirds of North America. (G. D. Stout, ed.). Viking Press, N.Y.

RECHER, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

REEDER, W. G. 1951. Stomach analysis of a group of shorebirds. Condor 53:43–45.

RITTER, J. R. 1969. Preliminary studies of sedimentation and hydrology in Bolinas Lagoon, Marin County, California, May 1967–June 1968. U.S. Dept. Int., Geolog. Surv., Water Resources Div., Menlo Park.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

STEEL, R. G. D. AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, N.Y.

SUGDEN, J. W. 1933. Range restriction of the Long-billed Curlew. Condor 35:3–9.

SWANSON, G. A. AND J. C. BARTONEK. 1970. Bias associated with food analysis in gizzards of Blue-winged Teal. J. Wildl. Manage. 34:739–746.

SWENNEN, C. 1971. Het voedsel van de Groenpootruiter *Tringa nebularia* tijdens het verblijf in het Nederlandse Waddengebied. Limosa 44:71–83.

TIMKEN, R. L. 1969. Notes on the Long-billed Curlew. Auk 86:750–751.

TUCK, L. M. 1972. The snipes. Environment Canada, Can. Wildl. Serv. Monogr. Ser. No. 5, Ottawa.

WICKERSHAM, C. W. 1902. Sickle-billed Curlew. Auk 19:353–356.

POINT REYES BIRD OBSERVATORY, BOX 321, BOLINAS, CA. 94924. ACCEPTED 20 MAR. 1975.

NOTICE TO CONTRIBUTORS

Effective with new manuscripts received after 10 June 1976, the maximum number of pages that will be published in the Wilson Bulletin without page charges being assessed will be 15. This policy is necessary because of increased publication costs, an increase in the number of manuscripts submitted, and an increase in the average length of manuscripts submitted.

OVERLAND MIGRATION BY COMMON EIDERS OF THE ST. LAWRENCE ESTUARY

J. Gauthier, J. Bédard, and A. Reed

The Common Eider (*Somateria mollissima*) is an abundant summer resident on and around the islands of the St. Lawrence estuary (Fig. 1). The birds usually arrive in early April and leave by mid-November. Band recoveries indicate that the wintering grounds of this population extend from southern Nova Scotia to Massachusetts and that migration is a gradual movement through Cabot Strait and along the southeast coast of Nova Scotia (Reed 1975). Some banding data and circumstantial evidence led us to believe that a more direct overland migration route might be used by some birds. That overland route, including a 300 km stretch over dry land, represents a distance one-fifth that of the route through Cabot Strait (450 versus 2350 km, total distances from center of breeding area to winter grounds).

In this paper we examine (1) the historical evidence which indicates the presence of an overland route, (2) the numbers and status of eiders undertaking the overland trip, (3) their behavior preparatory to the overland flight and (4) the possible significance of the alternative migration routes for this sea duck.

STUDY AREA AND METHODS

From 1963 to 1973, 2200 eiders were banded with conventional aluminum-alloy leg bands on a number of islands in the St. Lawrence estuary (Fig. 1). Our banding effort was evenly spread between islands on either side of the Saguenay River. In 1972 and 1973, 1400 were color-marked (in addition to leg bands) with patagial tags and sometimes leg streamers to permit individual recognition. Of the total marked birds, 97% were adult females.

Preliminary observations in 1972 and discussions with local residents made us select Anse-à-Giles, a small locality 3 km downriver from Cap-Saint-Ignace (Fig. 1) as the best vantage point for observing migrating eiders. Intensive observations were conducted from there between 2 October and 9 November 1973. During 29 of the 37 days, uninterrupted watches were kept from dawn till dusk and any eider movement quantified. On 4 of the remaining days, associate observers noted the passage of migrants without quantifying it. Weekly aerial surveys were also conducted in the estuary in the fall of 1973.

Weather records were obtained from the meteorological station at the Quebec (Ste. Foy) airport, 64 km SW of our observation post at Anse-à-Giles. Repeated observations at the latter site indicated no appreciable differences from the data provided by the airport records.

RESULTS

Historical evidence for an overland route.—As early as 1938, flocks of eiders were recorded in the inner estuary (near Montmagny) during the fall

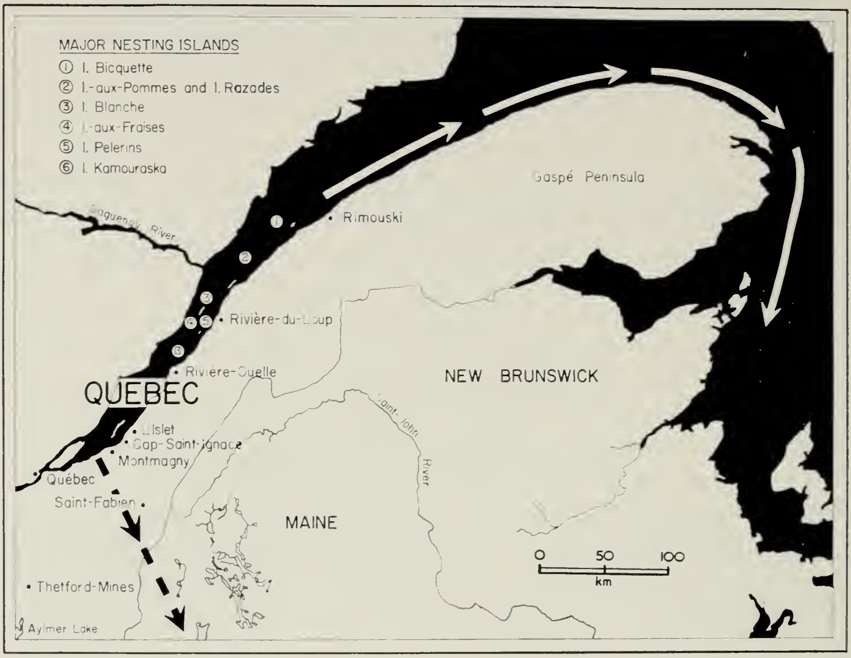

FIG. 1. The St. Lawrence estuary and the major nesting islands used by the common eider. The map shows the 2 migration routes discussed in the article. The position of either arrow is generalized and approximate.

(Lewis 1939). Only recently, band recoveries have shown that these birds belong to the breeding population of the estuary. The presence of eiders in this location, roughly 160 km upriver from the center of the breeding area would not be expected if all individuals followed the coastal route indicated by previous studies (Reed 1975).

H. Mendall of the Maine Cooperative Wildlife Research Unit speculated, on the basis of fall observations he made in Quebec during the 1950's, that an alternate overland route existed between the inner portion of the estuary and the coast of Maine. Thus, on 23 October 1958, he noted a flock of 300–400 eiders leaving the St. Lawrence river at a point about 15 km west of Montmagny and disappearing high overland in a southeasterly direction (pers. comm. to Reed).

Resident game wardens were aware of the presence of eiders in the area in the fall and of their flights inland from the St. Lawrence. Further, on 31 October 1972, A. Bourget of the Canadian Wildlife Service (pers. comm.) observed a flock of about 550 eiders flying inland in a southeasterly direction

Table 1

Number of Common Eiders Passing at Anse-à-Giles in the Fall of 1973[a]

Date	Number of eiders flying				Net number of eiders flying SW
	SW		NE		
	Flocks	Birds	Flocks	Birds	
Oct. 6	8	388	1	6	382
7	9	258	1	55	203
8	4	930	2	550	380
9	4	324			324
11	1	45			45
18	6	2880	1	60	2820
19	7	3975	2	2150	1825
20			1	1000[b]	
21	1	100	4	153	
22	2	390			390
25	9	2732			2732
26	1	261			261
27	6	1599			1599
28	10	2274	1	1721	553
Nov. 4	1	72			72
5	1	178	1	27	151
Totals	70	16406	14	5722	11737

[a] Flocks under 100 were counted individually and presumably carry no error. For flocks larger than 100 and smaller than 200 we assume a confidence interval of 15% and above 200 a confidence interval of 30%. So, the total migrants for a day may exceed 100 or even 200 and carry no error if the total was made up of several flocks smaller than 200 that could be counted singly.

[b] These birds were counted on water during low tide.

near Montmagny. He was able to follow the flock 6.4 km inland from the shore at which point it broke up with one group (250 birds) returning to the St. Lawrence and the other (300) maintaining a SE bearing until out of sight.

On 4 November 1972, a banded eider was shot by a hunter on Lake Aylmer, 130 km south of Quebec City. When questioned on the presence of eiders in that area, the hunter reported that small numbers occurred regularly each fall. Furthermore, on 27 November 1973 a female eider color-marked by us the preceding June on Ile aux Fraises was found dead on the shore of Lake William, 25 km north of Lake Aylmer.

Evidence of the use of this route by spring migrating eiders is restricted to the following observations. H. Mendall has observed flocks following the Penobscot River northwards in the spring (pers. comm.). J.-P. Savard (pers. comm.) sighted eiders on a lake about 60 km inland south of Montmagny

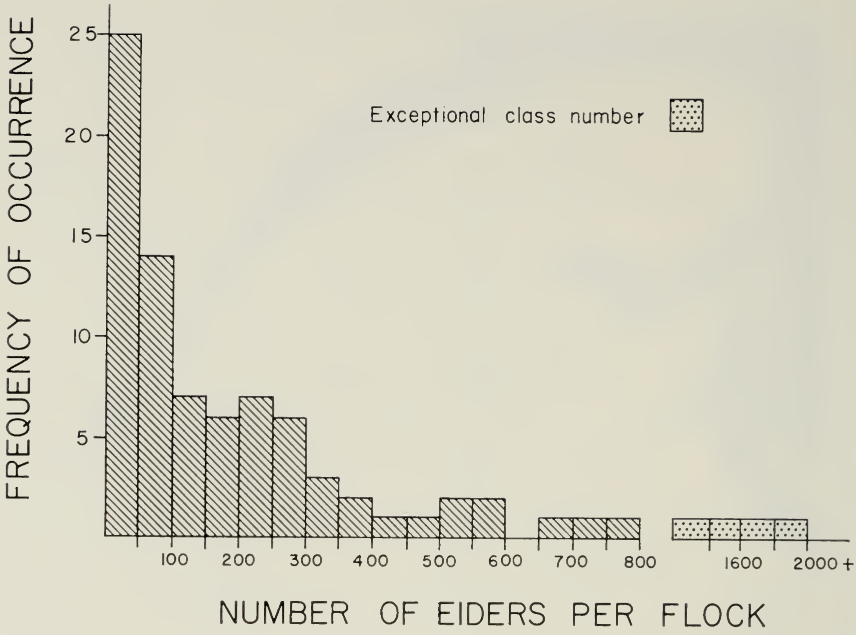

FIG. 2. Net number (only birds heading SW) of individuals in eider flocks passing at Anse-à-Giles in October and November 1973. Note change of scale on the X-axis beyond the 750–800 class.

on 22 May 1967. One male in nuptial plumage was found dead 40 km inland east of Montmagny on 31 March 1974. Finally, eiders are sighted regularly in late April on the St. Lawrence River between Montmagny and Quebec City (at this time, the maritime estuary and the southern part of the gulf are frequently ice-jammed, while the estuarine area near Montmagny is consistently ice-free).

The exact route of the inland corridor has not been determined as inland tracking of the migrating flocks was impossible. Two factors hindered observation: the absence of access roads and the occurrence of migratory activity during the twilight period.

Numbers and status.—Net numbers of eiders moving west beyond our vantage point were assumed to represent total numbers of birds about to engage in overland migration: we estimated that roughly 12,000 eiders used that migratory route over the period of observation (Table 1). Single eiders were seldom seen but modal flock size was fewer than 50 birds, while 78% of all flocks contained fewer than 300 individuals (Fig. 2).

Inspection of Table 1 reveals the existence of a seasonal peak of migration

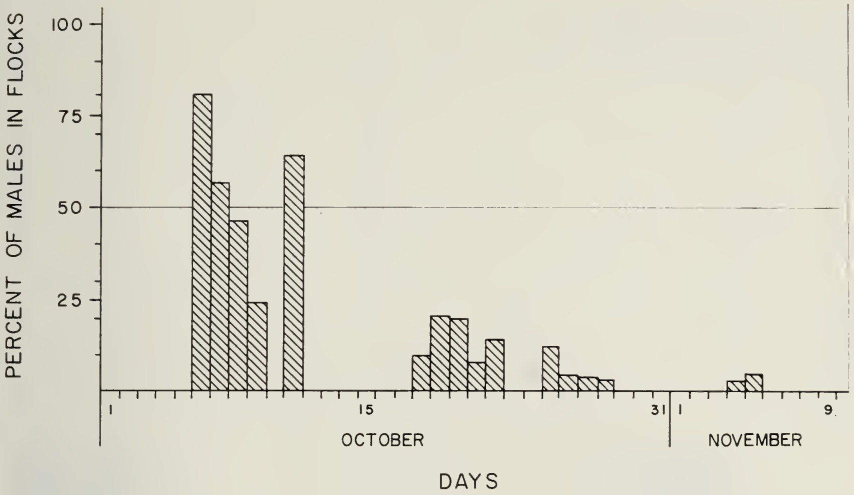

Fig. 3. Sex ratio in eider flocks seen at Anse-à-Giles during October and November 1973. Sample size as in Table 1.

between 18 and 27 October, with more than 80% of all the birds passing during that period.

The sex ratio in the flocks of migrants changed markedly as the season progressed (Fig. 3). In early October the number of males was higher than the number of females but by the last week in October and the first week in November, the number of females constituted 95% of the migrants.

The age of the birds in flocks could not be ascertained by direct observation. However, examination of eider wings received in the annual harvest surveys of the Canadian Wildlife Service in 1972 and 1973 indicated that all 8 birds killed in the vicinity of Montmagny were adults while only 24 of 88 birds killed east of Kamouraska were adults.

Seventeen sightings and recoveries of marked eiders were made in the upper St. Lawrence estuary. All but one of these birds had been marked on islands west of the Saguenay River.

All the birds seen or collected in the upper estuary in early fall were capable of flight. On the other hand, a substantial proportion of the birds seen or collected in the region east of Kamouraska during the same period had not completed the molt of the primaries: 35 of 88 eiders (40%) obtained during the 1972 and 1973 hunting seasons were not capable of flight.

Behavior.—The majority of flocks observed over the St. Lawrence at Anse-à-Giles behaved in a stereotyped manner: the birds flew low over the water in a compact group of variable formation (often comet-shaped). Eiders rest-

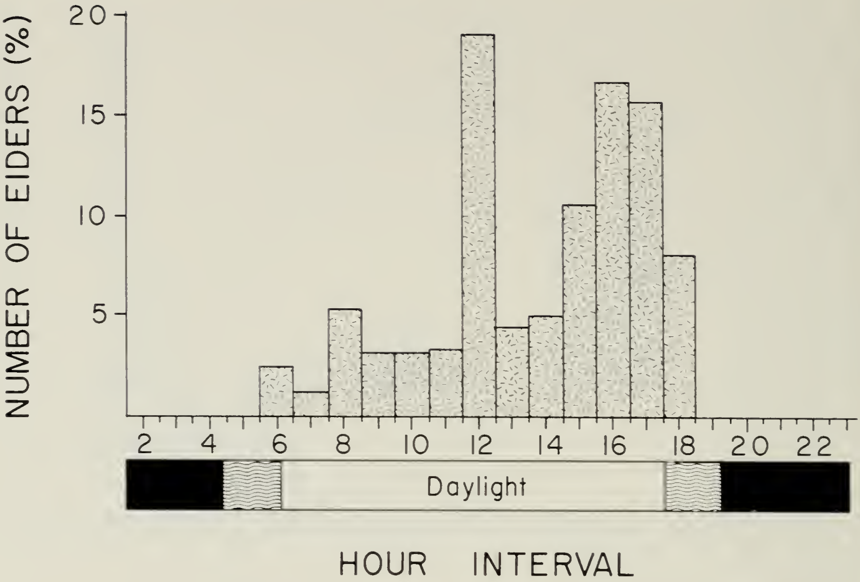

FIG. 4. Proportion of total number of eiders (21,128) involved in migration according to hourly intervals (EDT). Length of day adjusted to 6 October.

ing on the water maintained compact flocks, slowly drifting towards shore. They were never seen to feed and only rarely did they accompany other species.

On 3 occasions, we watched flocks initiating overland flights. In each instance, the flock hesitatingly circled over the shoreline while gradually gaining altitude. Once a few hundred meters high, the flock established a steady bearing (SE) which it maintained as long as it remained visible.

There was a tendency for flocks to pass along the St. Lawrence near our observation post during the afternoon. Thus, 62% of the flocks passed between 12:00 and dusk (about 18:15 in October) and 45% between 14:00 and dusk. The same tendency is also explicit when one examines the numbers of eiders involved in such flights (Fig. 4). However, all observations of departure on overland flights were made just before or during the evening twilight period. This contrasts markedly with Bourget's observation where the flight occurred at 08:30. We also observed a flock heading towards the St. Lawrence one morning, apparently returning from a night inland. This observation suggests that possibly some flocks observed initiating overland flights did not complete their migration on that same occasion.

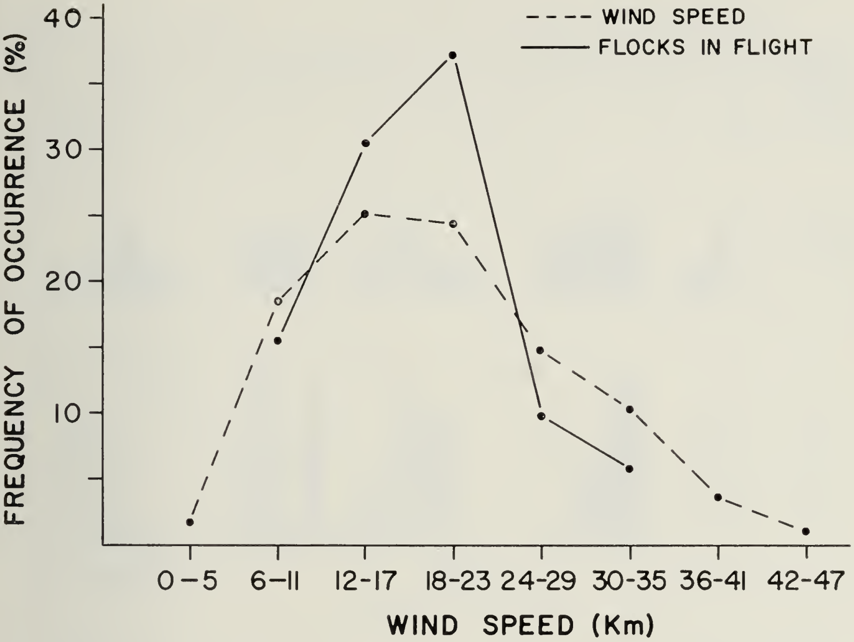

Fig. 5. Frequency of wind speed (km/h) and flight activity of eiders.

To examine the effects of weather on migratory activity we compared our data on flock behavior at Anse-à-Giles with the following weather variables: wind direction and speed, barometric pressure, cloud cover or insolation, and air temperature.

Migratory activity was observed irrespective of wind direction; yet, more than half of the flocks migrated with SW and W winds. At our observation post, birds flying in that general direction (SW, W) are heading upriver; hence, headwinds seem to be preferred by the eiders but only when relatively light to moderate (12 to 23 km per hour); headwinds above 24 km per hour seem to hinder most migration (Fig. 5).

A negative relationship clearly existed between cloud cover and eider movement; but overcast, as measured at the local weather station was expressed in a complex 4-point scale which rendered the correlation analysis rather cumbersome. Another independent variable expressing the same phenomenon, the number of hours of bright sunshine per day, produced a very strong positive relationship ($r = 0.789$, $P < 0.001$) between daily amounts of sunshine and eider movements (see Fig. 6).

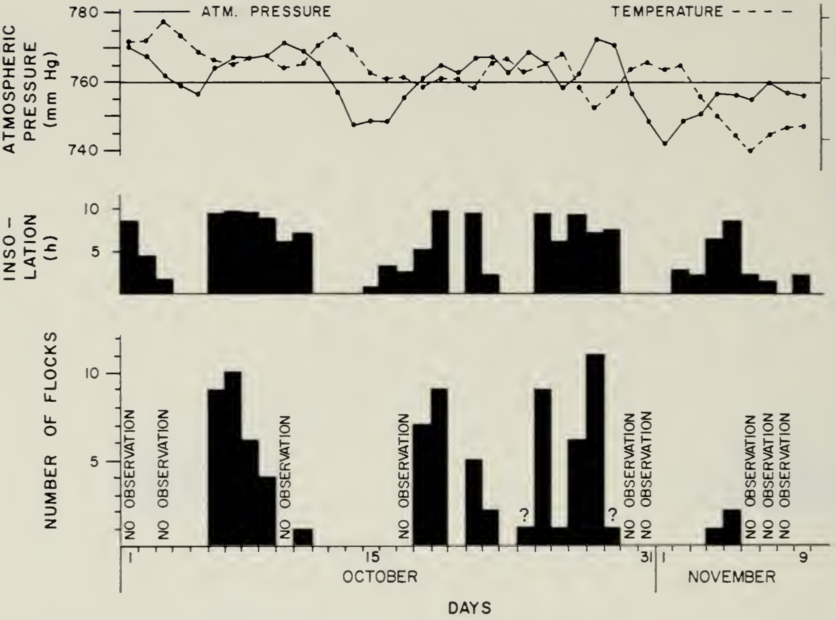

FIG. 6. Insolation (number of hours per day), temperature (daily average in °C) and barometric pressure (daily average in mm Hg) in relation to migratory activity of eiders at Anse-à-Giles. On 24 and 29 October, observations covered only a part of the day, hence the question marks.

A positive correlation was also found between absolute barometric pressure and the degree of migratory activity ($r = 0.583$, $P < 0.01$). As a rule, a rise in barometric pressure was a sure indication of recurring migratory activity while stable high pressure seemed to favor continuous movement (Fig. 6).

When considered individually, atmospheric pressure and insolation account for an important proportion of the variance in the migration data, but, obviously, the 2 are not independent, being different expressions of the same weather system. Further statistical analysis indicated that the increase in the amount of variance explained by adding the action of barometric pressure to that of insolation is not significant. Therefore, insolation is considered the best single predictor of migratory activity in eiders in the present situation.

No relationship was found between the number of flocks passing during a given day and average air temperature for that day. However, several pulses of migration occurred following periods of a few days during which the temperature had been falling (Fig. 6).

DISCUSSION

The Common Eider has been known to make inland flights for some time (Tufts 1962, Boyer 1966) but the documented cases involved short overland journeys of a few kilometers at the most, as for instance over the Isthmus of Chignecto between Nova Scotia and New Brunswick. The migration discussed in the present paper is clearly of a different nature.

Fall movements did not begin to any appreciable extent before October and reached a peak between 18 and 27 October. There was no evidence that the large numbers involved in the late October flights had accumulated in the area during the preceding weeks. Aerial surveys during September and October rather revealed the presence of numerous small scattered flocks between Montmagny and Riviere-Ouelle, all heading west.

The dominance of males among early migrants (Fig. 3) may be accounted for by their earlier postnuptial migration and molt, soon after the females begin incubation (Bent 1925). Shortly after, females that have lost their clutch or their brood early after hatching will also begin a post-breeding molt. Our observations reveal that between 80 and 90% of all females fall into this category. Finally, females with parental duties do not molt until the end of the brood rearing period in late August or early September (Cantin and Bédard, pers. obs.). Hence, males are able to migrate earlier than females. A similar progressive change in the sex ratio over the season of migration was noted in eider species near Point Barrow, Alaska (Johnson 1971, Thompson and Person 1963).

The number of birds involved in flight activity was greater after mid-day, reaching a peak in the 3-hour period before sunset (Fig. 4). A similar daily pattern has been shown by Johnson (1971) and by Nelson (1969) for eiders in Alaska. However, in Sweden, Roed (1971) observed that eiders migrated in the morning as well as in the evening. Bent (1925) quotes Hagerup's notes from Irictut, Greenland, also describing evening inland flights of Common Eiders.

Generally ducks are held back in migration by cloud cover (Hochbaum 1955, Bellrose 1967, Svardson 1953) and our observations support this. However, Roed (1971) observed that eiders migrating overland in Sweden did so only during fine weather while coastal migrants were not held back by overcast weather.

Examination of weather maps for the time period involved (U.S.D.C. 1973) revealed that the passage of a cold front was invariably followed by a pulse in migratory activity: these fronts generally move west to east in the area and are generally indicative of clear skies, dropping temperatures and rising barometric pressure. A persistent high pressure center over the area also enhanced migratory activity (Fig. 6).

We cannot explain why overland flights were initiated at dusk, but the initiation of migratory activity with clear skies may relate to the navigational means used by the eider. Ducks and geese have the ability to navigate at night and often at great heights above land (Bellrose 1967).

The total eider breeding population of the St. Lawrence estuary is estimated at 45,000 individuals (Reed 1973) and we estimate that approximately ¼ of the population uses the overland route.

The simultaneous existence of 2 distinct migration routes for this population needs to be accounted for. Eiders undertaking the long coastal migration apparently move leisurely from one bay to the next, never leaving their traditional habitat and feeding all along. Characteristically they fly low and for short distances over the water. The coastal migration likely takes several weeks. Eiders following the inland route devote a much shorter period of time to migration, with the overland leg of the trip probably lasting 4–8 hours. From the middle estuary, they move upstream to the point of overland departure in habitat unsuited for feeding; the estuarine waters near Montmagny are very poor in marine organisms (Bousfield and Filteau 1974). The 300 km overland journey covers inhospitable terrain, dense forests, fresh water lakes, and mountain ranges over 500 m.

Thus, part of the population takes a lengthy but "leisurely" migration while the remainder take a short but demanding and risky one. The status of the birds undertaking one or the other of these routes might shed some light on the factors influencing the choice.

Sightings of color-marked birds and band recoveries suggest that most overland migrants breed on the westernmost islands (west of the Saguenay River). Birds nesting closest to the entrance of the overland corridor are therefore more likely to take that route but other individuals from these same islands use the coastal route and at least one individual from the eastern group of islands was known to follow the overland route. Thus, the location of the nesting island is important, but not the sole factor involved in the choice.

There is evidence to suggest that the fall overland route is undertaken mainly by full-winged adult birds while many late-molting adults and juveniles take the coastal route. This might be interpreted as suggesting that the potential time-saving of the overland route is only practicable for birds with full flight capacities.

We have dealt only with the fall migratory activity, yet it is likely that a similar but reverse migration takes place in the spring, leading birds directly from the New England coast to the upper St. Lawrence estuary. Other than the scattered reports mentioned earlier, this spring movement has gone unnoticed. Probably these birds enter a migration corridor over a rather narrow path but arrive on a broad front, which would account for the spectacular character of the fall movement in the estuary and the unobstrusive nature of the spring arrivals.

The advantages of a direct overland flight may be greater during spring migration. In March, April, and May the upper estuary between Quebec City and the Saguenay is consistently ice-free while the waters of the gulf are frequently ice-choked (Berenger and Michel 1972). Therefore in some years it may be advantageous to use an overland route to return to the nesting islands. This may have been the case in 1967, a year when an exceptional accumulation of ice occurred in the gulf during April; only a relatively small number of eiders (overland migrants?) showed up to breed on the nesting islands on schedule (Reed 1975). However, a higher rate of mortality may accompany those taking the overland route. We have only 2 records of birds being found dead along the overland route but, in view of the very remote chances of birds being found in that area of low human population and poor access, they can be regarded as evidence of important losses. Thus, the advantages of reaching the nesting islands to breed at the optimum time even in years of heavy ice in the gulf may be balanced in the long run by greater adult mortality. The crucial question of whether individual adult birds can exercise a choice of route or whether they are restricted through tradition or heredity to a single one cannot be answered at this time.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bellrose, F. C., Jr. 1967. Orientation in waterfowl migration. *In* Animal orientation and navigation (R. M. Strom, ed.). Oregon State Univ. Press, Corvallis.

Bent, A. C. 1925. Life histories of North American wildfowl. Part II. U.S. Natl. Mus. Bull. 130.

Berenger, D. and B. Michel. 1972. Contribution à une étude systématique de la formation de la glace dans le St-Laurent. Université Laval, Québec, Génie Civil, Section Mécanique des Glaces. Rapport GCS-72-10-25. (A copy has been deposited in the Van Tyne Library.)

Bousfield, E. L. and G. Filteau. 1974. Ecologie de l'holoplancton et du meroplancton de l'estuaire moyen du St-Laurent. Groupe Interuniversitaire de Recherches Océanographiques du Québec. Rapport 1972–73. (Copy in Van Tyne Library.)

Boyer, G. F. 1966. Birds of the Nova Scotia–New Brunswick border region. Can. Wildl. Serv. Occ. Pap. No. 8, 52 pp.

Hochbaum, H. A. 1955. Travels and traditions of waterfowl. Univ. of Minnesota Press, Minneapolis.

Johnson, L. L. 1971. The migration, harvest and importance of waterfowl at Barrow, Alaska. M.S. thesis, Univ. of Alaska.

Lewis, H. F. 1939. A large flock of eiders near Montmagny, Quebec. Can. Field Nat. 53:123.

Nelson, R. R. 1969. Hunters of the northern ice. Univ. of Chicago Press, Chicago.

Reed, A. 1973. Aquatic bird colonies in the St-Lawrence estuary. Ministère du tourisme, de la chasse et de la pêche. Québec, Bull. 18.

———. 1975. Migration, homing and mortality of breeding females eiders of the St-Lawrence estuary, Quebec. Ornis Scand. 6:41–47.

Roed, U. 1971. Moulting migration in southern Jutland at Kalmarsund. Flora Fauna 77:45–51.

Svardson, G. 1953. Visible migration within Fenno-Scandinavia. Ibis 95:181–211.

Thompson, D. Q. and R. A. Person. 1963. The eider pass at Point Barrow, Alaska. J. Wildl. Manage. 27:348–356.

Tufts, R. W. 1962. The birds of Nova Scotia. Provincial Museum, Nova Scotia, Halifax.

U.S.D.C. 1973. United States Department of Commerce. Daily Weather Maps. Weekly Series, Washington, D.C.

DEPT. DE BIOLOGIE, FACULTÉ DES SCIENCES ET DE GÉNIE, UNIV. LAVAL, QUÉBEC, CANADA (J. G. AND J. B.) AND SERVICE CANADIEN DE LA FAUNE, ENVIRONNEMENT CANADA, 1141 RUE DE L'EGLISE, STE-FOY, QUÉBEC, CANADA. ACCEPTED 30 MAY 1975.

GENERAL NOTES

An early Pleistocene avifauna from Haile XVA, Florida.—The Haile XVA site is located near Haile, Alachua Co., Florida, in R17E, T9S, Sec. 25. This small deposit, a filled fissure in the Eocene Ocala Limestone, contained a modest number of mammalian remains and a small number of avian specimens. Through the mammalian fauna (Robertson, in press, Bull. Fla. State Mus.; Webb, Pleistocene Mammals of Florida, Univ. of Florida Press, 1974; and Kinsey, *in* Webb, op. cit.) it is possible to date the deposit as early Pleistocene (late Blancan). Although the small number of avian specimens, only 10, would normally bring only passing attention, the presence of a new species of green heron makes the avifauna worth noting.

The species represented are as follows:

Podilymbus podiceps.—Complete right femur, distal end of left tibiotarsus, and distal end of left tarsometatarsus.

Casmerodius albus.—Broken fragment of proximal end of tarsometatarsus.

Egretta sp.—Proximal end of left tibiotarsus. The great osteological similarity between *E. caerulea* and *E. thula* prevents a specific determination of this incomplete specimen.

Butorides validipes, n. sp. (Fig. 1).—*Holotype.* Complete right tarsometatarsus, University of Florida/Florida State Museum No. UF 17546, from early Pleistocene (late Blancan) of Haile XVA, Haile, Florida. Collected by S. David Webb and Jesse Robertson. *Diagnosis.* Tarsometatarsus agrees with that of *Butorides* and differs from that of all other North American genera of herons by having (1) anterior face of shaft only slightly channeled; (2) distinct internal curvature of shaft with external point of inflection located approximately ⅔ the shaft length distally; (3) similar size.

Tarsometatarsus differs from that of *Butorides virescens*, *B. striatus*, and *B. sundevalli* by having (1) intercotylar prominence more rounded proximally, more robust, and less clearly demarcated posteriorly; (2) anterior lip of internal cotyla deeply undercut in medial view (prominent ridge extending distad present in *B. virescens*, *B. striatus*, and *B. sundevalli*); (3) inner calcaneal ridge of hypotarsus very short and curved (long to moderate length in *B. virescens* and *B. striatus*, long in the one *B. sundevalli* available; slightly curved in all); (4) ridge leading distad from inner calcaneal ridge of hypotarsus long and slightly curved in medial view (short and sharply curved in *B. virescens*, *B. striatus*, and *B. sundevalli*); (5) proximal foramina and tubercle for tibialus anticus located slightly more proximad; (6) shaft very broad for entire length (narrows sharply immediately distal to cotylae in *B. virescens* and *B. striatus*; narrows similarly in *B. sundevalli*, but shaft broader than in previous two species); (7) edge of shaft straight internal to tubercle for tibialus anticus (locally curved in *B. virescens* and *B. striatus*; curvature present and less localized in *B. sundevalli*); (8) curvature of shaft in anterior view less pronounced; (9) intertrochlear grooves similar to those of *B. virescens* and *B. striatus* (larger in *B. sundevalli*); (10) trochlear surfaces wide (narrower in *B. virescens* and *B. striatus*; wide in *B. sundevalli*); (11) external trochlea extend farther distad; (12) depression in lateral surface of external trochlea deep and restricted (shallow in *B. virescens* and *B. striatus*, of moderate depth in *B. sundevalli*; restricted in all). The internal trochea of the holotype tarsometatarsus of *B. validipes* has the distal end missing.

Measurements (mm) of the holotype tarsometatarsus, with those of *B. virescens* ($N = 14$), *B. striatus* ($N = 3$), and *B. sundevalli* ($N = 1$) in parentheses, are as follows: length, 47.8 (*virescens*, 48.4–52.8, $\bar{x} = 51.8$; *striatus*, 48.6–50.0, $\bar{x} = 49.4$; *sundevalli*, 51.3); width of proximal end, 7.1 (*virescens*, 6.4–7.0, $\bar{x} = 6.7$; *striatus*, 6.3–7.1, $\bar{x} = 6.6$;

FIG. 1. Anterior, external, and posterior views of holotype tarsometatarsus of *Butorides validipes*, n. sp. (× 1.5; actual length, 47.8 mm).

sundevalli, 7.3); width of distal end, 6.6 (*virescens*, 5.9–6.6, x̄ = 6.3; *striatus*, 6.1–6.7, x̄ = 6.4; *sundevalli*, 7.0); length of inner calcaneal ridge, 4.0 ± 0.1 (*virescens*, 4.3–5.6, x̄ = 4.9; *striatus*, 4.7–4.8, x̄ = 4.7; *sundevalli*, 5.4); least width of shaft, 3.3 (*virescens*, 2.5–3.3, x̄ = 2.9; *striatus*, 2.8–2.9, x̄ = 2.9; *sundevalli*, 3.2); shaft width at metatarsal facet, 3.5 (*virescens*, 2.9–3.6, x̄ = 3.3; *striatus*, 3.1–3.2, x̄ = 3.2; *sundevalli*, 3.8).

Etymology. From Latin *validus*, strong, and *pes*, foot.

Anas crecca.—Complete left carpometacarpus. Additionally, a badly broken proximal end of a left humerus may be referred to *Anas*, but not to species because of its condition.

Colinus cf. *suilium.*—One right scapula. The variability found in scapulae make them very unsatisfactory elements upon which to base the identification of a species. The specimen referred to here is insignificantly larger than the scapulae referred to *C. suilium* from Reddick (Brodkorb, Bull. Florida State Mus. 4:269–291, 1959; Holman, Bull. Florida State Mus. 6:131–233, 1961), and for this reason it is not referred to the larger *C. hibbardi* (Wetmore, Univ. Kansas Sci. Bull. 30(pt. 1):88–105).

Meleagris gallopavo.—Distal end of one left tibiotarsus.

The geology, age, paleoecology, and zoogeographic affinities of the Haile XVA site are well discussed elsewhere (Robertson, in press). The combination of aquatic (*Podilymbus*, *Anas*, *Casmerodius*, *Egretta*, and *Butorides*) and forest, or forest edge, species (*Colinus*, *Meleagris*) supports the conclusions drawn from the mammalian evidence (Robertson, in press) that the deposit represents a stream passing through a forested area.

I wish to thank S. David Webb for the opportunity to study the specimens under his care and Pierce Brodkorb for use of his skeletal collection and many helpful comments.

—Kenneth E. Campbell, Jr., *Dept. of Zoology, Univ. of Florida, Gainesville, 32611.*

Accepted 16 May 1975.

An unusual clutch size of the Black-bellied Whistling Duck.—The phenomenon of compound or dump nests in the whistling or tree ducks (*Dendrocygna* spp.) has been reported by several investigators (e.g., Cottam and Glazener, Trans. N. Am. Wildl. Nat. Resour. Conf. 24:382–395, 1959; Weller, Ecol. Monogr. 29:333–365, 1959).

While studying the nesting biology of the Black-bellied Whistling Duck (*D. autumnalis*) in nest boxes described by Bolen (J. Wildl. Manage. 31:794–797, 1967), we discovered a nest box containing 17 eggs on 14 June 1971 at 11:55. This box was subsequently rechecked at 11:27 on 16 June 1971 and then contained 50 eggs. Since Black-bellied Whistling Ducks lay their eggs in late afternoon (Bolen, Ph.D. thesis, Utah State Univ., Logan, 1967), this nest received 33 eggs in the 2 days, indicating that at least 17 different females contributed to the clutch based on the premise that these waterfowl lay 1 egg daily.

At 12:35 21 June 1971 a Black-bellied Whistling Duck adult flushed from the nest box which then contained 90 eggs. The incubating female and male were captured at the nest box on 23 June and 24 June 1971 and were banded with U.S. Fish and Wildlife Service leg bands. When the male was banded the nest contained 101 eggs. The nest was observed thereafter on 14 occasions at 1 to 4 day intervals until 38 eggs hatched on 26 July 1971. At the time of hatching the nest contained 99 eggs.

These observations raise the following points of interest concerning Black-bellied Whistling Duck nesting biology. First, Black-bellied Whistling Ducks apparently remove broken eggs from their nests. The eggs were counted on 24 July 1971, 2 days before hatching and no shell fragments of the 2 missing eggs, presumably broken, were observed in the nest. Sowls (Prairie ducks, Stackpole, Harrisburg, Pa., 1959) described the removal of broken egg shells for several species of surface feeding ducks (*Anas* spp.).

Second, at least 11 additional eggs were deposited in the clutch after incubation began. It is generally accepted that waterfowl initiate incubation after the deposition of the final egg in clutches originating from a single hen.

Third, this nest took at least 36 days to hatch assuming incubation began on 21 June 1971 when the adult was flushed from the nest box at mid-day. Bolen (Ph.D. thesis, op. cit.) found a mean incubation period of 27.5 days for the species. Stotts and Davis (Chesapeake Sci. 1:127–154, 1960) indicated that the number of times a sitting bird is interrupted during incubation is related to the duration of the incubation period. Kendeigh (Auk 57:499–513, 1940) has shown that a narrow temperature range exists for optimum incubation so that interruptions may indeed lengthen the period required for embryonic growth. Accordingly, the temporary abandonment of the nest by the incubating birds during our inspections may have contributed to the lengthening of the incubation period for this clutch.

Fourth, although productive from the standpoint of numbers of young produced, only 38 of 99 of the eggs hatched. Reasons for the low hatchability include (a) the interval between the laying of the earliest eggs to the start of incubation may have been long enough to incur reduced viability in the older eggs (i.e. those laid first), and (b) the incubating birds were unable to physically cover the entire clutch with their bodies so that many eggs, including those deposited after incubation began, would not be fully developed when the properly covered eggs hatched.—Don Delnicki, Eric G. Bolen, *and the late* Clarence Cottam, *Rob and Bessie Welder Wildlife Foundation, Sinton, TX 78387 (present address for DD: P.O. Box 156, Challenge, CA 95925). Accepted 14 May 1975.*

An apparent hybrid goldeneye from Maine.—Recently there have been reports of male hybrids between Barrow's and Common goldeneyes (*Bucephala islandica* and *B. clangula*) based on specimens from New Brunswick, Canada (Snyder, Wilson Bull. 65: 199, 1953), and British Columbia (Jackson, Auk 76:92–94, 1959) and on sight records from Washington (Schultz, Murrelet 38:11, 1958) and Iceland (Bengtson, Bull. Br. Ornithol. Club 92:100–101, 1972). Fjeldsa (Bull. Br. Ornithol. Club 93:6–9, 1973) reported possible hybrid female specimens from Maine and Iceland.

At Perkins Cove, York Co., Maine on 3 March 1963, we observed an apparent hybrid male goldeneye for about 30 min. At a distance of 100 m through a 30 × telescope we noted several features which seem intermediate between the 2 goldeneye species. The forehead sloped upwards gradually from the bill and the hind crown sloped back gradually, imparting a triangular appearance not typical of either species. The fore and upper parts

Fig. 1. Adult male Barrow's Goldeneye (left) and hybrid male Barrow's-Common goldeneye right. Note the oval facial spot, reduced amount of black on side, and lack of black "shoulder" mark on hybrid. Photograph in Denver Municipal Zoo by Thomas Mangelsen; photograph used by courtesy of Dr. Paul A. Johnsgard.

of the head were distinctly brownish, this color merging into purplish toward the nape. Irridescent head colors are notoriously difficult to determine in the field, but the viewing conditions were good. The brown head color has been described in several of the above mentioned reports. The facial spot was oval in shape, the superior margin extending above the level of the eye. The side was blacker than in the Common Goldeneye, but the "ladder" effect of the Barrow's was not well-developed, nor did we note the vertical black "shoulder" mark anterior to the bend of the wing. Snyder (1953) discusses other intermediate characters apparent only in specimens (e.g., pattern and shape of bill, frontal bone, nape feathers and nostrils) which support a hybrid origin for his specimen.

In most of western North America, Barrow's Goldeneye breeds south of the range of the Common Goldeneye, although the latter migrates through lakes where Barrow's Goldeneye breeds (Munro, Trans. R. Can. Inst. 22:259–318, 1939). Johnsgard (Handbook of Waterfowl Behavior, Cornell Univ. Press, Ithaca, N.Y., 1965) describes the close behavioral similarity of the species, and presumably there would be little obstacle to interbreeding, particularly if one species occurs as a straggler in the range of the other. This is probably the case at Lake Myvatn, Iceland where a few Common Goldeneye have been observed recently during breeding seasons and where hybrids have been found (Bengtson 1972, Fjeldsa 1973). The hybrids previously reported and our observation suggest the occurrence of hybridization somewhere in eastern North America. Observations of behavioral interactions of the species where they breed sympatrically would be of great interest. Johnsgard (1965) reports that wild hybrids have been found involving *B. clangula* and 5 other species, and Ball (Peabody Mus. Nat. Hist. Yale Univ. Bull. 3:1–26, 1934) mentions additional hybrids in captivity. A hybrid between *B. clangula* and *B. islandica* has been produced at least once in captivity with the Barrow's as the female parent (P. Johnsgard pers. comm.). Figure 1 compares a male Barrow's (left) with the male hybrid (right), the difference in the facial spot and pattern of wing and side are well illustrated. We thank Dr. P. Johnsgard for comments on the manuscript and for permitting us to use the photograph.—MICHAEL GOCHFELD, *Dept. of Ornithology, American Museum of Natural History, New York, NY 10024* and GUY TUDOR, *380 Riverside Drive, New York, NY 10025. Accepted 8 May 1975.*

Cleptoparasitism by gulls of migrating shorebirds.—Facultative cleptoparasitism or interspecific robbing of food (Nettleship, Ecol. Monogr. 42:239–268, 1972) has been reported in several gull species. Bent (U.S. Natl. Mus. Bull. 113, 1921), Ansingh et al. (Ardea 48:51–65, 1958), Rooth (Int. Comm. Bird Preservation, 7th Bull. :117–119, 1958), and Hatch (Auk 87:244–254, 1970) have reported that Laughing Gulls (*Larus atricilla*) take food from the Brown Pelican (*Pelecanus occidentalis*), Sandwich Terns (*Sterna sandvicensis*), Common Terns (*S. hirundo*), and Arctic Terns (*S. paradisaea*). Meinertzhagen (Pirates and Predators, Oliver and Boyd, Edinburgh, 1959) reported that Great Black-backed (*L. marinus*), Glaucous-winged (*L. canus*), and Black-headed gulls (*L. ridibundus*) take food from ducks, coots, grebes, and loons. Nettleship (op. cit.) has seen Great Black-backed Gulls rob Common Puffins (*Fratercula arctica*). Hopkins and Wiley (Auk 89:583–594, 1972) reported Common Terns taking food from Arctic Terns at a Common Ternery. We have observed gull cleptoparasitism on Dunlin (*Calidris alpina*) and Black-bellied Plovers (*Squatarola squatarola*) by 2 additional species of gulls; the Ring-billed Gull (*L. delawarensis*) and Bonaparte's Gull (*L. philadelphia*).

Interactions between gulls and Dunlin and Black-bellied Plovers were watched for approximately 20 min in late afternoon on 24 May 1974 at the Nayanguing Game Re-

TABLE 1
INSTANCES OF SUCCESSFUL CLEPTOPARASITISM BY GULLS

Victim	Aggressor species Bonaparte's Gull	Aggressor species Ring-billed Gull
Dunlin	ca 60	3
Black-bellied Plover	1	0
Bonaparte's Gull	0	1
Ring-billed Gull	0	1

serve, Saginaw Bay, Bay Co., Michigan. Approximately 200 Dunlin and 30 plovers were feeding on large earthworms in a plowed field recently flooded by rains. In the group as a whole, the birds caught 3 worms averaging 100 to 130 mm long each 20 sec, and this food-getting rate yielded approximately 180 worms during 20 min of observation. About 30 Bonaparte's and 10 Ring-billed gulls were scattered among the shorebirds. They stood quietly without attempting to probe for or capture food, but watched the Dunlin and plovers around them. A gull gave chase when a nearby Dunlin caught a worm. The Dunlin sometimes dropped the worm as the gull approached, but usually flew with the worm until the gull forced the smaller bird to drop its food by swooping close to it. When the Dunlin dropped the worm, the gull landed and ate the catch. Chases seldom were farther than 60 m; if longer the gull circled back to the Dunlin group and the Dunlin which had escaped landed and ate its worm. Occasionally 2 gulls gave chase at once, but 18 out of 21 chases were one to one. One chase occurred about every 20 sec of observation and most chases were successful for the gull. Thus the Dunlin lost nearly a third of their catch (Table 1). Aggression between gulls and between gulls and smaller shorebirds was qualitatively similar. Bonaparte's were never observed to chase the larger Ring-billed gulls, although the opposite was seen (Table 1). Dunlin did not avoid nor mob gulls. Similar numbers of Dunlin feeding nearby in standing water were apparently eating smaller food and were not disturbed by gulls.

Intraspecific cleptoparasitism occurred in Ring-billed Gulls (Table 1) and Dunlin. In the latter case birds either lunged directly at conspecifics with worms or performed a Wing-up display before taking the worm. Instances of intraspecific aggression were not counted but were much less common than interspecific interactions. Goss-Custard (*In* Crook, Social Behaviour in Birds and Mammals, Academic Press, New York, 1970) reported another case of intraspecific aggression over food in the Dunlin as well as isolated cases in other wading birds.

Resistance of Dunlin to gulls was limited to flying away, and this rarely prevented the gull from gettting the worm. This is noteworthy in view of the high risk of loss of each Dunlin's food to gulls. Three non-exclusive hypotheses might account for the failure of the Dunlin to avoid feeding near gulls or otherwise prevent robbery.

(1) Dunlin normally feed on smaller items of food (Holmes, Ecology 47:32–45, 1966) and have had little past selective pressure to avoid cleptoparasitism by the larger species.

(2) The geographic ranges of the sandpiper and these 2 species of gulls do not ordinarily overlap and the small bird has had little chance to evolve a defense against their behavior.

(3) Large worms were so easy for Dunlin to find and capture that it was not worth-

while to expend much energy fighting or fleeing gulls or to sacrifice feeding in optimal sites to avoid gulls. This presumes that a Dunlin robbed by a gull has ample opportunity to find another worm if it stays in habitat where worms (and gulls) are abundant, and that the risk of mobbing or energetic cost of evasive action would be considerably greater than the cost of losing the item of food.

These hypotheses cannot be rigorously distinguished without further data and analysis, and insufficient evidence exists for speculation on (1). Wintering ranges of Ring-billed and Bonaparte's gulls and Dunlins overlap broadly and the Dunlin normally migrates through the ranges of several gull species known to rob other birds of food, so (2) is unlikely to be important. Bird et al. (Wilson Bull. 85:480–482, 1973) noted that American Robins (*Turdus migratorius*) are passive when Starlings (*Sturnus vulgaris*) regularly steal worms from them. Explanation (3) may be sufficient; it may simply not be worthwhile to respond to gulls by mobbing response or a more complex evasive behavior to avoid losing an easily replaced food which is available for only a short time—the water in the field, the worms on the surface, and the birds were all gone two days later. —Robert B. Payne and Henry F. Howe, *Museum of Zoology, Univ. of Michigan, Ann Arbor 48104. Accepted 5 Mar. 1975.*

Rapid tail molt and temporarily impaired flight in the Chuck-will's-widow.—The annual molt of the Chuck-will's-widow (*Caprimulgus carolinensis*) has been studied in detail by Rohwer (Auk, 88:485–519, 1971). He found that specimens replacing rectrices are very rare in collections (only 8 of more than 500 specimens examined) and concluded that tail molt must be highly compressed in time. The primaries are molted from innermost to outermost (P1–P10). No specimens were replacing P8 but Rohwer thought that most Chuck-will's-widows must rapidly replace the rectrices while that primary is being renewed, because only one bird replacing P7 showed any tail molt and the only bird replacing P9 had all of the rectrices about ¼ to ⅔ grown (Rohwer, op. cit.:495). In any case, tail molt seems rarely to begin during the replacement of P7 and is usually complete by the time P10 is full grown.

Rohwer inferred that at least some Chuck-will's-widows have trouble flying during the late stages of molt when they would not only be missing much or all of their tails but also a surface of each wing equivalent to about 2 of the longest primaries and approximately 4 secondaries. He suggested that, although the birds probably could fly, their ability to catch aerial prey might be rather severely impaired.

Recently I collected a Chuck-will's-widow which was replacing P8 and which tends to confirm these inferences. The bird (Univ. Kansas Mus. of Nat. Hist. No. 68716) was taken at about 17:30 on 4 September 1974, in Douglas Co., Kansas, on a gravel road traversing a disturbed oak-hickory hillside regularly frequented by the species in summer. This bird was an adult female (ovary 5 × 3 mm). The innermost primary being renewed was P8 (35 mm sheathed, total length 105 mm); P9 was smaller (32, 65 mm); and P10 had just been dropped (13 mm, all sheathed). The rectrices ranged from 60 to 80 mm in length and their sheaths varied from 28 to 37 mm (Fig. 1). Ridgway (U.S. Natl. Mus. Bull. 50 [part 6]:508, 1914) gives the average tail length of 16 females as 136 mm. The rectrices had clearly been molted simultaneously or nearly so. Secondaries 4, 6, 7, and 10–12 of the bird's left wing, and 1, 5, 7, and 9–12 (numbering from outermost inward) of the right wing were less than full length and were variously sheathed. The bird was in heavy molt of all body tracts and its rictal bristles were uniformly very short and fully sheathed, as in the specimen figured by Sutton (Bull. Okla-

Fig. 1. Tail of a molting female Chuck-will's-widow showing essentially simultaneous replacement of the 10 rectrices.

homa Audubon Soc., 2:9. 1969). Sutton's specimen was the one studied by Rohwer that was replacing P9, and the latter concluded that the simultaneous loss of the rictal bristles, while disadvantageous to aerial foraging, might be adaptive in possible ground feeding during this period. While watching Chuck-will's-widows walking about and swallowing pebbles (Jenkinson and Mengel, Condor 72:236–237, 1970), I formed the impression that they could easily forage on the ground and that they may well do so.

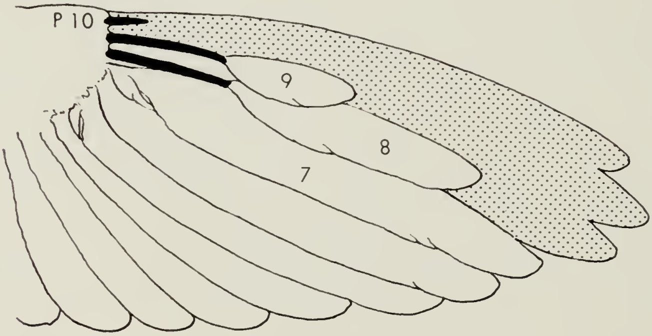

Fig. 2. Diagram of the outer wing of a molting female Chuck-will's-widow. Black = sheaths of growing feathers; stippling = area missing from the wingtip of the specimen. Scale approximately × ½.

The present Chuck-will's-widow was flushed 4 times before it was taken. In each case it flew 15 to 30 m before alighting, 3 times in the roadway and once on the tip of a broken snag where it perched erectly, owl-fashion. Its flight was direct but seemed relatively slow and labored. I have estimated that the primary surface of the wing (Fig. 2) lacked about ¼ of its normal surface, this at the critical tip, and the tail approximately 50%—surely enough to impair the maneuvers required in aerial feeding.

Finally, the bird was virtually emaciated, weighing 86.7 g. Other Chuck-will's-widows in the University of Kansas collection weighed 109, 109, 146, and 153 g (females, the last 2 with shelled eggs in their oviducts), and 97, 111, 119, 125, and 128 g (males, the first extremely lean). The bird's stomach was empty save for one scute from a large beetle. The weather for several days had been unseasonably cold with periodic heavy rainfall. The capacity for short-term torpidity—undemonstrated thus far in this caprimulgid—would be highly adaptive under these circumstances.

I thank Richard Lattis for the photograph and my co-worker Marion Jenkinson for helpful comments on the manuscript.—Robert M. Mengel, *Dept. of Systematics and Ecology and Museum of Natural History, Univ. of Kansas, Lawrence 66045.* *Accepted 20 Mar. 1975.*

Throat obstruction as a mortality factor among Willow Ptarmigan chicks.—Mortality among ptarmigan (*Lagopus* spp.) chicks is often high during the first week after hatching (Jenkins et al., J. Anim. Ecol. 32:317–376, 1963; Watson, J. Anim. Ecol. 34:135–172, 1965) though the causes are poorly documented. The following account describes some cases of mortality affecting new born chicks from late clutches of Willow Ptarmigan (*Lagopus lagopus*).

On 23 July 1974 we found a 1–2-day-old dead chick on Karlsøy Island in Troms County, Norway on a territory known to contain a renest brood. This was an unusual discovery as dead chicks are not commonly found. The chick had hatched approximately one month later than the normal peak hatching period.

The chick appeared unharmed exteriorly. Necropsy disclosed that the crop contained 2 crowberries (*Empetrum* spp.) and a third crowberry had become wedged in the posterior opening of the crop and was pressing against the bronchial tubes. The lungs contained bloody foam and death was apparently due to strangulation. Six similar cases of mortality due to obstruction or strangulation from both ripe and unripe blueberries (*Vaccinium myrtillus*) occurred among approximately 50 late, newly hatched chicks raised in captivity during the same summer.

The diet of wild Willow Ptarmigan consists mainly of insects during the first week of life (Lid and Meidell, Nytt. Mag. Naturvidensk. 73:75–114, 1933; Christiansen and Kraft, Nor. Jeger og Fiskerforbunds Tidsskr. 4:1–10, 1953). Insect consumption then decreases rapidly while the relative amount of plant material increases. Flowers and the vegetative parts of blueberry plants are often included in the diet of young chicks. Berries are not (Christiansen and Kraft 1953), as most chicks normally hatch before *Vaccinium* (and *Empetrum*) berries are available. Chicks from renest broods, often hatch during the early part of the berry season at which time berries could be consumed and result in mortality as described here. Whether newly hatched chicks prefer berries to insects is not presently known.

We are grateful to Dr. Svein Myrberget for his review of the manuscript.—Ingolf Hanssen and Howard Parker, *Univ. of Tromsø, Institute of Medical Biology, Division of Wildlife Biology, Box 977, 9001 Tromsø, Norway.* *Accepted 1 Mar. 1976. Page costs paid.*

Gray-backed Terns eat lizards.—On 15 June 1973 while on Enderbury Island (3° 08′ S, 171° 05′ W) in the central Pacific Ocean, I made some observations of an unusual feeding habit of the Gray-backed Tern (*Sterna lunata*). Initially about 5 adult terns were seen swooping low over an area of coarse coral rubble sparsely covered by low bushes (*Sida fallax*), a prostrate herb (*Boerhavia diffusa*), and dry moribund clumps of a bunch grass (*Lepturus repens*). The first bird I saw clearly rose from a swoop with a lizard in its beak. The lizard was almost certainly a snake-eyed skink (*Cryptoblepharus boutoni*) because the only other species of lizard found on Enderbury, the mourning gecko (*Lepidodactylus lugubris*) is nocturnal. Another tern, which I watched for about 8 min caught skinks on 2 of 3 swoops. At least twice during this period the tern made incomplete swoops probably because the lizard had seen the tern and had taken evasive action. Captured lizards were held across the mid-body and swallowed head first while the birds were in flight.

As far as is known, the normal diet of this species consists primarily of small fish and squid (Munro, Birds of Hawaii, 1944; Pacific Ocean Biological Survey Program. unpubl. data filed at the U.S. National Museum of Natural History). Small crustaceans and insects are also eaten but apparently quite uncommonly (POBSP, unpubl. data).

None of the species of terns treated in Bent (U.S. Natl. Mus. Bull. 113, 1921) was noted as having fed on lizards. However, Rowher and Woolfenden (Wilson Bull. 80:330–331, 1968) reported green anoles (*Anolis carolinensis*) in the digestive tracts of 4 of 6 Gull-billed Terns (*Gelochelidon nilotica*) collected in Florida. As these authors have indicated eating of lizards by this species was also noted by Jensen (Dan. Ornithol. Foren. Tidsskr. 40:82–83, 1946). Anderson (Dan. Ornithol. Foren. Tidsskr. 39:199, 1945) also recorded Gull-billed Terns eating lizards (*Lacerta vivipara* and *L. agilis*).

Such a feeding habit of the Gray-backed Tern is apparently unusual because no mention of it is made in the extensive files of the Smithsonian Institution's Pacific Ocean Biological Survey Program. Further, none of the Gray-backed Tern stomachs collected for the Program held anything other than that indicated above. It seems likely that this feeding pattern was an opportunistic response to the great abundance of these lizards on Enderbury at that time.—Roger B. Clapp, *National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560. Accepted 8 May 1975.*

Leaf-scratching in White-crowned Sparrows and Fox Sparrows: test of a model.—Many emberizine species turn leaves by a 2-footed scratching movement somewhat resembling hopping (Hailman, Wilson Bull. 85:348–350, 1973). To account for the number of successive leaf-scratches in a bout I offered a simple stochastic model in which the probability of adding another scratch to a bout is constant (Hailman, Wilson Bull. 86:296–298, 1974). The model predicts the relation between the number of scratches per bout (s) and the frequency (f_s) of bouts having s or more scratches as:

$$\log f_s \propto s.$$

Quantitative models aid understanding only if they accurately predict reality, and data from the White-throated Sparrow (*Zonotrichia albicollis*) and Dark-eyed Junco (*Junco hyemalis*) conformed to the relation (Hailman 1974, op. cit.).

I now have sufficient data to test the model against foraging in the White-crowned Sparrow (*Z. leucophrys*) and Fox Sparrow (*Passerella iliaca*). In the present test, data were collected from migrant Fox Sparrows in Madison, Wisconsin during October

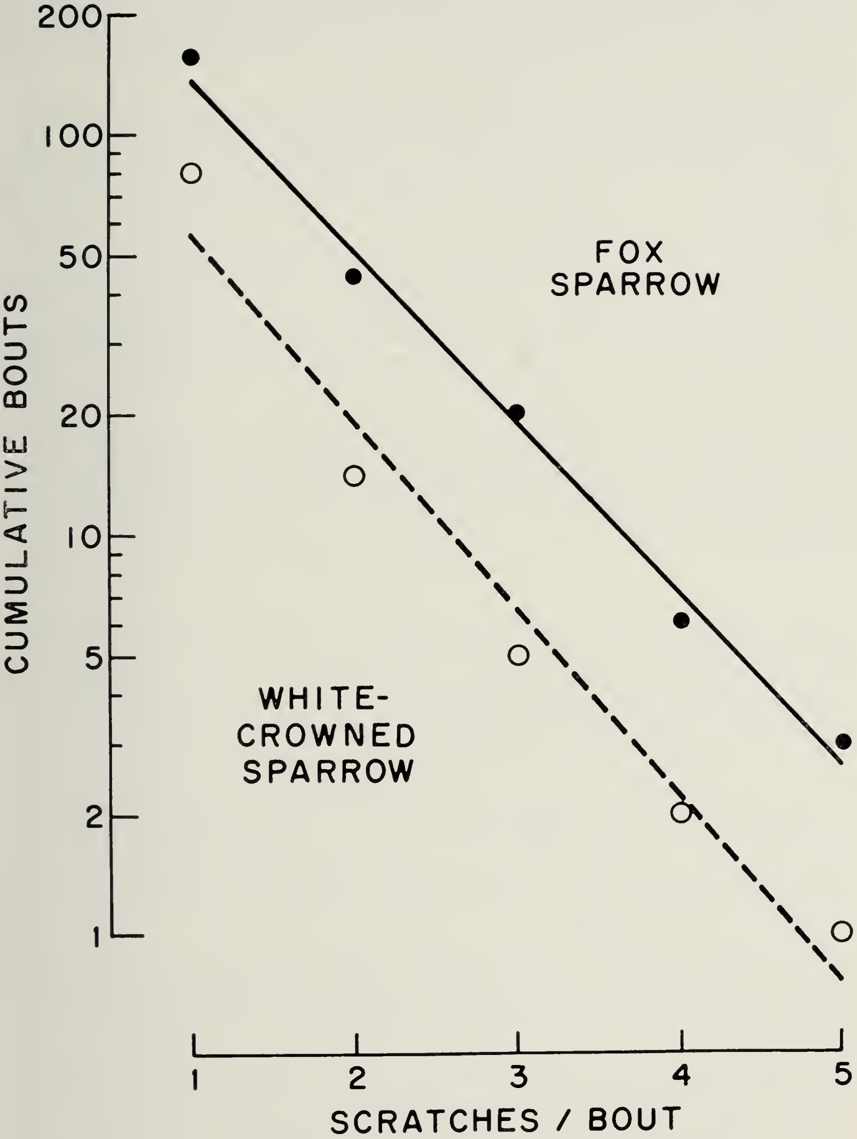

Fig. 1. The linear correlation between the logarithm of the cumulative number of bouts and the number of scratches per bout is predicted by the model of foraging in emberizines. Negative correlation coefficients exceed 0.98 for both Fox and White-crowned sparrows; the lines drawn are those of least-squares regression.

1972 and November 1973. All birds were observed outside my study window in an area baited with mixed bird seed, for a total of 157 bouts. White-crowned Sparrows rarely migrate through this area, but I made some observations of an immature on 28 October 1972 and further observations of a flock of adults at Falcon State Park, Texas on 4 January 1974 for a combined total of 80 bouts.

The data (Fig. 1) conform to the predicted "geometric decay" function, with correlation coefficients being –0.996 for the Fox Sparrow and –0.984 for the White-crowned Sparrow. Slopes of the least-squares regression lines are virtually identical, meaning that the constant probability of adding another scratch is the same for the 2 sets of data.

The match between prediction and data for all 4 emberizine species now observed seems sufficient to suggest that scratching bouts obey the same rules for all emberizines, although a check on the rather different towhees (*Pipilo*) would be desirable. The generality of results encourages investigation of the factors that dictate the value of the parameter (slope), which I suggested (Hailman 1974, op. cit.) might be governed by the environmental circumstances, particularly the amount of leaf-litter. The leaf-scratching of emberizines thus provides an opportunity for a detailed, quantitative understanding of how ecological variables affect avian foraging behavior.

For comments on the manuscript I thank E. H. Burtt, Jr., B. D. Sustare, and my wife Liz.—JACK P. HAILMAN, *Dept. of Zoology, Univ. of Wisconsin, Madison 53706.* *Accepted 25 Feb. 1975.*

Aerial fishing by Pied Herons.—Certain species of herons occasionally pursue prey in the air and may hover over the water, stirring it with their feet (see figure by G. Tudor *in* Meyerriecks, Nat. Hist. Mag. 71(6):48–59, 1962). Kushlan (Wilson Bull. 84: 199–200, 1972) and Mock (Wilson Bull. 86:280–282, 1974) have discussed aerial feeding in herons. At Waigani Sewage Farm, 10 km NW of Port Moresby, Papua New Guinea, I observed Pied Herons (*Notophoyx picata*) feeding in flight on 3 visits, 21 and 25 August and 20 September, 1972. About 120 to 175 Pied Herons were usually standing or foraging on foot at the margin of the ponds, but at almost any time, 1 to 10 birds were observed feeding in a tern-like fashion (often with Gull-billed Terns, *Gelochelidon nilotica*) over open water near the end of a sewage pipe. Cichlid fish (apparently *Tilapia* spp.) and perhaps other forms were abundant, and both terns and herons caught fish about 5 to 10 cm in length.

The herons circled or hovered about 1–2 m above the surface, their feet usually dangling down, but not touching the water. Fish were caught on downward swoops with the bill barely entering the water, the same manner in which the terns were fishing. One heron caught fish on 2 of 5 swoops, and a group of 4 caught 7 fish on 19 swoops. The manner of flight with extended neck and dangling feet was similar to behavior described by Mock (op. cit.) for the closely related Little Blue Heron (*Florida caerulea*). Only once, however, did I see a bird land and pursue prey on foot.

Kushlan (op. cit.) and Mock (op. cit.) discuss food scarcity as predisposing to aerial feeding. Fish were clearly abundant at Waigani, but were perhaps not uniformly dispersed. Possibly in sewage flats with high biological oxygen demand, fish concentrate near the surface offering an unusual advantage to herons that can exploit them by feeding in flight. The energetic costs and benefits of such behavior, habitual aerial feeding by individuals, and comparative success of aerial and ground feeders would be interesting to examine. I thank G. S. Keith, A. Keith, W. Keith and P. V. Rich for help in the field. E. Lindgren and A. W. Layton provided valuable information.—Michael Gochfeld, *Dept. of Biology, Queens College, Flushing, NY and Dept. of Ornithology, American Museum of Natural History, NY 10024. Accepted 8 May 1975.*

American Kestrel eating carrion.—On 8 February 1975 near Lebanon, Pennsylvania at approximately 16:00, my wife and I observed a male American Kestrel (*Falco sparverius*) eating a quite decomposed gray phase Screech Owl (*Otus asio*). We drove to within 6 m of the falcon at which time it attempted to carry the owl off, although it could only drag the carcass and after a few seconds' struggle, let go and flew to a small tree. We were road trapping at the time for kestrels, made a pass at the falcon and threw out a bal-chatri with a mouse. The kestrel struck the trap and was captured. The falcon appeared to be in good condition. His weight of 124 g is consistent with the range of male kestrel weights I have recorded in the same area. His crop was near empty.—G. Robert Ganis, *Route 5, Box 383, Lebanon, PA 17042. Accepted 28 Apr. 1975.*

House Sparrows usurp Hornero nests in Argentina.—The Hornero or Rufous Ovenbird, *Furnarius rufus*, is a very common bird in Argentina nesting in trees near houses and on fenceposts in the pampas (Olrog, Las Aves Argentinas, Inst. Miguel Lillo, Tucuman, 1959). Horneros construct dome-shaped nests of mud, rootlets, straw, and horsehair (MacDonagh, El Hornero 8:250–256) with a tunnel entrance leading to an inner chamber.

House Sparrows (*Passer domesticus*) were introduced into Argentina from Europe for agricultural purposes (Bibiloni and Baez, El Hornero 6:512–513, 1937). They nested for the first time in 1905, expanded into new areas in the 1910's, and became very abundant by the 1920's (Castellanos, El Hornero 5:307–338, 1934). House Sparrows were first reported using Hornero nests in the early 1920's (Castellanos, El Hornero 5: 1–40, 1932). Little mention has been made of interactions between Horneros and House Sparrows since that time.

I observed the interactions and competition for Hornero nests between House Sparrows and Horneros on the ranches La Estanzuela, near Venado Tuerto, and San Jose, near Murphy in the province of Santa Fe, Argentina, from October through November 1972. I drilled holes in the sides of nests and inserted corks. Nesting birds were marked with paint at night by inserting a brush through the holes. This procedure was effective although some pairs repaired light leaks around the corks each day.

Hornero nests were censused between 20 and 30 October and 20 and 30 December 1972 to ascertain the extent of nest use by House Sparrows. Only new Hornero nests that appeared to be constructed in the current year were counted. Old nests usually began to break open in the rains the year after construction. Of 46 Hornero nests I located, 28 (60%) were used by Horneros, 11 (24%) were unused, and 7 (16%) were used by House Sparrows. If House Sparrows take over active Hornero nests, Horneros might selectively defend their nests against House Sparrows.

I made observations of bird behavior at Hornero nests from 20 to 30 October and from 10 to 20 November 1972. Any time any bird landed within 5 m of an Hornero's nest, I recorded the species of intruder, and the reaction of the resident Hornero. Twelve species landed near Hornero nests, *Columba picazuro*, *Columbina picua*, *Guira guira*, *Colaptes campestroides*, *Pitangus sulphuratus*, *Muscivora tyrannus*, *Molothrus bonariensis*, *Passer domesticus*, *Sicalis flaveola*, *Poospiza nigrorufa*, *Embernagra platensis*, *Zonotrichia* *capensis.* Usually there was no reaction by the resident pair of Horneros unless the visitor was a House Sparrow. These were recorded more frequently than any other species (32 times) and when one landed in the same tree, the resident pair of Horneros usually flew to the nest and vocalized (93%), often chasing the House Sparrows (53% of the time). Thus, Horneros are selectively defending their nests against House Sparrows. In all but one case the Horneros were successful in driving away the intruders.

One Hornero nest was built in a tree on the marshes of the San Jose estancia. The nest and a pair of Horneros were present on 13 October. The Horneros carried bits of grass into the nest on 13, 14, and 15 October, and were near the nest nearly all day. On 16 October at 11:00 a pair of House Sparrows landed near the nest. The resident Hornero flew to the nest, vocalized, and chased the sparrows. During the next 2 hours the sequence was repeated 11 times. From 17:00 to 19:00 that same day, the sequence was repeated 6 times. On 17 October from 21:00 to 22:00 House Sparrows landed near the nest 6 times but were chased away only 5 times. On 18 October during an hour observation period, the House Sparrows landed at the nest 7 times and were chased away 4 times. The sparrows were unmolested for longer periods of time before the Horneros came to chase them away. The Horneros no longer vocalized and only chased the intruders. On 19 October the Horneros were seen in the vicinity of the nest, but did not chase away the sparrows. The Horneros were not seen after 19 October. The House Sparrows subsequently added nest material and laid eggs.

My research in Argentina would have been impossible without the constant help and encouragement of Peter and Martha Miles of the estancia La Estanzuela. I thank Carlos Itturalde for the unrestricted use of the marshes on the San Jose estancia.—JOANNA BURGER, *Dept. of Biology, Livingston-Rutgers Univ., New Brunswick, NJ 08903.* *Accepted 10 Mar. 1975.*

A westward extension in the breeding range of the Mountain Plover.—The Mountain Plover (*Charadrius montanus*) is typically a breeding species of the Great Plains of North America, with the westward limits of its breeding range in Wyoming, Colorado, and New Mexico (A.O.U. Check-list, 1957). In New Mexico, the species extends as a breeder to the vicinity of or slightly beyond the Continental Divide in the central-west and southwest, but it has not previously been found breeding in the northwest (Hubbard, Check-list of the birds of New Mexico, New Mexico Ornithol. Soc. Publ. 3, 1970). On 1–3 June 1974, Alan P. Nelson and I found up to 3 adult Plovers and a nest with eggs in the latter region, specifically in San Juan Co., about 5 km NNW of Burnham Trading Post, on the Navajo Indian Reservation. This is an area where animals typical of the grassland and basin sagebrush biociations (as defined by Kendeigh, Animal Ecology, Prentice-Hall, Inc., Englewood Cliffs, N. J., 1961) intermix. The record is particularly interesting (1) because it appears to be the first documented breeding record of this species in an area influenced by animals associated with the basin sagebrush biociation, and (2) because this species is included on the "status undetermined" list of the U. S. Department of the Interior (Threatened wildlife of the United States, Fish and Wildl. Serv. Resour. Publ. 114, 1973).

The nest was a slight depression in mixed sand-and-gravel soil, with a lining of a few small twigs. It contained 3 extremely light-buffy-brown eggs that were flecked with dark brown (one measured 37 x 28 mm). These egg colorations contrast with the typical colors of an olive background with black spots (Bent, U. S. Natl. Mus. Bull.

146, 1929). The adult that was flushed from the nest ran away while performing a "broken wing" display. The nest and the birds were in flat to slightly rolling terrain, with sparse, overgrazed, shrubby vegetation interspersed with bare areas. The nearest water was over 4.5 km away. Since each of the 3 sightings of adult plovers were over 1 km apart, it is possible that 3 different nesting birds were observed. This is especially likely, since only one adult attends each nest (Graul, Living Bird 12:69–94, 1973). Photographs of the nest and associated bird are in the National Photoduplicate File, Migratory Bird and Habitat Research Laboratory, U. S. Fish and Wildlife Service, Laurel, MD 20810 (numbers 281–1Ta and 281–1Tb, respectively).

The only record that I can find that might suggest breeding by the Mountain Plover in a similar biociation is a bird seen in northwestern Utah in Box Elder Co., on 27–28 June 1929 (Bent, op. cit.). In addition, Bent reports breeding records for Fort Bridger, Wyoming, and the Pahsimeroi Valley, Idaho. Authoritative sources that I have read or contacted show no recent summer records in these areas, or in adjacent parts of Colorado. In Arizona, the only summer record is of several flocks seen in August near Springerville (Phillips et al., The birds of Arizona, Univ. Arizona Press, 1964), but these may well have been migrants, since Walter D. Graul (pers. comm.) found that fall flocks sometimes form in mid-July on his Colorado study area.

I would like to thank Alan P. Nelson for field assistance and William H. Behle, Walter D. Graul, John P. Hubbard, and Clayton M. White for various help. Western Gasification Company (WESCO) and Utah International Inc. provided project funding.—Duane A. Tolle, *Ecology and Ecosystems Analysis Section, Battelle, Columbus Laboratories, 505 King Avenue, Columbus, OH 43201.* *Accepted 15 Apr. 1975.*

The nesting site of the Northern Oriole in Amherst, Massachusetts.—During the winter of 1965–66, we collected quantitative and qualitative data on the nest sites selected by the Northern Oriole (*Icterus galbula*) in Amherst, Massachusetts (Graf, Senior Honors thesis, Univ. of Massachusetts, Amherst, 1966). Data on nest tree species, ground cover beneath the nest, and the nest height are reported in this note.

An intensive effort was made to locate all oriole nests visible from roads within the town boundaries. After leaf-fall (during October and November 1965) an open convertible automobile was used to survey roadsides for oriole nests. Species of tree used for nesting and the nature of the ground beneath the nest were recorded at each nest. Height of the nest tree, and nest height were recorded at a random sample of 70 nest locations taken from 143 nests initially located (6 more nests were found later). A Haga altimeter and 12 × 50 binoculars were used to gather most of the data.

Most of the 149 nests found were in elm (*Ulmus americanus*, 66%) or sugar maple (*Acer saccharum*, 23%). There was a significant difference in frequency of species of trees selected for nesting (χ^2, $p \leqslant .05$, 1 df). Nests were also found in red maple (*Acer rubrum*), white oak (*Quercus alba*), apple (*Malus* spp.), shagbark hickory (*Carya ovata*), weeping willow (*Salix* spp.), black willow (*Salix nigra*), black oak (*Quercus velutina*), ash (*Fraxinus* spp.) and lombardy poplar (*Populus nigra* var. *italica*). One elm included 3 nests and 8 elms had 2 nests. In an extension of this study in 1966 and 1967 Pank (M.S. thesis, Univ. of Massachusetts, Amherst, 1974) found similar distribution of species of nest trees and a statistically significant difference between the frequency of species selected for nesting and the frequency of occurrence of roadside tree species. American elm was selected more frequently, and sugar maple and other species, less frequently than expected.

The height of oriole nests above the ground ranged from 4.5 to 22 m in the random sample of 70 nest sites. In elms, the nest height ranged from 4.5 to 21 m (mean = 10.6 ± 0.5 m) while in sugar maple, nest height ranged from 8.5 to 22 m (mean = 13.0 ± 1 m). The difference in nest height between the elms and sugar maples was not significant (χ^2, $p < .05$). Nest tree height varied from 12.7 to 29 m in the random sample of 70 nest sites. The height of elms varied from 15 to 27 m (mean = 20.1 ± 0.5 m) while sugar maple height ranged from 12.7 to 29 m (mean = 19.4 ± 1.2 m).

The ground cover beneath the nest (based on the 70 random sample nest locations) included: 34% lawns, but nests occurred over paved road-surface almost as often (28%). Nests were built over grazed pastures, road shoulders and uncut grass less frequently. Among the miscellaneous habitats found below nests were a dirt road, a road shoulder adjoining a cornfield, a cultivated field, a lightly grazed pasture with shrubs, and a secondary forest stand of red maple (12–15 m tall).

Results of our studies confirm that Northern Orioles tend to select elms to nest in more frequently than other species of trees in which they were seen to nest. It did not appear that Northern Orioles had selected nesting sites on the basis of the surface below them although any nests in a roadside sample of this kind would have a high probability of occurring over rather open surfaces such as road surfaces and lawns.—RUDOLPH L. GRAF, *Box 450, Wisconsin Dept. of Natural Resources, Madison, 53701*; and FREDERICK GREELEY, *Dept. of Forestry and Wildlife Management, Univ. of Massachusetts, Amherst, 01002.* *Accepted 9 Feb. 1976. Page costs paid.*

ORNITHOLOGICAL NEWS

ALEXANDER WETMORE RESEARCH FUND

The American Ornithologists' Union has announced the formation of an Alexander Wetmore Research Fund for the support of research in avian systematics, zoogeography, and palaeornithology to which all who have known Dr. Wetmore or admired his great contribution to ornithology are invited to contribute. All money received will be handled as endowment and the income distributed annually in the form of grants-in-aid to applicants in these fields by our Committee on Research Awards, which also administers the Van Tyne awards. This is a great opportunity to join in honoring Dr. Wetmore and to contribute to one of the A.O.U.'s most worthy activities. Please send your checks, marked "Wetmore Fund," to Dr. John A. Wiens. Treasurer, Department of Zoology, Oregon State University, Corvallis, OR 97331.

ORNITHOLOGICAL LITERATURE

An Introduction to Ornithology. 3rd Edition. By George J. Wallace and Harold D. Mahan. Macmillan Publishing Co., Inc., New York, 1975: xiv + 546 pp., drawings, graphs, maps, photographs. $14.95.

The Life of Birds. 2nd Edition. By Joel Carl Welty. W. B. Saunders Company, Philadelphia, 1975: xv + 623 pp., drawings, graphs, maps, photographs. $18.50 (U.S.) and $19.50 (Canada).—In the 12 years or so since the earlier editions of these 2 books appeared there have been many new developments in avian biology. Not only are there new facts, but attitudes and the general orientation toward certain topics have changed as well. Both of these revised editions show evidence of the 2 types of change.

An Introduction to Ornithology by Wallace and Mahan is just what the title implies. Although it has an extensive bibliography, it is by no means an exhaustive treatment of ornithology today. It does present a generally excellent summary of the main topics in avian biology. Basically the new edition is organized like the previous one, but there are minor rearrangements of the contents into different chapter divisions. The chapter on behavior (ch. 8) was revised by Harold D. Mahan with an expansion of the discussion of ethological terms and concepts.

Although much of its content has been retained, the chapter on ornithological methods from the 2nd edition has been eliminated. It strikes me as a regrettable loss that the suggestions on note-taking and methods of describing bird song in the field have been omitted from this edition. To be sure, the more modern, more technical methods of song analysis by sound spectrographic procedures are described, but these are not readily available to the average field observer, and much valuable information can be obtained from old-fashioned note-taking with pen and paper in the field.

Diane Pierce's new drawings and her revisions of old ones improve the appearance and in some cases the accuracy of the illustrations, although in a few instances (e.g. fig. 6.9, Structure of an egg) there is poor correlation between the text and the illustration. The directions for preparing a bird skin have been supplemented with photographs of the main steps, helping to clarify the descriptions, but I find the photographs less explicit than drawings might have been.

One feature of the book that I find objectionable is the arrangement of the references. A few major references are listed at the end of each chapter, while others are relegated to a much longer listing at the end of the book. Since the "more important" ones are not listed there, it is often necessary to look both places. I found it safest to look first at the end of the book, since the majority of sources are there. I understand that the omission of the basic references at the end is a space-saving (and cost-saving) arrangement, but the space saved is relatively small, whereas the increased trouble of finding a source is considerable.

Welty's new edition of *The Life of Birds* is arranged exactly like his first, except for the addition of a new chapter on birds and man. Some of the topics in this new chapter have been lifted from various places in the earlier versions, but much of the material, as far as I can tell, is new. All the chapters are considerably revised, and those treating the most active areas of avian research, such as chapter 8 on environmental controls of reproduction, chapter 9 on behavior, chapter 11 on songs, calls and other sounds, and especially chapter 23 on the origin and evolution of birds, show some of the reorientation of current thought, and very extensive revision of factual detail. Like Wallace and Mahan, Welty also gives basic references at the end of each chapter, but they are by title and author only, with the complete references in the list at the end of the book.

There are relatively few typographical errors in either volume. The new Wallace and Mahan book has gone from glossy to nonglossy paper, while the new Welty has gone from nonglossy to a semigloss. I found the old Welty much easier to read than the new. There is something about the new print on the paper that made me feel I was reading through a haze. The old nonglossy paper and dark print had great contrast, and facilitated reading. Having the old and new editions side by side made the difference very conspicuous.

Which book would be preferable for a course in ornithology depends on the instructor's philosophy toward textbooks. Wallace and Mahan are less explicit and expansive on basic biological concepts, but do include other types of information that a beginning ornithologist might find helpful, such as the procedure for making a bird skin, some information on ornithological collections, and a listing of foreign ornithological publications.

Welty, on the other hand, deals at length with such topics as flight mechanisms, speciation, and photoperiodism, which are rather glossed over in Wallace and Mahan. The latter have missed some of the more recent literature on fundamental topics such as that by Schmidt-Nielsen on the mechanics of breathing in birds. *The Life of Birds* has a greater wealth of detail on avian biology (there are roughly 3 times as many references listed in Welty as in Wallace and Mahan), and less on ornithological procedures and organizations. If you prefer a work that introduces the subject and whets the appetite, but does not probe very deeply, you will like Wallace and Mahan. On the other hand, if you want a broader treatment, in greater depth, you will probably prefer Welty.—William L. Thompson.

Birds of New York State. By John Bull. Doubleday/Natural History Press, Garden City, New York, 1974: xii + 655 pp., many maps, black-and-white photographs, 9 color plates. $29.95.—This long-awaited updating on the birds of New York is a welcome addition to the library of any serious birder or student of the state's bird life. This work will serve as an often-quoted reference for years to come and therein lies the justification for its price: it is an investment for the future.

The author covers an interesting range of background matter. He reviews the diverse habitats of the state and discusses some of the more noteworthy birding areas. Because numerous changes have occurred in the birdlife over the past 60 years, he uses the works of Eaton (1912, 1914. *The Birds of New York.* Two volumes. 64th and 66th Annual Report of the New York State Museum, Albany.) as a basis for comparison in dealing with changes in occurrence and distribution of the state's 410 recorded species and 228 breeders.

Each species is given rigorous treatment. The author's critical style on record verification and acceptance, which became apparent in his earlier work, *Birds of the New York Area* (1964), is preserved here. Typically, he discusses each species' range, status (breeding and non-breeding), occurrence, egg and nestling dates, and clutch size. Data on maximum field sightings are given for coastal and inland areas. Reference is also made to specimen and photographic records for some of the more unusual reports. The breeding records for unusual or newly recorded species are graphically represented on maps. These as well as other graphic representations add much to the value of the text.

Noteworthy in a work of this sort is the author's treatment of banding data. The recovery distribution on 55 species are represented on maps, and there is commentary on some extraordinary banding records including longevity. I would question, however, the completeness of the recovery data represented on some of the maps. Surely for a species that is as frequently banded and recovered as the Evening Grosbeak, one would expect considerably more congestion on the recovery map. Nevertheless, it is heartening to see some of these banding data represented.

The work is liberally graced with photographs, many of which represent various habitat types. Having been contributed by the state's birders, whose photographic skills vary, the photographs themselves are of variable quality. In that regard, the publisher can be relieved of responsibility for their reproduction quality. However, for the 9 colored plates, the publisher must accept responsibility for a poor quality job in the harshness of contrast and reproduction of the plates of Eckleberry and Malick, whereas Singer and Tudor's plates are superb.

These liabilities, while unfortunate, are very minor in comparison to the overall authoritative character of the work. Its value as a comprehensive reference cannot be emphasized too strongly. It will serve the serious researcher as a landmark of the times, and it will provide the list chaser a mark at which to aim for many years. An enormous amount of effort went into collecting, organizing and presenting the information. The birders of the state are indeed indebted not only to the author for his considerable effort and sacrifice, but to those people who financed and encouraged this review of New York's ever changing avifauna.—Robert P. Yunick.

Vergelijkende Studie van de Pterylosis in Enkele Afrikaanse Genera van de Ploceidae. Bijdrage tot de Morfologie en de Systematiek van de Passeriformes. (Comparative Study of Pterylosis in certain African Genera of the Ploceidae. Contribution to the Morphology and Systematics of the Passeriformes.) By Maria Morlion. Verhandelingen van de Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van Belgie, 33 (119), 1971:584 pp. Order from the Secretariat, Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van Belgie, 43 Kunstlaan, 1040 Brussels, Belgium. No price given.—This work is bound in 2 soft-covered volumes, the first being part I, the text (xvi + 328 pp) and the second comprising part II, the figures and part III, the tables (iv + 256 pp). Unfortunately it is written in Flemish. This drawback, however, is offset to some extent by the clarity of the diagrams and tabulated data. There is a 3½ page English summary.

The object of the investigation was to provide a basis for future studies and to this end detailed descriptions of the pterylosis of some African ploceids are given. Morlion examined 179 alcoholic specimens representing 40 species in 19 genera, although the generic classification used is not that currently employed by most students of African birds. In the Ploceinae, Estrildinae, and Viduinae the distribution of feathers is very constant. The general configurations and regional subdivisions of tracts are similar. "No striking differences are found, but several minor distinctions can be seen." Morlion believes that the long-debated recognition of 2 families, Ploceidae and Estrildidae, would not be justified on the basis of these small pterylographic differences alone. She concludes that additional studies of passerine and nonpasserine families are needed before the "exact taxonomic value" of pterylosis can be assessed.

The bibliography is convenient, though incomplete in some respects. However, the fact that different papers published by the same author in a single year are not distinguished by "a", "b", etc., can lead to confusion. Citation errors are common. In the first 12 pages there are 6 instances in which the years of publication given in the text are not found in the list of references.

Factual information in this work should be useful to systematists, particularly if it is considered with material in other recent publications (e.g.: Clench, Auk 87:650–691, 1970; Markus. A preliminary survey of the occurrence of neossoptiles in South African passeriform birds, with special reference to natal pteryloses, order no. M-2297, Univ. Microfilms, Ann Arbor, Mich., 1969; Sibley, Bull. Peabody Mus. Nat. Hist., no. 32, 1970; Stettenheim, pp 1–63 *in* Avian Biology, Vol. 2, Farner and King, eds., Academic Press, N.Y.; Lucas and Stettenheim, Avian Anatomy: Integument, Agriculture Handbook no. 362, U.S. Gov. Printing Office).—MILES B. MARKUS.

ECOLOGY OF POMARINE, PARASITIC, AND LONG-TAILED JAEGERS IN NORTHERN ALASKA. By William J. Maher. Pacific Coast Avifauna. Number 37, Cooper Ornithological Society, 1974: 148 pp., 27 figs., 37 tables. Paper cover. $3.75.—In recent years some of the most widely heralded ecological studies of birds have been based largely on theory. Some of these have provided important insights, but in too many cases critical readers have been forced to discount the conclusions because the author's understanding of the subject did not extend to the *biology* of the species. At times, it has almost seemed as if knowledge about real birds evolving in a dynamic environment was no longer as important, say, as a speculative interpretation of the length of their bills.

William J. Maher's important paper on the comparative ecology of 3 species of jaegers should do much to redress the balance. It is based on 5 seasons of solid field work in northern Alaska, and contains a wealth of information on ecological adaptations that allow these potentially competing species to coexist. All 3 jaeger species are treated, but most information concerns the Pomarine Jaeger which nests along the low-lying coastal plain. Maher shows that breeding in this species is totally dependent on the presence of microtine rodents, particularly the brown lemming, for prey. To exploit this unpredictable fluctuating resource, which may be superabundant one year and unavailable the next, the Pomarines migrate into potential breeding grounds in loose flocks of up to 100 individuals; this maximizes their chance of encountering high prey concentrations. The birds settle and breed in great density—up to 23 pairs per sq. mile—where lemmings are common. Since territories are small and must provide nearly all of the requirements for the pair, they are defended virogously for the entire season. This species is essentially nomadic, and "forms no permanent territorial attachment".

Feeding habits and foraging techniques of the Parasitic and Long-tailed jaegers are more varied, though Parasitics depend to a large degree on birds and Long-tails on rodents. Because these species can usually depend on an adequate and predictable food supply, they migrate to the nesting areas in pairs or small flocks and apparently return to territories of past years. Territories are much larger but are defended strongly only early in the season, until spacing is accomplished. Densities never approach those of the opportunistic Pomarines: the highest recorded for the Parasitic was 0.36 pairs per square mile, for the Long-tail 2.3.

All 3 species are physiologically capable of breeding at the time of their arrival, and all have similar incubation periods and growth rates. However, the pre-egg stage of the Pomarine is longer and more variable, and the fledging period is several days to a week longer than in the smaller species. These factors, Maher argues, are probably significant in limiting the northern extent of the Pomarine's breeding range, and give the Long-tail "an advantage in areas where the potential breeding season is critically short."

The annual breeding success of jaegers, like that of other arctic species, varies considerably, but that of the Pomarine is extreme. Between 1949 and 1960, the species bred in significant numbers at Barrow only 5 times, and then only when lemming numbers were high. In 1958, Pomarines were not known to nest anywhere in northern Alaska. Although the extent to which this species may wander in search of breeding opportunities is unknown, it seems clear that most individuals do not nest annually—and some might nest as infrequently as 1 year in 4. The corollary—that survivorship is highest in this species—remains to be tested. Further, the presence of lemmings is no guarantee of nesting success. Despite a high in 1956 apparently no Pomarine chicks fledged because of an early snowfall. This also suggests greater longevity and adult survivorship in the Pomarine.

One of the most important aspects of this paper is the inclusion of data on the behavior of non-breeding birds. Such data—for any species—are almost non-existent in the literature, and in the present case they are essential for understanding variations in annual breeding patterns. These data emphasize the importance of making long-term studies in one area.

The paper is also important for the questions it raises that cannot yet be resolved. For example, in 1956, when lemmings were abundant, Pomarine Jaegers migrated into and bred at Barrow in large numbers; in 1957 and 1958, when lemmings were rare, spring migrants into the area were virtually nonexistent and no birds bred. How, then, does this species assess the presence of a potential food supply without even visiting an area? Do jaegers instinctively recognize lemming cycles and shift their explorations to new regions after years of (usually) successful breeding? Did they not return in 1957 because of the nesting failure in the previous year? Or did they perhaps not return to the breeding grounds at all, remaining at sea? Students of pelagic birds on the west coast might be able to clarify the situation by making more detailed observations on summering jaegers.

Much remains to be learned about jaegers. Maher's study deals only with adaptation and interactions on the breeding grounds. But for 9 months of the year jaegers are pelagic, and adaptations that may allow them to coexist are unstudied. Data will be hard to get but are essential to a full understanding of jaeger ecology.

The paper is well presented, and the occasional redundance necessitated by the volume of material presented is not objectionable, but serves to reinforce important points. Except for pp. 109–114, where scientific names are misspelled with distressing frequency, there are few typographical errors. The offset printing suffers from unevenness, and the format of the Avifauna series is quite dated and deserves an overhaul. I would have appreciated photographs of the habitat and even of the species, but the paper stock is probably inadequate for successful reproduction of photographs. But no quibbles are really justified. Maher's paper deserves wide circulation. It is an important reminder that hard and prolonged field work remain the only basis for sound ecological studies. Editor Tom J. Cade is due congratulations for making such an important publication available at a bargain price.—J. R. JEHL, JR.

Bird Ringing. By Chris Mead. British Trust for Ornithology Guide No. 16, 1974: 68 pp., illus. by many drawings, maps, photos, and graphs. Paper cover. $2.00. (includes surface mail postage) from B.T.O., Beech Grove, Tring, Hertfordshire, England HP23 5NR.—An authoritative, interesting, and occasionally delightful treatise on British banding, written for the bird *watcher.* American birders, banders, and research ornithologists alike will find much of interest here, for it includes concise and well-written discussions of the purposes, history, techniques, and practical and research potential of banding—most of which is world-wide in application. Particular emphasis is placed on non-game species (refreshing to an American bander) and on the information that can be obtained from the live bird in the hand as well as from recoveries. "Spectacular" recoveries of 100 species are mapped, as are selected records from 25 species that have interesting or typical migration patterns. Each map is accompanied by several paragraphs on the species, some of which discuss the contributions banding has made to environmental, biological, or conservation problems. Mixed in with the purely expository writing and the technical explanations are several captivating bits, such as the difficulties of coding the cause of death in cases like the rather sad Blue Tit that "Entered kitchen, flew against closed window, fell into bowl of custard and drowned" or the Mute Swan that "hit wires, chased by a cow which sat on it." These compete successfully with my favorite (now discontinued) American code of "Caught by or due to: Clam."

It is particularly gratifying to see a national, but privately-financed, banding program go to the effort and expense of producing such an excellent pamphlet on its work. Note to the USF&WS Bird Banding Laboratory: go thou and do likewise.—Mary H. Clench.

Alauda, Supplément Sonore, 1974. Disque No. 1. "Les Oiseaux de l'Ouest Africain". Accompanying commentary by Claude Chappuis. "Illustration Sonore de Problèmes Bioacoustiques Posés par les Oiseaux de la Zone Ethiopienne", *in* Alauda 42:197–222.

An announcement accompanying the disc states that beginning in 1974, the Société d'Études Ornithologiques will publish a sound supplement to *Alauda*, consisting of a series of high-fidelity 12-inch discs accompanied by corresponding studies in the Journal *Alauda.*

This disc is the first of a series, which is good news, assuming the others maintain its excellent quality. Side A contains the voices of 12 species and 5 hybrids of Columbidae, and Side B illustrates 18 species of Cuculidae. I have been informed by the Editor of *Alauda*, J. Vielliard, (pers. comm.) that future discs will include not only further African species but also birds from South America and other continents. Such an ambitious program must be applauded by the ornithological community, since the expense of publishing records and their limited market have tended to dry up the flow of such productions in recent years. Generally the jacket costs more than the disc to produce; herein lies the secret of *Alauda*'s budget. The discs do not have individual jackets (my review copy came in a plain cardboard mailer) though in the announcement we are promised "boxes", presumably to house a series. Lack of a jacket means that extra care must be taken lest the discs be scratched and some loss of sales on the popular market may occur since an attractive jacket can add greatly to a record's aesthetic appeal. However, if the resultant savings mean that a larger series of jacketless discs can be produced, the omission is worthwhile.

Technically the production is excellent, and the recordings are of high quality. Most are by Chappuis himself, other contributors being André Brosset, J. Brunel, C. Erard, M. Laferrère, and Dale Zimmerman. The birds are correctly identified, something that cannot always be taken for granted. Most recordings were made during trips spanning 1967–1972, all in West Africa except for one trip to Kenya-Tanzania.

The only spoken words on the disc are the names of each species; this results in a commendable saving of space. Commentary is confined to the pages of *Alauda* which are bound separately and accompany the disc. The commentary includes general introduction to the proposed program of discs, an outline of the scientific objectives, and comments on each species. For the latter, French, English, and scientific names are given with details of each recording (locality, date, recordist, and symbols for technical details).

The introduction states that the discs are not intended merely to aid identification or give aesthetic pleasure, but also to illustrate or resolve certain bioacoustical problems or suggest further avenues of research. The tone is a little apologetic, as though there is some doubt that the material is "scientific" enough to warrant publication by *Alauda.* I feel that no apology is necessary even if the records confined themselves to identification, since anyone who has worked with birds in a tropical forest knows the immense amount of time that would be saved could one but identify the birds he hears all the time but cannot see. I suspect that some sort of catalog of vocalizations is hoped for because for *Columba arquatrix* and *Pachycoccyx audeberti,* which do not appear on the disc, there is an insert in the text to the effect that "we have not yet received a recording of this species". Also, a number of species' vocalizations appear to have no particular "point" to them, since they are simply listed in the text without comment.

The disc contains only new, unpublished material, of which Chappuis and others have gathered a vast amount; nearly 700 African species have been recorded. Nevertheless, I am a little disappointed that this grand enterprise could not have become an even grander international production, with material from already published discs and contributions solicited. For Africa, the student will still have to dart back and forth from the *Alauda* discs to the works of North, Haagner, Stannard, myself, and others in order to make comparisons. Perhaps one day such a grand design can be achieved. I do not mean to fault the Supplément Sonore for not going further, but congratulate it for going this far. The most important thing is to make the material available for study, which is being done. Later, we may hope that some dedicated soul will piece the whole thing together in systematic order.

Going beyond simple identification, the scientific problems that it is hoped the discs will illustrate include behavior (especially the duet), speciation and taxonomy, species recognition, and the evolution of song types. In the present disc, Chappuis contends that vocalizations evolve more slowly than do morphological characters, especially plumage. He illustrates this with a recording of wild *Columba livia,* whose voices are essentially the same as those of our city birds, though the latter appear in a wide variety of plumages. The point is further illustrated by the song of *Streptopelia roseogrisea,* which closely resembles that of its descendant, the domesticated *S. risoria,* though the 2 are morphologically different. *Streptopelia lugens* is shown by vocalization to be the African dove most closely related to *S. turtur* of Europe. A most interesting section contains recordings of *Streptopelia* hybrids, with input from *S. roseogrisea, S. risoria, S. decaocto, S. senegalensis,* and *S. turtur.*

The African Green Pigeons (*Treron*) have weird voices, quite unlike any other bird, but I would not on that account take the bold step proposed by Chappuis and elevate the Treroninae to family rank. Apart from general considerations of "how different is different?" at the family level, one must also consider the green pigeons of Asia which certainly belong in *Treron* but have more "normal" pigeon voices, quite unlike their African cousins.

There is further interesting material among the cuckoos. Chappuis believes that the vocal differences between *Cuculus canorus* of Europe and *C.* (*canorus*) *gularis* of Africa show that 2 different species are involved, and I have long believed this myself. It is a pity that alongside his excellent recording of *C. gularis* he couldn't have inserted one of *C. canorus* for comparison. The tremendous variation in plumage of the Black Cuckoo, *Cuculus cafer*, has resulted in the description of numerous races and even the erection of a full species, *C. gabonensis*, for birds from Uganda west. Chappuis here provides a recording of *C. gabonensis* that shows it is clearly just another morph of *C. cafer*. The recording of *Chrysococcyx flavigularis* is another of Chappuis' many "firsts", of special merit since the call has never been properly described before, let alone recorded. Finally, we have a fine selection of the voices of *Centropus* species which are notoriously difficult to tell apart in the field.

In conclusion, if the succeeding discs in this series maintain the quality and interest of the prototype, all those involved in bird vocalizations are in for a great treat. M. Chappuis and the editors of *Alauda* are to be congratulated on having made a fine beginning to a grand undertaking.—Stuart Keith.

TO THE ARCTIC BY CANOE 1819–1821. THE JOURNAL AND PAINTINGS OF ROBERT HOOD, MIDSHIPMAN WITH FRANKLIN. Edited by C. Stuart Houston. McGill-Queen's University Press, Montreal and London, 1974: xxxv + 217 pp., 14 col. pls., 5 maps, numerous other illus., cloth. $17.50.—This is an outstanding contribution to the literature of the north. The book is beautifully produced, with large type, fine illustrations, and a sturdy sailcloth binding. Its editor knows the north and its natural history and he has real knowledge of and empathy for native peoples. Furthermore, there are plenty of medical topics in this narrative and Dr. Houston's expertise is obvious in the relevant footnotes.

Hood was born in Lancashire, England, and became a midshipman in 1811 at age 14. In 1819, he and George Back (their names are perpetuated in the names of two great rivers) were chosen to accompany Franklin's overland arctic expedition. Hood had many talents. He performed diverse duties, such as studying the weather (including magnetic phenomena), terrestrial magnetism, making maps, collecting natural history specimens, and making a pictorial record of matters of interest. He was not strong physically and, while in debilitated condition, he was shot through the back of the head by an Iroquois member of the party who was suspected of having turned cannibal. Although Hood's journal and pictures have survived, his specimen collections disappeared.

Ornithology does not bulk large in this book. Yet, in view of Hood's many duties and often appalling circumstances, the wonder of it is that he recorded as much as he did. The book includes 4 bird plates in color and one in monochrome; all are composites, having 5 to 8 species per plate. All figures appear to be based on close observation of dead specimens. They are stylized in various ways; most, for example, have undersized heads. Some are of considerable historical and scientific importance: Wood Duck, Eskimo Curlew, Evening Grosbeak, Hoary Redpoll, and others. The birds and other subjects depicted—seascapes, landscapes, native peoples, quadrupeds, and fishes—are discussed in important commentary by Dr. Houston. He also has provided a short account of each member of the expedition (with portraits of some of them) and a brief bibliography. There is a detailed index. An excellent book in every way.—Ralph S. Palmer.

Spirit of Survival/a Natural and Personal History of Terns. By John Hay. Dutton and Company, New York, 1974: x + 175 pp. $7.95.—John Hay has found that the lives of terns reveal something central and common to all manifestations of life: the primacy of association and integral connection in the natural order. Exploring the "otherness" of a tern's world as something apprehended only by an empathic fascination with another form, the author tries, while engaged in a personal odyssey of identification with his subject, to grasp what the common essentials of existence are, what primal roots of being "imply a lasting trust in the face of all finality" (p. 2).

In *Spirit of Survival*, we are treated to the gradual unfolding of the author's perceptive awareness of terns, from his happening upon the deceptive simplicity of a pair of Least Tern eggs ("What is more common than an egg?"—p. 1) through his informational and emotional survey of the breeding season of terns in general. Because it is very much a personal vision, the book defies classification as pure natural history; it appears at times to be more a critique of the clinicism of the strictly scientific investigation of otherness. There are consequently minor errors which reveal the author's bias toward a broad and poetic revelation of natural affinities: in discussing various aspects of tern behavior, the author states: "Their habits have worked well enough, on balance, to keep the race alive; to think of them only in terms of adaptability might not be wise enough on our part" (p. 2). In a biological sense, working "well enough, on balance, to keep the race alive" is the very essence of what is meant by the adaptability of a trait. One must keep in mind that John Hay may not intend strictly biological definitions for "biological" terms. More specifically (p. 13) he indicates that Roseate Terns have an all-black bill during the breeding season. Breeding roseates undergo a series of bill-color changes and actually have a red and black bill during much of the breeding season (Donaldson, Auk 85:662–668, 1968.) The seemingly authoritative description of the terns' route southward during fall migration (p. 13) is actually a tentative overview that awaits further investigation. It is perhaps unfair to continue an analysis of *Spirit of Survival* on the "fact" level: the author's ultimate objective is clearly outlined in the Acknowledgments: "As far as the book itself is concerned, I only hope to convey the dimensions of the subject and some of the fascination I found in it" (p. x). The author's style is poetically evocative of his own subjective experience of another living form, of an alien cycle of life closely attuned to the vagaries of the environment, a life whose "discipline" he admires: "I envied its constancy" (p. 21). The human desire to be other is trapped in the eternal paradox; desiring the apparent spontaneity of a tern's life means desiring the state of what appears to be "non-reflection" (p. 7). Perhaps the human burden of transcending self weighs too heavily upon John Hay. He dedicates his book to those who are trying to "narrow the gap between men and nature" (p. 1). One hopes that narrowing the gap means returning periodically to tap the sources of the "spirit of survival" in other living forms, while rejoicing in the separateness and reflectiveness that makes that gap real, the gap that permits the creation of the poetic prose at which John Hay often excels: "Water currents shifted in the sunlight, and I heard the 'wheep, wheep' of a startled shorebird. In the distance, the terns uplifted and drew across the water again, and I felt in me all the tugs of water and wind and the long, long, pressure of change in that smoky sky. September was beginning to pull away" (p. 5).

John Hay's ultimate message, garnered from his observations of terns, is a plea for a more responsive relationship to our environment; in this sense, *Spirit of Survival* is a didactic, revelatory work. We cannot know what it is to be a tern. Our ignorance about the lives of terns and other living things is emenable to reduction by what we like to think of as rigorous investigation. John Hay appreciates the fascination of scientific study: "Could I not usefully spend another lifetime on this formality of daily change?" (p. 129). But his approach is poetic. His book cannot be judged as an information source; it possesses no index. It may be easily dismissed by those currently engaged in scientific studies of the lives of terns, as reminiscent of the vitalism of such early ornithologists as Eliot Howard (i.e. *A Waterhen's Worlds.* 1940). But it should be read for an insight into another human viewpoint, replete with its own insights; in it one could perhaps glimpse some of the "unguarded" thoughts about the lives of terns and humans, not admitted to in writing, that have materialized in the subconscious minds of the most meticulous field workers.—KATHLEEN E. DUFFIN.

LOUISIANA BIRDS. 3rd Edition. By George H. Lowery, Jr. Louisiana State University Press, Baton Rouge, 1974: xxxii + 651 pp., frontis., 41 plates (12 in color), 147 figures. many photographs (1 colored). $15.00.—Although the author's stated objective is ". . . to introduce the people of Louisiana to the absorbing subject of ornithology . . . ." the appeal of this book should be wider. Much of the appeal derives from the varied avifauna of Louisiana. A major factor contributing to the avifaunal diversity of that state is the extensive, indented coastline, which provides breeding habitat for many aquatic birds, the first landfall for trans-Gulf migrants, and a barrier to the further progress of vagrants from more westerly regions. Other factors include a mild climate that permits an exceptional number of insectivorous land bird species to winter there, and occasional tropical storms. The list of visitors from the southwest (southern Texas and Mexico) presents intriguing problems.

Another area of interest is in the changes that have occurred since the 1st edition was completed in 1954. In that interval the State List has grown from 377 to 411 species, despite the net loss of four species as a result of changes in the A.O.U. Check-list. Most of the increment is a consequence of additional coverage and the contributions of colleagues are acknowledged generously in this respect. However, 2 species (Cattle Egret and Black-whiskered Vireo) have been added through expansion of their ranges, and some others unknown earlier have been recorded several times, suggesting more or less regular occurrence. A few species (e.g., White-winged Dove, Great Kiskadee), admitted to the state list earlier, now nest locally. Changes in status are evident in many accounts, notably the Northern Gannet (sighted more frequently), Red-headed Woodpecker (diminishing rapidly) and, sadly, the Brown Pelican. The last-mentioned account should be studied by anyone contemplating the restocking of a species that has been extirpated locally. The updating in this 3rd edition serves to orient observers to gaps in knowledge, and may, for example, lead to confirmation of nesting status for some of those summer resident species not presently starred in the convenient charts of seasonal occurrence (Table 3).

As in the 1st edition the format is in keeping with the author's objectives. Thus, chapters on topics such as "How to Identify Birds" and "Attracting Birds" are included. I was surprised that the section on "Migration" was unaltered in view of the recent contributions of the author and his colleagues cited in the annotated bibliography. The text presents few problems. Information on habits and field marks is presented in a style that is easily read, conveying the author's enjoyment of his wealth of field experiences. However, the term "fully webbed" toes in the discussion of loons (p. 102) may be confusing when the uninitiated reader encounters ". . . full, or totipalmate, webbing . . ." in the introduction to pelecaniform birds (p. 119). The legend for Fig. 31 ignores the letter designations for the component elements. Endangered species are not mentioned as such in the chapter on conservation, but the topic appears in individual accounts (e.g., Wood Stork). The breeding range of the Green-tailed Towhee (p. 568) does not extend, as stated, to central western Texas. In my judgment the pastel backgrounds of the black and white plates of the 1st edition provided a sharper contrast than the present gray ones (especially Plate III).

Trusteeship of the state list is executed with reason, and the need for documentation with specimens is justified repeatedly. One senses here and there a minority report relative to the actions of the A.O.U. Checklist committee. One case is the author's retention (amply justified) of the Baltimore Oriole in preference to Northern Oriole as a vernacular for the consolidated species. The use of the long-established name has particular merit in this case since many casual observers in the West never were aware of Bullock's Oriole as a separate entity anyway. Some of the author's proposals concerning the wood warblers (notably the inclusion of *Oporornis* in *Geothlypis*) also represent departures.

Too frequently the publication of a state bird book marks the author's crowning achievement. It is gratifying, therefore, to see as a chronicle of change the 3rd edition of "Louisiana Birds." This continuing enterprise should accelerate the progress of ornithology in Louisiana, and it may promote ornithological tourism as well.—KEITH L. DIXON.

THE RED-TAILED TROPICBIRD ON KURE ATOLL. By Robert R. Fleet. Ornithological Monographs No. 16. American Ornithologists' Union, 1974: vi + 64 pp., 34 figs., 5 tables. Paperbound. $5.50 ($4.50 to A.O.U. members).—Except for the presentation of numerical data, this account of the breeding biology of the Red-tailed Tropicbird, *Phaethon rubricauda*, could be regarded as a model for the conduct and write-up of a 2-year study of a single species.

The introduction is brief, concise and informative. It clearly introduces the bird, the study area, the methodology and its limitations, and the relevant literature. The main body of the text covers: population dynamics, aerial display, role of non-breeding birds at the colony, molt in relation to the breeding season, nest site selection, nest construction, territory and nesting density, eggs, egg-laying, incubation, hatching, brooding, development and feeding of nestling, fledging, causes of nest failure, renesting, nest site attachment, pair bond maintenance and successive breeding cycles.

The discussion contains a good argument for the hypothesis that the breeding cycle is regulated mainly by seasonal changes in the availability of food. Social synchronization and predators are discounted as having a major influence on the breeding cycle.

The description of the aerial nuptial display (p. 14) is the best I have read for any species of tropicbird. Marked birds were found to perform the flight only in the vicinity of the nesting colony where they were marked. This is at variance with the conclusion reached by Diamond (Auk 92:21–23, 1975) regarding birds at Aldabra, where he found the display "performed over open water and dense vegetation on the main islands as well as over the islets used for nesting." My own unpublished observations at Christmas Island, Indian Ocean and Lord Howe Island, Tasman Sea, agree with Fleet rather than Diamond in that the courtship flights of the Red-tailed Tropicbird were over the sea and over the forest in the vicinity of nesting colonies on steep cliffs, and rarely over other areas of these islands.

Table 2 (p. 40) is unfortunately an example of how not to present measurements. It would have been quite sufficient to have given the range and mean to the nearest millimeter and gram. The remaining figures, decimal fractions of millimeters and grams, obscure the presentation of information and are biologically and statistically meaningless. It is not clear whether the figures after the ± symbol are standard deviations, standard errors or some other statistical parameter. At several places on pp. 39 and 40 it should be "tarsus" and not "tibiotarsus."

The author and the A.O.U. are to be congratulated on producing a first rate monograph on a scientifically interesting and beautiful bird.—GERARD F. VAN TETS.

THE SEABIRDS OF BRITAIN AND IRELAND. By Stanley Cramp, W. R. P. Bourne, and David Saunders. Taplinger Publishing Co., Inc., New York. 1974: 287 pp., 12 photographs, 4 color plates, 32 maps, drawings, tables. $14.95.—This recent addition to the swelling volume of information on seabirds has resulted from "the strenuous labours of more than a thousand observers who surveyed all the coastal breeding seabirds of Britain and Ireland during 'Operation Seafarer' in 1969–70." Operation Seafarer attempted to bind together all the scattered and continuously accumulating knowledge on British seabirds in order to provide a comprehensive view of the breeding distribution and abundance of every coastal-nesting species. It was designed as a baseline study that could provide a reference point against which future censuses of equal scope could be compared, for the authors and organizers were keenly aware of the need to measure the effect of man's increasing activity upon the birds that nest on their shores. Throughout the book, the changing fortunes of each species are discussed in terms of the probable forces, most of them human, that have resulted in the waxing or waning of local or area-wide seabird populations. Interestingly, the majority of species have increased in the last century, primarily because of protective legislation.

The book begins with introductory chapters on seabird biology, threats to seabirds, and an overview of their population trends within the study area. The main body of the text consists of accounts of each of the 24 species breeding in the British Isles (2 procellariids, 2 hydrobatids, 1 sulid, 2 phalacrocoracids, 2 stercorariids, 11 larids, and 4 alcids), each headed with a black and white drawing by Robert Gillmore. David Lack once remarked how indispensible Gillmore's drawings were in increasing the interest in what he liked to call his "dull books." This book is not dull, and Gillmore's drawings greatly enhance it. Each account is divided into 6 sections: "identification," "food and feeding habits," "breeding," "movements," "world distributions," and "status in Britain and Ireland in

1969–70 and past history." Very useful maps, locating all major colonies and their sizes, and 27 appendices, conclude the work. As the authors point out, this is the first time all the coastal colonies of a large country have been mapped, and the total numbers estimated accurately enough for meaningful comparisons in the future.

The first 5 sections of each account are essentially summaries of known information, and are very good. The sections on status form the major new contributions in the work, and they are dependent upon the degree of accuracy of the "more than a thousand observers" conducting the censuses. The difficulties in estimating the number of breeding pairs (the unit used) of such divergent species, over a 2-year period, and under such greatly differing colony conditions are fully discussed by the authors, who freely admit that it is a "formidable undertaking." How well did they do? The author's candid assessments seem the best. They feel that the estimates of 17 of the 24 species are accurate enough to detect changes of 10% to 20% of total population if comparable future censuses are conducted. The 4 alcids and 3 of the Procellariiforms presented the most difficult problems. The alcids could be counted, but the numbers seen do not tell how many are nesting. Population figures for them are estimates only, and only major changes in future censuses would show up, although accurate surveys of the extent of many colonies will provide some indication of future population trends. The nocturnal, burrow-nesting storm petrels (*Oceanodroma leucorhoa* and *Hydrobates pelagicus*) and Manx Shearwater (*Puffinus puffinus*) are nearly impossible to estimate, and the authors candidly present only orders of magnitude for them. Given these difficulties, it is best to consider Table 1 (p. 42), which ranks all except the above Procellariiformes in order of abundance, as only a general guide to relative abundance. Some rank positions may not be reliable, because differences in censusing accuracy between species may preclude discerning which have the greater total population.

This book has been well edited and has few errors. Most noticeable are the misnamed gulls in Table 1 (p. 42): *Larus fuscus* and *L. marinus* are called the Lesser and Greater "Black-headed," rather than "Black-backed," Gull, respectively. Leach's Petrel has been spelled in alternate ways by different authors over the years, and both *O. leucorrhoa* (p. 42) and *O. leucorhoa* are found here. Gillmore did an excellent job depicting all species in his 4 color plates, especially the terns, but somehow has stretched the wings of his soaring adult Gannet (*Sula bassana*) into an albatross-like length.

In summary, it seems clear that Operation Seafarer achieved in large measure what it set out to do, and the results of this impressive survey have been brought together in a highly readable manner, with the wealth of information clearly presented and easy to find. The authors are to be complimented.—CAMERON B. KEPLER.

PELAGIC STUDIES OF SEABIRDS IN THE CENTRAL AND EASTERN PACIFIC OCEAN. Warren B. King (ed.). Smithsonian Contrib. Zool. No. 158, 1974: iv + 277 pp., many maps, charts, graphs, and black-and-white photos. Paper cover. $3.70. For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402.—This report on the distribution of pelagic seabirds is based mainly on the results of the Pacific Ocean Biological Survey Program organized by the Smithsonian Institution and carried out during 1963–1968. Following a general introduction to the program by Patrick J. Gould, there are chapters on the Sooty Tern (*Sterna fuscata*) by Gould; the Wedge-tailed Shearwater (*Puffinus pacificus*) by Warren B. King; the Black-footed Albatross (*Diomedea nigripes*) by Gerald A. Sanger; the Laysan Albatross (*Diomedea immutabilis*) by

Sanger; the storm petrels (Hydrobatidae) by Richard S. Crossin; the Red-tailed Tropicbird (*Phaethon rubricauda*) by Gould, King, and Sanger; and on recoveries of banded albatrosses by Chandler S. Robbins and Dale W. Rice. The general emphasis is on a detailed account of the distribution of these species in relation to their ecology.—R. J. R.

AUTUMN HAWK FLIGHTS. By Donald S. Heintzelman. Rutgers University Press, New Brunswick, New Jersey, 1975: 398 pp., 88 photographs, 48 maps, 60 tables, 40 charts, drawings, and graphs. $30.00.—*Autumn Hawk Flights* is divided into 6 parts. Part 1 contains an introductory chapter that is devoted to field study methods and a chapter on hawk identification. The emphasis of Part 2 is on hawk lookouts and contains 7 chapters, each of which covers a particular geographical area. Raptor morphology, anatomy, and flight are the subjects of Part 3, and Part 4 elaborates on hawk migrations in relation to general weather systems, local weather variables, mountain updrafts, and thermals, and includes a chapter on daily rhythms and noon lulls in autumn hawk flights. Part 5 covers migration routes, diversion lines, and wind drift in relation to geography, and discusses hawk counts as indices to raptor population trends. An interesting and speculative account on the migration and evolution of Broad-winged Hawks completes the regular text of the book as Part 6. The book contains 2 appendices: one gives the scientific names of the birds mentioned in the text, and the other contains the tables of data referred to in the various chapters. The literature cited section has 22 pages of references, and I found the 20-page index compiled by Lisa McGaw very thorough and helpful.

This book, although somewhat useful to the serious student of migration, is written primarily for the amateur or non-professional. Technical terms are avoided whenever possible, and those that are used are defined in footnotes. For instance, on p. 205 Heintzelman gives an accurate description of roll vortices but never uses the term. In contrast, terms like *wind drift*, *thermals*, and *accidentals* are footnoted and defined when they first appear. In general I found the text quite easy to read.

The book contains too many black-and-white photographs, some of which are not of the best quality and are redundant. There are 7 photographs of Red-tailed Hawks in the text and at least 6 photographs showing kettles of migrating Broad-winged Hawks. Many of the photographs portray hawk lookouts with observers staring into the sky. One or 2 of these would suffice instead of 11. Chapter 2 on hawk identification occupies 20 pages and does not contribute enough new identification points to justify its inclusion. Little that is not already in field guides appears in the chapter.

The diagrams are well done, especially those in Parts 4 and 5. Parts 3 through 5, consisting of 150 pages, are Heintzelman's best and contain most of the real biology in the book. It is here that Heintzelman speculates that pesticides or other factors, by reducing energy production of flight muscles in Ospreys, have contributed to the increasing numbers of Ospreys using updrafts at mountain flyways in recent years. One finds that most hawk flights along the northeastern mountain ridges occur more or less with the typical weather pattern of a low-pressure area in New England and a cold front passing the vicinity of the hawk lookouts. In the discussion related to wind drift and diversion lines, Heintzelman mentions the Trans-mountain Drift hypothesis that he and Armentano put forward in 1964, in an attempt to explain the interaction of mountain ridges and coastlines with broad-front hawk migration. The hypothesis also explains why observers at nearby lookouts along a line of flight do not record the same birds and may tally markedly different counts of hawks on the same day. Based on this and other factors, it is Heintzelman's opinion that the greatest caution must be exercised in considering northeastern raptor population indices based on autumn hawk counts. If this is indeed so, why has he devoted 40 pages containing 44 tables to data on yearly hawk counts and the number of hawks banded? Perhaps more synthesis and less tabulation of the data would have been in order.

On page 96 there is mention that many hawks do not cross water gaps, because no thermals develop over water, but thermals or at least convection cells do develop over water at night when the water temperature is warmer than the air above it. This has important implications for the Broad-winged Hawks that move southwest from Key West and Dry Tortugas, Florida. Another question that was left unanswered in the book was whether hawks deposit fat reserves for their migrations in the same manner as other migrant birds.

Admittedly most studies of hawk migration have originated in the Northeast, but is the almost cursory treatment of hawk migration south of the Great Lakes, the Appalachians, and Virginia the result of no data or an oversight on the part of the author? Whatever, there is clearly a need for more work in these geographical areas. Two omissions in the book are bothersome. There is no mention of the migration of kites, and more importantly, the word "spring" does not even appear in the index, and for good reason. The only mention of spring hawk migration in the book appears on p. xxix in the Preface. How a book of 398 pages can be devoted to autumn hawk flights without making comparisons with spring hawk flights is a bit staggering.

My final comment concerns the price of the book. As is usual, the smaller the projected audience for a given book, the higher the price per copy, but $30.00 for this book is the best guarantee that sales will be limited. If the price were halved the circulation would certainly more than double.—SIDNEY A. GAUTHREAUX, JR.

TRAITE DE FAUCONNERIE. By Hermann Schlegel and A. H. Verster de Wulverhorst. Chasse Publications, P.O. Box 906, Denver, Colorado, 1973: viii + 115 + 90 + viii pp.; 16 monochrome lithographs. $32.50.—This is a translation from the original French edition published in 3 parts between 1844 and 1853. The authors saw a need for a modern treatment of falconry, encompassing the methods of acquiring, training, and caring for raptorial birds. Much of the book traces the history of the sport in the lands where it was practiced and with the various birds used.

The authors went to considerable effort to describe 3 variations of *Falco rusticolus* (Gyrfalcon) which they maintain are distinct species. We mention this in order to illustrate the confusion at the statement (p. 20) that "The Gyrfalcon is irritable and obstinate, ill-tempered and so malicious as to attack other falcons of any species." We are uncertain about what bird they are really referring to as the Gyrfalcons of our experience are usually one of the easiest of all raptorial birds to tame and often develop a strong attachment to their trainer. It is further stated (p. 14) that the progeny of the White Falcon (Gyrfalcon) "Are already capable of propagation the year after they are born." Our research suggests that the time is closer to 4 or 5 years of age. Similar confusion exists with respect to other species discussed.

Methods of capturing hunting birds begin on p. 47, and although the descriptions of the various trapping devices may be difficult to understand, it is interesting to note the elaborate pains that early falconers went to. A line on p. 47 describes a man seated in a blind on the plains of Holland, patiently waiting for a falcon to approach his trapping station. "Seated on a chair in the small hiding place with his gaze constantly fixed on the shrikes (used to alert the trapper of an approaching falcon), he has no pastime except his pipe." Much of the equipment and furniture described in the book is no longer in use. This is also true of many ancient training methods.

Falconers of the 19th century shared with modern falconers an understanding of the non-social attitude of most raptorial birds. In the section on training a good comparison is made between the temperament and treatment of dogs and hawks while in training. Much unnecessary effort and energy was expended by 19th century falconers to train and fly birds. The book states that 4 to 5 months are needed to train a falcon. Modern falconers rarely take more than a month to accomplish this.

The authors worked extensively to describe the history and practice of falconry in many parts of the world. This section of the book contains a great deal of extraneous rambling interspersed with a few interesting stories. The Shahs of Persia made gifts of falcons to great nobles and provincial governors. "They put jeweled hoods and bells of gold on the birds. The lords also had gloves which are bordered with jewels for holding the birds and they put jesses and swivels of gold on their birds." A description of an eagle trained to kill men ended with the bird plucking out the eyes of the dying man.

On p. 20 is described a particularly good year of falcon trapping and subsequent destruction of the excess birds "for fear that their abundance would cause a subsequent depreciation in price." Yet a law in the code of the Burgundians says that "anyone who is guilty of stealing a hunting bird shall pay the owner of the bird six sows or shall suffer the punishment of having the bird take six ounces of flesh from his buttocks."

The circumstances that caused the decline of falconry in Europe were "The French revolution and the wars which followed it and enveloped almost the entire continent of Europe. The complete overthrow of the old order of things and ideas and more than twenty years of troubles the like of which Europe had not suffered for centuries sufficed to bring about the disappearance of a sport which recalled the luxury and extravagances of the past far too openly not to incur henceforward the disapproval of the public."

We feel that the authors spent too much time delving into historical rhetoric for the book to have been of much value to aspiring novice falconers of the 19th century. Besides, the aristocracy of the time had on their payrolls professional falconers who learned their trade through apprenticeships. For the modern falconer, the book would serve well as an addition to his library on falconry. We have never read a more complete historical account of the subject. The book provides a feeling of identity and an explanation of some of the terminology used by modern falconers.

We experienced difficulty in locating the footnotes. On p. 2 footnote 14 is missing, and on p. 8 footnotes 6-2, 6-4, and 6-6 are missing. The introduction by the translator and editors does not make it immediately clear that the book is a translation of an old work. Some areas of the book are a bit vague, but readers of the era in which it was first published might not have found this to be so. The book is attractive in its binding and printing and the type of paper used adds greatly to the look of the facsimile.—William F. Johnston, Jr. and Heinz Meng.

This issue of *The Wilson Bulletin* was published on 30 June 1976.

THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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The Wilson Bulletin

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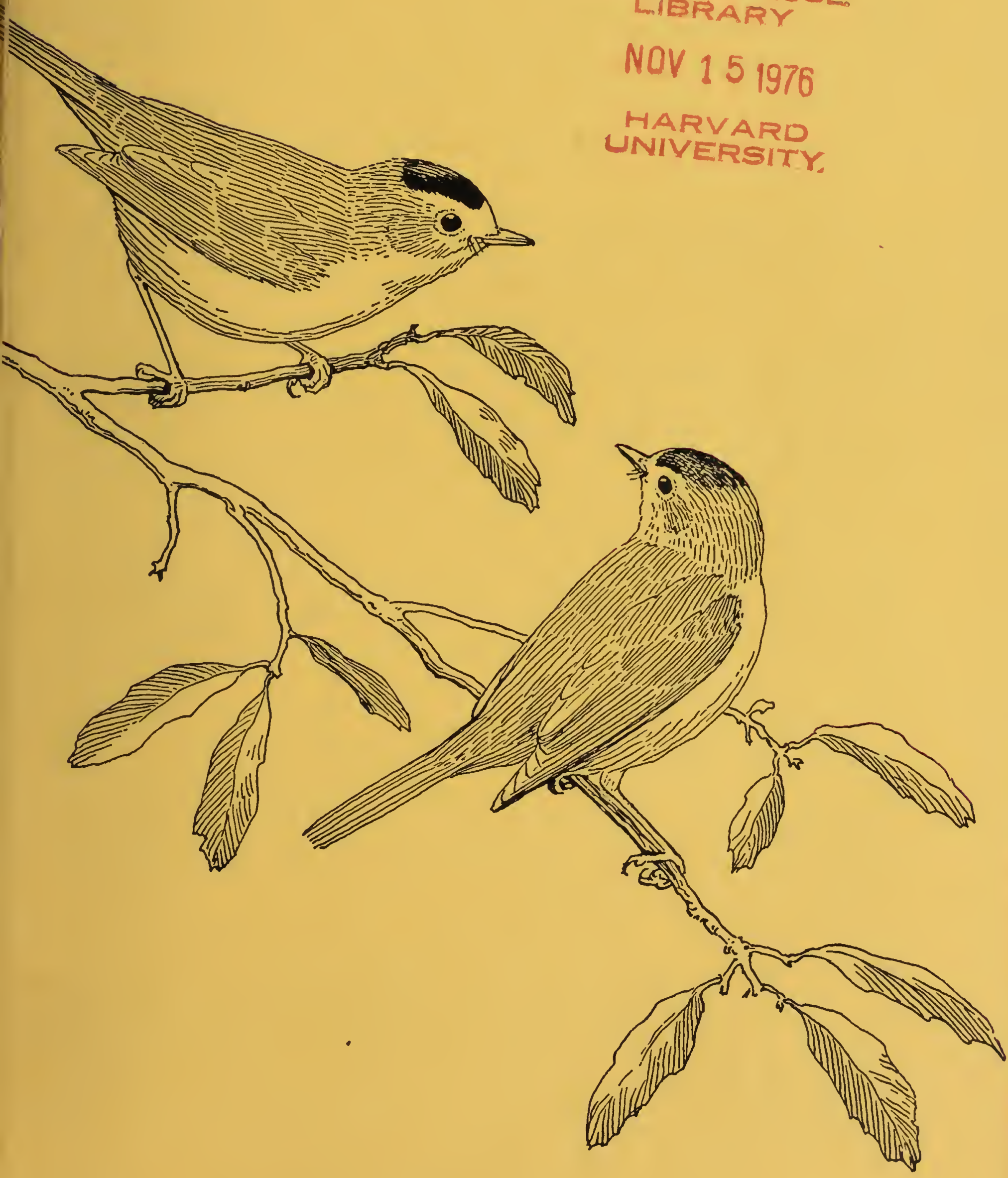

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ROSEATE TERN BILL COLOR CHANGE IN RELATION TO NESTING STATUS AND FOOD SUPPLY

GRACE DONALDSON CORMONS

In a previous paper (Donaldson 1968) I described the change in bill color of Roseate Terns (*Sterna dougallii*) breeding on Great Gull Island, New York, (41°12′ N. Lat., 72°07′ W. Long.), at the eastern end of Long Island Sound. Briefly, when the Roseates arrive at the island in early May the bill is all black. During incubation red appears at the base of the bill. The extent of red increases until about the time the young fledge. At the end of the season the bill becomes all black again.

At the time of the 1968 paper, data were not available on the exact nesting status of most of the birds measured, and it had not been possible to follow the bill color change of individual Roseates. These data, and more, are now available.

In this paper I describe the bill color change of a marked pair of Roseate Terns followed from the time the first red began to appear during incubation through the time their young fledged. I compare the average of measurements of the extent of red on the bills of Roseate Terns trapped on Great Gull Island for 1968–1970, 1972, and 1974 and discuss these figures in relation to estimates of food available. I also present the bill color measurement data in relation to sex, weight, clutch size, and age. Finally, I discuss some data on bill color of Roseates in the Caribbean and speculate on the possible adaptive significance of bill color change in the Roseate Tern in light of the unique timing of this change.

METHODS

The pair of adult Roseate Terns illustrated in Plates 1 and 2 had been individually color-marked 21 June 1969 as part of our program of color-banding adult terns (Hays 1970b). The sexes of the pair were determined by H. Hays in late August 1972 when she observed one bird (USFWS 742–75155) mount the other (USFWS 742–75165). I refer to the former as M for male and the latter as F for female. This sexing was consistent with observations in 1974 of their display behavior and their roles in incubation and feeding the young.

In 1971 and 1974 M and F nested in the grass at the top edge of a 4m high retaining wall opposite a tower from which they were observed and photographed. In 1971 I photographed this pair daily from 15 June–11 July, when they moved their young into the rocks below the tower. We then set up a blind near where they fed their young and I photographed them 18 July–14 August. This 1971 series showed no detectable difference in extent of red from day to day. Comparison of photographs taken at 3- and 4-day intervals did show a perceptible change. In 1974 Joan Black photographed M and F on 8 June. My husband and I then photographed them twice a week from 22 June through 18 July, and on 25 June I photographed M held in the hand.

In both years M and F were photographed through the last day they were seen on the island, and all photos both years were taken between 11:00 and 13:00. The slides from 1974 were sharper than those from 1971. The plates are based on the 1974 slides except for the figure of F on 14 August 1971.

J. Black photographed with a Nikon F2 camera body and 500 mm reflex lens. All other photos were taken with a Konika FP camera body with a 450 mm Soligor lens. In 1971 Kodachrome II film was used. In 1974 high speed Ektachrome was used for all photos except those taken 8 June, when Ektachrome X was used. I have included the 8 June 1974 and 14 August 1971 pictures in the plates, although they were taken with different films, because they show the extremes early and late in the change. In the 8 June slide the bills are almost completely black with only a trace of red at the base. The 14 August picture shows the faded red of the bill late in the season. That this color is not an artifact of the difference in film type is demonstrated by comparison of leg color (which does not change during this period); the legs appear identical in slides made with the 3 film types. Use of the Kodachrome II slide was further validated by comparisons of slides of the same birds taken in 1971 on Kodachrome II and in 1974 on high speed Ektachrome.

Referring to the slides for each date, Kathleen Duffin painted the tern heads using the guache technique with Guitar brand watercolors. In the case of the figures for the female on 8 and 18 July, the *extent* of red is as shown for these dates, but the *shade* of red is that of the slides from 5 and 15 July respectively, as the slides of her from 8 and 18 July were overexposed.

In 1968–1970, 1972, and 1974 I measured the extent of red on the bills of 872 Roseate Terns trapped on nests that had been numbered when the first egg was laid. Using dial calipers I measured to the nearest mm the red on the side of the upper mandible along a line from the edge of the feathering to the tip of the bill, passing along the line of the nostril. I use gross measurements rather than a percentage of red because the variation in distance from the base of the feathers to the distal end of the nares among Roseates is negligible (Donaldson 1968). As I measured adults only at the time their eggs hatched, the red on the bill rarely extended beyond the distal end of the nares.

I have compared the measured extent of red on the bills of the Roseates we trapped during the first part of each nesting season for all years (Table 3). The varying calendar dates of these periods reflect differences in the timing of first eggs and of the peak dates of newly established Roseate nests. The nesting status of the birds trapped in each of these periods was directly comparable. All adults were trapped on newly hatched or 1-day-old chicks and the measurements of those birds trapped on the first nest to hatch each year are compared.

The 1972 season was exceptional. On 22 June 1972 Hurricane Agnes destroyed many nests; birds subsequently renested, so that there were more birds nesting late than in any other year of the study. We were able to continue trapping Roseates in August. I have, therefore, grouped the birds trapped after 7 July 1972 into a second and third period for that year: 8–22 July, and 23 July–1 August.

In 1970 and 1972 I weighed the birds to the nearest gram using a Pesola balance. In 1974 I weighed them to the nearest tenth of a gram on a triple beam balance.

RESULTS

Plates 1 and 2 show the bill color change of a pair of Roseate Terns from the middle of incubation to about 6 weeks after the young have hatched. I have notes on this pair taken 2 June, 6 days before the first picture in Plate 1 and 18 days before the first egg hatched: I describe M as having the bill completely black on both sides, and F as having a trace of red at the base on the right side with no red on the left.

Table 1 represents an expanded legend for Plates 1 and 2. The side of the bill actually illustrated in the plate is discussed first, then the opposite side if it was different.

In 1974 we did not see M and F after their second chick flew on 18 July. In 1971 they were seen through 14 August, thus allowing me to photograph the faded bill of F. The first slide from 1971 that shows fading of the red is that of F on 2 August. The red continued to fade as is shown in the slides for 7 August, yet between 27 July and 7 August in 1971 the extent of red on F's lower mandible increased to the amount shown for her on 14 August (Plate 2). The slide record of M's fading bill is not so complete as that of F, but his bill appears to have reached its maximum brightness about 27 July also, and was beginning to fade on 9 August.

In both 1971 and 1974 the extent of red on the female's bill was consistently greater than that of the male. It appears likely that there is no consistent sexual dimorphism in bill color, as in 10 of the 235 pairs trapped and measured, there was no difference in extent of red on the bills of mates (Table 2).

The acquisition of red for most Roseate Terns in the Great Gull Island colony appears to follow the pattern shown for M and F, the first red appearing at the base of the bill during incubation (Donaldson 1968). In 1969 I noted a single exception to this pattern. On 16 May I picked up a freshly dead Roseate Tern with 2 mm of red at the base of the bill. This bird had several developing ova, but no ruptured follicles. The first Roseate egg marked on Gull Island in 1969 was found on 21 May, 5 days later. The 15 May bird beginning to show red was thus exceptionally advanced.

TABLE 1
LEGEND FOR PLATES 1 AND 2

Date	Nest Status	Ind.	Side	Description
6/ 8/74	12 days before hatching	M	L	LM*trace of dark red
		F	L	LM dark red coming in on lower part. UM** red extending down from base of culmen to distal end of nares.
6/25/74	chicks 3 and 5 days old	M	R	LM, red extending less than on side of UM, where it reaches beyond nares.
			L	No slide
		F		No slides
7/ 1/74	chicks 9 and 11 days old	F	L	Red now solidly filled in at base of bill and much increased in extent and brightness since 8 June.
			R	Same as left side, but with a light diffused red over the nares on culmen.
		M	L	Extent similar to that on 25 June, but red brighter.
7/ 8/74	chicks 16 and 18 days old	F	L	Red brightened and extended in last week, especially along culmen.
			R	Red extends 2mm farther beyond naris and 3mm more along cutting edge of LM, than on left side. This was the greatest difference between the sides for any date for either bird.
		M	L	Red brightened and filled in at base since 1 July, and extends somewhat farther along culmen.
7/18/74	chicks 26 and 28 days old (The elder had flown from the wall. The younger flew 18 July.)	F	L	Bright red extending along almost 50% of the side (i.e. from the point where the black and white feathers meet with the UM, to the distal point of red).
		M	L	Red extending along about 40% of the side of the upper mandible.
			R	No slide.
8/14/74	chicks 41 and 44 days old	F	L	Red is very faded, diffused with black and there is a definite area of black at the base of the UM.

* LM = lower mandible
** UM = upper mandible

♂ 8 June

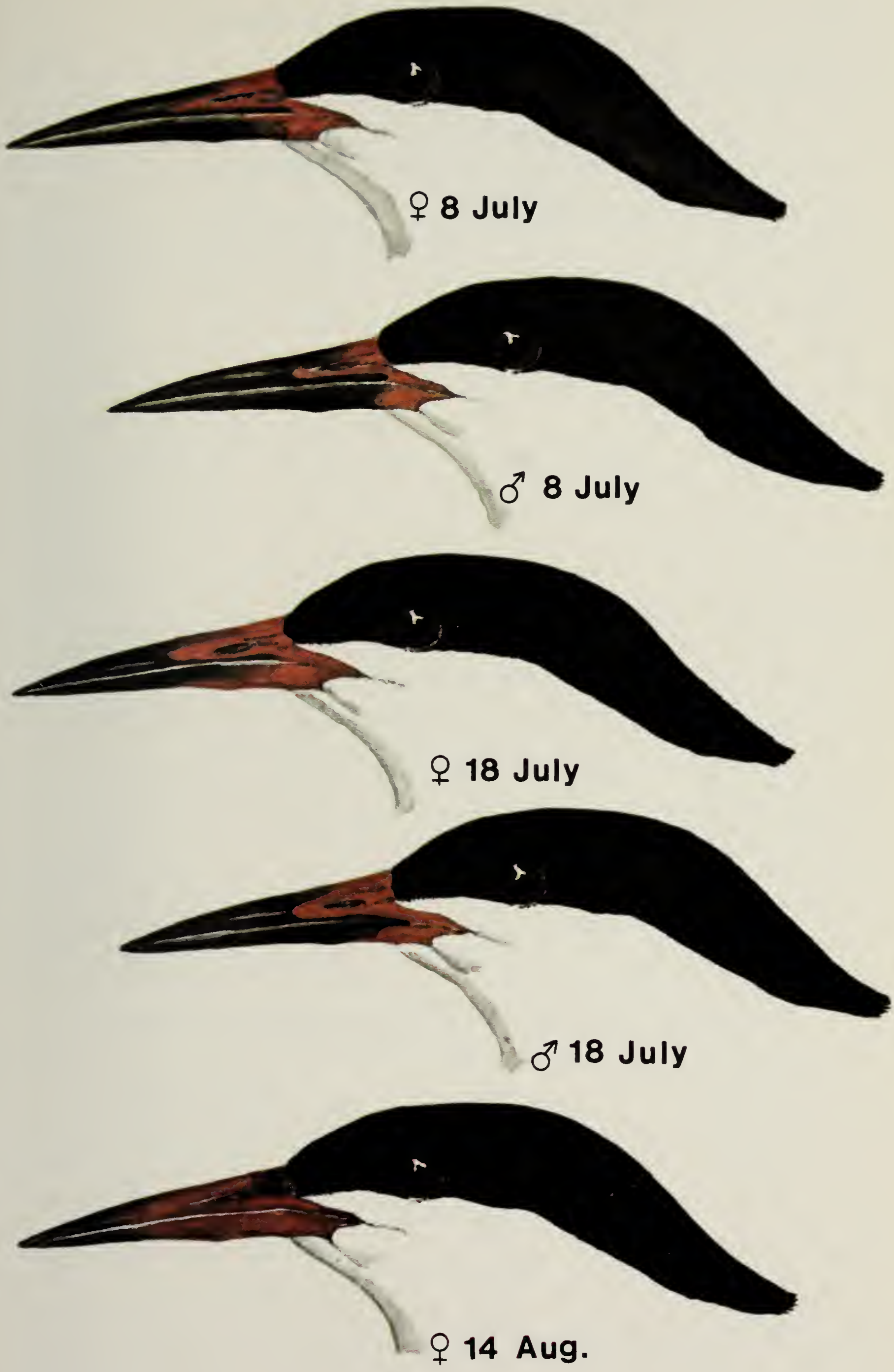
♀ 8 June

♂ 25 June

♀ 1 July

♂ 1 July

KED 1975



KED 1975

Plate 2

TABLE 2
DIFFERENCE (MM) OF RED ON RIGHT SIDE, BETWEEN MEMBERS OF PAIRS TRAPPED WITHIN ONE DAY OF EACH OTHER

	Number of Birds						
Difference	1968	1969	1970	1972	1972*	1972**	1974
0	2	4	2				2
.1–1.0	4	12	15	6	8	13	10
1.1–2.0	8	17	9	6	7	10	7
2.1–3.0	4	8	7	2	5	6	9
3.1–4.0	3	5	3	1		3	3
4.1–5.0	1	4			2		3
5.1–6.0		3			4	1	1
6.1–7.0		1			2		1
7.1–8.0		1			3	2	
8.1–9.0						1	
9.1–10.0		1					1
11.1–12.0							2
12.1–13.0		1					

* Second period of 1972.
** Third period of 1972.
All other dates are for the first trapping periods, as detailed in the methods section.

TABLE 3
RED ON THE BILLS OF ROSEATE TERNS IN DIFFERENT YEARS[1]

Dates	No. of terns	Mean	S. D.	Range
14 June–3 July 1968	30	4.47	2.26	0–11.4
14 June–4 July 1969	115	6.24	2.53	0–17.4
15 June–5 July 1970	63	5.57	1.80	0–10.0
24 June–7 July 1972	84	5.56	3.07	0–15.4
22 June–5 July 1974	89	6.65	2.86	0–18.3

Significance of difference in means of extent of red between years:

	Value of t	P =
1968 vs. 1969	3.462	.01
1968 vs. 1970	2.502	.02
1968 vs. 1972	1.764	.1
1968 vs. 1974	3.763	.01
1969 vs. 1970	1.849	.1
1969 vs. 1972	1.701	.1
1969 vs. 1974	1.079	.3
1970 vs. 1972	0.024	.5
1970 vs. 1974	2.263	.05
1972 vs. 1974	2.404	.02

[1] Measurements (mm) of red on the side of the bill of birds whose first chick was newly hatched or one day old.

TABLE 4
WEIGHTS (G) OF ADULT ROSEATE TERNS

Dates	Number	Mean	S. D.	Range
15 June–5 July 1970	144	109.8	6.8	96–128
24 June–7 July 1972	72	107.9	6.4	96–120
22 June–7 July 1974	83	112.6	7.3	98–133

Table 3 compares the measurements of the extent of red on the bills of Roseate Terns trapped in all years. Comparison of the means for like periods shows significant differences: the 1974 mean is greatest (i.e. the bills had the greatest extent of red), followed closely by 1969, then by 1972 and 1970 which are very similar; 1968 is lowest. Individual Roseates remeasured in succeeding years (Fig. 1) tend to bear out the pattern of annual differences shown for the total sample in Table 3.

These differences in the extent of red from year to year coincide with apparent differences in the fish supply. For instance, in 1968, when the extent of red on the Roseates' bills was low, there was a scarcity of fish in the colony (Hays 1970a; LeCroy and Collins 1972). In 1969 and 1974, when the average extent of red was much greater, there were apparently more fish (LeCroy and LeCroy 1974; pers. observ.).

I found some correlation between weight and bill color, with heavier Roseates tending to have a greater extent of red on the bill. I compared the average weight of birds with 0–10 mm red with that of birds with 10–20 mm of red. The group with less red averaged lighter in weight, although the difference was not statistically significant.

There was a significant (P = .05) difference between the mean of the weights for 1974 and the mean of the weights for both 1970 and 1972 (Table 4). This pattern, with 1970 and 1972 similar and 1974 higher, is the same as the yearly pattern for extent of red on the bills. Both the weight and the bill color differences thus appear to reflect differences in food supply from year to year.

I found no consistent relationship between clutch size and bill color. In 1968, 1969, and 1974, birds on 1-egg clutches averaged slightly redder bills than birds on 2-egg clutches, but the differences were not statistically significant. In 1970 and all 3 periods of 1972, birds on 2-egg clutches had more red than did those on 1-egg clutches, but the difference approaches significance only for the last period of 1972.

Within the large samples of birds measured each year, there was considerable individual variation in the extent of red on the bills of birds of the same nest status. For instance, in 1972 (Fig. 2), some Roseates had

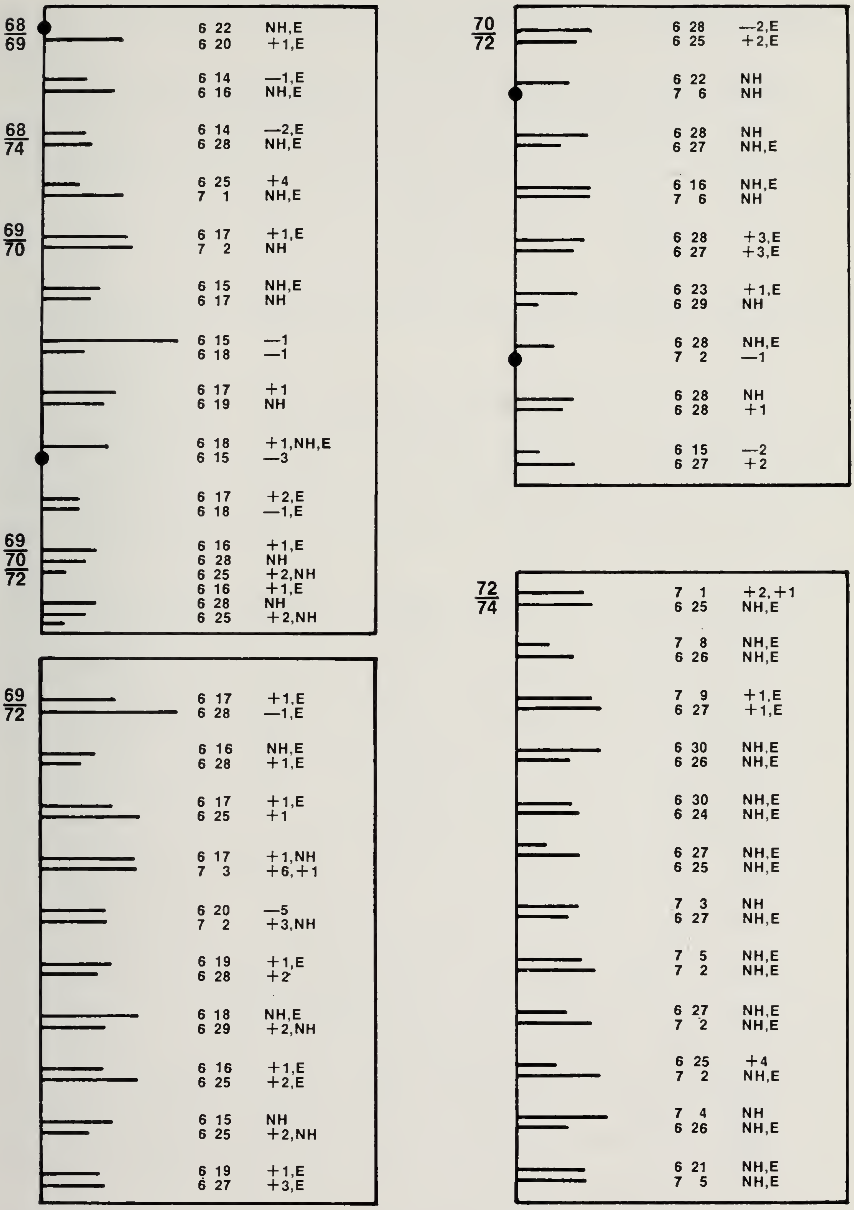


FIG. 1. Each grouping of lines represents the extent of red on the bill of an individual Roseate measured in more than 1 year, e.g. (19)68/(19)69, followed by the date on which it was measured each year and its nest status at the time of measurement. NH = newly hatched chick, E = egg, –5 to +4 = days before (–) or after (+) hatching.

TABLE 5

RANGES OF RED ON THE BILLS OF KNOWN AGE BIRDS WHOSE FIRST CHICK WAS NEWLY HATCHED OR ONE DAY OLD

Age in years	Extent of red (mm)[1]	No. of birds
2	1.5–17.0	3
3	2.5–14.5	13
4	3.4– 8.0	7
5	3.0–14.5	8

[1] These ranges are a summary taken from all years trapping was done (1968–1970, 1972, and 1974).

more than 10 mm of red in June while others had none. There was a marked increase in the number of birds having more than 10 mm of red that were trapped on new chicks late in the 1972 season (Fig. 2). It may be that these were birds that had first nested during June and their bills had already started to become red before the hurricane destroyed their nests.

Even birds of the same age, all measured at the time their first young hatched, varied in the extent of red on their bills (Table 5). Most of these known age birds were trapped in 1972, and are shown individually in Fig. 2, where their ages are indicated by the numeral next to their symbol. The two-year-olds are of particular interest. In addition to the one shown in Fig. 2, I have data on 3 two-year-olds from other years. One, trapped on a nest of unknown age 23 June 1967, had 1 mm of red on its culmen. Another, trapped over a 1-day-old chick, measured 17 mm of red on 3 August 1971 (Donaldson 1971). The third, also trapped 3 August 1971, one day before its chick hatched, had 17 mm red.

Roseate Terns in other parts of the world may differ from the Gull Island birds in the timing and rate of acquisition of red on their bills. Between 22 and 26 May 1968, Helen Hays and I surveyed 275 Roseate Terns on small islands off St. Thomas in the Virgin Islands. Thirty of these Roseates had all black bills. The rest had amounts of red on the bill varying from a few millimeters to ⅔ of the bill red. These birds were standing along the shores of the islands. The islanders are permitted to collect eggs of seabirds until the end of May, and as our search of 4 islands where the birds breed yielded only 6 nests, it seemed likely that the first clutches of most of the birds we saw had been collected.

We aged the eggs by flotation (Hays and LeCroy 1971) in the 6 nests we found, and all but one, which had been incubated 1 or 2 days, were fresh. I trapped an adult on a fresh egg 22 May and the measured red on its culmen was 8.7 mm. These measurements are comparable in extent

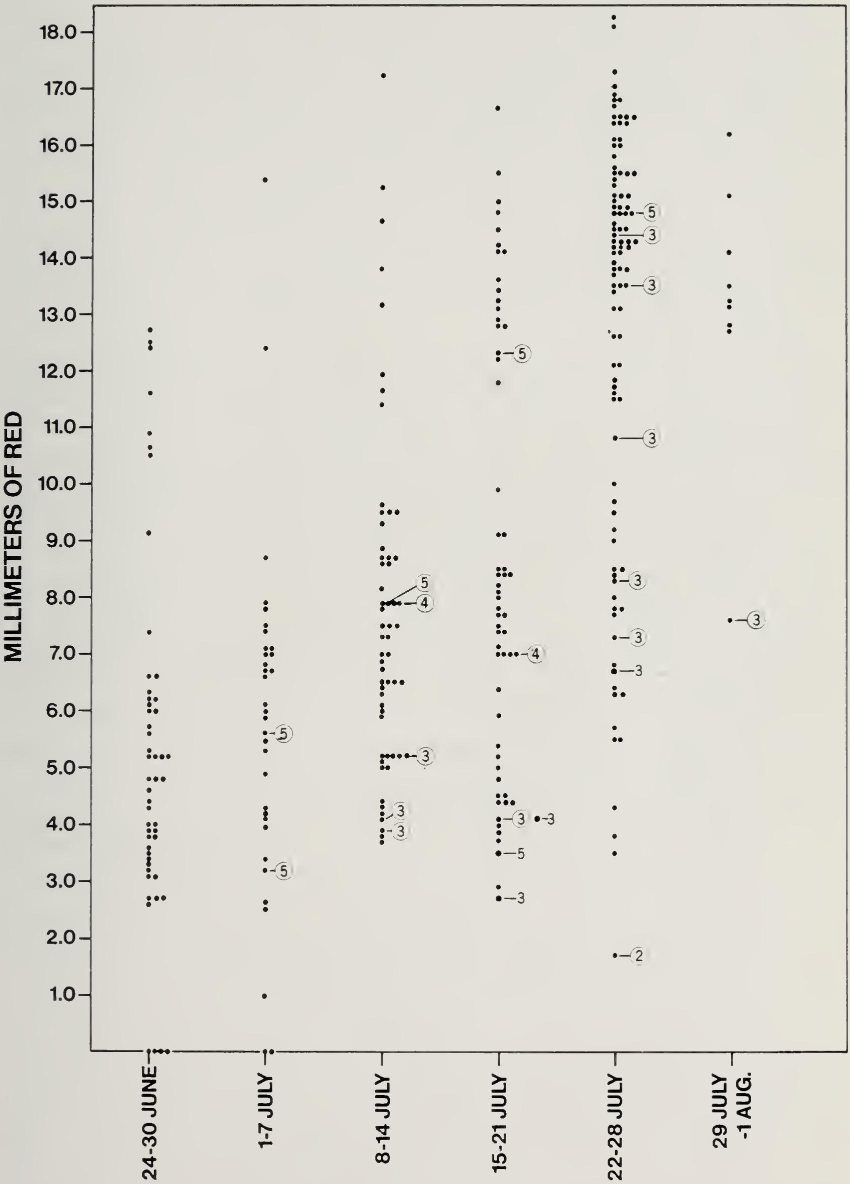


Fig. 2. Each Roseate Tern measured in 1972 is represented by a dot indicating the extent of red on its bill. The numerals indicate the age of known-age birds. Numerals without circles are known-age birds trapped over chicks 2–4 days old. All other birds were trapped when their first chick was newly hatched or one day old.

to those for M and F on Great Gull Island when their young were 16 and 18 days old.

I find little specific information on egg dates for Roseates in the Caribbean. Beatty (1941) said 200 Roseates nested at Bivoni Bay, St. Thomas, and had downy young 26 June 1939, and at Little Saba Cay a colony of 200 Roseates was nesting 2 July 1940. Wetmore and Swales (1931) reported 200 pairs of Roseates nesting in the Dominican Republic on 11 May, and Voous (1965) said eggs of Roseates may be found in the Netherlands Antilles May–July. According to Phelps and Phelps (1959), Roseate nests were found on the Islas Los Roques, Venezuela, 26 May, 14 and 24 June, and 25 July.

If the rate of acquisition of red for birds in the Virgin Islands was the same as that for Roseates on Great Gull Island, the bird I trapped 22 May would have had to start incubating its presumed first clutch in mid-April. If, as the scanty information on egg dates suggests, the birds in the Virgin Islands do not begin laying until early May, then their bills must become red faster than do those of the birds breeding on Great Gull Island, or, start to become red before the birds have eggs.

More specific data on the timing of bill color change are needed for populations of Roseate Terns in different parts of their range. Mack's (1969) observation at Isle of Palms, South Carolina 28 April 1968, further emphasizes this point. He describes a Roseate on this date with "basal 40 to 50% of bill reddish-orange." This extent of red is even more than that on the bills of most of the Roseate Terns we saw in the Virgin Islands at the end of May, and is comparable to the extent on a Great Gull Island Roseate in late July with a 6-week-old chick.

By contrast, a pair of Roseate Terns on a nest with eggs in North Carolina 23 May (Soots and Parnell 1975) had, as would be expected of Great Gull Island Roseates, entirely black bills. The authors misinterpreted my previous paper (Donaldson 1968) when they concluded that breeding Roseates at this stage should have partially red bills.

DISCUSSION

Bill color change in species like the Black-headed Gull (*Larus ridibundus*, Van Oordt and Junge 1933), House Sparrow (*Passer domesticus*, Keck 1934), and European Starling (*Sturnus vulgaris*, Wydoski 1964) takes place well before the birds are paired. As far as I know the Roseate Tern is unique in that the change in bill color takes place after the birds are in breeding plumage and pairing has taken place.

This unique timing of the bill color change in the Roseates may function in one or more ways. Possibly the Roseates' black bills early in the breeding season serve as one means of species recognition where Roseates nest in colonies with other species of terns that are red-billed when mating takes place. Probable Common × Roseate hybrids have been described (Hays 1975), and it is interesting to speculate that if indeed bill color is used for species recognition, then hybridization would be most likely to occur involving a Roseate with a partially red bill, perhaps after the destruction of its initial clutch.

Another hypothesis, arrived at independently by Helen Hays and myself, is that the timing of the change may help reduce interspecific competition for nest sites in northern colonies where Roseates nest with Common Terns (*Sterna hirundo*) and/or Arctic Terns (*Sterna paradisaea*) in dense colonies. Common and Arctic terns are more aggressive species than Roseates and both arrive on the breeding ground with bills that have already changed from all black to all or partially red. The Roseates' all black bills at the time nest sites are chosen and laying begins may make them appear less aggressive, thus making it easier for them to establish themselves in areas where either Common or Arctic terns are nesting.

We further speculate that since the great increase in red on the Roseates' bills parallels the time they are bringing in increasing numbers of fish to feed the growing young, the red may serve an aggressive function. Interspecific piracy of fish has been observed in the Great Gull Island colony (D. Duffy, pers. comm.). It may be that at the time when they are carrying fish for the greatest distances as well as when interspecific competition for fish may be the greatest, the red on the Roseates' bills makes them better able to compete for food in feeding flocks of terns and permits them to deliver the fish to their young with a minimum of interference from other terns.

SUMMARY

The bill color change of Roseate Terns breeding on Great Gull Island, New York is illustrated and discussed. Bills of 872 Roseate Terns of known nesting status, including 235 mated pairs, were measured in 1968–1970, 1972, and 1974. The mates in 10 pairs had identical amounts of red, suggesting that there is not necessarily a sexual dimorphism in bill color. There is extensive variation in extent of red on individuals of similar nesting status measured within the same week, and also among birds of the same age. Significant differences in the extent of red in different years correlated with estimates of food available and weights of the birds. No consistent relationship was found between clutch size and extent of red.

The black bill of the Roseates when they are pairing may be a means of species recognition. It may also make the Roseates appear less aggressive when they are choosing nest sites and thus facilitate their establishment in mixed colonies with the more aggressive Common or Arctic terns. The extent of red on the bill of Roseates on Great Gull Island is greatest when their chicks are 4 to 6 weeks old. The presence

of red may serve an aggressive function at this time, helping the adults to deliver fish to their young when competition for food may be at a peak.

Roseate Terns in the Virgin Islands, where egg collecting obscures the normal breeding cycle, had bills as much as ⅔ red at the end of May. These appear to become red more quickly than do those of Great Gull Island Roseates.

ACKNOWLEDGMENTS

This research was supported by the Frank M. Chapman Fund and the Mae P. Smith Fund. This study would not have been possible without the understanding of Malcolm Arth, Chairman of the Education Department of the American Museum of Natural History, who granted me the time to work on Great Gull Island. I also wish to thank Joseph Sedacca, Manager of Graphics at the museum, for advising on, and Betty Halp, for executing, the graphs and the labels for the plates; and especially Helen Hays, Chairman of the Great Gull Island Project, for teaching me many field techniques, discussing with me all aspects of bill color change, and facilitating this study in countless other ways. Kenneth C. Parkes and Helen Hays critically read the manuscript. I am grateful to Mary LeCroy and Kenneth C. Parkes for suggesting references. I especially thank Kathleen Duffin for painting the tern heads for the plates, and Joan Black for photographing the pair on 8 June. Lou Di Paolo photographically reduced the graph. Benjamin and Joanne Trimble suggested where to find Roseates in the Virgin Islands, and Anne Chambers typed the tables. I am indebted to everyone who has worked on the Great Gull Island Project: all aspects of this project are so interrelated that I could not have done this study without the cooperation and contributions of everyone else. Finally, I thank my husband Matt, whose photographs of M and F and whose encouragement helped make this possible. This paper is contribution #44 from the Great Gull Island Project.

LITERATURE CITED

BEATTY, H. A. 1941. New bird records and some notes for the Virgin Islands. J. Agr. Puerto Rico 25:32–36.

DONALDSON, G. 1968. Bill color changes in adult Roseate Terns. Auk 85:662–668.

———. 1971. Roseate Tern breeding during its second year. Bird-Banding 42:300.

HAYS, H. 1970a. Common Terns pirating fish on Great Gull Island. Wilson Bull. 82:99–100.

———. 1970b. Great Gull Island report on nesting species 1967–1968. Proc. Linn. Soc. N.Y. 71:105–118.

———. 1975. Probable Common × Roseate Tern Hybrids. Auk 92:219–234.

——— AND M. LECROY. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. Wilson Bull. 83:425–429.

KECK, W. N. 1934. The control of the secondary sex characters in the English Sparrow, *Passer domesticus.* Exper. Zool. 1967:315–347.

LECROY, M. AND C. COLLINS. 1972. Growth and survival of Roseate and Common tern chicks. Auk 89:595–611.

——— AND S. LECROY. 1974. Growth and fledging in the Common Tern (*Sterna hirundo*). Bird-Banding 45:326–340.

MACK, B. 1969. The Roseate Tern in the Carolinas. Chat 33:85–87.

PHELPS, W. H. AND W. H. PHELPS, JR. 1959. La nidification de las aves marinas en el archipelago de Los Roques. Bol. Soc. Venezolana Cien. Nat. 92:325–336.

SOOTS, R. F. AND J. F. PARNELL. 1975. First record of the Roseate Tern nesting in North Carolina. Chat 39:20–21.

VAN OORDT, G. J. AND G. C. A. JUNGE. 1933. Die hormonale wirkung der gonaden auf sommer-und prachtkleid. Der einflub der kastration bei mannlichen lachmowen. (*Larus ridibundus*). Archiv. fur Entwicklungsmechanik der Organismen 128:166–180.

VOOUS, K. H. 1965. Nesting and nest-sites of Common Terns and Dougall's Terns in the Netherlands Antilles. Ibis 107:430.

WETMORE, A. AND B. H. SWALES. 1931. The birds of Haiti and the Dominican Republic. U.S. Natl. Mus. Bull. 155.

WYDOSKI, R. S. 1964. Seasonal changes in the color of Starling bills. Auk 81:542–550.

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NEW LIFE MEMBER

Mr. Martin K. McNicholl, a new life member of the Wilson Society, is presently working on a Ph.D. at the University of Alberta. His ornithological interests include behavior, ecology, and zoogeography, and he has published several of his studies. Mr. McNicholl's current research deals with the Blue Grouse. A member of many ornithological organizations, he has served as an officer of several. In addition to his ornithological interests, Mr. McNicholl enjoys flower photography, art, and music.

HABITAT SELECTION AND TERRITORIAL BEHAVIOR OF THE SMALL GREBES OF NORTH DAKOTA

JOHN FAABORG

The Horned (*Podiceps auritus*), Eared (*P. nigricollis*), and Pied-billed (*Podilymbus podiceps*) grebes all have extensive ranges that overlap in the northern interior of North America. Munro (1940) has suggested some slight habitat differences among these species on the lakes of British Columbia, and he also described differing preferences for fish in the diets of these species there. Storer (1960) described subtle differences in feeding techniques employed by the *Podiceps* grebes on their marine wintering grounds.

The small, shallow lakes and ponds of the glaciated prairie region form the major portion of the zone of sympatry of these 3 species. Fish are not usually present there so all 3 species must feed on insects and other invertebrates. The bills of these species are different, but each shape is the result of evolution throughout the species range, not just in the relatively small zone where these grebes coexist. The foods available to grebes in the glaciated prairie region are more limited, suggesting a large overlap between species despite differences in bill shape. During the summer of 1972 I studied habitat selection, territorial behavior, and nest dispersion in order to identify the ecological conditions allowing coexistence of these 3 species.

STUDY AREAS AND METHODS

The study was conducted in the vicinity of Kenmare, Ward County, North Dakota. Extending from Kenmare to the north and east is a glacial drift plain (Stewart and Kantrud 1972), characterized by slightly rolling terrain, poor drainage, and, in wet years, abundant small bodies of water (potholes). About 25 km west of Kenmare is the "Coteau du Missouri," a rolling terminal moraine region that extends in a narrow belt across the Dakotas and also contains large numbers of potholes and scattered large alkaline lakes.

I selected 3 study areas totaling 65 km^2 for quantitative measurements and observations. The largest of these (31 km^2) is just north of Kenmare in typical prairie pothole country. Even in wet years most of the ponds are small and nearly all of the area has been cultivated at one time or another. Over 200 semi-permanent ponds were recorded here, excluding small, ephemeral ponds.

A second study area of 15.5 km^2 is located 16 km east of Kenmare. This agricultural area is exceptionally flat and in wet years contains some very large, yet very shallow ponds. I surveyed 43 ponds here in 1972, including one of over 120 ha that was just 1 m deep at its deepest point.

I selected a third study area (18 km^2) in the north portion of the Lostwood National Wildlife Refuge in the Coteau region. Here I surveyed 244 ponds plus 4 lakes of up to 89 ha in size.

The ponds of the first 2 areas were similar, with a wide variety of pond types present. Ponds which had been cultivated in dry years had emergent vegetation that would naturally appear in less permanent areas. These ponds had fewer of the more typical emergents such as cattail (*Typha* sp.). Water levels were high in 1972 and ponds with shorelines that were cultivated in 1971 had few emergents; ponds totally cultivated in 1971 had no emergents or submergents until at least mid-summer.

The potholes of the Lostwood area had a very different vegetation, apparently due to more stable surroundings and somewhat more alkaline waters. Sedge (*Carex*) dominated small ponds, while white-top (*Scholochloa feustacea*) predominated on larger ponds. The largest ponds and small lakes were very alkaline and generally had only scattered patches of bulrush (*Scirpus*).

In the 3 study areas, I surveyed all ponds and classified them according to pond permanence as determined by the presence of various indicator species of aquatic plants (following Stewart and Kantrud 1971). Ponds were placed into such classes as ephemeral, seasonal, semi-permanent, permanent, alkali, etc. Pond cover types were graded from 1 to 4, with type 1 having 95% or more of the pond area covered with emergent vegetation and type 4 being 95% or more open water. Thus, the typical cattail-lined pothole is usually classed as a type IV, semi-permanent pond, but its cover type may vary from 1 to 4 depending on the distribution of the cattails.

For each pond with nesting grebes, I recorded the number of pairs, found nests when possible, and determined the size of the pond either through cover-mapping or aerial photographs. When possible, I also observed aggressive behavior, area of defended territories, and other general habits of these grebes.

RESULTS

Habitat selection.—I found one or more pairs of grebes on 75 of the over 500 ponds and lakes surveyed. The ponds used by grebes were easily separable into 2 size classes. Small ponds of 7.3 ha or less had (with 1 exception) 1 species of grebe per pond, although in some cases several pairs were found. These ponds were all seasonal or semi-permanent with many in cultivated areas classed as seasonal-tilled due to past agricultural activity. Ponds of 19.4 ha or more had 2 or 3 species of grebe in nearly all cases. These ranged from large, very shallow seasonal ponds through large alkaline lakes.

I found a single species of grebe (78 grebe pairs) on 67 small ponds (Table 1). Pond type (seasonal, semi-permanent, etc.) appeared to be unimportant to grebes, while pond size and cover-type seemed to be the factors used by grebes in selecting ponds. Of the 67 ponds, 3 were very open and each contained one pair of Eared Grebe. The remaining small ponds were divided between Horned and Pied-billed grebes.

The Pied-billed Grebe avoided the 100% open water, seasonal-tilled ponds but used a wider range of cover types than the Horned Grebe (Table 1).

TABLE 1

CHARACTERISTICS OF SMALL (<7.3 HA) PONDS CONTAINING ONLY ONE GREBE SPECIES PER POND[1]

	Horned	Eared	Pied-billed
Total number of pairs	27	3	48
Number of ponds used	20	3	44
Average number of pairs per pond	1.4	1.0	1.1
Range of number of pairs per pond	1–6	1	1–2
Average area of pond per pair (ha)	0.9	1.5	2.2
Range of pond sizes used (ha)	0.1–5.2	0.4–3.0	0.6–7.0
Frequency of occurrence of pairs by pond classification[2]			
Seasonal Pond	8	1	26
Semi-permanent Pond	9	1	22
Seasonal-tilled Pond	10	1	0
Frequency of occurrence of pairs by pond cover-type[2]			
Type 1	0	0	2
Type 2	3	0	17
Type 3	11	0	23
Type 4	13	3	6
Average cover type used	3.4	4.0	2.7

[1] Only one example of a small pond with 2 species was observed, a 0.6 ha pond with both a Horned and an Eared Grebe pair.

[2] Following the methods of Stewart and Kantrud (1971) as described in the text.

Figure 1 is a finer analysis of the pond-use data and plots pond size against percent open water. The dotted line is added to show the general division of Horned and Pied-billed grebes along these coordinates. The Pied-billed Grebe was also found in a wider range of pond sizes (Fig. 2). Figure 3 shows the distribution of Horned and Pied-billed grebes on ponds less than 2 ha in size. This includes over 80% of the Horned Grebe ponds compared to 45% of the Pied-billed Grebe ponds. Of the 24 Pied-billed Grebe ponds, 13 were rather heavily vegetated (only 20–40% open water), suggesting that where pond size selection overlaps the most, habitat separation is more pronounced. Very small ponds were used almost solely by Horned Grebes, and 60% of all Horned Grebe ponds were less than 1 ha.

The 7 large ponds and lakes used by grebes all had extensive areas of open water which were sometimes bordered by emergent vegetation. The Eared Grebe accounted for 218 of 235 grebe pairs on these ponds (Table 2). All but 6 of the Eared Grebe nests were on large, very open ponds and lakes. The only large lake with just one breeding species was an 89 ha alkaline lake that lacked shore vegetation and had but a few small patches

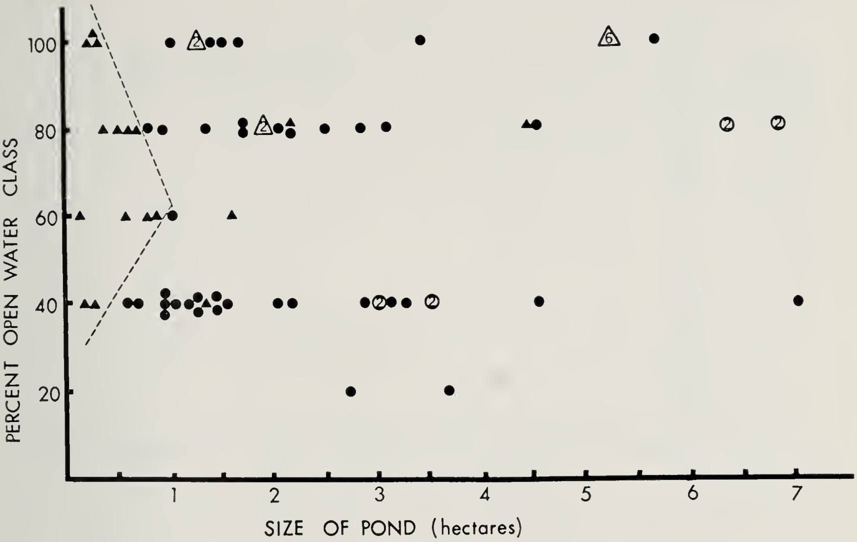

FIG. 1. Size and percentage-cover class of small ponds used by Horned and Pied-billed grebes. Triangles mark Horned Grebe ponds; circles mark Pied-billed Grebe ponds. Figures with numbers represent multiple-pair ponds. Open water classes are designated by the larger value of each class. The dashed line marks the region of pond types used exclusively by Horned Grebes.

of emergent bulrush for Eared Grebe nesting sites. The 10 pairs of Horned Grebes found on large ponds used bays or portions of the lake separated from the main lake by emergent vegetation. Pied-billed Grebes were always associated with dense stands of emergent shoreline vegetation and just 7 pairs were found on these large ponds.

Nest dispersion and territorial behavior.—In most cases the Horned and Pied-billed grebe had but one nesting pair per pond, while the Eared Grebe was usually colonial with all the nests on a lake or pond tightly clumped. Of 222 Eared Grebe nests, only 4 were solitary and one colony included 110 nests.

On ponds with 2 or more Horned Grebe nests, the nests were widely separated either by open water (at least 45 m of water between visible nests) or a barrier of vegetation or land. This species was very aggressive in defense of its pond or portion of pond against other Horned Grebes. Attacks on an intruding bird continued until the intruder was chased out of sight, either into emergent vegetation or out of the pond. An average of only 0.9 ha of water per pair was recorded on the small ponds, and one pair successfully raised young on a pond of only 0.1 ha.

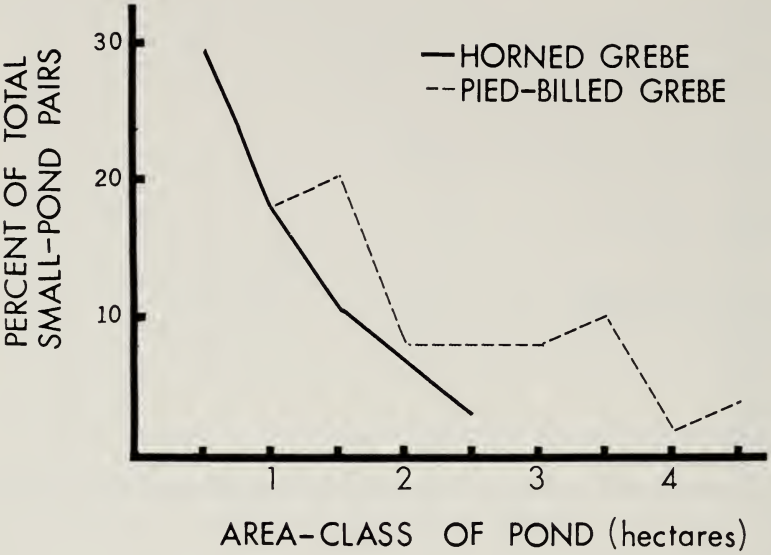

Fig. 2. Frequency distribution by pond size for Horned and Pied-billed grebe ponds computed as the percentage of total small pond pairs for each species.

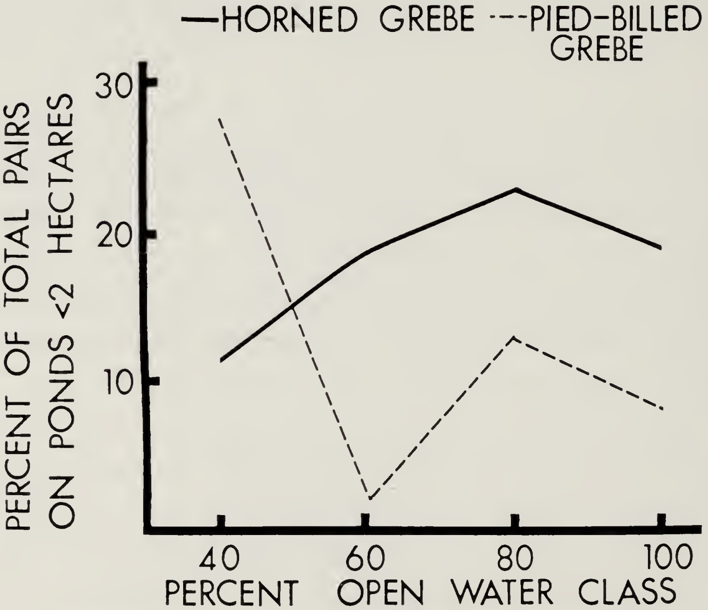

Fig. 3. Frequency of pond use by open water class for those Horned and Pied-billed grebe pairs found on ponds less than 2 ha in size.

TABLE 2

SUMMARY OF GREBE OCCURRENCE ON LARGE (>7.3 HA) PONDS AND LAKES

Pond Size (ha)	Pond Description	Cover Type*	Number of Grebe Pairs		
			Horned	Eared	Pied-billed
19.6	shallow seasonal	4	4	44	1
21.0	alkaline semi-permanent	3	0	4	3
22.5	shallow seasonal	4	0	8	1
24.1	shallow seasonal	4	1	34	1
28.8	permanent lake	3	3	2	0
89.7	alkaline permanent lake	4	0	16	0
128.9	large, very shallow seasonal	4	2	110	1
		Total Pairs	10	218	7

* Following the methods of Stewart and Kantrud (1971) as described in the text.

Two or more Pied-billed Grebe pairs using a pond also spaced their nests widely. In sharp contrast to the readily visible nests of the Horned Grebe, the nests of this species were nearly always hidden in emergent vegetation. Although the species nested in many ponds of about 1 ha, the smallest pond with 2 pairs of Pied-billed Grebe was over 3 ha. Glover (1953) described the Pied-billed Grebe territory as an arc of 150 feet (45 m) around the nest and observed that birds were amicable away from their territories. Of the grebes I studied, only the Pied-billed Grebe had a vocalization that appeared to be associated with territorial behavior.

DISCUSSION

Species which share limited resources likely influence each other's abundances reciprocally to the extent of their overlap in resource use (Gause 1934). Thus, to coexist, closely related species must differ either in habitat, range, or foods (Lack 1971). Range is not a factor here, and studies of the foods used by these species (Munro 1940, Wetmore 1924, Palmer 1962) suggest a high amount of overlap among the species of this area. This suggests that separation by habitat is the most important component allowing the coexistence of these species in the glaciated prairie region.

The separation of the Eared Grebe from the Horned and Pied-billed grebes is obvious, for the former prefers large, open ponds. Here, nesting sites are more limiting than food supply, a condition ideally suited for the colonial nesting habits of the Eared Grebe where only the nest site is defended (Palmer 1962). In contrast, I found the Horned Grebe and Pied-billed Grebe to be solitary nesters and to prefer small ponds or just portions of large ponds. The Horned Grebe was most common on very small, open ponds, a habitat well suited to its observed method of terri-

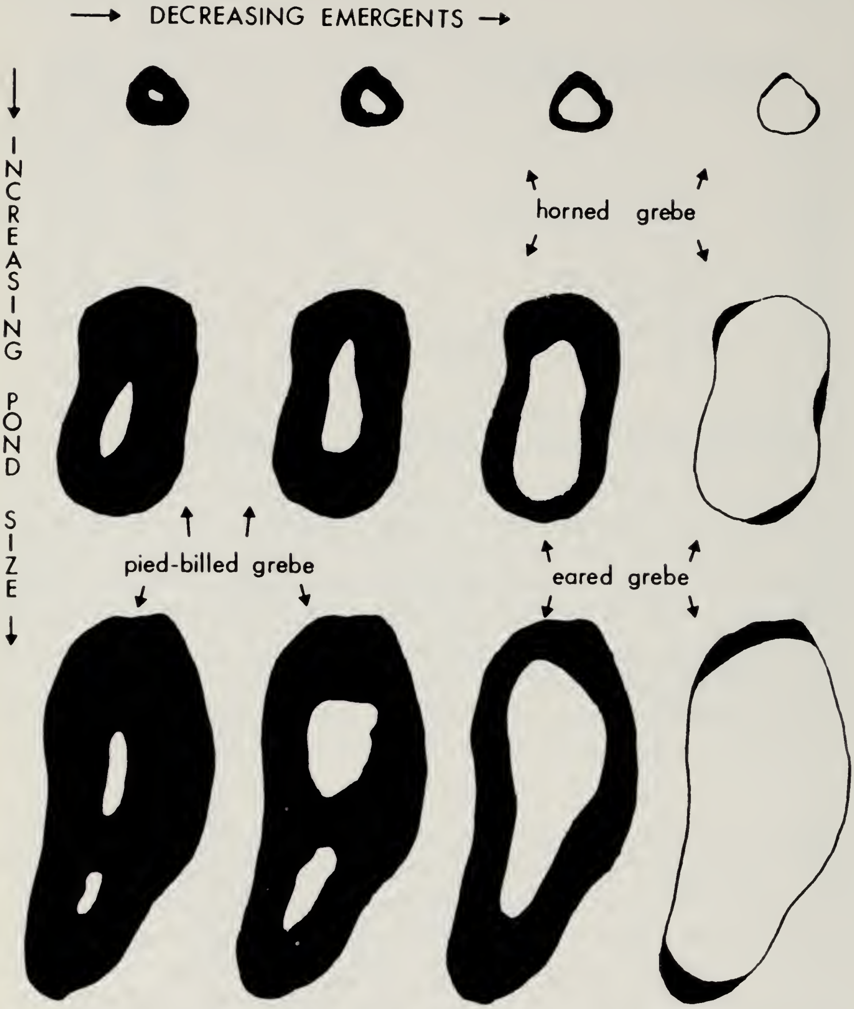

FIG. 4. Schematic diagram showing how the 3 grebe species generally separate their habitat preferences among ponds varying in size and emergent vegetation. Dark areas signify emergent vegetation; species names signify the general area in which they predominate.

torial defense by visual cues. On the other hand, the Pied-billed Grebe used more heavily vegetated and generally larger ponds and used a distinctive vocalization to aid in the defense of its territory in such a visually restricted habitat. Figure 4 illustrates the method used by these species to divide ponds of varying size and cover-type.

Another factor possibly contributing to the distribution of these species was the aggressiveness of the Pied-billed Grebe towards the *Podiceps* species. Wetmore (1920) observed the Pied-billed Grebe harassing Eared Grebes and he states (1924) that the Pied-billed is a savage fighter that even attacks coots (*Fulica americana*). No direct confrontations between Horned and Pied-billed grebes were observed, but in 2 cases Pied-billed replaced Horned grebes which had appeared first on a pond. This suggests that the Pied-billed may have been dominant on the wide variety of pond sites it occupied. The Horned Grebe used ponds either too small or too open for the Pied-billed, while the Eared Grebe could effectively populate large, open ponds where vegetation might have been limiting for the Pied-billed Grebe. The amount of overlap in habitat preferences might have been related to the presence of many more available ponds than breeding grebe pairs in 1972. Even so, each species had one type of pond that it occupied exclusively.

Since both *Podiceps* species commonly build their nests in shallow water away from emergent vegetation, the idea that nest sites may be relatively more limited on a large, open pond should be clarified. Glover (1953) found that 50% of the destruction of Pied-billed Grebe nests in Iowa could be attributed to wind damage. A similar pattern prevailed in North Dakota in 1972 with many nests destroyed by the rough water resulting from strong prairie winds. These winds varied greatly in direction during the spring and thus limited the number of sheltered nesting sites. On large, open ponds containing several pairs of Horned Grebes, the first pair arriving in the spring usually picked the most sheltered site and nested successfully. Late arriving pairs were forced to put their territories and nests in portions of the pond more vulnerable to wind and water damage and were correspondingly less successful. Contrastingly, when Eared Grebes nested on large ponds or lakes they effectively put the whole colony of nests in the most sheltered location and thus greatly reduced nest loss.

The fairly complete division of these species by habitat implies indirectly the highly overlapping or identical foods that I discussed earlier. If foods were different, 2 or 3 species might be able to coexist on smaller ponds. Even though 2.2 ha per pair was needed on small ponds, a pond of nearly 20 ha was needed to support 2 species. The existence of 2 or 3 species on a pond may be the result of the larger area being able to supply separately the habitat requirements of each species. This suggests certain parallels between grebe distribution and bird species packing on islands (MacArthur and Wilson 1967). Large ponds may act like large islands which contain more species than small islands because they contain more habitats and thus can support more habitat specialists. Large islands also contain more species because they allow closely-related species with overlapping habitat or dietary requirements to coexist. On a small island, this may not be possible and perhaps only one of these species could survive. In this way small ponds may act like small islands which can support just one of a set of similar species. Certain of these ponds may match the habitat specifications of only one species of grebe, while others could be suitable for 2 species. In the latter case, the species present may be a matter of who arrived first, dominance behavior between species, subtle differences in available foods, or, perhaps, habitat differences finer than those analyzed here. Further work would be needed to determine this, but it is apparent that even if we allow a certain amount of variation among the diets of these species, small ponds would still be able to support just one species while the overlapping diets could be tolerated on larger ponds and lakes.

SUMMARY

Patterns of habitat selection and territorial behavior of the Horned, Eared, and Pied-billed grebes were examined in North Dakota. Each species seemed to prefer a distinct pond type which could be explained in part by the species-specific methods of nest dispersion and territorial defense. The Eared Grebe preferred large, open ponds with abundant feeding grounds but where a compact colony of nests could be situated in a sheltered site. Horned Grebes seemed to prefer small ponds with open water where they could defend a territory visually. The Pied-billed Grebe occupied the widest variety of pond types but was always associated with heavy emergent vegetation. As this species has a distinct vocalization, it was suggested that it was the best adapted of the species for defending its territory in low-visibility habitats.

Possible dominance interactions were discussed to explain the presence of certain species on ponds suitable for 2 or more species. The advantages of being colonial on open ponds were also discussed. Parallels between pond selection by grebes and island biogeography were noted.

ACKNOWLEDGMENTS

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LITERATURE CITED

Gause, G. F. 1934. The struggle for existence. Hafner, N.Y.

Glover, F. 1953. Nesting ecology of the Pied-billed Grebe in northwestern Iowa. Wilson Bull. 65:32–39.

Lack, D. 1971. Ecological isolation in birds. Blackwell Scientific Publ., Oxford.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J.

Munro, J. 1940. The grebes. Occ. Papers B.C. Prov. Mus. #3, Victoria, B.C.

Palmer, R. S., ed. 1962. Handbook of North American birds, Vol. I. Yale Univ. Press, New Haven, Conn.

Stewart, R. E. and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Resource Publ. 92. Bureau of Sport Fisheries and Wildlife, Washington, D.C.

——— and ———. 1972. Population estimates of breeding birds in North Dakota. Auk 89:766–788.

Storer, R. W. 1960. Evolution in the diving birds. XII Int. Ornithol. Congr. 2:644–707.

Wetmore, A. 1920. Observations on the habits of birds at Lake Buford, New Mexico. Auk 37:221–247, 393–412.

———. 1924. Food and economic relations of North American grebes. U.S. Dep. of Agric. Bull. 1196.

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NEW LIFE MEMBER

Dr. Walter D. Maddox of Kankakee, Illinois, is a life member of the Wilson Ornithological Society whose professional interests and research are in oral surgery. Dr. Maddox's ornithological interests include avian biogeography and evolution. He is also a member of the AOU, the COS, Sigma Xi, and several professional dental organizations. He is married and has 2 sons and 2 daughters. In addition to his professional and ornithological interests, Dr. Maddox is a student of Civil War history and the Illinois Community College Movement, and he enjoys golf and photography.

NESTING BIOLOGY OF THE LONG-TAILED MANAKIN

Mercedes S. Foster

The Long-tailed Manakin (*Chiroxiphia linearis*) is a strongly dimorphic species in which the brightly colored males perform conspicuous communal displays (Slud 1957, Foster pers. observ.). The dull olive-green females, however, who are solely responsible for nest building and rearing of the young, are considerably more secretive. Thus, very little is known about the nesting biology of this species although it is common over much of its range from southern Mexico to northwestern Costa Rica (Friedmann et al. 1957).

For 19 months in 1971 through 1974 I studied this manakin in Guanacaste Province, Costa Rica. Although the study focused primarily on ecology and social organization, some data on breeding biology were gathered. I discovered 39 nests, 12 of which contained eggs or young. Herein I provide an analysis of these nests and observations on eggs, young, and nesting behavior of females.

METHODS

The study was conducted on the property of Estación Experimental Enrique Jiménez Nuñez (Finca Jiménez), a research station owned and operated by the Costa Rican Ministry of Agriculture and Livestock. It is located approximately 13.6 km SW Cañas in Guanacaste Pr. Two nests located at the Palo Verde Field Station of the Organization for Tropical Studies were examined also. Except where noted specifically, Palo Verde nests did not differ from Finca Jiménez nests, and data for both are combined.

All nests were checked at least once a day to determine their progress. Nests under construction and those containing eggs or young were observed for extended periods as often as possible concomitant with other studies. Observations were made with 7 × 35 binoculars at distances of 6 to 10 m with and without the use of a blind. By climbing a tree, standing on a stump, etc. I was able to see into all nests from a distance of 3 m or more. Therefore, in an attempt to minimize disturbance and its effects on nest success, nests were approached closely only when absolutely necessary, for example, to mark and measure eggs or young.

Nests were measured and collected after I was certain that they no longer were in use. Some nests were destroyed by predators before data were taken. Data taken in the field include location in the study area, height above ground (measured to the top of the nest rim), distance from the trunk of the nest tree, and greatest inner and outer depths and diameters. In addition notes about nest form and habitat were taken, the nest tree was measured, and plant material was pressed for later identification. Voucher specimens of the trees are deposited in the herbarium of the University of South Florida, Tampa. Although most nest measurements were made in the field, they represent only an estimate of actual dimensions at the time of nest completion. Nest dimensions may be modified by weather, predators, and normal use by the birds. Measurements of associated branches were made in the laboratory along with analyses of nest construction and composition.

One nestling, briefly and unsuccessfully maintained in captivity, also was observed. Another unsuccessful attempt was made to hatch 2 eggs deserted by a female. The young contained in these eggs were sufficiently developed to provide some morphological and anatomical information although their ages are unknown. Pterylographic designations follow Clench (1970). Young were preserved in 10% formalin. Measurements taken of young include wing chord (bend of the unflattened wing to the tip of the longest primary), tarsus length (juncture of the tibia and metatarsus to the anterior, distal edge of the lowest undivided scute), length of the middle toe without the claw (anterior distal edge of the lowest undivided scute to the tip of the toe pad on the ventral surface of the toe), and bill length (anterior margin of the nostril to the bill tip), depth (culmen to lower edges of rami), and width (one tomium to the other). Bill depth and width were measured at the level of the nostril.

Females were aged using degree of skull pneumatization and external measurements. Ovaries were examined macroscopically in dead or laparotomized individuals. Ovum measurements are diameters in millimeters.

Vocalizations were recorded at a speed of 7.5 ips with a Uher 4000 Report-L tape recorder and M516 microphone on 1 mil polyester tape. Sound spectrograms were made using a Kay Electric Co. Audio Spectrum Analyzer, model 7029A, at a wide band, 80–8000 Hz setting. Weights were taken with a Pesola balance graduated in 0.5 g divisions. Measurements were made with a 30 m tape, a 15 cm plastic rule, and Helios dial calipers.

Data on 9 nests and 18 eggs from Oaxaca, Mexico were provided by L. F. Kiff from material in the collections of the Western Foundation of Vertebrate Zoology (WFVZ). Localities represented by nests are Rancho Sol y Luna (5), Rancho Sol y Luna, 10 km NW Tapanatepec (1), El Novillero, 3.2 km N Tapanatepec (1), and 16 km NW Rancho Vicente, Cerro Baúl. All eggs were collected at the second locality noted above. N. G. Smith provided a nest of the Lance-tailed Manakin (*Chiroxiphia lanceolata*) which he collected at Rodman Ammo Dump, West Bank of Canal Zone, Panama.

RESULTS

Habitat and nest placement.—The Long-tailed Manakin occupies primarily tropical dry forest habitat (Holdridge et al. 1971) although it may extend into areas of tropical moist forest or "cloud forest" (Griscom 1932, Dickey and van Rossem 1938, Slud 1964, Monroe 1968). My observations were concentrated in a riparian woodland located in the arid tropical zone of northwestern Costa Rica. The water table in the woodland is higher than in nearby areas resulting in a taller, more luxuriant, and largely evergreen forest. However, manakins are abundant on the adjacent drier hillsides as well. Some parts of the study area are greatly disturbed, having been subjected to grazing by cattle and patchy clearing. The greatest portion, however, shows only minimum disturbance, this from occasional selective cutting for lumber. The canopy is closed for the most part, resulting in a shady forest floor. The understory is quite open and characterized by many small trees and saplings, lianas, and a lack of shrubby undergrowth. Several detailed descriptions of the area are available (Holdridge et al. 1971, Janzen

Fig. 1. Long-tailed Manakin nest from Finca Jiménez, Guanacaste Province, Costa Rica. Note roofing provided by adjacent leaves and camouflaging leaves hanging vertically from the rim and underside of the nest.

1973, Sawyer and Lindsey 1971). The nests from Palo Verde were taken in a very similar though somewhat drier habitat.

The nests were placed throughout this woodland although they generally were absent from the more open areas associated with tree falls or cutting by man (e.g. along fence lines). They usually were built in small trees (36 in trees < 3m, 2 in trees > 5m) although one was found in a moderate sized shrub. Within the tree the nests are suspended from a fork at or near the end of a small branch. The fork selected invariably is located so that adjacent shoots and leaves provide a roof over the nest (Fig. 1). Quantitative aspects of nest placement are summarized in Table 1.

Manakins apparently are quite selective with regard to species of tree used. Of 39 nests, 17 (43.6%) were placed in trees of 2 species, 25 (62.4%) in trees of 4 species (*Eugenia* sp., 9; *Terminalia lucida*, 8; *Ardisia revoluta*, 4; *Psychotria* sp., 4). The remainder were in individuals of another 8 species. Although no complete list of tree species present is available, a preliminary survey of trees in the Cañas area (Hartshorn 1971) cites more than 140 species. The relative abundance of these forms is not known. However, it is generally apparent that *Ardisia revoluta* and *A. belizensis* are the most

TABLE 1

QUANTITATIVE ASPECTS OF NEST PLACEMENT BY THE LONG-TAILED MANAKIN IN GUANACASTE PROVINCE, COSTA RICA, 1971–1974

Character	No.	Range	Mean
Height nest tree (m)	38	1.3–8.0	2.47
DBH nest tree (cm)	38	0.8–12.0	2.65
Distance, nest from trunk (cm)	34	20.0–142.0	55.65
Height, nest above ground (m)	38	0.7–1.7	1.26
Diam. fork rami (mm)	73	2.1–7.5	3.55

abundant components of the understory. Only 10.3% of the nests were found in individuals of the former species. None was found in the latter.

Nesting period.—Nesting occurs in both the dry (Dec.–April) and wet (May–Nov.) seasons. Nests with eggs or young were located in the months of April, May, June and July. However, several lines of evidence suggest that nesting begins in March or perhaps in February. Males initiate reproductive displays in late February (C. R. Carroll, pers. comm.). Such displays rarely, if ever, are given in the absence of a receptive female (pers. observ.). In addition, several females captured in March had developing brood patches and/or enlarging ova. One female taken 21 March contained a yellow-orange ovum 8 mm in diameter. Several completed nests located in the first half of April and followed for several weeks never were observed to contain eggs. Possibly these nests were built and abandoned, but it is more likely that at one time they contained eggs or young which fledged or were preyed upon prior to their discovery (nests do not persist from year to year, see below). They easily could have been initiated in March.

Although no active nests were located, I also believe that Long-tailed Manakins are reproductively active into September. Males display actively until about 1 September, and one female collected on 17 August carried a shelled egg in her oviduct. A second female mist-netted on 13 August had an active brood patch. Nests with eggs and one with recently hatched young were located during the last half of July, indicating fledging in August or perhaps September. One nest was initiated on 30 or 31 July 1974, but construction was not completed on 13 August when I left the area. Another nest was discovered on 10 September 1973, when it contained a broken egg shell. It was located in a small tree within a few cm of a quadrat boundary line which I set out on 21 August. Finally, I have located a few nests in late August and September which appeared quite new. During the rainy season, abandoned nests rarely persist intact for more than a few weeks, if that. The combined effects of weather and perhaps theft of nest materials by other species rapidly bring these delicate structures to a state of marked disarray.

Although nesting is confined to a 7-month period, data suggest that once the ovary becomes active, it remains in an active state continuously. Adult females from all months except October, January and February were examined. All had ovaries with well defined ova. For example, 9 individuals examined between 22 November and 14 December had ova of at least 1 mm. Young females breed the year following hatching. Their ovaries probably first become active at this time. Three immature females examined between 23 and 28 November contained smooth ovaries showing no evidence of ova externally.

Nest form and composition.—The nest of the Long-tailed Manakin is a small, shallow cup suspended from the fork between 2 small branches (Fig. 1). Usually the nest is attached to each branch only at 2 points though occasionally fibers are wound around the entire length of the twig. Attachment sites range from 3 to 30 mm in width, averaging around 16.5 mm. The anterior connections often are heavier than posterior ones and may reach a thickness of several millimeters. The connection is formed by a dense mat of fibers tightly wrapped around the branch and extending into the cup of the nest. A single fiber may form several loops of the connection. As much as 50% of the attaching fibers may be delicate white or silvery-gray strands apparently from some type of spider web, egg case, or insect cocoon. These fibers are sticky, elastic, and quite strong. Equally common in the connecting mass are black rhizomorphs of the fungus *Marasmius* sp. which measure only a few tenths of a millimeter in diameter. Occasionally larger fibers, usually extensions of components of the nest cup, are included. Pieces of crushed leaf blade, moss and other materials often are bound up in this mass.

The nest proper is a circular cup although the attachment areas and supporting twigs give the nest as a whole a trapezoid appearance. The nest is not lined with any soft material but can be separated into 3 (rarely 4) relatively discrete layers. The outermost layer consists of a very sparse network of fungal hyphae which extends between the connection points. These hyphae form a sling supporting the middle layer which is composed of leaves or of mixed leaves and moss (Leskeaceae). Very rarely, both a layer of leaves and then a layer of moss are present. In about 35% of the nests the fungal hyphae also provide a site for the attachment of leaves which hang vertically from the outer surface of the nest for a distance of up to 8.5 cm. These may be few or many, but usually they are concentrated around the outer perimeter of the cup. The hanging leaves generally are quite large and often different from those in the middle layer and

TABLE 2

QUANTITATIVE ASPECTS OF LONG-TAILED MANAKIN NESTS IN GUANACASTE PROVINCE, COSTA RICA, 1971–1974

Character	No.	Range	Mean
Inner Diam. (cm)	23	4.3–6.0	5.87
Outer Diam. (cm)	25	5.8–8.8	7.22
Inner Depth (cm)	24	1.5–3.0	2.24
Outer Height (cm)			
A[1]	22	3.5–4.5	3.84
B[2]	11	6.0–11.0	9.08

[1] Excluding vertically hanging leaves.
[2] Including vertically hanging leaves.

apparently serve to camouflage the nest against predators. The middle layer always contains leaves, or more often pieces of leaves, of many species and may be from one to several leaves thick. Four nests also included grass blades in the leaf layer; 10 nests included strips of bark. Nineteen included pieces of moss (Leskeaceae) and 20, leaflets of the fern *Lygodium venustum*.

Beneath the leaf layer is the innermost and thickest layer which forms about half the bulk of the nest. It consists primarily of fungal hyphae (*Marasmius*) and leaf midribs from various species, although small diameter twigs, grass blades, bark fibers and fern petioles (*Adiantum*) also are found occasionally. The fibers forming the rim of the nest and the centimeter just below the perimeter are wound circularly while those in the cup usually are interwoven at right angles across the nest.

Palo Verde nests showed only minor differences from those at Finca Jiménez. They contained a greater percentage of fungal hyphae (*Marasmius*), and the leaf layer of one nest consisted primarily of blades of grass (*Panicum fasciculatum*). Both lacked leaflets of *Lygodium venustum*.

Measurements of various nest parameters are summarized in Table 2.

Nest construction and use.—I did not observe nest building from its inception but did locate 3 nests in which construction had been in progress for less than half a day. The female building one of these nests was observed for 9.2 hours. The other 2 nests were checked periodically to determine their progress toward completion.

Construction begins at the attachment sites. A limited amount of material is added at these sites throughout the building process, but attachment is quite strong from the beginning. The circular fibers forming the upper centimeter of the rim and the outer sling of fungal hyphae extending between the various attachment sites are added next. By this time the

FIG. 2. Long-tailed Manakin nest under construction at Finca Jiménez, Guanacaste Province, Costa Rica. Note the leaf midrib lying across the upper perimeter of the nest; it is partially interwoven with other fibers but not shaped into the cup of the nest.

general shape of the nest is apparent. Approximately half a day is required for construction to reach this point. Next the leaves hanging from the rim or bottom of the nest are added, if they are to be included. At approximately the same time the leaf-moss layer is laid down from the inside. The innermost layer of hyphae and midribs is the last to be added. This is done in several ways. The most common is by placement of several strands of material across the nest so that they protrude on either side (Fig. 2). The female then lands on the center of the nest cup bending the strands with the weight of her body. She wiggles her body laterally as if settling in on the nest at the same time rotating her body slightly. Initially then, the nest is a half sphere which is periodically pushed down in the center. Often when settled in the nest the female leans over to the outside reaching with her bill to poke and rearrange material. She also perches on the rim of the nest or on the supporting twig between connection points leaning to the inside to rearrange material or to reinforce connections. Some fibers are poked into the outside of the nest, brought up over the supporting twig and attached on the inside.

The leaflets of *Lygodium venustum* are green when brought to the nest as are the tufts of moss. The *Marasmius* rhizomorphs used probably are live also. Other leaves and nest materials always are brown and dry, even those apparently coincidentally of the same species as the nest tree. I never observed a female collecting nest material from the tree in which the nest was built. Although these dry materials must be brittle, there is little evidence of broken twigs or midribs. Leaf blades, however, often are represented by nothing more than an extensive vein network. During the rainy season, of course, materials are considerably more pliable.

It takes a female approximately 3 days to build a nest. She works at it throughout the day, though work bouts periodically are interrupted by absences from the nest of 30 to 60 min. When actively building, the female visits the nest fairly regularly at intervals of approximately 5 min. On entering the nest area she usually perches 3 to 5 m from the nest carefully scanning the area. This may last for a few seconds or several minutes involving several perch changes. Occasionally she will leave the area without visiting the nest site. Usually the female carries only a single piece of nest material at one time. The visit to the nest site may last only a few seconds, the length of time required to leave the material carried, or it may last up to 35 sec.

Observations at one nest indicate that the female may interrupt nest building for several days. This nest was begun on 24 May. No work was done on 25 May nor any day thereafter until 1 June. It was completed on 2 June. Another nest observed was begun 31 July. No additional building occurred between 1 and 13 August when I left the area. In each instance the initiation or reinitiation of building directly followed one or several days of rain. Once the rainy season begins, usually in late May, interruptions of building seem to coincide with dry periods. Therefore, it is tempting to suggest that rainfall in some way stimulates or controls nest building behavior. However, nesting apparently occurs in both March and April when rains are absent, or at best rare, sporadic and unpredictable. Records of several nests built during this dry period indicate construction following periods of up to two weeks without rain. One would suspect that nest building would be easier after a rain as construction materials would be more pliable.

Eggs, egg laying, and incubation.—The Long-tailed Manakin eggs from Costa Rica are covered by a thin, delicate shell of beige-tan ground color. It is lightly to heavily marked with medium to dark chocolate brown spots. They may be present over the entire shell or just toward the larger end where they usually are concentrated, especially in a 4–5 mm band at the point of greatest egg diameter. Nine clutches from Oaxaca, Mexico, are of the same color and markings (L. Kiff, pers. comm.). Egg dimensions, weights, and clutch size data are summarized in Table 3. These parameters

TABLE 3

EGG DIMENSIONS AND CLUTCH SIZES OF MANAKINS OF THE GENUS *CHIROXIPHIA*

Character	No.	Range	Mean
C. linearis—Costa Rica (this study)			
Length (mm)	10	20.3–24.0	22.40
Greatest width (mm)	9	15.5–18.0	16.52
Weight (g)[1]	9	2.5–3.25	2.94
Clutch size	10	1–2	1.6
C. linearis—Oaxaca, Mexico (L. Kiff, pers. comm.)			
Length (mm)	18	21.1–22.8	22.13
Greatest width (mm)	17	15.6–16.8	16.09
Weight (g)	0	–	–
Clutch size	9	2	2.0
C. lanceolata—Panama, Colombia (Allen 1905, Hallinan 1924)			
Length (mm)	7	21.0–22.0	21.67
Greatest width (mm)	7	14.7–16.0	15.31
Weight (g)	0	–	–
Clutch size	5	1–2	1.8
C. pareola—Brazil, captivity (Burmeister 1856, Pinto 1953, Olney 1973)			
Length (mm)	7	21.5–25.0	–
Greatest width (mm)	7	14.5–17.0	–
Weight (g)	1	2.2	2.2
Clutch size	7	2	2.0
C. caudata—Brazil, Paraguay (Burmeister 1856, Nehrkorn cited in Ihering 1900, Euler 1900, Ihering 1902, Chubb 1910)			
Length (mm)	?[2]	21.6–26.0	–
Greatest width (mm)	?[2]	16.0–17.0	–
Weight (g)	0	–	–
Clutch size	?[3]	2	2.0

[1] Includes fresh eggs (N = 2, R = 2.75–3.25) and eggs located some time after laying (N = 7, R = 2.50–3.25, $\bar{x}$ = 2.93).

[2] No. = at least 7.

[3] No. = at least 3.

do not differ significantly between the countries. The 9 clutches from Mexico all consisted of 2 eggs. Of 10 from Costa Rica, 6 included 2 eggs and 4 one egg, which suggests a difference. Sample sizes are too small for meaningful statistical testing. Three of the 1-egg clutches were located after completion of egg laying and may reflect partial loss of the clutch.

In 2 instances eggs were laid in nests whose construction had been followed. At both, 2 full days intervened between the day of nest completion and the day the first egg was laid. A second egg was laid in one nest the following day. Four eggs for which information is available were laid

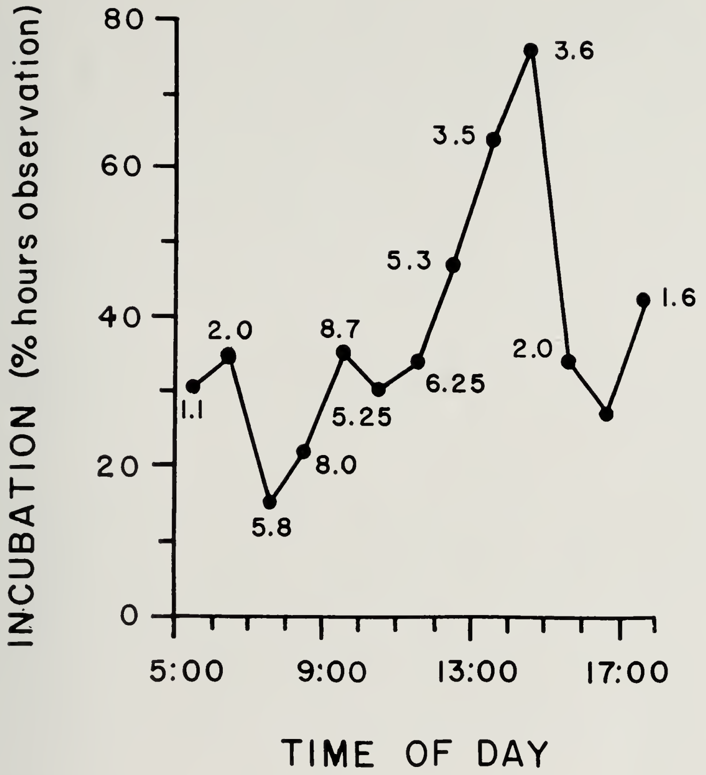

Fig. 3. The amount of incubation by females during each daylight hour expressed as a percentage of hours of observation (numbers adjacent to dots) during each of those daylight hours.

in the morning, 2 prior to 07:30 and 2 between 09:00 and 10:00. In no instance were nests observed to be used more than once.

Incubation was observed at 6 nests for approximately 55 hours. Because hours of observation were not equal for each daylight hour, data were transformed by hour into the percentage of observation time spent by the female on or off the nest (Fig. 3). Females do not incubate during much of the morning. This absence may be attributed in part to time spent feeding, but I suspect that this is a relatively minor factor. Manakins are frugivores feeding in trees that are quite abundant in the study area. Observations on feeding suggest that they know the location of the trees and travel directly to them. Feeding bouts are usually quite short, a few minutes at most. In addition, much of the time when a female is not incubating, particularly during the morning hours, she is present at the nest site. A female often was seen perching quietly in a tree adjacent to her nest tree, preening, or quite alertly examining the area. Sometimes it appeared as if she sensed some disturbance in the area and for that reason was avoiding the nest. For example she would settle on the nest for a minute or 2 and then with no apparent provocation would leave the nest and perch in an adjacent tree. After carefully eyeing the area for 15 to 20 min, she would return to the nest again only for a minute or 2. However, this behavior was observed only during the morning, not in the afternoon. The dip in incubation time in the late afternoon also may represent absence for feeding although again, the birds appear to be absent for more time than necessary, and the female may remain near the nest during this period. The increase in incubation time between 17:00 and 18:00 hours is indicative of females coming to the nest to spend the night. The number of hours of incubation each day also seems to increase as the incubation period progresses.

Although my data are limited, they suggest that females do not incubate right after laying. Three nests with a total of 4 eggs were observed at length or spot checked several times on the days the eggs were laid and for several days thereafter. It was noted for the 2-egg clutch that the female did not incubate until the second day following the laying of the second egg. At another nest the female did not incubate the day she laid the first egg. The nest was destroyed by a predator the next day. At the third nest no incubation was observed the first day after laying. The nest was not checked again until 3 days later at which time the female was incubating one egg.

No nest was observed from egg laying through hatching, so the length of the incubation period is not known. The longest any nest was observed was 10 days. In this instance, eggs were present, and the female was incubating when the nest was located. One egg hatched on the tenth day of observation.

When I first located a manakin egg and weighed and measured it, I also numbered the shell with India ink. I was thus able to determine that the position of the eggs changed during the day, throughout the incubation period. Individual eggs were rotated side to side and end to end and even were moved to new positions relative to another egg in the nest. I do not know if this was an accidental result of movements by the female during incubation or if she actively changed their position from time to time.

Nestlings.—Only 3 young were observed in the nest. The first, one of a clutch of 2, apparently hatched prior to 07:00 when I arrived at the nest to begin observations. The female was incubating, and the contents of the nest were not observed until 10:10. No shell or remnants were present in or under the nest at that time, and the female did not dispose of them between 07:00 and 10:10. She also did not feed the young bird during this period, and it did not have the bulging stomach often characteristic of nestlings. The nestling weighed 3.0 g, hatching from an egg weighing 3.15 g nine days before. When disturbed, the nestling repeatedly gaped widely but made no sound. Its mouth lining was golden-yellow, its eyes were closed, and the black-tipped bill was 3 mm long with a small distal caruncle. Grayish-tan natal down was present in the superciliary and occipital elements of the capital tract, all elements of the dorsal tract, the scapulohumeral and femoral tracts, and the area of the secondaries in the alar tract.

The other 2 young were present in a single nest. They weighed 9.5 and 8.5 g, 50 to 60% of the average adult weight. Their measurements (mm) were, respectively, bill length, depth and width: 3.0, 2.5, 4.0 and 3.0, 2.7, 3.5; chord of the wing: 15, 13; tarsus plus middle toe: 22, 19. Neither had rectrices. Their gapes and mouth linings were golden-yellow, their skin reddish to light brown, and their natal down grayish-brown. These feathers were present in the superciliary and occipital elements of the capital tract, all elements of the dorsal tract, and the femoral tract. All pterylae were clearly defined by developing pins just beneath or barely protruding through the skin. Sheath tips were unruptured.

The young were observed from 13:45 until 17:00 on the day of discovery. They were not visited by the female during this period nor was any female seen in the vicinity. However, the young must have been fed shortly before my arrival as they were regurgitating seeds in the nest. All seeds but one (unidentified) were from fruits of *Trichilia cuneata* on which the adults feed commonly. The regurgitated seeds landed in the nest, and all seemed relatively fresh. No seeds were apparent on the ground beneath the nest. This suggests that the female removes the seeds after the young regurgitate them. No food or fecal remains were present in or under the nest which was quite clean. All 39 nests examined were noticeably clean and free of any fecal material.

The young were able to flex their appendages but did not seem capable of moving around the nest. When the nest was jiggled, they raised their heads and gaped repeatedly; when they were not begging, however, their heads drooped, and they crouched low in the nest. When handled, the nestlings made a series of soft *cheeps.*

Because I was to be away from the area for the 4 days subsequent to the discovery of the nest, I took one nestling in an attempt to rear it. This effort was unsuccessful. The nestling rapidly lost weight, and so I preserved it 20 hours after collection. However, a few observations were made in

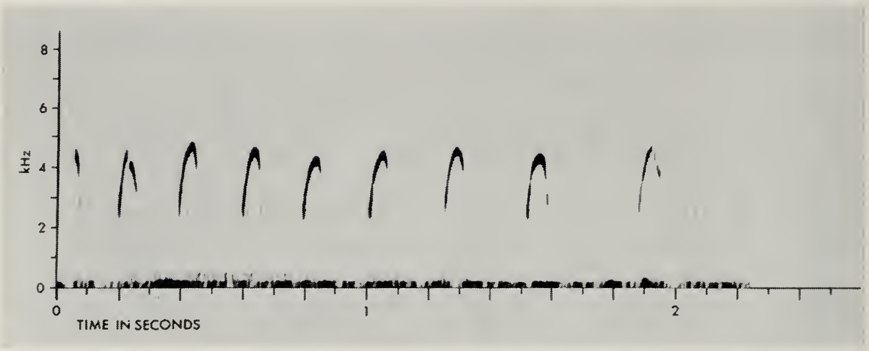

FIG. 4. Sound spectrograph of *cheep* notes of a nestling Long-tailed Manakin from Guanacaste Province, Costa Rica.

the laboratory. Vibration of the nest (apparently simulating the arrival of the female) stimulated the bird to gape. If the nestling accepted a food item, it would not gape again for several minutes. Food was taken into the bill and "mouthed" for a second or 2 before swallowing. If the food item was too large or too dry, it was dropped. The preferred size of items seemed to be about 5 mm in length and 3 mm in diameter, although larger pieces were taken. This means that fruits such as those of *T. cuneata* would have to be broken up by the parent into component carpels before feeding. The seeds regurgitated in the nest ranged to 9 mm in length and 4.5 mm diameter. The nestling in captivity was fed field collected fruits of *T. cuneata* and *Muntingia calabura* as well as a few insects. Seeds of the *Trichilia* were regurgitated, usually several in succession. The tiny *Muntingia* seeds and insect exoskeletal parts were voided in the feces.

Fecal material contained in a sac-like membrane was voided directly into the nest. Apparently the female removes these sacs in the wild. Birds would not gape when about to void a fecal sac. This act was preceded by a series of peristaltic contractions running posteriorly along the length of the body, and by lifting and rhythmic contraction of the anal protuberance.

The nestling cheeped almost continuously except immediately after being fed, so this vocalization may function in begging. Spectrographic analyses of several calls are shown in Fig. 4. The *cheep* begins at an average frequency of 2.258 kHz (N = 15). It has a rapid upward inflection to an average of 4.519 kHz followed by a turn downward. The depth of the downward inflection is variable, reaching frequencies ranging from only 3.875 kHz to 2.375 kHz. Each *cheep* element lasts an average of 0.062 sec. The *cheep* is given in series of varying length (R = 19–64 calls; $\bar{x}$ = 31.8;

N = 12) without any observable pattern. Within each series from beginning to end, however, the calls are spaced at intervals of increasing length. Initially, *cheeps* are given at a rate of 6 calls/sec; toward the middle of the series they occur at a rate of 5/sec and at the end, at 4/sec.

The *cheep* call is characterized by a well-defined beginning and end, and covers a wide frequency range. Thus, it should be easy to locate. However, it is not likely to attract predators from any great area as it is a very low intensity vocalization inaudible to my ear at a distance of about 1.5 m. Despite its low intensity, some variation between calls is noticeable (this is not evident in the spectrograms). "Louder" calls appear to alternate with "softer" ones at a ratio of one to one.

Two other young nestlings taken from unhatched eggs that had been abandoned were examined. They had been incubated for at least 6 and 7 days though probably more. Both weighed approximately 1 g without the yolk sac and though both were well developed, one was obviously more advanced. Each had a well developed egg caruncle, and the pterylae were moderately to well defined. Down feathers with intact sheaths were present in the areas noted above for the other nestlings.

Nesting success and predation.—Although only a small number of eggs and nestlings was followed, nesting success seems to be quite low in the Long-tailed Manakin. Only one of 15 eggs observed (6.67%) hatched. This nestling plus one from another nest (I collected a third) did not fledge.

Though nest predation never was observed, it was presumed on the basis of egg or nestling disappearance, and in some instances on the basis of nest damage. In 3 instances pieces of broken shell were found in or beneath the nest. Predation apparently is accomplished in at least 2 different ways. In one instance the nest seems perfectly intact with only its contents missing. In the second, the central portion of the nest is pushed (pulled?) downward and occasionally completely separated from the four connection points and adjacent portions of the nest rim. It appears as if an animal of considerable weight has rested on or pulled down the central part of the nest.

Snakes would appear to be the most likely predators in the first instance. The nests generally are placed low enough so that ground dwelling as well as arboreal forms may be responsible. Of the many snakes known from the area, at least *Boa constrictor*, *Drymarchon corais*, *Leptophis mexicanus*, *Mastigodryas melanolomus*, *Oxybelis aeneus* and *Trimorphodon biscutatus* may be expected to prey on eggs or nestlings (Keiser 1975, D. R. Paulson, R. W. McDiarmid, N. J. Scott, W. van Devender pers. comm.). Various species of birds also may rob the nest causing minimal damage. Likely candidates common in the area include Turquoise-browed Motmots (*Eumomota superciliosa*), White-necked Puffbirds (*Notharchus macrorhynchos*), toucans (*Pteroglossus torquatus*, *Ramphastos sulfuratus*), Magpie Jays (*Calocitta formosa*) and others.

Nests that were pulled apart could have been damaged by large lizards or mammals. Both *Ctenosaura similis* and *Basiliscus basiliscus*, which are common arboreal lizards in the area, might be expected to take bird eggs or nestlings (R. W. McDiarmid, W. van Devender pers. comm.). Local mammals reported (Goodwin 1946, Leopold 1959) to feed on birds and eggs include several opossums (*Didelphis marsupialis*, *D. virginianus*, *Philander opossum*, *Caluromys derbianus*), White-throated Capuchins (*Cebus capucinus*), Kinkajous (*Potos flavus*) and probably Coatis (*Nasua nasua*). At one nest between my observations late one afternoon and early the following morning, some large predator weighed down the limb with the nest far enough to hook the limb on a bush below. Although the nest was undamaged, the eggs had fallen to the ground. I restored the eggs and nest to their former positions, but the female never returned to incubate.

DISCUSSION

Nest site selection.—Trees used for nesting apparently are selected on the basis of growth form, size, and fruiting time. The suspension of the nest requires the presence of forked branches of approximately equal diameter lying in the same horizontal plane. Although this criterion would seem to be one easily met by a large number of species, some trees are particularly suitable and are commonly selected. *Terminalia lucida*, in which the branches occur in whorls in a single horizontal plane, is one of these. In addition, branching must be such that adjacent rami will form a roof over the nest site without hindering access by the female (Fig. 1). The roof probably is of great value in mediating the effects of the physical environment. Although none of the nests was directly exposed, all received filtered sun for several hours each day. The adjacent leaves helped to shade eggs, young, and the attending female. Protection provided from rain during the wet season would be of equal importance. In most instances, the shading vegetation appeared to reduce substantially the amount of water falling into the nest during a storm or from adjacent vegetation afterward.

The roof of leaves also tends to camouflage the nest from above and sometimes from the side. Additional camouflage is provided by the leaves which hang vertically from the rim and underside of the nest. Some nests closely resemble piles of detritus caught in the fork between branches. I can attest to the fact that this camouflage is very effective at reducing discovery by ornithologists. It undoubtedly reduces predation to some degree also.

Predation may be the selective factor controlling choice of tree species and size. Many of the trees common in the study area produce an abundant fruit crop heavily used by birds and mammals also expected to prey on eggs and nestlings (e.g. *Eumomota superciliosa*, *N. nasua*). Thus the placement of manakin nests in trees of species not in fruit or in individuals below fruiting size minimizes the probability of encounters between fruit eating predators and the nest. Predation also may favor the use of small trees for nesting if the trunks and branches are too small to support the weight or provide free movement of many of the large mammals and lizards. This probably also influences the distance from the trunk at which the nests are built because animals too large to traverse small side branches would be unable to reach into the nest from a position on the trunk.

Although advantageous with regard to predation, the use of distal rami of small branches of saplings and small trees may be disadvantageous during the dry season because of wind. The months of November through April are characterized by strong tradewinds from the northeast. These winds commonly cause small trees or their branches to bend deeply. On one occasion I watched while the wind tipped a branch with a nest from which the female was absent far enough to cause the eggs to roll out.

Other nests of C. linearis.—Wagner (1945) reported on 3 nests from Chiapas, Mexico, which he attributed to the Long-tailed Manakin. However, according to the data he provided, the nests and their eggs differ considerably from those taken in Costa Rica and Oaxaca, Mexico (WFVZ).

Wagner indicated that he found his nests at the borders of woods, in direct sunlight, and at heights of 2.5 to 3 m. The nests I located were in the forest proper, received only filtered sunlight and averaged 1.26 m (Table 1) above ground. Eight of the nests from Oaxaca averaged 1.49 m (R = 0.91–1.83) above ground, and the 5 with data all were in deep shade. Wagner also states that the nests were not hidden by leaves in contrast to my findings.

On the basis of the descriptions and diagrams which he provided, the Chiapas nests also appear to differ in plan of construction and composition from the Costa Rican nests and the single Oaxacan nest that I have seen. The latter, apparently typical of all of the Oaxacan nests (L. F. Kiff, pers. comm.), is strikingly similar to those from Costa Rica. It is approximately the same size and was suspended from a small fork. Primary components include spiders' web, leaf midribs, fungal rhizomorphs (*Marasmius*?), leaflets of *Lygodium venustum*, and an outer covering of dead leaves. Differences in the Chiapas nests include (1) crossing of small adjacent branches with the principal ones of suspension to increase nest stability; (2) extensive use of extremely large squares and strips of bark and their deployment in the nest; (3) interior lining of leaves and bark. The suspension of the nest in a small fork, the use of spiders' web and long animal hairs (which I assume were actually fungal rhizomorphs), and the manner of nest construction agree with my findings.

Wagner (1945) also supplied a variety of nest measurements. For one nest illustrated he gave interior and exterior diameters of 4.2 and 8 cm, and an interior depth and exterior height of 4.5 and 7 cm, respectively. He also stated that the upper diameter of the nests varied between 4.2 and 4.7 cm and the height between 4.6 and 7 cm. The diameter measurements are similar to those of the Costa Rican nests, but the other measurements are more difficult to evaluate. He did not mention the presence of leaves hanging vertically from the nest, and in the general diagram of nest construction (Wagner 1945: Fig. 2) they are clearly absent. His diagram of an intact nest, in situ (Wagner 1945: Fig. 1), although not very clear, may show such components. This would account for the differences in height values. The single measurement for inner depth, 4.5 cm, is extremely difficult to explain. The mean depth of the Costa Rican nests was only 2.24 cm ranging to a maximum of 3.2 cm. Long-tailed Manakins are small birds with an average body length (tip of bill to tip of tail, excluding the central pair of rectrices) of only 10 cm (Land 1970), 3 to 3.5 cm of which comprise the tail. It seems unlikely that a bird this size would occupy so deep a nest.

Finally, Wagner described the eggs found in one of his nests as whitish-cream in color with dark spots, which is different from both the Costa Rican and Oaxacan eggs (see above).

On the basis of the data provided in his paper, it seems likely that all or at least one of Wagner's nests were misidentified. Although various aspects of nests may vary between widely separated parts of the range of a species (e.g. Skutch 1969:114, 216), it is unlikely that the nests of Oaxaca and Costa Rica would be extremely similar to each other while markedly different from those in Chiapas. Wagner never mentioned how species identification was determined and did not indicate that any females were sighted in the vicinity of the nest.

The eggs and nests which he described and diagrammed are strongly reminiscent of those of the Barred Antshrike (*Thamnophilus doliatus*) which I have seen commonly in my study area in Costa Rica and which are described by Belcher and Smooker (1936) and Skutch (1969). The distribution of this species overlaps that of the Long-tailed Manakin in Chiapas

(Edwards 1972) where Wagner made his observations. The nests he described should be excluded from a consideration of manakin nests at least until more conclusive data concerning the nature of the Long-tailed Manakin nest in Chiapas are available.

Comparisons with other Chiroxiphia.—The genus *Chiroxiphia* includes 3 species in addition to *C. linearis.* All species show striking similarities in external morphology (de Schauensee 1970, Land 1970) and male reproductive behavior (Sick 1967). Although very few comparative data about nesting biology are available, it appears that the 4 species are very similar in this respect also.

Nests of the Lance-tailed Manakin (*C. lanceolata*) have been described from Colombia (Allen 1905) and Panama (Hallinan 1924) where they were found in low forest shrubs. The nests consisted of a mat of fine circularly woven fibers with dead leaves forming an exterior covering and hanging loosely from the sides and bottom. Spiders' web was used for binding the nest to its supporting twigs, although Allen suggested that dried, glutinous bird saliva might be used also. The Colombian nests had outside diameters ranging from 6.35 to 7.62 cm, inside diameters ranging about 2.54 cm less, and a depth of less than 2.54 cm (Allen 1905). I also have examined a nest of this species collected by N. G. Smith in Panama. It agrees with the above description but also includes some fungal rhizomorphs (*Marasmius* sp.). The average height of these nests was 1.13 m (R = 1.0–1.2; N = 3) above ground. Burmeister (1856) briefly mentions a nest of the Blue-backed Manakin (*C. pareola*) found in Brazil by R. Schomburgk. It was in the forest and made of moss. Pinto (1953) also described nests of this species from Brazil. They were located in the forest, especially adjacent to waterways, and suspended from forks in small trees at an average height of 1.4 m (N = 4). One nest, treated in detail and pictured, consisted of a small cup of curved petioles and long dark fibers resembling horsehair, neatly arranged in layers. Presumably the horse-hair-like fibers were fungal rhizomorphs, perhaps *Marasmius* sp. Pinto also noted that the outer surface of the nest was covered with dry leaves or pieces thereof, but included no moss. The single nest measured had an outer diameter of 6 cm. Several authors (Burmeister 1856, Euler 1900, Ihering 1902, Sick 1957) have mentioned nests of the Swallow-tailed Manakin (*C. caudata*). These nests generally are suspended from the forks of small branches in forest shrubs and small trees. They are rather weakly built and measure about 7 cm in diameter. Dry plant fibers, black fibers of *Tillandsia usneoides*, rhizomorphs of *Marasmius*, and sometimes moss and wool (?) are used in construction. Dry leaves are affixed to the outsides and may hang beneath the nest.

Egg dimensions of the 4 *Chiroxiphia* species are similar (Table 3), though *C. caudata* is a noticeably larger bird than the others (pers. observ.). Egg color and markings also are quite similar. Eggs of the Lance-tail are described (Hallinan 1924) as brownish-white with reddish-brown markings, or (Allen 1905) as dull creamy-white with markings of a very pale chocolate color mixed with shades of lilac. In both instances, markings are concentrated at the wide end of the egg. Remnants of broken eggs of this species supplied by N. G. Smith are of a beige-tan background with medium brown spots and closely resemble eggs of *C. linearis.* The eggs of the Blue-backed Manakin described by Pinto (1953) ranged from dirty-white to light-brown with chocolate brown, rusty-wine or yellow-brown spots. Thus they differ slightly from those laid in captivity (Olney 1973) which were bluish-buff and heavily spotted with chocolate brown. According to Euler (1900) and Nehrkorn (cited in Ihering 1900), the eggs of *C. caudata* are yellowish-white with light brown spots and dark elongated markings concentrated in a band at the blunt end. The cream-colored eggs described by Chubb (1910) also had spots and blotches concentrated at the large end, but these markings were pale chestnut and lilac. Eggs described in Burmeister (1856), in contrast, were grayish-yellow, covered with a pale reticulum, and marked with bluish-green spots.

With the exception of a notation that the female was incubating at a nest of *C. caudata* (Euler 1900), the only *Chiroxiphia* other than the Long-tail for which data on nesting behavior are available is the Blue-backed Manakin. Pinto (1953) noted incubating females at 4 nests. Additional information was provided by Olney (1973). However, his observations were made on a female nesting at the London Zoo and so do not necessarily reflect activity in the wild. An incubation period of 17 days was suggested, and the fledgling first left the nest after 14 days. The nestling was fed primarily, if not wholly, on fruit. Olney did observe some participation by the male in nest building.

SUMMARY

The nesting biology of the Long-tailed Manakin (*Chiroxiphia linearis*) was studied over several months in 1971–1974 in Guanacaste Province, Costa Rica. Thirty-nine nests were discovered, 12 of which contained eggs or young. These nests were shallow cups suspended from forks in small trees. They were placed so that adjacent branches provided camouflage and protection from weather. Nest materials included primarily spider web or insect cocoon fibers, fungal rhizomorphs (*Marasmius*), moss, leaf blades and petioles, bark fibers, grass blades, and other dry plant fibers.

Nest building normally took about 3 days when not interrupted. Females did not incubate over much of the morning and in the late afternoon, although they often remained in the vicinity of the nest. Clutch size was 1 or 2. Young were sparsely covered with grayish-tan natal down; gapes and mouth linings were golden-yellow.

Older young, at least, were fed on fruit, and they repeatedly made soft, *cheep* notes. Nesting success was very low, presumably because of high predation. Only one of 15 eggs which were followed hatched; neither of 2 nestlings observed fledged.

Growth form, size, and fruiting time are probably the most important features of the tree controlling the selection of trees for nest placement because of their influence on nest suspension, camouflage, and protection from weather and predators.

Long-tailed Manakin nests described from Chiapas, Mexico by Wagner (1945) were probably misidentified. The Costa Rican nests and eggs also are compared to those from Oaxaca, Mexico and to those of the other 3 species of the genus *Chiroxiphia*. All are strikingly similar.

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LITERATURE CITED

Allen, J. A. 1905. Supplementary notes on birds collected in the Santa Marta District, Colombia, by Herbert H. Smith, with descriptions of nests and eggs. Bull. Am. Mus. Nat. Hist. 21:275–295.

Belcher, C. and G. D. Smooker. 1936. Birds of the colony of Trinidad and Tobago. Pt. IV. Ibis 6:792–813.

Burmeister, H. 1856. Systematische uebersicht der thiere Brasiliens. II. Georg Reimer, Berlin.

Chubb, C. 1910. On the birds of Paraguay.—Part IV. Ibis 4:571–647.

Clench, M. H. 1970. Variability in body pterylosis, with special reference to the genus *Passer*. Auk 87:650–691.

de Schauensee, R. M. 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pa.

Dickey, D. R. and A. J. van Rossem. 1938. The birds of El Salvador. Field Mus. Nat. Hist. Publ., Zool. Ser. 23:1–609.

Edwards, E. P. 1972. A field guide to the birds of Mexico. E. P. Edwards, Sweet Briar, Va.

Euler, C. 1900. Descripção de ninhos e ovos das Aves do Brazil. Rev. Mus. Paul. 4:9–148.

FRIEDMANN, H., L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico. Pt. II. Cooper Ornithol. Soc. Pac. Coast Avif. 33:1–436.

GOODWIN, G. G. 1946. Mammals of Costa Rica. Bull. Am. Mus. Nat. Hist. 87:271–474.

GRISCOM, L. 1932. The distribution of bird-life in Guatemala. Bull. Am. Mus. Nat. Hist. 64:1–439.

HALLINAN, T. 1924. Notes on some Panama Canal Zone birds with special reference to their food. Auk 41:304–326.

HARTSHORN, G. 1971. Checklist of Costa Rican trees. *In* The book, (C. E. Schnell, ed). Organization for Tropical Studies, San Jose, Costa Rica.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHEWAY, T. LIANG, AND J. A. TOSI, JR. 1971. Forest environments in tropical life zones. A pilot study. Pergamon Press, New York.

IHERING, H. v. 1900. Catálogo crítico-comparativo dos ninhos e ovos das aves do Brasil. Rev. Mus. Paul. 4:191–300.

———. 1902. Contribuiçoes para o conhecimento da ornithologia de São Paulo. Rev. Mus. Paul. 5:261–329.

JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distribution. Ecology 54:659–686.

KEISER, E. D., JR. 1975. Observations on tongue extension of vine snakes (genus *Oxybelis*) with suggested behavioral hypotheses. Herpetologica 31:131–133.

LAND, H. C. 1970. Birds of Guatemala. Livingston Publ. Co., Wynnewood, Pa.

LEOPOLD, A. S. 1959. Wildlife of Mexico. The game birds and mammals. Univ. Calif. Press, Berkeley.

MONROE, B. L., JR. 1968. A distributional survey of the birds of Honduras. Ornithol. Monogr., Am. Ornithol. Union 7:1–458.

OLNEY, P. J. 1973. Breeding of the Blue-backed Manakin *Chiroxiphia pareola* at London Zoo. Avic. Mag. 79:1–3.

PINTO, O. 1953. Sobre a coleção Carlos Estevão de peles, ninhos e ovos das aves de Belém (Pará). Pap. Avulsos Dep. Zool. (São Paulo) 11(13):111–222.

SAWYER, J. O. AND A. A. LINDSEY. 1971. Vegetation of the life zones in Costa Rica. Indiana Acad. Sci. Monogr. 2:1–214.

SICK, H. v. 1957. Rosshaarpilze als nestbau-material brasilianischer vögel. J. Orn. 98:421–431.

———. 1967. Courtship behavior in manakins (Pipridae): a review. Living Bird 6:5–22.

SKUTCH, A. F. 1969. Life histories of Central American birds. III. Cooper Ornithol. Soc. Pac. Coast Avif. 35:1–580.

SLUD, P. 1957. The song and dance of the Long-tailed Manakin, *Chiroxiphia linearis.* Auk 74:333–339.

———. 1964. The birds of Costa Rica. Bull. Am. Mus. Nat. Hist. 128:1–430.

WAGNER, H. 1945. Observaciones sobre el comportamiento de *Chiroxiphia linearis* durante su propagacion. An. Inst. Biol. Univ. Nac. Auton. Mex. 16:539–546.

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CHEMICAL RESIDUE CONTENT AND HATCHABILITY OF SCREECH OWL EGGS

Erwin E. Klaas and Douglas M. Swineford

A close relationship between organochlorine insecticide residues in avian tissues and eggs and reduced reproductive efficiency has been demonstrated for a variety of species, both in controlled experiments and in field situations (Cooke 1973). Poor reproduction is generally accompanied by the production of eggs with reduced shell weight and thickness (Hickey and Anderson 1968, Enderson and Berger 1970, Ratcliffe 1970). Certain birds of prey, because of the high percentage of birds in their diet, seem to be particularly vulnerable to contamination, and recent declines in population numbers have occurred in certain areas where organochlorine residues in eggs or tissues are found to be high (Fyfe et al. 1969, Cade et al. 1971).

No assessment has been made of chemical residues in wild Screech Owls (*Otus asio*) in North America. These small birds of prey are at the top of their food chain, and feed on a wide variety of prey including crustacea, insects, small mammals, and birds. In a controlled study with captive Screech Owls, McLane and Hall (1972) demonstrated that 2.8 ppm (wet wt.) of DDE mixed in the diet would reduce eggshell thickness an average of 12%. Hence, we thought it possible that chemical residues might accumulate to relatively high levels in Screech Owls in nature.

This study was undertaken to obtain baseline information on organochlorine residues in the eggs of wild Screech Owls, to determine whether eggshell thinning is occurring, and to attempt to associate chemical residues with hatching failures in individual clutches. The population occurring in northwestern Ohio was selected for study because data concerning food habits and reproductive success over a 30-year period were available for the area (VanCamp and Henny 1976). Many of the owls in VanCamp's study area nested in artificial nest boxes and were easily accessible for acquiring a statistically adequate sample of nests. Moreover, many of the owls used in McLane and Hall's (1972) study were acquired from this area.

METHODS

In 1973, 19 nests were located during egg-laying or the early stages of incubation. Soon after laying was completed, 1 egg was removed from each clutch. Nests were revisited after young had hatched and 14 unhatched (addled) eggs were collected. Four other nests were found for the first time after young had hatched. Each of these nests contained 1 addled egg, 2 of which were collected and are included in discussions of unhatched eggs.

Collected eggs were refrigerated until the contents could be removed and placed in bottles that had been rinsed in hexane and acetone. Caps for the bottles were lined with aluminum foil. Samples were then frozen (–8°C) until they could be analyzed for residues.

Eggshells were rinsed with cold water and allowed to air dry at ambient temperatures for about 3 months before measuring. Shell thickness was measured with a Starrett Model 1010M dial gauge graduated in 0.01 mm increments. This same gauge, modified to measure archival eggshells having a small blow-hole, was used to measure eggs collected prior to 1935 that are presently in various museum collections. The thickness of each eggshell was determined as the mean of 3 measurements taken near the equator.

The contents of the owl eggs, albumen and yolk, were prepared for chemical analyses by homogenization. A 5-g aliquot of the homogenate was mixed with anhydrous sodium sulfate and extracted for 7 h with hexane in a Soxhlet apparatus. The extract was cleaned up on a Florisil column. Organochlorine pesticides and polychlorinated biphenyls (PCB's) were separated into 3 fractions on a Silicar column and analyzed by electron capture gas chromatography on a 4% SE–30/6% QF-1 column. The lower limit of sensitivity was 0.10 ppm. Eggs were analyzed for p,p′-DDE, p,p′-DDD, p,p′-DDT, dieldrin, heptachlor epoxide, mirex, oxychlordane, *cis*-chlordane and/or *trans*-nonachlor, *cis*-nonachlor, hexachlorobenzene (HCB) and PCB's. Average recovery of spiked Mallard (*Anas platyrhynchos*) carcass tissue ranged from 96% to 110% for all compounds, except hexachlorobenzene which had an average recovery of 69%. Residues in 10% of the samples were confirmed on a combined gas chromatograph-mass spectrometer. A more detailed description of the analytical procedure is presented by Cromartie et al. (1975). Residues were adjusted to fresh wet weight, assuming specific gravity of 1.0 as suggested by Stickel et al. (1973).

Analysis of variance and t-tests followed procedures given in Sokal and Rohlf (1969).

RESULTS

Eggshell thickness.—Thickness measurements from 2 groups of archival eggs (1 egg selected at random from each of 12 clutches from Ohio, and 37 clutches from Pennsylvania) were compared with thicknesses of 19 eggs (collected early in incubation from 19 clutches) from northwestern Ohio in 1973. No statistical differences were detected in the means for the 3 groups of eggs (anova, $p > 0.50$). A 4th group of 16 unhatched eggs (11 of which came from 3 clutches in which no eggs hatched) from 8 clutches did not differ in mean thickness from the other 3 groups (Table 1).

Chemical residues and nesting success.—DDE and PCB's occurred in all 35 Screech Owl eggs analyzed. These eggs were laid by 21 different females. The mean level of DDE was 1.29 ppm (range, 0.33–2.8) and PCB's averaged 1.32 ppm (range 0.26–3.4). Dieldrin averaged 0.13 ppm (range, 0.10–0.24) in 8 eggs, each from a different clutch. Other organochlorines detected among the 35 eggs analyzed are given in order of frequency: Mirex (5 eggs from 3 clutches, $\bar{x} = 0.12$ ppm), HCB (3 eggs from 3 clutches, $\bar{x} = 0.11$), DDD (2 eggs from 2 clutches, 0.12 and 0.11 ppm),

TABLE 1

SHELL THICKNESS (MM) FOR SCREECH OWL EGGS COLLECTED IN OHIO AND PENNSYLVANIA

Locality	Collected	Eggs measured	Mean	S.E.	Range
Pennsylvania	Pre-1947	37	0.241	0.003	0.197–0.277
Ohio	Pre-1947	12	0.244	0.004	0.230–0.287
Ohio (early[1])	1973	19	0.234	0.004	0.197–0.260
Ohio (addled)	1973	16	0.243	0.007	0.157–0.270

[1] Eggs collected early in incubation.

heptachlor epoxide (2 eggs from 2 clutches, 0.10 and 0.22 ppm), DDT (1 egg, 0.19 ppm), oxychlordane (1 egg, 0.31 ppm) and *cis*-chlordane (1 egg, 0.20 ppm).

The 19 nests located at the start of the nesting season contained an average of 4.6 eggs per nest. After collecting 1 egg from each nest, 68

TABLE 2

NESTING SUCCESS OF SCREECH OWLS IN NORTHERN OHIO IN 1973 AND RESIDUES OF DDE AND PCB'S IN THEIR EGGS

No. of nests	Eggs laid[1] per nest	Young fledged per nest	Unhatched eggs per nest	Early or unhatched	No. of eggs	ppm, Wet Wt.[2] DDE	ppm, Wet Wt.[2] PCB's
2	6	5	1	—	—	—	—
1	6	3	0	Early	1	2.8	2.8
1	6	1	4	Early	1	0.81	0.88
				Unhatched	4	(0.96)	(1.03)
1	6	0	5	Early	1	1.5	1.4
				Unhatched	3	(1.63)	(1.40)
5	5	4	0	Early	5	(0.93)	(0.93)
1	5	0	4	Early	1	1.7	1.3
				Unhatched	4	(1.45)	(1.18)
5	4	3	0	Early	5	(1.74)	(2.05)
2	4	2	1	Early	2	(1.23)	(0.80)
				Unhatched	2	(0.73)	(0.63)
1	4	1	Unknown	Early	1	0.63	0.54
1	4	0	Unknown	Early	1	1.3	2.1
1	3	1	1	Early	1	0.89	0.51
				Unhatched	1	0.47	0.26
1	Unknown	2	1	Unhatched	1	2.1	3.4
1	Unknown	Unknown	1	Unhatched	1	1.2	2.2

[1] Represents number of eggs before 1 was removed for analysis.

[2] Values in parentheses are arithmetic means; estimated variances based on total sample: DDE, 0.322; PCB's, 0.651.

eggs remained. A total of 49 eggs (72%) hatched, or an average of 2.6 per nest. An average of 2.5 owls fledged per nest and 16 of the 19 nests produced at least 1 young. Fourteen eggs (in 6 clutches) failed to hatch and were recovered, 5 eggs disappeared near the time of hatching and may have hatched, and 2 young disappeared.

DDE residues averaged 1.2 ppm in 16 unhatched eggs and 1.3 ppm in 19 eggs collected early in incubation. PCB's averaged 1.2 ppm in unhatched eggs and 1.4 in eggs collected early in incubation. Neither of these differences in means was significant (t-tests, $P > 0.10$). Also, mean residue levels of DDE and PCB's in 11 eggs collected early in incubation from nests in which all of the remaining eggs were known to have hatched were not different statistically ($P > 0.01$) from residue levels in unhatched eggs. (PCB chromatograms most closely resembled a profile for Aroclor 1260.)

One egg containing residues of 7 different compounds totaling 3.4 ppm came from a nest in which all 4 remaining eggs in the nest hatched. In another instance, an egg contained 5 compounds totaling 3.8 ppm but the 3 remaining eggs in this nest disappeared before hatching.

The 2 nestlings that disappeared were survived by 3 nestmates and we doubt that their loss was related to residue levels. Yet, the egg analyzed from this nest contained the highest level of total organochlorines (5.88 ppm) found during the study.

DISCUSSION AND CONCLUSIONS

No apparent relationship was found between hatching failures and the presence of organochlorine residues in eggs from a wild population of Screech Owls. Moreover, eggshell thickness in 1973 was unchanged from that of eggs collected before the widespread use of organochlorine pesticides. Although the shells of Screech Owl eggs can be experimentally thinned by feeding low levels of DDE in the birds' diet (McLane and Hall 1972), the wild owls examined in this study are apparently not accumulating enough residues in their tissues to cause any adverse effects on shell thickness or hatchability. Also, mean DDE residues are below the levels that have been associated with detrimental effects on reproduction in other raptorial species (Fyfe et al. 1969, Cade et al. 1971, Snyder et al. 1973, Wiemeyer et al. 1975). The Ohio Screech Owls have sustained good reproductive rates and stable numbers for many years (VanCamp and Henny 1976). Thus, it is probable that residue levels have never been much higher than those found in 1973.

The relatively low residue levels are consistent with the healthiness of the population. The owls nest principally in narrow strips of riparian habitat bordering streams that drain large areas of cropland (corn, wheat, soybeans). Although specific information concerning pesticide use in this area was not obtained, it is generally known that DDT and dieldrin were widely used to control pests on these grain crops throughout the midwestern United States for many years. Thus, it is surprising that higher residue levels were not found since most of these chemicals are known to be persistent and widespread, and to accumulate in food chains. Also, Screech Owls are at the top of their food chain. A possible explanation is that the Screech Owl preys on a wide variety of animals, some of which are less contaminated than others. VanCamp and Henny (1976) show that small birds make up a large portion of the Screech Owl's diet in spring and may be the major source of contamination; in other seasons, mammals and invertebrates are more important. The latter forms could be expected to carry lower residue levels than birds, allowing for a period in which tissue levels could be reduced through metabolism and excretion.

SUMMARY

Eggs of wild Screech Owls were collected from nests in northwestern Ohio in 1973. One egg was taken from each of 19 nests near the start of incubation. Mean shell thickness in these 19 eggs and mean thickness of 16 unhatched eggs did not differ from 49 archival eggs collected in Ohio and Pennsylvania prior to the widespread use of organochlorine pesticides. Residues were generally low although all eggs contained DDE and PCB's. No relationship was found between hatching failures and the presence of organochlorine residues. Low residues are consistent with a long history of good nesting success and a stable population.

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LITERATURE CITED

Cade, T. J., J. L. Lincer, C. M. White, D. G. Roseneau, and L. G. Swartz. 1971. DDE residues and eggshell changes in Alaskan falcons and hawks. Science 172: 955–957.

Cooke, A. S. 1973. Shell thinning in avian eggs by environmental pollutants. Environ. Pollut. 4:85–152.

Cromartie, E., W. L. Reichel, L. N. Locke, A. A. Belisle, T. E. Kaiser, T. G. Lamont, B. M. Mulhern, R. M. Prouty, and D. M. Swineford. 1975. Residues of organochlorine pesticides and polychlorinated biphenyls and autopsy data for Bald Eagles, 1971 and 1972. Pestic. Monit. J. 9:1–58.

Enderson, J. H. and D. D. Berger. 1970. Pesticides: eggshell thinning and lowered production of young in Prairie Falcons. BioScience 20:355.

Fyfe, R. W., J. Campbell, B. Hayson, and K. Hodson. 1969. Regional population declines and organochlorine insecticides in Canadian Prairie Falcons. Can. Field-Nat. 83:191–200.

Hickey, J. J. and D. W. Anderson. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science 162:271–273.

McLane, M. A. R. and L. C. Hall. 1972. DDE thins Screech Owl eggshells. Bull. Environ. Contam. and Toxicol. 8:65–68.

Ratcliffe, D. A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol. 7:67–115.

Snyder, N. F. R., H. A. Snyder, J. L. Lincer, and R. T. Reynolds. 1973. Organochlorines, heavy metals, and the biology of North American accipiters. BioScience 23:300–305.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco.

Stickel, L. F., S. N. Wiemeyer, and L. J. Blus. 1973. Pesticide residues in eggs of wild birds: adjustment for loss of moisture and lipid. Bull. Environ. Contam. and Toxicol. 9:193–196.

VanCamp, L. F. and C. J. Henny. 1976. The Screech Owl: Its life history and population ecology in northern Ohio. N. Am. Fauna, No. 71.

Wiemeyer, S. N., P. R. Spitzer, W. C. Krantz, T. G. Lamont, and E. Cromartie. 1975. Effects of environmental pollutants on Connecticut and Maryland Ospreys. J. Wildl. Manage. 39:124–139.

U.S. FISH AND WILDLIFE SERVICE, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MD. 20811 (PRESENT ADDRESS: EEK, IOWA COOPERATIVE WILDLIFE RESEARCH UNIT, AMES 50011). ACCEPTED 1 MAR. 1976. PAGE COSTS PAID.

LOON PRODUCTIVITY, HUMAN DISTURBANCE, AND PESTICIDE RESIDUES IN NORTHERN MINNESOTA

CATHERINE H. REAM

Olson (Olson and Marshall 1952) studied the Common Loon (*Gavia immer*) in the Knife Lake area of the Superior National Forest of Minnesota during 1950. Magnus and Karns (unpublished cooperative survey, Superior National Forest and the Minnesota Department of Conservation, Division of Game and Fish) later found decreased loon reproduction in the same area. I participated in the latter survey in 1966 and 1967. During 4 months of work and travel by canoe through the Boundary Waters Canoe Area (BWCA) from 1 July until 1 November 1966, I did not observe young loons. Massive loon die-offs in Lake Michigan during the falls of 1963, 1964, and 1965 gave additional cause for concern for the loon populations, although those loons as well as many gulls apparently died of poisoning from *Clostridium botulinum* Type E (Fay 1966).

I initiated the present study in order to further document the status of the Common Loon population in the Superior National Forest and to evaluate the possibilities that decline in the population might be related to pesticide contamination and/or increased human activity in the area.

METHODS

Observations were made on as many pairs of loons in the Superior National Forest as possible. Travel in the BWCA was coordinated with the ecological survey team of the North Central Forest Experiment Station (NCFES). This team was working on a 10-days-on and 4-days-off schedule, making 8-day canoe trips into the BWCA. During the 4 "off" days, territories of loons which were accessible by road or less than 1 day's canoe paddle were visited. In this manner, 2 readily accessible loon territories were kept under surveillance throughout the summer. Methods and distances made systematic observations on all known loon territories impossible. However, most pairs were observed for several days and at more than one time during the summer. Supplementary observations were contributed by members of the ecological survey team of the NCFES who were traveling separately from me.

Five fish, 5 loon eggs, and tissues from 3 loons I collected in the BWCA were analyzed by the Wisconsin Alumni Research Foundation for pesticide residues. One smallmouth bass (*Micropterus dolomieui*), 3 northern pike (*Esox lucius*), and a walleye pike (*Stizostedion vitreum*) from 5 different lakes with loon populations were analyzed. Four of the loon eggs obtained for analysis were being incubated and apparently viable. The fifth (abandoned) had a slight crack and was putrid at the time of collection. Two immature loons were shot and appeared to have been healthy. Each came from a nest in which 2 young had been produced. A mature bird was found dead and tangled in aquatic vegetation at Burntside Lake. It had buckshot embedded in its neck and I presumed that this was the cause of death. This loon had been killed

TABLE 1

LOON PRODUCTIVITY IN THE KNIFE LAKE CHAIN

Year	No. territories checked	No. young loons
1950*	42	21
1964**	45	19
1965	31	10
1966	21	1 (plus 4 unhatched eggs)
1967	49	5 (plus 1 pipped egg)

* Olson and Marshall 1950.
** Magnus and Karns, unpublished data, 1964–1967.

very recently and showed no signs of decomposition. Samples of fat, liver, brain, and breast muscle were analyzed for each of the loons.

RESULTS

We observed 85 loon territories in the Superior National Forest between 1 May and 15 October, 1967. The majority of these were on lakes in the BWCA and inaccessible by road. Many territories were observed too early in the summer to ascertain reproductive success. Thirty-six pairs of loons were known to have attempted nesting and, of these, 11 pairs successfully hatched 18 young. Two of the 18 young were collected for pesticide residue analyses. The figure of 18 young for 36 pairs of loons is a biased record since assisting teams on several occasions reported territories where young loons were present, but did not report all of the territories they observed which were occupied by adults only. I checked several territories where young had been observed by other parties. Omitting this bias, 6 young were produced by 31 pairs of loons. Renesting was observed in both pairs which were under observation throughout the summer, however neither pair brought off young.

Forty-nine of the 85 loon territories observed in 1967 were in the Knife Lake chain. Table 1 presents loon productivity data for this area from 1950 through 1967.

The number of paddling canoeists using the BWCA increased 54% from 1961 to 1966. Motoring canoeists increased 44% during the same period (Lucas 1967). On some major canoe routes, over 14,000 people travel through in a summer. On some lakes, nearly every suitable site is used for camping. When fishing season opens the last of May, nearly every campsite is occupied on lakes which are known to have good fishing and are accessible by motor. All of the loon nests we found were on islands

TABLE 2

RESIDUE ANALYSES PPM LIPID WEIGHT

		DDE	DDD	PP′DDT	Dieldrin
Loon #5444	Muscle	4.13	1.01	1.11	<.52
	Liver	4.71	2.25	1.12	<.72
	Brain	1.72	<.37	.49	<.37
	Fat	4.07	.65	1.48	<.02
Loon #5445	Muscle	3.23	.88	.91	<.59
	Liver	2.68	<.72	<.72	<.72
	Brain	4.83	1.48	2.76	<.49
	Fat	3.22	1.59	.68	<.03
Loon #5446	Muscle	1030.88	797.06	69.49	18.27
	Liver	1214.49	1023.83	25.36	23.83
	Brain	552.2	265.56	530.00	6.56
	Fat	1624.43	685.52	1469.01	5.44
Loon eggs	1	176.29	5.96	16.26	4.97
	2	323.88	.64	1.80	16.19
	3	240.51	16.95	40.89	8.26
	4	223.83	12.89	32.55	4.56
	5	173.31	19.23	25.04	5.97
Fish	1	11.66	3.50	2.94	13.92
	2	12.53	6.98	6.77	<1.39
	3	14.21	2.79	4.83	<1.24
	4	6.85	<3.70	<3.89	<3.70
	5	6.05	1.09	9.07	<.34

or sedge mats. Nine of the 18 nests we located were on campsite islands or on islands that had been used for lunch stops as indicated by fireplaces. Six of these nests were unsuccessful. Hatching results were not known for the remaining 3, but the chances of successfully hatching eggs seemed very slim for 2 of these. The third was on a large island on the far side from the campsite and may have been successful.

On an island campsite in Agnes Lake, fishermen were seen throwing fish entrails into an alder thicket 0.3 m from a loon nest. Subsequently, ravens (*Corvus corax*) arrived and began to eat the fish remains. I collected the egg for pesticide residue analysis. Loons do not actively defend their nests. They may either sneak off the nest at the approach of intruders or display, racing on the water surface and treading water and calling, attempting to draw the intruders away. They return to disturbed nests only after a considerable period of time, leaving the eggs subject to predation by crows

(*Corvus brachyrhynchos*), ravens, otter (*Lutra canadensis*), muskrat (*Ondatra zibethica*), etc. We found several nests with pieces of eggshell in them and no young loons surviving. In one territory 2 eggs had holes pecked in them, apparently by crows or ravens. The eggs had been pushed off the nest into the surrounding sweet gale (*Myrica gale*). In another instance, eggshell was found in the water in front of the nest, suggesting an otter may have been responsible. One abandoned nest contained an egg which was cracked, perhaps by an adult loon leaving the nest hastily.

The Boundary Waters Canoe Area has not been sprayed since 1963. Lakes peripheral to the BWCA, where resorts and summer homes are located, are sprayed regularly throughout the summer. Personal communication with property owners and personal observation on Burntside Lake in 1967 indicated that mosquitoes and black flies were no problem around this lake in spite of the fact that the habitat was excellent and in 1967 these insect populations were high. Apparently spraying occurred several times during the summer on this lake and probably many others. Some of these pesticides arrive in the BWCA either directly or through drainage patterns and animal movement.

The results of the pesticide residue analyses on a lipid weight basis are presented in Table 2.

DISCUSSION

Water clarity and physiographic features of lakes in the study area have remained constant and therefore do not explain the decline in reproduction. Changes in fish abundance and species composition in these lakes are not known. Two factors affecting loons have changed significantly. One is the increased number of human visitors at a critical time of year and the other is the spraying of pesticides.

The opening of fishing season coincides with the beginning of the loon nesting season. Loons are more inclined to desert their nests when disturbed early in the nesting season than after incubation has progressed (Olson and Marshall 1952). So, at the time when loons are most susceptible to disturbance, many lakes have every campsite occupied and new ones being made by fishermen.

Canoeists favor island campsites and loons prefer to nest on islands of 1 ha or less. Of 54 nests located by Olson, 50 were on islands. The use of nesting islands for campsites may be a key factor limiting loon reproduction in the BWCA. In most cases, campers do not destroy eggs or even locate nests, but they do, by their mere presence, keep the loons away from their nests. Loon nesting sites are established a week or 2 before the arrival of the first campers. Fortunately islands which are used for nesting by loons on some lakes are too small and/or marshy to attract people.

The loon eggs and fish analyzed for pesticide residues gave fairly constant results in spite of the fact that they were collected from widely separated lakes. The immature loons collected on Tofte Lake (#5444) and Hub Lake (#5445) gave similar, comparatively low results. The adult female (#5446), found dead on Burntside Lake, was highly contaminated (Table 2).

Since the young birds were not yet able to fly, the pesticides they contained came either from their parents or from the lake on which they were taken. Hub Lake is fairly inaccessible; Tofte can be reached by road and has a cabin on it. The mature bird from Burntside Lake could have been contaminated from many sources: on the wintering grounds, during migration, and from any lakes on which she fed during the summer.

The DDT residue levels in loons 5444 and 5445 are similar to those given by Locke and Bagley (1965) for loons killed by botulism. Loon 5446 certainly contained residue levels that would be considered fatal on the basis of studies of other species of birds (Stickel et al. 1966). The loon eggs contained residues of DDE within the range of other aquatic bird eggs recorded by Faber and Hickey (1973).

Loons in the BWCA are to some degree affected by high levels of pesticide residues, but the main factor limiting reproduction appears to be the disturbance of nesting sites by canoeists.

SUMMARY

In recent years there has been a decline in loon reproduction in the Superior National Forest. The biota of certain lakes in the Superior National Forest on which resorts are located contain high concentrations of pesticides and these may affect reproductive success of loons, but, the most important factor seems to be the increasing number of canoeists in the area. Virtually every island in some of the lakes is occupied several times a week by campers during the critical early nesting period. Campers usually do not destroy loon eggs directly, but do frighten loons off of their nests, leaving them susceptible to predators.

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LITERATURE CITED

Faber, R. A. and J. J. Hickey. 1973. Eggshell thinning, chlorinated hydrocarbons, and mercury in inland aquatic bird eggs, 1969 and 1970. Pestic. Monit. J. 7:27–36.

Fay, L. E. 1966. Type E botulism in Great Lakes water birds. Trans. 31st N. Am. Wildl. Nat. Resour. Conf. 139–149.

LOCKE, L. N. AND G. E. BAGLEY. 1965. DDT in loons. The effects of pesticides on fish and wildlife, 1964. Fish and Wildl. Serv. Circ. No. 226:13–14.

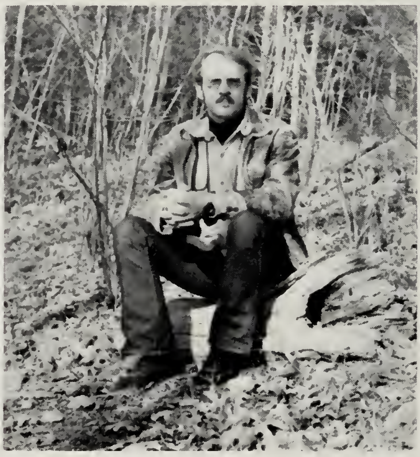
LUCAS, R. C. 1967. The changing recreational use of the Boundary Waters Canoe Area. U.S. Forest Service, Research Note NC–42.

OLSON, S. T. AND W. H. MARSHALL. 1952. The Common Loon in Minnesota. Minn. Mus. Nat. Hist., Univ. of Minn., Occas. Pap.: No. 5.

STICKEL, L. F., W. H. STICKEL, AND R. CHRISTENSEN. 1966. Residues of DDT in brains and bodies of birds that died on dosage and in survivors. Science 151: 1549–1551.

NEW LIFE MEMBER

Dr. Harry M. Ohlendorf is now a life member of the Wilson Ornithological Society. Dr. Ohlendorf is presently a wildlife research biologist and assistant director of the Patuxent Wildlife Research Center. His principal interests in ornithology are the effects of environmental contaminants on fish-eating birds. He has published several of his studies, including 2 papers on flycatchers that have appeared in recent issues of the Wilson Bulletin. In addition to his ornithological interests, Dr. Ohlendorf enjoys gardening, canoeing, and woodworking.



ON THE RELATIVE ABUNDANCE OF MIGRANTS FROM THE NORTH TEMPERATE ZONE IN TROPICAL HABITATS

James R. Karr

Each year beginning in July or August and continuing as late as May in the following year many areas in Latin America, Africa, and the Indomalaysian region are inundated by migrants from the nearctic or palearctic regions. Although no systematic comparative studies have been done on these areas, many comments have appeared in the literature which hint at assessment of the impact of these migrants on the tropical faunas that they visit. Unfortunately these studies vary in intensity and objectives to the extent that synthesis of results is difficult.

Willis (1966) presents an intensive study of the roles of migrants at army ant swarms, while Leck (1972a,b) discusses the impact of North American migrants at fruiting trees in Panama. Other studies in the neotropics have been concerned with ecological isolation in wintering warblers (Lack and Lack 1972), or the impact of migrants on seasonal breeding cycles (Miller 1963). Tramer (1974) presented data on proportions of wintering North American birds in dry habitats in tropical Mexico. Many studies in Africa have dealt with the seasonal movement patterns, distributions, and/or abundance of palearctic migrants (Morel and Bourliere 1962, Elgood et al. 1966, Brosset 1968, Morel 1968, Pearson 1971, Britton 1974, Thiollay 1970a,b). Moreau (1972) presents an excellent summary of what is known of the Palearctic-African bird migration system. In Asia little is known of the impact of migrant birds on their host ecosystems. Ward (1968, 1969) comments briefly on the significance of the influx of migrants on the annual cycle of Malaysian birds, as does Brosset (1968) on the abundance of migrants in India. The extensive studies of McClure and Medway have contributed materially to the clarification of migration of Palearctic species to Southeast Asia (McClure 1964, 1974, McClure and bin Othman 1965, Medway 1972, Nisbet and Medway 1972).

Unfortunately, few of these studies adequately define the habitats under consideration, the size of area examined, *and* the densities of tropical resident and migrant species in the same area. Although these individual studies are often excellent, it is difficult to derive a comparative synthesis from their results.

Between 1968 and 1972 I visited a number of forest areas on several continents as part of a study of the organization of tropical forest avifaunas. A routine procedure in each area involved use of mist-nets at 0–2 m. In this paper I present results which relate to the impact of northern migrants in the tropics. Initially, I present data from a number of habitats studied intensively in Panama. Subsequently, more restricted data from Africa and Indomalaysia are presented. Finally, I attempt a summary of the scattered literature on north temperate migrants in the tropics.

"Tropical resident" refers to species that reside throughout the year in the region of the study area. Although it is not widely recognized, many of these species show considerable propensity for seasonal movements (Moreau 1972, Elgood et al. 1966, Karr 1976a). "Migrants" will refer to species that move long distances and chiefly to species that breed in the north temperate zone and spend the temperate winter in the tropics. These species may occur as "transients" on an area or as "winter visitors." "Winter visitors" occur as residents in a study area for some period of time, especially in the December to February period. Generally, the status "winter visitor" is used when reasonable evidence of winter residence is available, e.g. when a banded bird is captured on several occasions or a bird is observed through a regular molt sequence.

There is a tendency for biologists with a primarily temperate zone background to refer to these migrants as temperate-zone birds when what is meant is temperate-zone breeders. Clearly, this phraseology should be so understood since these birds spend nearly as much time, and in some cases more time, on their tropical wintering grounds as they do on the north temperate breeding grounds. I will focus on the birds of terrestrial environments and not consider migrant shorebirds, although shorebirds will be included in discussions of Panama study areas so that data are complete.

FIELD METHODS

Panama study areas.—The data presented in this paper derive from a combination of field techniques (Karr 1971a). Study plots in Panama were surveyed from July 1968 through July 1969 by walking the study areas for several hours, usually in the morning, and recording on maps the location and species of all birds. Mist-nets were used in shrub and forest habitats to clarify ambiguities about species composition and abundance. Generally, twelve 30 and/or 36 mm mesh nets, 12 m long were placed in the study area with the lower shelf on the ground.

Nets were opened 30 to 90 min before sunrise and checked hourly until about noon when they were closed for the day. Birds captured in the nets were identified, weighed, individually marked, and released at the capture site. Generally, a color slide was taken of each species captured to confirm identifications.

Since migrant birds do not sing regularly during this period and many are only transient on the intensive study areas, no attempts were made to quantify abundance of the migrant species from census data. A reasonable index of their abundance relative to the resident birds can be obtained if we assume that both migrants and residents are captured in mist-nets in proportion to their abundance. Migrants may be captured with somewhat higher frequency than expected by their abundance since they may be moving more than residents (see below). The ratio of migrant individuals to total individuals captured should be a reasonable first approximation of migrant densities.

African and Asian study areas.—Most of the study areas in Africa and Asia were mist-netted for relatively short periods so comprehensive censuses were generally not possible. However, I used mist-nets as described above for several days on each study area.

STUDY AREAS

Extensive discussions of the study areas have been presented previously for the Panamanian (Karr 1971a) and African (Karr 1975, 1976b) study areas. All Panama study areas were in the lowlands. Vegetation types varied from grassland to forest. There were 2 grazed and 2 ungrazed grassland study areas. Two shrub areas included mosaics of grass and thicket habitat; early shrub was predominated by grass, while a late shrub area was a similar mosaic with shrubs predominating. Temperatures near all of the study areas averaged near 27°C, but rainfall was somewhat higher in the forest (2600 mm) than near the grasslands (1900 mm) or shrub areas (2000 mm).

In Liberia I studied birds of several study areas near Mt. Nimba at 500 m. The study areas included forest and late shrub similar in vegetation structure to the Panamanian sites, and an intermediate area of disturbed forest. Mean annual temperature in the vicinity of each study area is near 23°C with annual rainfall slightly below 3000 mm. The only other African site visited during the season when Palearctic migrants might be expected was the Sokoke Forest in coastal Kenya about 90 km north of Mombasa. This is a coastal deciduous forest growing on a dry sandy soil.

I netted in only one forest in India. This area, located near the athletic field at Mahabaleshwar in Maharashtra (17° 56′ N, 73° 40′ E), is part of the western Ghat forest that extends from just south of Bombay to the southern tip of India. At 1370 m the forest has a distinctly montane appearance with a canopy height of about 15 m. The sparse ground cover of the area is similar to that of lowland forest. Signs of recent human (wood-gathering) and cattle activity were common. Vegetation cover was low in the 1–5 m levels and canopy coverage reached a maximum of about 60% at 6–15 m. Mahabaleshwar has a mean annual temperature of about 19.5°C and an annual rainfall of 6200 mm, with most of the rain falling in the June to September monsoon period. Common trees in the forest around Mahabaleshwar include *Syzigium cumini*, *Memecylon edule*, *Actinodaphne hookeri*, *Randia brandisi*, *Lassiosiphon ericephalus*, *Glochidia hohenackeri*, and *Mappia foetida.*

I also netted in the Pasoh Forest Reserve, about 72 km from Kuala Lumpur, Malaysia. This relatively undisturbed reserve is used in an intensive study of the dynamics and productivity of lowland dipterocarp rain forest as part of a Malaysian/United Kingdom contribution to the International Biological Program. The study area is located at about 2° 59′ N, 102° 18′ E at an elevation of less than 100 m. The mean annual temperature at nearby Kuala Pilah is near 26°C and annual rainfall averages near 1900 mm. Trees on the area include many species with *Shorea* spp. and *Dipterocarpus* spp. being especially abundant. Canopy height commonly exceeds 40 m.

RESULTS

Seasonal distribution of migrants to Panama.—Before the end of the North American summer the first migrants begin to arrive in central Panama. Upland Sandpiper (*Bartramia longicauda*) and one of the northern forms of the

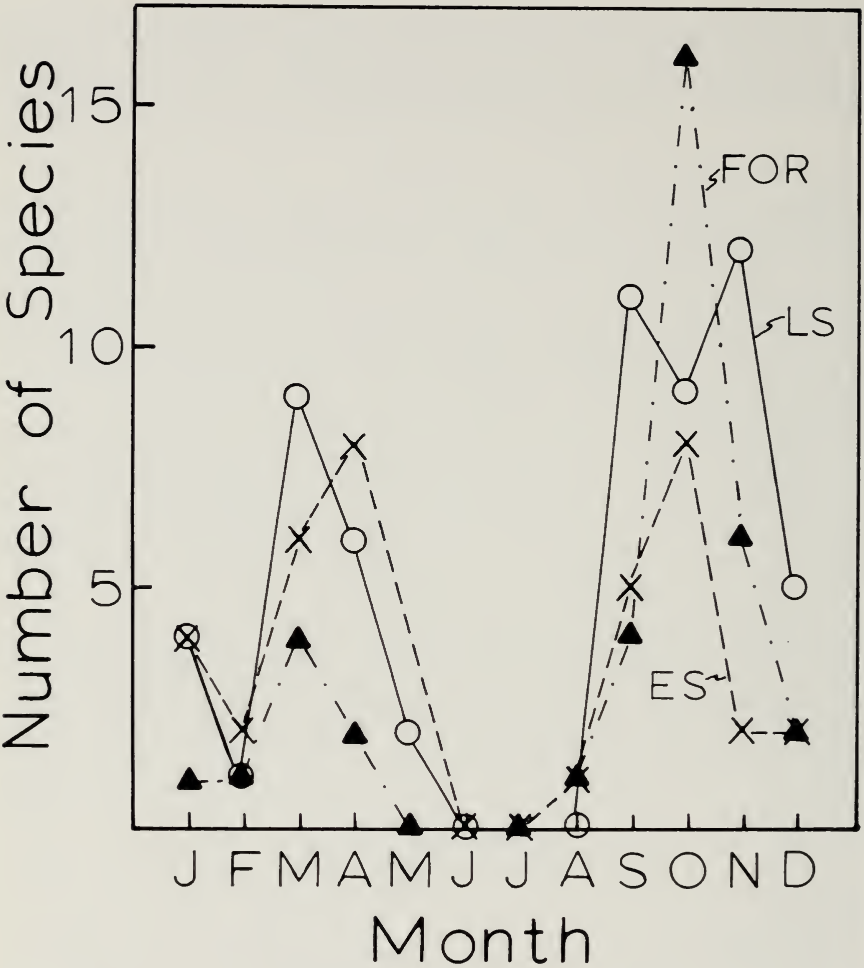


FIG. 1. Number of migrant species seen in each month on the early shrub (ES), late shrub (LS), and forest (FOR) study areas in central Panama.

Rough-winged Swallow (*Stelgidopteryx ruficollis*) are first seen in the grasslands in August. September through November are peak months with several species of sandpipers, flycatchers, and warblers as well as the Barn Swallow (*Hirundo rustica*) arriving in September. There is a sharp decline in the number of migrant species from December to February (Fig. 1).

The influx of northward moving species begins in late February or early March and peaks in April. In the forest the movement apparently has stopped before May but 2 species from northern Middle America are still noted in the shrub areas well into May (Table 1, Fig. 1). No north temperate breeding species were seen in the study areas in June or July. The fall peak in number of migrant species was about 30% higher than the spring peak in the 2 shrub habitats and 400% higher in the forest. The spring peak was more protracted than the fall peak. However, many species that were abundant in the fall, especially thrushes and warblers, were rare or not observed on my study areas in the spring.

Migrant species on the Panama study areas.—Species that visited the Panama study areas either as non-breeding transients or as winter visitors are classed as migrants. Most of these species breed north of Panama, either in temperate North America or in 4 cases in northern Middle America or the West Indies. One species, the swallow *Phaeoprogne tapera*, is a visitor from southern South America during the southern hemisphere winter. The number of migrant species varied from as few as 5 on the dry grazed grassland to a high of 28 on the late shrub area (Table 1). Those on the dry grazed grassland were mostly swallows (4 spp.) but included the Yellow-rumped Warbler (*Dendroica coronata*). This warbler, a very irregular, sporadic winter visitant to Panama, was observed in late December and January. Migrants on the wetter portion of the grazed study areas included 4 sandpipers, 1 snipe, 4 swallows, an icterid (*Dolichonyx*) and the Yellow-rumped Warbler. The ungrazed study areas had similar groups of species but added 1 raptor, and 2 tyrant-flycatchers.

The early shrub migrants included 6 Falconiformes, 6 tyrant-flycatchers, 3 swallows, 6 wood-warblers, and 1 each of thrush, vireo, and tanager (Table 1). The late shrub study area had a similar species distribution with 10 wood-warblers. Twenty-three of 25 migrants observed on the early shrub area and 25 of 28 on the late shrub were from North America. One migrant from South America (*Phaeoprogne*) occurred on both areas. One on the early shrub and 2 on the late shrub were from northern Central America.

I observed 22 migrant species on the forest study area (Table 1). The species were similar to those on the shrub areas, but included more thrushes.

I observed 48 migrant species (seen, heard, or netted) on all study plots, although most occurred as transients, rather than as winter visitors.

Relative abundance of migrants and residents.—Total winter densities of migrant species are difficult to assess because of the mobility of many species and problems of visibility. However, mist-nets operated in the undergrowth of shrub and forest habitats can provide an index of migrant abundances.

On the Pipeline Road forest study area, no migrants were captured in September but nearly one-fourth of the individuals captured in October were migrants (Table 2). The capture rate declined for 2 months, increased

TABLE 1

MIGRANT SPECIES RECORDED ON THE STUDY AREAS IN CENTRAL PANAMA.†

Species	Grassland				Early Shrub	Late Shrub	Moist Forest
	Grazed		Ungrazed				
	Dry	Wet	Dry	Wet			
Ictinia misisippiensis					4		
*I. plumbea***						3,4,5	8,9
Buteo swainsonii					3	3	9,10,11
B. platypterus					4,5	3,4,11	9,10,11
Circus cyaneus			3,11				
Falco peregrinus					3	3	
F. sparverius					10		
Charadrius wilsonia			4,5				
Bartramia longicauda		4	4,8,9,10	4			
Tringa melanoleuca		9					
T. solitaria		9					
Actitis macularia		9					
Capella gallinago	11						
Calidris melanotos			10				
*Muscivora tyrannus***					9	9	

TABLE 1. (*Continued*)

Species	Grassland				Early Shrub	Late Shrub	Moist Forest
	Grazed		Ungrazed				
	Dry	Wet	Dry	Wet			
Tyrannus tyrannus			4	4	3,4,5	4,5,9	9,10
*T. dominicensis****			3	3			
*Myiodynastes luteiventris***						9	
Myiarchus crinitus					1,10	1,3,11,12	10
Contopus virens					8,9,10,11	9,10,11	10
Empidonax virescens					1,4,10	4,9,11	11
E. traillii					1,4,10	4,9	
Petrochelidon pyrrhonota	3,5	3,5	10	10			
Hirundo rustica	3,5,10,11,12	3,5,10,11,12	4,10,11	4,10,11	3,4,5,9,10	9,10	
Stelgidopteryx ruficollis	3	3	8	8	3,4	3,4	
Riparia riparia	4	4	5,10	5,10			
*Phaeoprogne tapera**					2	2	
Catharus ustulata						10,11	3,4,10,11
C. minima					10		10
C. fuscescens							10,11
Vireo olivaceus					9	10	10

TABLE 1. (*Continued*)

Species	Grassland						
	Grazed		Ungrazed				
	Dry	Wet	Dry	Wet	Early Shrub	Late Shrub	Moist Forest
V. flavifrons						12	
Mniotilta varia					11	10,11,12	10
Vermivora peregrina					12	1,11,12	10,12
Dendroica pensylvanica					1,12	10,11,12	1,3
D. coronata	1,12	1					
D. castanea						10	10
D. petechia					9	1,3,9,10,12	
Seiurus aurocapillus					10		
S. noveboracensis						9,11	4
Oporornis formosus						9,11	2,3,4,10,11,12
O. philadelphia						3	
Wilsonia canadensis					10	10,11	10
Setophaga ruticilla						9	11
Icterus galbula							10
Piranga rubra					2	1,3,11	10
Dolichonyx orizyvorus		11		10			
Pheucticus ludovicianus							3
Total Number of Migrants	5	11	10	8	24	28	22

† Coded by month from January (1) through December (12).
* Migrant from southern South America.
** Migrant from northern Middle America.
*** Migrant from South Florida or West Indies.

TABLE 2

DISTRIBUTION OF INDIVIDUALS AND SPECIES AMONG RESIDENT AND MIGRANT SPECIES IN PANAMA MIST-NET STUDIES

Study Area (Habitat)	Month	# Net Hours	Total Number Captures	Number of Captures		Number of Species		Captures/Species		% Migrant Individuals	Captures/Hour	
				R[1]	M	R	M	R	M		R	M
Pipeline Road (Lowland Forest)	Sept.	126	61	61	0	26	0	2.3	0.0	0.0	.48	.00
	Oct.	258	120	93	27	31	5	3.0	5.4	22.5	.36	.10
	Nov.	238	91	85	6	31	3	2.7	2.0	6.6	.36	.03
	Dec.	201	84	82	2	28	1	2.9	2.0	2.4	.41	.01
	Feb.	149	44	41	3	24	1	1.7	3.0	6.8	.28	.02
	Mar.	280	72	70	2	28	2	2.5	1.0	2.8	.25	.01
	Apr.	129	53	52	1	22	1	2.4	1.0	1.9	.40	.01
	May	192	73	73	0	22	0	3.3	0.0	0.0	.38	.00
Chiva Chiva Road (Late Shrub)	Sept.	92	46	42	4	18	3	2.3	1.3	8.7	.46	.04
	Oct.	139	82	73	9	32	7	2.3	1.3	11.0	.53	.06
	Nov.	102	45	43	2	23	2	1.9	1.0	4.0	.42	.02
Fort Clayton (Disturbed Forest)	Oct.	108	59	29	30	18	8	1.6	3.8	50.8	.27	.28
End of Chiva Chiva Road (Disturbed Forest)	Dec.	165	115	107	8	36	4	3.0	2.0	7.0	.65	.05
Puercos Island (Island Forest)	Jan.	547	110	83	27	14	5	5.9	5.4	24.5	.15	.05

[1] R = resident, M = migrant.

slightly in February, and again declined. Seven of the 14 captures from November to April were of a single Kentucky Warbler (*Oporornis formosus*) (Karr 1971b).

Mist-net data for the late shrub study area are limited to the late rainy season (September to November) (Table 2). Netting activities on the shrub area were restricted to this season because of the danger of losing nets and birds to fires during the dry season (December–April). October capture rates were highest in this area but less than for the same month in the forest.

Mist-net data for 2 other mainland areas are available for comparison (Table 2). Both areas had disturbed forest with denser undergrowth than that on the Pipeline Road study area. The first area, located on Fort Clayton, was netted in October of 1968. Fifty-nine birds were captured in 2 mornings (8 migrant species, 30 individuals; 18 resident species, 29 individuals).

A similar area on Chiva Chiva Road was netted in December. Only 8 of 115 captures (7%) were of migrants. These 8 captures included 4 species: *Oporornis formosus*, *Seiurus noveboracensis*, *Empidonax traillii*, and *Helmitheros vermivora*. I captured 36 resident species.

The migration peak occurred in October in all habitats, and involved the largest number of species and individuals in forest habitats. At mist-net levels (0–2 m) migrants made up about 20% of the avifauna, but were as high as 50% in some areas (Ft. Clayton).

September data indicate that early migrants seemed to favor the shrub habitat (9% of captures) rather than forest (no captures). The fact that net captures in the shrub area began almost a week before that in the forest strengthens that conclusion. Later in the migration season relative densities of migrants in shrub habitat exceeded those in forest areas.

An index of the relative rarity of the migrants can be obtained by determining captures per species for migrant and resident species (Table 2). It is clear that the migrant species are generally rarer than their resident counterparts, despite the general rarity of tropical forest species (Karr 1971a). Major exceptions to this pattern occurred in the peak migration months of October and February when the number of individuals per species was higher for migrants than for residents.

Summarizing data from the Panama studies, migrants reached their greatest proportion of the community in forest during the peak of the fall migration. However they wintered at higher densities in areas which contained a mixture of second growth and disturbed forest than in extensive areas of mature forest. A few species occurred as transients in (or over) grassland habitats, but none were winter visitors on grassland study plots.

Migrants on the African study areas.—Three study areas netted in Liberia —lowland forest (relatively undisturbed), disturbed forest, and late shrub—

were chosen to correspond to the areas studied in Panama (Table 3). Samples on these areas included from 295 to 650 mist-net hours; not a single capture of a Palearctic migrant was made (Table 3). This includes both forest and late shrub habitats. (The late shrub area had been relatively undisturbed for 6 years.) Nearby grassland and garden areas however contained many migrant species (25+) and individuals during my visit.

Similarly, in East Africa many migrants were observed in savanna and grassland habitats but a mist-net sample in the coastal deciduous forest of Kenya yielded no migrants (Table 3).

During 7 months of field work in Africa when migrants were present, I did not observe a Palearctic migrant in wet forest habitat. On one occasion I observed the cuckoo *Clamator levaillantii* about 15 m inside a forest in Liberia. This is unusual, however, as this migrant from within the Ethiopian region (breeds in the drier areas of Africa south of the Sahara) is more commonly found in open habitat.

Migrants on Indomalaysian study areas.—Mist-netting at Mahabaleshwar, India during January of 1972 yielded capture rates of about one bird per 10 mist-net-hours (Table 3). Forests in Liberia and Panama yielded one bird per 2–4 hours. Clearly the total populations of the Indian forest are significantly below those for lowland forests on the other 2 continents. My limited experience at netting in mid-elevation forests (1000 m) in the neotropics yielded very high capture rates. In 3 days of netting at San Vito in southern Costa Rica, I captured one bird every 1.5 hr. (Unfortunately these Costa Rican data were collected in the north temperate summer—July—so no migrants were present.) A brief netting attempt in forest at Wau, New Guinea in May gave capture rates similar to those of the San Vito site. No migrants were included in the New Guinea sample, but palearctic migrants and migrants from Australia are relatively rare in New Guinea except for some aquatic forms and 2 swifts (Rand and Gilliard 1967). Generally New Guinea resembles Africa in the absence of migrants from rainforest although migrants are often abundant in open habitats at low and medium elevations and on some satellite islands (Diamond 1975; pers. comm.).

The low densities of birds in the Indian forest are particularly striking when one considers that 10 of 18 birds captured were migrants. Although I did not net in other Indian forests, surveys of forest areas near Bombay, Baroda, New Delhi, Agra, Varanasi, and Calcutta had low resident abundance and high abundance of Palearctic migrants. Generally these were relatively open, dry forests. In south India at Manjolai in Tamil Nadu, residents appeared higher and migrants lower in abundance than in northern India, but I have no quantitative data for this region.

In March 1972 I visited 2 areas in Malaysia. In 3 days of netting at the

TABLE 3

DISTRIBUTION OF INDIVIDUALS AND SPECIES AMONG RESIDENT AND MIGRANT SPECIES IN AFRICAN AND INDOMALAYSIAN MIST-NET STUDIES

Country	Study Area (Habitat)	Month	Number of Net Hours	Total Number Captures	Number of Captures		Number of Species		Captures/ Species		% Migrant Individuals	Captures/Hour	
					R[1]	M	R	M	R	M		R	M
Liberia	Airport Forest (Lowland Forest)	Feb. thru Apr.	650	194	194	0	38	0	5.1	0.0	0.0	.30	0
	Forest Road I (Disturbed Forest)	Apr.	295	84	84	0	23	0	3.7	0.0	0.0	.28	0
	Forest Road II (Late Shrub)	Mar. thru Apr.	374	131	131	0	30	0	4.4	0.0	0.0	.35	0
Kenya	Sokoke (Coastal Semideciduous Forest)	Nov.	176	33	33	0	11	0	3.0	0.0	0.0	.19	0
India	Mahabaleshwar (Lower Montane Forest)	Jan.	179	18	8	10	4	3	2.0	3.3	55.5	.04	.06
Malaysia	Pasoh (Lowland Forest)	Feb.	$\simeq$ 1500	185	152	33	34	4	4.5	8.3	17.8	.11	.02
		Mar.	211	36	33	3	14	2	2.4	1.5	8.3	.16	.01

[1] R = resident; M = migrant.

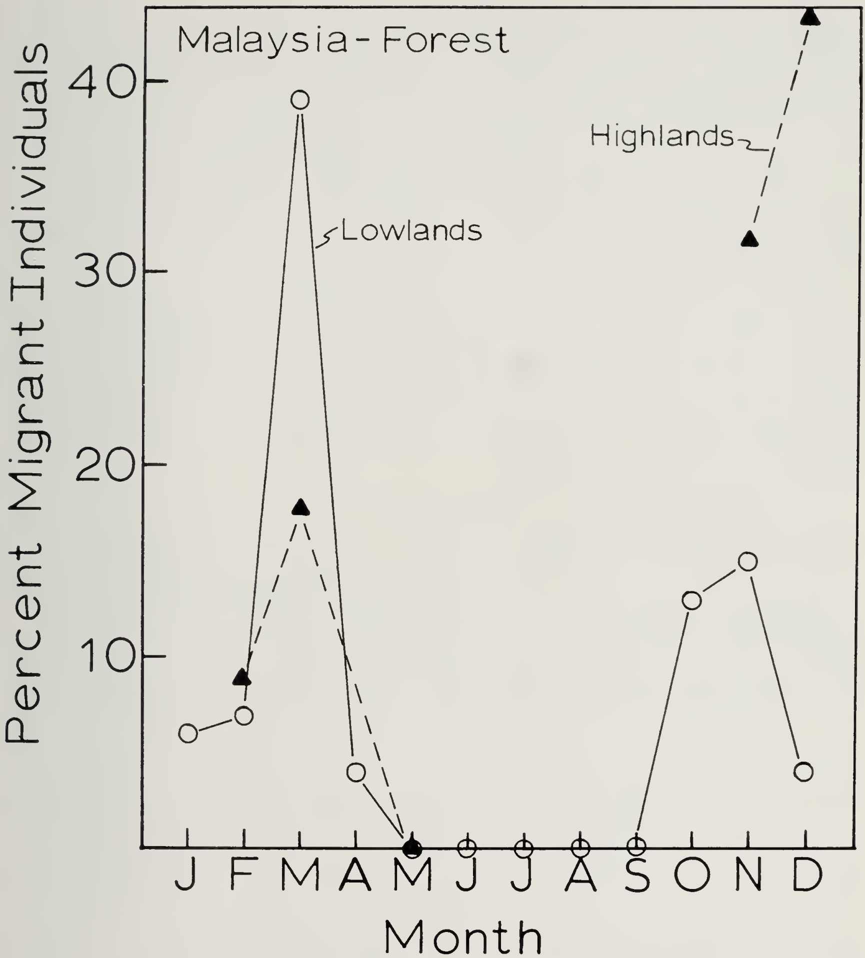


FIG. 2. Percent migrant individuals in mist-net samples from the lowlands and highlands of Malaysia. (From data in McClure 1964 and McClure and bin Othman 1965.)

Pasoh forest I captured 36 birds in 211 hours (1 bird per 6 hours) (Table 3). Only 3 of the individuals (8.3%) were migrants. Dr. David Wells of the University of Malaya kindly provided me with an extensive set of data for a mist-net sample from the same forest area. His data, collected in February, include 33 migrants in 185 captures (17.8% migrants; Table 3). Although the exact number of net hours is not known, about 1500 hours of netting were conducted during the daylight hours of 4 days, yielding a capture rate of about one bird every 8 net hours.

I have limited mist-net data for another Malaysian forest site—Bukit Lanjang—which has been studied by the Institute for Medical Research at Kuala Lumpur. I netted in this area in mid-March and caught 40 birds in 3 days (160 net hours), giving the highest capture rate of the Asian samples at 1 bird per 4 net hours. Intensive research in this area for several years has resulted in a modified foliage configuration. From experience in the neotropics in similar circumstances I expected capture rates higher than at Pasoh. Although I expected high migrant densities, no migrants were among the 40 captures.

In summary, these observations from the Indomalaysian region suggest 2 major points: (1) for those species sampled by ground level mist-nets, densities of birds in Indomalaysian forests are significantly below those in African and neotropical forests; and (2) winter densities of migrants are higher in lowland and mid-elevation Indomalaysian forests than in similar African and neotropical habitats.

DISCUSSION

This and other studies clearly indicate several general patterns with respect to the magnitude of interactions between migrant and resident birds in tropical environments. There are (1) seasonal changes in number of migrants in the tropics that are correlated with changes in available food supply on their temperate breeding ground. In addition, the importance of migrants varies with (2) vegetation type, (3) elevation, and (4) food type within each of the major geographical areas. Finally, there is variation (5) among the continents and (6) between continents and adjacent islands in the significance and abundance of migrants. Other factors which may influence patterns of migration such as climate, distance, shape and position of host continent, topography, and location and orientation of mountain masses will not be discussed here. In the following discussion I shall summarize my own observations and will also freely draw on the studies of many others. No doubt many significant studies have been overlooked in this review, and much unpublished, relevant work is not cited. The volume of relevant literature is tremendous, and scattered in many publications. My apologies to those whose work I have overlooked.

Seasonal abundance of migrants.—Very few migrants occur in tropical areas from May to August. (For this and subsequent discussion, I exclude the shorebirds, osprey, and larids. Some individuals of these species spend the north temperate summer in Panama.) A few early arrivals are often noted in August and some of the last individuals to depart may remain into early May. October is generally the month of greatest migrant density as transients predominate (this study, Galindo and Mendez 1965, Morel 1968, Willis 1966, Leck 1972a). After the October peak, wintering densities are generally low. An increase occurs in the northward spring migration that is well below the fall peak in both number of species and number of individuals (Table 2, Fig. 1). In perhaps the most intensive study to date, Willis (pers. comm.) found that about 12% of the individuals on Barro Colorado Island were migrants in October. However, only 4% of the biomass was migrants as the average migrant individual is smaller than the average resident individual. One difficulty in interpreting the seasonal results of Willis is that they are for a composite of forest, second growth, and aquatic habitats. The low numbers of northward moving birds in March through May result from most species returning by the more direct route over the West Indies (Smith 1975). In addition, some migrants to Panama change habitats during the north temperate winter as food availabilities change (E. Morton, pers. comm.).

Peak migrant abundances in African savanna occurred in October with 47 individuals per 25 ha (Morel 1968). Rather than a decline followed by an increase in the spring migration as observed in Panama, there was a general decline until the next spring when all individuals had departed. This decline was presumably due to the long dry season in Morel's area which begins in late September and continues for 8–9 months.

In gallery forest migrant abundances were high in October, decreased in the November to January period, and then increased in the north temperate spring (Morel 1968). Morel attributed this to the movement of birds from the nearby savanna into the gallery forest where food resources were more abundant and regularly available.

In western Kenya the abundance of migrants in secondary thicket habitat declined from 60% of individuals (50% of biomass) in the fall passage period to 27% of individuals and 25% of biomass in the winter (Britton 1974). Similar seasonal changes occurred in acacia and cultivated habitats studied by Britton.

In the lowlands of southeast Asia the peak in migrant abundance occurred in March (39% of captures) (Fig. 2). Another peak occurs in November but it appears to be somewhat smaller than the March peak (McClure and bin Othman 1965). Densities in the overwintering period (December to February) are lower, averaging about 6% of captures. Generally only 1 or 2 migrant species are represented in these samples. At 1500 m on Mt. Binchang, McClure (1964) recorded the highest migrant densities (35–40% of captures) in November and December with lower densities in February and March (5–18%).

Vegetation type.—Several workers have examined changing abundances of migrants among habitats or vegetation types. Most recently Tramer (1974) determined the abundances of migrants and residents in dry tropical habitats in the Yucatan peninsula of Mexico. His studies were conducted on disturbed (garden), partly disturbed, and undisturbed habitats. Densities ranged from 3 to 8 birds per ha in the disturbed and undisturbed areas. Excluding one coastal study area, migrant species made up from about 8 to 36% of the individuals in his communities. The variance was high among study areas with the same degree of disturbance. In a study of wintering parulids in Jamaica, Lack and Lack (1972) tabulated the number of warblers of a variety of species seen per hour in several different vegetation types. In the wet lowlands, mangrove (12.4 warblers/10 hrs) and lowland park and garden habitats (9.0 warblers/10 hrs) yielded migrants at the most rapid rate and lowland forest (1.5) had relatively smaller numbers of parulids. A similar tabulation for limestone forest indicated the greatest abundances in periodically flooded areas at sea level (15.5). In riverine forest they observed 10.9 wintering warblers per 10 hours. Moderately moist secondary and cutover areas yielded birds at a more rapid rate (4.7–9.6) than did arid areas (0.7–2.5 birds per 10 hours). Tramer (1974) found his lowest density of migrants in a disturbed coastal area bordered by mangrove, while mangrove and flooded sea level forest had the highest migrant densities in the study by Lack and Lack (1972).

Migrants are more abundant in scrub and early forest habitats although they do use forest habitats to some extent, particularly in the northern portions of Central America (Willis 1966, pers. comm.). Moving to the south Willis found that the abundance of migrants decreased in tall forest. In South American forest, migrants were very rare, and in the Amazonian lowlands even forest edges and second growth had few migrants (Willis 1966). As discussed below this may be due to the cost of continued migration exceeding the disadvantage of staying in Middle America.

On Barro Colorado Island residents exceed migrant densities (including transients) in virtually all habitats. In old forest there are 26 resident individuals for each migrant while the numbers decrease to 12 to 1 and 2 to 1 for young forest and scrub habitats, respectively (Willis, pers. comm.).

I did not find any species of migrant that regularly used grassland habitats for wintering in my Central American studies but it was common to see large numbers of migrants in the dense thickets associated with riverine habitats. Similarly, Willis (pers. comm.) found that migrants were about 8% of the individuals in lakeshore habitats. In another paper (Karr 1976b), I have suggested that these riverine habitats may have played a significant role in the evolution of a distinct forest edge avifauna in Central America, while no such forest edge fauna seems to have developed in Africa. Perhaps riverine habitats also have been important in providing a wintering ground for migrants from North America. The activities of man in clearing of forests

(Slud 1960) during the last 10,000 to 20,000 years may have increased the habitat available to these 2 groups of birds. As E. S. Morton has emphasized (pers. comm.) large areas of cleared forest are not optimal for migrants; rather many migrants are well adapted to using mosaics of cut over and mature forest.

In Africa, also, there are significant variations in the density of migrants with vegetation type. As early as 1952, Moreau pointed out that desert and evergreen forest habitats supported few if any Palearctic migrants. In a comprehensive analysis of the Palearctic migrants of Nigeria, Elgood et al. (1966) found that most species winter in dry woodlands (Guinea savanna) and in the semi-arid (Sahel) savanna. These 2 habitats and "derived savanna" (savanna modified by human disturbance) each contained 20 or more wintering species. Coastal habitats in Nigeria (including mangrove) harbored 14 Palearctic species. Mangrove forests of the Gambia were found to contain large numbers of migrants (Cawkell 1964, Cawkell and Moreau 1963). For the terrestrial birds of the Accra Plains in Ghana, about 15% of the species are migrants, including both Palearctic and Ethiopian birds that do not breed in Ghana (Grimes 1972). In general, the results of Elgood et al. (1966)—most migrant species winter in savanna and dry woodland habitats—agree with studies throughout Africa (Morel and Bourliere 1962, Brosset 1968, Morel 1968, Pearson 1971, Thiollay 1970a,b, Moreau 1972, Karr this study and pers. obs.). Neotropical birds use cutover, parkland, and late second growth in areas of high rainfall while relatively few Palearctic migrants in Africa use the rarer high rainfall habitats. Rather they prefer the more open dry savanna and parkland areas, habitats that are little used by migrants in the neotropics.

A few studies in Africa have presented quantitative data on the densities of migrants, either absolutely or relative to resident species. Elgood et al. (1966) suggest that there may be 78 migrants per km^2 in Nigeria. Moreau (1972) uses this figure in one derivation of his estimate of 5000 million Palearctic migrants entering sub-Saharan Africa. Regrettably, this becomes circular as Elgood et al. used a 1961 estimate of Moreau's to derive their estimate of 78 per km^2. Moreau (1972) cites estimates of Pearson (1971) that wintering passerines number 2 to 5 per ha in cultivated areas. In the rank grass adjacent to the lake at Kampala, Uganda he estimated densities of 75 per ha with densities somewhat lower (about 25) in a variety of habitats near the lake. However, I found no references to densities of wintering passerines in Pearson (1971).

Several habitats studied by Britton (1974) in western Kenya contained strikingly different numbers of wintering migrants. In second-growth thickets, for example, 27% of passerines were migrants. In lowland wet forest 2%

were migrants (mostly at forest edge) while cultivated and acacia habitats had 18–19% migrants.

In West Africa the best studies are those of Morel in Senegal and Thiollay in Ivory Coast. Morel (1968) found that Palearctic migrants made up about 43% of the wintering individuals in dry acacia savanna of Senegal. Of the 97 species in his 25 ha study area, 32% (31 species) were migrants. In his gallery forest Morel (1968) found considerable year to year variation in the densities of wintering individuals. In the December to February periods of 1960 to 1962 he found densities varying from 9.5 to 20.5 per ha, which varied from 11 to 33% of the birds on the area. In a similar study of the Lamto savanna in Ivory Coast, Thiollay (1970a,b) found 165 species of birds with only 7% (11) of the species being migrants from the Palearctic. If one considers all migrants (Palearctic and Ethiopian), 30 species (18% of the fauna) are "grands migrateurs." According to Thiollay (1970a,b) densities of migrants on his savanna are much lower than those of Morel in Senegal mentioned above—only 6% of the species and 5% of the individuals. Several reasons for this striking dichotomy can be suggested. First, it is possible that the relative isolation of the Lamto savanna "protects" it from the large influx of migrants. Second, perhaps the increased distance to be travelled may limit the number of migrants that reach Lamto.

Willis (1966) suggested that the decline in migrants in Amazonia is due to the "general decline in numbers of migrants away from" North America. Since migration is so costly, it would be to each bird's advantage to end migration as soon as possible. This is especially true if mortalities on the wintering ground are as low as indicated below. If food resources are adequate in Middle America and the West Indies, little migration to South America would be expected. It seems unlikely that lack of food resources in the north prevents the movement of migrants into coastal areas of West Africa. When such West African areas contain savanna habitats many migrants are present. For example, a number of migrants visit the Accra plains of Ghana (Grimes 1972), and within a few years of the clearing of forest at Mt. Nimba in Liberia many migrants had moved into the newly opened grassland areas (Forbes-Watson, pers. comm.; Karr, pers. obs.). In addition many of the migrant species go farther south in the East African portion of their wintering grounds. For example, see maps in Moreau (1972) for *Oenanthe oenanthe* and *Saxicola rubetra.* A third and more reasonable alternative is suggested by Willis (1966); that is, migrants are not able to encroach in relatively stable areas. They are better able to "exploit environmental irregularity." From my own observations at Lamto I suspect that the complex interdigitation of ronier palm savanna and gallery forest habitats allows many species to get through the most severe season in much the same way that many insects survive the dry season better in areas where gallery forest is available (Janzen 1973). This seems to be true in Senegal (Morel 1968).

Relatively few studies seem to have been done on the numbers of species of migrants and their abundances in the Indomalaysian region. Brosset (1968) indicates that migrants are particularly numerous in Indian habitats, especially those modified by man. As outlined earlier in this paper perhaps 50 to 75% of the individuals in the forests across India at latitudes between Bombay and Delhi are migrants from the Palearctic. The lusher forests of south India contain relatively fewer but still large numbers of migrants (Karr, pers. obs.).

According to Medway (1972) 161 bird species are migrants to Malaysia during the northern winter, and most are found in "open or largely deforested country," including aquatic habitats. Ward (1969) also suggests that migrants avoid forest in favor of deforested areas. However, my own data and those of Wells (Table 3) and McClure (Fig. 2) indicate that perhaps 6–15% of the birds in Malaysian forest are Palearctic migrants. Only 24 of the 161 migrants to Malaysia occur in undisturbed forest, and their "importance in the ecology of this habitat is unknown" (Medway 1972). In a survey of Gunong Benom, Medway (1972) found only 11 migratory species in a transect from 200 to 2100 m. Fifteen of 173 (9%) species observed at the Gombak Valley forest in Malaysia and 25 of 145 (17%) species observed at the Khao Yai National Park were migrants (McClure, pers. comm.).

A lowland forest site in Malaysia studied for only 5 days by Medway and Wells (1971) contained 141 species in an area of 200 ha. Adding the observations of several others they accumulated a list of 156 species known from their Kuala Lompat study area. Twelve of these species were migrants and 8 more were partial migrants, species in which "at least some individuals leave Malaysia to breed further north." All species were classified according to habitat. Of the 12 Palearctic migrants, 8 were classed as forest or forest-edge species, 2 as aerial insectivores and 2 were found along rivers or in river bank vegetation. The 8 partial migrants included 6 forest and forest-edge species and 1 each from river edge and aerial sweep species.

In summary, lowland forest habitats seem to be avoided by migrant birds in Africa, and to a much lesser extent in the neotropics. Wintering migrants are more abundant in the lowland forests of India and Malaysia. Forests in India and southeast Asia with high rainfall often have relatively high densities of wintering migrants. Mahabaleshwar for example receives over 6200 mm of rain per year as compared with the 2600 mm for the Panama forest study area. However, over 95% of the rain at Mahabaleshwar falls in the 4-month period—June to September. Nine months of the rainy season are required to accumulate over 95% of the rainfall at the Pipeline Road in Panama. Perhaps the long dry season in the Indian area has resulted in a low diversity fauna which can easily be invaded by Palearctic migrants. Grassland and open savanna habitats are generally avoided in the neotropics but used very heavily in Africa. The habitats in the lowlands of Africa that harbor greatest densities of migrants are the various forms of semi-arid and dry woodland, while dry forest and second growth and river edge forest in wet areas are used by most migrants that overwinter in the neotropical lowlands. The nearest equivalent to the African semi-arid habitats in Panama is the Cocle Plains areas west of Panama City. Very few migrants occur in that area as winter visitors (Karr, pers. obs.).

Elevation.—For mainland Central and South America there is general agreement that montane and highland (1000 to 2500 m) provide winter homes for more migrants than do similar lowland habitats (Miller 1963, Willis 1966, Leck 1972a, pers. obs.). The Jamaican studies of Lack and Lack (1972) included surveys of mid-level and montane areas of both natural and disturbed habitat. Natural forest above 1000 m elevation contained about the same number of individuals (birds observed per 10 hours) as lowland forest (1.67 vs. 1.49). However, since we will see that migrant densities in the lowland forests are high, we cannot conclude that the high elevation forests of Jamaica have low densities of migrants; rather both lowland and highland areas have high migrant densities. Censuses in mid-level garden and parkland habitats have even higher encounter rates (14.5). No good data on the migrant portion of the fauna are available for mainland Latin America to my knowledge. Miller (1963) suggests that migrants made up about 10 to 15% of the winter avifauna in his cloud forest area at 2000 m elevation in Colombia. This seems a reasonable estimate in my experience. It is similar to the results of Tramer (1974) in dry forest in northern Central America where 6 to 18% of the wintering individuals were migrants. Smith (1975) estimated migrant densities at 1600 m in western Panama at 150 per ha, or 6000 per 40 ha. This seems high to me and may not reflect a general pattern as much as a peculiar local circumstance.

Lowland wet forest data in Panama indicate that winter visitors make up about 1 to 3% of the avifauna. The densities of warblers are much higher in the mid-level forests of Jamaica than in lowland forests but their percentage of the passerine fauna is about the same in the 2 areas, near 30% (Lack and Lack 1972). Despite the high parulid densities, however, there are very few or no birds of groups such as orioles, grosbeaks, thrushes, tyrant-flycatchers, or vireos (Lack and Lack 1972, Ridgely, pers. comm.).

There are conflicting reports on the importance of highland areas as wintering areas for migrants in Africa. Brosset (1968) suggests that highland forests are of some significance in hosting Palearctic migrants but Elgood et al. (1966) state that the number of wintering species in highland areas is only slightly above the number wintering in wet forest areas. In the forests of Mt. Elgon in Kenya migrants are 10–12% of wintering passerines (Britton 1974). In agreement with Elgood et al., Moreau (1972) says that montane areas in Africa "harbour only a minute proportion of migrants and no species exclusively." That "elevation does not affect the distribution of migrants per se" in Africa (Moreau 1972) is not true in the neotropics. This general pattern is probably related to the extensive savanna and few montane habitats in Africa while in the neotropics the reverse is true.

In southeast Asia, B. King (pers. comm. *in* Leck 1972a) felt that migrants were especially abundant in the mountains of Thailand. My limited observations in the Malaysian highlands (Fraser's Hill) did not yield densities as high as those in neotropical forest at the same elevation, and at the same time of year. Of the 11 migrant species observed by Medway (1972) on Gunong Benom all were restricted to elevations below 1000 m and only 2 were observed above 700 m although some were taken as passage migrants at higher elevations. McClure (1964) reported high migrant densities in the highlands of Malaysia, especially in November and December. Migrants are more abundant in the highlands of Malaysia during southward migration and more abundant in the lowlands during the northward migration (Fig. 2).

Food resources.—Some of the best studies on the impact of migrants deal with patterns of food exploitation. In general, migrants in the tropics harvest superabundant and/or sporadically available resources. These include fruit and nectar (Leck 1971; 1972a,b,c), army ant swarms (Willis 1966), and grass fire and termite-emergence situations (Thiollay 1970b, Moreau 1972). Migrants are usually subordinate to resident species and they generally feed at peripheral or poorer foraging sites whenever residents are present. For example, Willis (1966) points out that migrants are frequently found at the less desirable swarms of *Labidus praedator* rather than swarms of *Eciton burchelli.* In general, it has been concluded that migrants exploit food resources not fully harvested by resident species (Morel and Bourliere 1962, Willis 1966, Thiollay 1970a,b, Moreau 1972). However, Miller (1963) felt that migrants might displace residents in Colombia, forcing them to feed in less competitive situations and even to the extent of restricting their reproductive season. Evidence accumulated to date seems to refute Miller's suggestions. In Sarawak, for example, Fogden (1972) found that the first 3 months of breeding in resident birds coincides with the time when visiting migrants are laying down migratory fat.

Lack and Lack (1972) examined the patterns of resource subdivision among Jamaican warblers (2 residents, 18 migrants) and found marked ecological differences segregating the 20 species. In addition they felt that the warblers did not significantly share ecological niches with other Jamaican birds. With respect to food types taken, Lack and Lack (1972) found that most species obtain at least 90% of their food as insects. The Cape May Warbler (*Dendroica tigrina*) is the only species that takes major amounts of fruit and nectar in its diet. Ridgely (pers. comm.) found the Tennessee Warbler (*Vermivora peregrina*) feeding on fruits and nectar in Panama. One hallmark of success of a number of migrants in Panama is their ability to switch food resources opportunistically; that is, to exploit available resources as they become available.

Leck (1972a) found that 10% of the feeding visits to fruit trees in Panama lowlands were by migrants compared to 45% in the highlands. In Puerto Rico 60% of the feeding visits to fruit trees were by migrants (Leck 1972c).

Of 34 migrants in Barro Colorado Island forests, 24 (76%) feed on small and 6 (18%) on large arthropods, 3 on small fruit, and 1 species feeds on reptiles and amphibians (Willis, pers. comm.).

Elgood et al. (1966) thought that virtually all terrestrial migrants from the Palearctic to Africa were insectivorous. More recent evidence indicates that perhaps 5% of the migrant species are primarily or exclusively seed eaters (Moreau 1972). However, most of these species winter north of 12° N, and are therefore out of the area considered here. Blondel (1969), Morel (1968) and others have shown that a number of migrant species exploit fruit resources rather heavily. Warblers of the genus *Sylvia* are known to exploit such fruits as *Lantana cantana* (Moreau 1972, Britton 1974). In my experience in Africa, concentrations of frugivorous species (migrants or residents) typical of the neotropics are rare (Karr 1975).

The competitive interactions of migrants in Africa have been examined from 2 perspectives. Of 90 migrant species in 6 African habitats 14 were without related native species as potential competitors (Moreau 1972). Nineteen others are segregated from native birds by feeding station and 32 differ significantly in size, an indication that they exploit different resources (Moreau 1972). Lack (1971) asked how much competition occurs among congeneric migrants in Africa and found that 64% had no contact with each other due to non-overlapping ranges. Habitat segregated 23%, foraging ecology separated 2%, and no obvious pattern of segregation was discovered for 10% of the species.

I have not been able to find discussions of food resources exploited by Palearctic migrants in Indomalaysia. Insects seemed to me to be the dominant source of food, although fruits are likely taken by some species.

Island vs. mainland.—Previous discussions have already hinted at the differences in migrant abundances and distributions between mainland and island areas. MacArthur et al. (1972) found wintering migrants to be about

25% of the fauna on Puercos Island in the Bay of Panama. This frequency is slightly higher than in the Pipeline Road forest area (Table 2) during the peak of the fall migration, and about 10 times higher than the overwintering (December) density in that forest. Similarly, Terborgh and Faaborg (1973) found island densities in Puerto Rico and Mona Island to be about 10% of the total avifauna. Abundances of migrants on Jamaica were as high as 30% of the total passerine fauna (Lack and Lack 1972).

Leck (1972c) found that the proportion of a fauna composed of migrant species increased from the mainland to islands and as island size decreased. This change was a result of the rapid decline in number of resident species, while the numbers of migrant species remained relatively constant.

Site faithfulness on wintering grounds.—Winter territoriality and long term residence is well documented for migrants on wintering areas. Examples from the neotropics can be found in Schwartz (1964), Willis (1966), Loftin and Child (1967 and papers cited therein), Karr (1971b) and Leck (1972a). Similar results have been reported for Africa (Moreau 1972, Table 19) and Malaysia (Medway 1972). However, as noted above, a number of species are known to change habitats as food availabilities change. Conservation efforts centered on the wintering grounds of migrants must exercise caution in formulating policies.

Conservation efforts in tropical wintering areas.—In a symposium on the avifauna of northern Latin America (Buechner and Buechner 1970) several contributors commented that wintering migrants in Central America are not in danger due to the destruction of forest since most use second-growth habitats as wintering grounds. This may be true for a majority of species but some, such as the Kentucky Warbler, may be specially adapted to wintering at low densities in tropical forest. Such species may be significantly affected by the recent rapid loss of lowland forest. Furthermore, small cleared areas in a mosaic of forest may be the optimal wintering habitat for many species. Extensive cleared areas do not provide that mosaic and will likely provide wintering grounds for few migrants.

In Africa it appears that habitat destruction by man adversely affects migrants (Moreau 1972). This is true not in the early stages of destruction where much second growth remains but rather in the intensively farmed areas south of Lake Victoria and in Nigeria. In these areas the destruction of virtually all shrub and tree growth has a significant effect, reducing migrant densities to near zero. Since no species winter in lowland wet forest of Africa the cutting of these areas should have little or no effect on Palearctic migrants.

SUMMARY

Variation in the intensity and objectives of studies on species which winter in tropical regions makes the derivation of a comparative synthesis difficult. An examination of my

own data combined with a review of published literature shows that the abundance of migrants from the temperate zone varies with (1) vegetation type, (2) elevation, (3) food type, and (4) season within each of the 3 major geographical areas considered in this paper. In addition, there is variation (5) between continents and adjacent islands and (6) among the continents.

With respect to vegetation type, lowland forest habitats are avoided in Africa, but support some birds in the neotropics and in southeast Asia. Grasslands and savannas are generally avoided in the neotropics but used heavily in Africa. Middle to high elevation areas support large numbers of migrants in the neotropics but relatively few in Africa. In southeast Asia the situation varies seasonally and among areas to a greater extent than in Africa and the neotropics.

In general, migrants harvest superabundant and/or sporadically available food resources. This often involves opportunistic shifting of food and habitat types during a single winter season. Migrant abundances seem generally to be highest during the fall passage period, lowest in the winter, and intermediate during the northward migration of the north temperate spring. Some seasonal movements associated with wet and dry season shifts and varying food abundances have been documented in various parts of the tropics. Finally, densities of migrants on islands tend to be higher than densities on nearby mainland areas.

In general, it appears that the evolutionary strategies of migrant birds are keyed to the exploitation of superabundant and/or sporadically available resources in their tropical wintering areas. These resources are often most easily exploited in disturbed, transitory, or isolated patches of habitat.

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LITERATURE CITED

Blondel, J. 1969. Synécologie des Passereaux Résidents et Migrateurs dans le Midi Méditerranean Francais. Centre Régional de Décomentation Pédagogique, Marseille.

Britton, P. 1974. Relative biomass of Ethiopian and Palaearctic passerines in West Kenya habitats. Bull. Br. Ornithol. Club 94:108–113.

Brosset, A. 1968. Localisation écologique des Oiseaux migrateurs dans la forêt équatoriale du Gabon. Biol. Gabonica 4:211–216.

Buechner, H. K. and J. H. Buechner. 1970. The avifauna of northern Latin America. Smithson. Contrib. Zool. 26:1–119.

Cawkell, E. M. 1964. The utilization of mangroves by African birds. Ibis 106:251–253.

——— and R. E. Moreau. 1963. Notes on birds in The Gambia. Ibis 105:156–178.

Diamond, J. M. 1975. Distributional ecology and habits of some Bougainville birds (Solomon Islands). Condor 77:14–23.

Elgood, J. R., R. E. Sharland, and P. Ward. 1966. Palearctic migrants in Nigeria. Ibis 108:84–116.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114:307–343.

Galindo, P. and E. Mendez. 1965. Banding of thrushes and catbirds at Almirante, Panama. Second year of observations. Bird-Banding 36:233–239.

Grimes, L. 1972. The birds of the Accra Plains. Univ. of Ghana, Accra.

Janzen, D. L. 1973. Tropical Agroecosystems. Science 182:1212–1219.

Karr, J. R. 1971a. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41:207–233.

———. 1971b. Wintering Kentucky Warblers (*Oporornis formosus*) and a warning to banders. Bird-Banding 42:299.

———. 1975. Production, energy pathways, and community diversity in forest birds. *In* Tropical ecological systems: trends in aquatic and terrestrial research (F. B. Golley and E. Medina, eds.), Springer-Verlag, New York.

———. 1976a. On the ecological correlates of rarity in a tropical forest bird community. Auk in press.

———. 1976b. Within- and between-habitat avian diversity in African and Neotropical lowland habitats. Ecol. Monogr. in press.

Lack, D. 1971. Ecological isolation in birds. Harvard Univ. Press, Cambridge, Mass.

——— and P. Lack. 1972. Wintering warblers in Jamaica. Living Bird 11:129–153.

Leck, C. F. 1971. Overlap in the diet of some neotropical birds. Living Bird 10:89–106.

———. 1972a. The impact of some North American migrants at fruiting trees in Panama. Auk 89:842–850.

———. 1972b. Seasonal changes in feeding pressures of fruit- and nectar-eating birds in Panama. Condor 74:54–60.

———. 1972c. Observations of birds at *Cecropia* trees in Puerto Rico. Wilson Bull. 84:498–500.

Loftin, H. and G. I. Child. 1967. Returns in 1965–66 of North American migrant birds banded in Panama. Bird-Banding 38:151–152.

MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. Ecology 33:330–342.

McClure, H. E. 1964. Avian bionomics in Malaya: 1. The avifauna above 5000 feet altitude at Mount Brinchang, Pahang. Bird-Banding 35:141–183.

———. 1974. Migration and survival of the birds of Asia. U.S. Army Medical Component, SEATO Medical Project, Bangkok, Thailand. 476 pp.

——— and H. bin Othman. 1965. Avian bionomics of Malaya. 2. The effect of forest destruction upon a local population. Bird-Banding 36:242–269.

Medway, L. 1972. The Gunong Benom Expedition 1967. 6. The distribution and altitudinal zonation of birds and mammals on Gunong Benom. Bull. Br. Mus. (Nat. Hist.; Zool.) 23:105–154.

——— and D. R. Wells. 1971. Diversity and density of birds and mammals at Kuala Lompat, Pahang. Malay. Nat. J. 24:238–247.

Miller, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. Calif. Publ. Zool. 66:1–78.

Morel, G. 1968. Contribution à la synécologie des oiseaux du Sahel sénégalais. Mem. ORSTOM 29, Paris.

——— and F. Bourliere. 1962. Relations écologiques des avifaunes sédentaire et migratrice dans une savane sahélienne du bas Sénégal. Terre Vie 109:371–393.

Moreau, R. E. 1972. The Palaearctic-African bird migration systems. Academic Press, New York.

Nisbet, I. C. T. and L. Medway. 1972. Dispersion, population ecology and migration of eastern great reed warblers *Acrocephalus orientalis* wintering in Malaysia. Ibis 114: 451–494.

Pearson, D. J. 1971. Weights of some Palaearctic migrants in southern Uganda. Ibis 113:173–184.

Rand, A. L. and E. T. Gilliard. 1967. Handbook of New Guinea birds. Weidenfeld and Nicolson, London.

Schwartz, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:169–184.

Slud, P. 1960. The birds of Finca "La Selva", Costa Rica: A tropical wet forest locality. Bull. Am. Mus. Nat. Hist. 121:1–148.

Smith, N. G. 1975. Spshing noise: Biological significance of its attraction and non-attraction by birds. Proc. Natl. Acad. Sci. 72:1411–1414.

Terborgh, J. and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk 90:759–779.

Thiollay, J.-M. 1970a. Le peuplement avien d'une savane préforestière (Lamto, Côte d'Ivoire). Thèse doctorat 3eme cycle, Institut Universitaire d'Ecologie Tropicale, Abidjan.

———. 1970b. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): Le peuplement avien. Terre Vie 24:108–144.

Tramer, E. J. 1974. Proportions of wintering North American birds in disturbed and undisturbed dry tropical habitats. Condor 76:460–464.

Ward, P. 1968. Origin of the avifauna of urban and suburban Singapore. Ibis 110: 239–255.

———. 1969. The annual cycle of the Yellow-vented Bulbul *Pycnonotus goiavier* in a humid equatorial environment. J. Zool., Lond. 157:25–45.

Willis, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187–231.

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EGGSHELL QUALITY: ITS ECOLOGICAL AND PHYSIOLOGICAL SIGNIFICANCE IN A DDE-CONTAMINATED COMMON TERN POPULATION

Glen A. Fox

Recent ornithological literature contains many references implicating organochlorine environmental pollutants, particularly DDE, in eggshell thinning and decreased reproductive success in bird- and fish-eating birds (see reviews by Cooke 1973, Jefferies 1973). The avian eggshell serves as a rigid container, a microbial barrier, the source of skeletal calcium, and the principal resistance to gaseous exchange for the developing embryo. All of these functions are presumably important to the successful hatching and survival of young birds.

In this paper I discuss the first field study in which the fate of individual eggs, *of known shell quality*, was followed in a single DDE-contaminated nesting population, and in which the chemical, ultrastructural, and respiratory characteristics of shells of eggs which failed to hatch were examined.

METHODS

Between 20 May and 20 August 1972, I made 44 visits to a colony of Common Terns (*Sterna hirundo*) nesting on a small island in Buffalo Lake, Alberta, Canada (52° 20′ N, 112° 50′ W). Each fresh egg was marked with the nest number and its sequence within the clutch and weighed to the nearest 0.01 g. I searched the colony for new nests on each visit, and recorded the contents of each nest at 48-hour intervals, weather permitting. All eggs were examined for cracks, dents, or evidence of pipping each time the nest was checked. Eggs which were cold when examined were placed on their large pole, and if they remained in that position on the next visit, they were regarded as abandoned.

Eggshell quality.—I measured the shell quality of each egg with a specially built portable beta-backscatter (BBS) gauge equipped with a 10 μc^{106} Ruthenium beta source (Fox et al. 1975, James and Retzer 1967, Voisey et al. 1969). The egg was suspended over the weak beta source and those beta particles which were reflected (backscattered) by the shell were detected by a Geiger-Meuller tube connected to a timer and counter. Backscattering is a simultaneous response to 3 distinct properties of the target: the mass of the constituents, their depth distribution, and crystalline structure (Nicolet et al. 1972). Hence, BBS is a simultaneous measure of thickness, density, and ultrastructure. It correlates highly ($r_s = 0.96$, $P < 0.01$) with the thickness index of Common Tern eggshells. The procedure adopted measured 3 well-separated areas on the waist of the egg, each of which was about 1 cm in diameter, and should be representative of the shell as a whole. Exposure of eggs to beta radiation, under these conditions of measurement, had no effect on hatchability.

Evaporative water loss of 50 randomly selected eggs was determined by weighing the egg on 2 or more visits. The surface area of the egg was calculated as 4.835 × fresh egg $\text{weight}^{0.662}$ (Paganelli et al. 1974) and used to calculate the evaporative water loss in mg/cm^2 per day. Only 46 of these eggs were incubated to term.

Eggs which failed to hatch, were damaged, or were abandoned, as well as samples of fresh eggs representing the range of BBS values encountered, were collected. Their contents were blown into labeled, pre-weighed hexane-rinsed glass jars with aluminum foil-lined lids and stored at 15°C. The inside of the shell was rinsed repeatedly with distilled water and then allowed to drain and air dry for 4 months at room temperature.

Lengths and breadths of air-dried shells were measured to the nearest 0.1 mm with a dial caliper. Their weight was determined to the nearest 0.001 g, or in the case of eggs in museum collections, 0.01 g. These measurements were used to calculate the thickness index (Ratcliffe 1967). Thickness indices were calculated for 87 Common Tern eggs from the collections of the National Museum of Natural Sciences (Ottawa), the Royal Ontario Museum (Toronto), and the Museum of Vertebrate Zoology (Berkeley). These eggs were collected from 9 colonies in Alberta, Saskatchewan, and Manitoba in 8 years spanning the period of 1894 to 1940 and should represent the geographic, temporal, and intra-clutch variability which existed in shells of this species on the Canadian Prairies prior to the introduction of DDT.

Samples (ca 1 cm^2) were cut from the waist of 31 shells using an abrasive disc. The average thickness of these samples with attached membranes was measured to 0.005 mm with a modified dial micrometer. The samples were weighed to 0.001 g, boiled in 2.5 N sodium hydroxide until the membranes were released, rinsed in distilled water, and allowed to digest in 10.0 ml of 0.1 N hydrochloric acid. Calcium content of the digest was determined by flame emission spectrophotometry, the magnesium content by atomic absorption spectrophotometry, and the phosphorus content colorimetrically by the method of Harwood et al. (1968). Calibration was based on dilutions of an aqueous standard.

Small fragments (ca 3 mm^2) were removed from the waist of selected shells for scanning electron microscopy. Three fragments were mounted on a single stub. One, untreated, was mounted face up. Another, treated with boiling 2.5 N sodium hydroxide to remove the membranes, was mounted face down. Pieces of untreated shell which had been cleanly broken from the egg were mounted in a perpendicular position. Thus it was possible to view the external surface, the internal surface with membranes removed, and the structural elements in sagittal section by examining 1 stub. The stubs with mounted shell fragments were coated with gold and examined using a Cambridge Stereoscan 4 scanning electron microscope. Photographs of representative and selected portions of these fragments were taken at standard magnifications. Contact prints of the resulting 58 cm^2 images were used for study and quantification. The total number of pore openings and the total number of mammillary bodies present in a representative field of the internal surface were recorded. All other observations were of a qualitative nature. There was much variation in the distribution of ultrastructural elements within the total surface area. However, by selecting the sample from the waist, which is the most uniform region of the shell, and by quantifying a representative rather than an exceptional field, I hoped that bias would be reduced and statistical comparison would be valid.

Organochlorine analysis.—The frozen egg contents were thawed and weighed to the nearest 0.01 g. The weight of the homogenate used in the clean-up procedure was corrected to the equivalent of 5.0 g of fresh egg contents by the following formula: 5.0 g × weight of total homogenate ÷ (weight of fresh egg − weight of air-dried shell). Food items were homogenized in their entirety. The homogenate was transferred to a mortar containing 50 g of florisil and ground to a free-flowing powder. This was added to a glass chromatographic column containing 50 g of florisil prewashed with methylene chloride:petroleum ether (1:1, V/V). The mortar and pestle were washed twice with 100 ml of petroleum ether:methylene chloride (4:1, V/V) and these washes added to the column. The eluate was collected in a 1-liter round bottom flask and flash evaporated to dryness. The residue was then dissolved in 10 ml of n-hexane. A Varian Aerograph 600 D gas-liquid chromatograph with a 250 μc tritium source electron capture detector and a 1.6 m glass column packed with a matrix of 10% DC-200 and 15% QF1 on 80/90 mesh Anakrom ABS was used for the separation and quantification of the compounds. The carrier gas was purified nitrogen at a flow rate of 70–85 ml/min. The oven temperature was 175° to 185°C. Only p′, p′DDE was quantified as it was the only organochlorine present in appreciable quantities. Sensitivity of detection of DDE was 0.05 ppm, and repoducibility of recoveries was ±0.25%.

Behavior.—One egg in each of 80 nests was displaced approximately 10 cm from the nest scrape, early and late in incubation, during special visits to the colony. The observer returned to the colony 30 min later and recorded whether or not the eggs had been returned to the nest scrape in the test period. Baerends (1969) has recommended egg displacement as a method of measuring the intensity of incubation instinct in larids.

All chicks were banded with a Fish and Wildlife Service band when first observed, and every attempt was made to ascertain the identity of the egg from which they hatched. The identity and condition of all chicks encountered was recorded on each visit. Depth perception and motivation of 55 chicks were tested on a visual cliff at 3 to 8 days post hatching. The visual cliff consisted of a 40 cm × 35 cm clear plexiglass platform immediately overlaying a sliding plywood "cliff" 30 cm deep, which was painted in a 2.5 cm^2 black checkerboard pattern, surrounded by a 15 cm high wooden fence. The testing procedure was to locate the "cliff edge" in the middle of the fenced field, and to place the chick on the plexiglass so it was looking over the "cliff edge." Chicks were allowed 3 min to choose the shallow or deep side by stepping backward or forward, respectively. Care was taken to ensure that the chick actually looked down at the plexiglass floor and "cliff edge" at least once during the test period. If the chick did make a choice, the procedure was repeated by sliding the "cliff" into a new position to correspond with the chick's new position, and the test repeated. Chicks which did not react in 3 min were recorded as "no response." If for any reason the response was questionable, the individual was retested later during the same visit or on the next visit. Chicks which were tested on 2 or more occasions were consistent in their response. An animal's response to the lack of visual support is unlearned (Walk and Gibson 1961). In the gulls, *Larus argentatus* and *L. atricilla*, a negative edge response is detectable in chicks less than 24 hours old (Emlen 1963, Hailman 1968).

Statistical analysis.—Non-parametric statistics were applied whenever possible as they are sensitive to differences in small samples and make no assumptions as to the nature of the population distribution or its variance (Siegel 1956).

NESTING SUCCESS

The Common Terns laid 473 eggs in 226 nesting attempts, resulting in a mean clutch size of 2.1 eggs. Of these eggs, 288 (61%) hatched. At least 133 of these 288 chicks (46%) survived 14 days. Eighty-three % of chick mortality occurred within the first 14 days, hence the figures of 0.28 14-day-old chicks per egg laid (0.59 per nesting attempt) closely approximates nesting success. Nisbet (pers. comm.) estimates that a minimal production of 1.1 fledged chicks/pair per year is necessary to maintain stability in the eastern seaboard population.

Langham (1968) and Nisbet (pers. comm.) have made intensive studies

TABLE 1

FATE OF EGGS FROM 3 POPULATIONS OF COMMON TERNS EXPRESSED AS A PERCENTAGE OF TOTAL EGGS LAID

	Location of colony		
	Buffalo Lake Alberta 1972[a]	Coquet Island Northumberland 1965[b]	Bird Island Massachusetts 1971[c]
	n = 456	n = 580	n = 103
Hatched	61***	88	97
Disappeared	5***	0	0
Cracked or dented	4*	1.5	0
Embryo failed	21***	3	2
Abandoned	6	5	0
Fledged young	28***	52	71

[a] This study, [b] Langham (1968), [c] Nisbet (pers. comm.).
* = $P < 0.05$; *** = $P < 0.001$; test for equality of 2 percentages (Sokal and Rohlf 1969).

of colonies on Coquet Island, Northumberland, and coastal Massachusetts, respectively. Their findings are presented in Table 1 as an arbitrary standard with which to measure the relative nesting success of the Buffalo Lake terns. The reproductive effort of Buffalo Lake terns was significantly less successful than these arbitrary standards. The poor success was largely the result of embryonic failure, egg disappearance, and egg damage.

Embryonic failure was responsible for at least 53% of the eggs which failed to hatch. Sixty-one % of these were addled, 17% died during the first week, 4% during the second, and 18% during the third week, including 14% which died while pipping. This distribution differs significantly from a constant rate ($P < 0.005$, χ^2), which might be expected if disturbance was the cause. Embryonic mortality and/or infertility occurred in 15–17% of eggs laid by Arctic Terns (*Sterna paradisaea*) nesting on Machias Seal Island, New Brunswick (Pettingill 1939, Hawksley 1957). Embryonic failure was observed in less than 5% of 868 eggs produced in recent nestings of Caspian Terns (*Hydroprogne caspia*) in Finland (Soikkeli 1973).

Thirteen % of eggs which failed to hatch disappeared. Gulls were repeatedly driven from the vicinity of the tern colony. The few eggs which were destroyed by the gulls were located in peripheral nests. Unincubated single eggs (dump eggs) were laid in all areas of the colony and remained intact as long as 28 days. This suggests that it was not unattended eggs which disappeared. The stage of incubation at which eggs disappeared differed significantly from random ($P < 0.025$, χ^2). Forty-eight % disappeared during the last week of incubation and another 36% after they had been incubated for at least the modal incubation period of 21 to 22 days. The distribution is very similar to that of eggs which were broken. Seventy-two % of broken eggs showed signs of microbial decomposition (malodor, discoloration, and abnormal consistency). Cracking and microbial decomposition were not independent ($P < 0.005, \chi^2$). Hence, there was an association among microbial decomposition, cracking, and egg breakage, and a similarity in timing and circumstances under which eggs disappeared or were broken. This suggests that nonviable and/or cracked eggs were detected by the parents and were broken (and eaten?) at the nest, or more frequently, carried away. This suggestion is supported by recent studies of DDE-fed Black Ducks (*Anas rubripes*) (Longcore and Samson 1973) and wild European Sparrowhawks (*Accipiter nisus*) (Newton 1973).

SHELL QUALITY AND ITS RELATIONSHIP TO NESTING SUCCESS

Shell quality, egg weight, and lipid content decrease in successive eggs of the clutch in the Common Tern (Dunn 1972a). Hence, any toxicant-induced variability in shell quality is superimposed upon natural individual and intra-clutch variability. This natural variability may mask any correlations resulting from the effects of toxicant-induced variability if eggs are considered independent of laying sequence.

Eggs were subdivided on the basis of their sequence within the clutch (*A*-, *B*-, and *C*-eggs) and were placed in 1 of 7 beta-backscatter (BBS) classes of equal width. Each class was ranked in the order of increasing shell quality. The various components of nesting success listed in Table 2 were calculated for each BBS class as percentages, and the values ranked on an ascending ordinal scale. The relationship of BBS to the components of nesting success was determined by comparing the rank of the component with the rank of the BBS class using Spearman's rank correlation coefficient (Table 2). As *A*-eggs are present in all clutches, and are usually of the highest quality, they were considered separately. The percentage of eggs with defects, and the percentage of eggs laid which disappeared were negatively correlated ($P < 0.05$) with shell quality, while the percentage of incubated embryos which hatched was positively correlated ($P < 0.01$) with shell quality. No correlation between shell quality and chick survival existed. Eggs which hatched had significantly ($P < 0.001$, Mann-Whitney U test) higher BBS values than those which were dented, cracked, or which disappeared, or in which the embryo died.

EGGSHELL CHARACTERISTICS WHICH ACCOMPANIED EMBRYONIC FAILURE

Shell thickness.—The distribution of thickness indices of the 87 eggs collected during this study was significantly different from the pre-1945 sample ($P < 0.01$, Kolmogorov-Smirnov 2-sample test, Fig. 1). Clearly, the thick-

TABLE 2
CORRELATION BETWEEN SHELL QUALITY AND SUCCESS OF EGGS OF KNOWN LAYING SEQUENCE

		BBS Classes (ranked in order of increasing shell quality)							Spearman Rank Correlation Coefficient
		1	2	3	4	5	6	7	
Percent of									
Eggs with defects[1]	A-eggs[2]	38.5	16.7	38.2	31.2	13.9	0.0		– 0.829*
	All eggs[3]	21.9	30.4	32.7	25.6	15.5	9.0	0.0	– 0.750*
Eggs laid which disappeared	A-eggs	23.1	12.5	3.6	4.2	0.0	0.0		– 0.900*
	All eggs	12.5	7.6	5.4	5.8	0.0	0.0	0.0	– 0.857*
Incubated embryos which hatched	A-eggs	57.1	82.3	78.9	93.9	94.1	100.0		+ 0.943**
	All eggs	78.3	82.7	85.5	94.9	89.6	100.0	100.0	+ 0.956**
Chicks hatched surviving 14 days	A-eggs	75.0	42.8	53.3	61.3	71.9	41.2		– 0.428
	All eggs	50.0	41.9	41.5	50.0	63.5	45.8	20.0	– 0.223

[1] Infertile, rotten, dented, or cracked.
[2] 1st egg laid, $n = 195$.
[3] $A + B + C$ eggs, $n = 416$.
$* = P < 0.05$; $** = P < 0.01$.

ness indices of the eggshells collected during this study are not normally distributed, hence the median is the appropriate measure of central tendency. The median pre-1945 thickness index is greater ($P < 0.0001$, median test) than that of the 1972 sample. The mean thickness index of the 1972 sample (omitting 3 anomalous very thick shells) was 0.889, 3.8% lower than the pre-1945 mean of 0.920. The mean thickness index of dented shells was 13.5% less ($P < 0.025$, Mann-Whitney U test) than the pre-1945 mean.

Shell chemistry.—The avian eggshell is composed primarily of calcium carbonate in the form of calcite (Heyn 1963, Simkiss and Taylor 1971). However, a large number of elements are present in trace quantities, some of which exist as impurities while others, including phosphorus and magnesium, are present in the form of salts. The chemical and physical characteristics of 28 shells collected in the Buffalo Lake colony in 1972, and 3 collected prior to the introduction of DDT, are summarized in Table 3. Although the calcium content of shells of eggs in which the embryos died did not differ from those of viable and pre-1945 eggs, their molar phosphorus concentration was 3 times higher. This increased phosphorus content is sufficient to bind calcium ions in the form of tricalcium phosphate or hydroxyapatite in equal numbers to those combining with carbonate ions to form calcium carbonate under normal conditions. The substitution of PO_3^{-3} for CO_3^{-2} ions in the calcite lattice has the following deleterious structural effects: (1) it distorts the calcite crystal because the foreign metaphosphate ions fit the crystal in

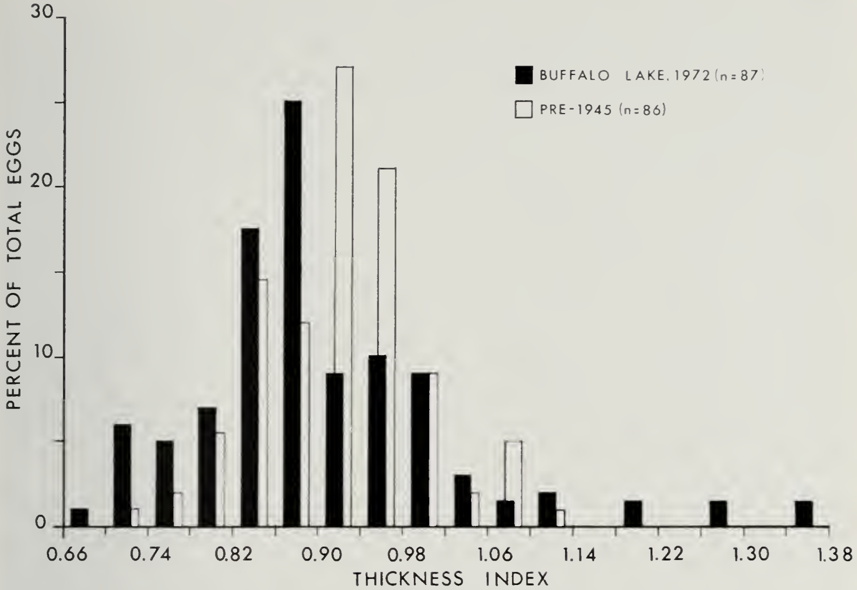

FIG. 1. Distribution of thickness indices of Common Tern eggshells collected in the Buffalo Lake colony in 1972 and of a pre-1945 sample from the Canadian Prairies.

2 dimensions but not in the third, and (2) it removes the electrostatic potential for the absorption of another layer of calcium ions, limiting crystal growth (Simkiss 1964). Dented shells were significantly thinner and weighed 13.3% less per unit surface area than shells of viable eggs but did not differ in their calcium content. Their increased phosphorus content may have been in part responsible for their reduced thickness and strength, and their higher Mg:Ca ratio may have increased brittleness (Brooks and Hale 1955).

Shell structure.—The calcified shell lies immediately external to the shell membranes. Its innermost or mammillary layer consists of roughly hemispherical knobs in the center of which there is an organic core of matrix substance representing the initial nucleation site of crystal growth. Fibers of the outermost shell membrane pass through these cores and firmly attach the membrane to the shell. Mammillae increase in diameter with distance from the membranes and ultimately fuse. The mammillary layer is continuous with the palisade or spongy layer which comprises most of the shell's thickness. The palisade layer has the mammillary bodies as its nucleation sites and thus the crystals are arranged in columns whose junctions are plainly visible in tangential section. Channels arise from some of the spaces between mammillae and pass through the palisade layer and open onto the outer shell

TABLE 3
PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE SHELLS OF COMMON TERN EGGS

	Pre-1945	Present Study		
		Living Embryo	Dead Embryo	Dented
n	3	12	11	5
Thickness, μ	200	197	205	175*
Thickness index	0.933	0.852	0.947	0.807*
Ca, mg/cm^2	13.18	10.54	11.34	10.80
Percent Ca	39.08	34.68	34.14	37.78
Percent Mg	1.80	1.54	1.43	2.10*
Percent P	0.27	0.24	0.86*	0.63*
Ca : P, molar	111.1	111.1	30.8*	45.5*
Mg : Ca, molar	0.076	0.073	0.069	0.092*

* Mean significantly different from shells containing living embryos ($P < 0.05$, t-test). Pre-1945 eggs not included in statistical comparisons.

surface in small depressions. These pores make gaseous exchange between the embryo and the atmosphere possible. The outer surface of the shell is covered with an organic cuticle. See Becking (1975) for a more detailed description of eggshell structure.

The differences in structure between shells of 10 eggs in which the embryo died and 4 from which chicks hatched are illustrated in Figs. 2–4. During the latter stages of normal embryonic development, calcium is withdrawn from the shell. This occurs at the mammillary cores, hence the eroded central depressions in the bases of the mammillae in Fig. 2A. This decalcification does not alter the number of mammillae, their size, or distribution, nor does it alter the number of pores. Egg failure was accompanied by a generally less-organized structure. Non-viable eggs had 21% fewer ($P < 0.025$, Mann-Whitney U test) mammillae per microscopic field and this decrease in number was accompanied by marked variation in size and shape. Pore openings visible on the inner surface were reduced by 44% ($P < 0.05$, Mann-Whitney U test). The columns, which normally fit tightly together, had irregular-shaped gaps between them, composed of crystals of varying orientation which appeared to replace pores in some cases (Fig. 3D). The palisade layer contained larger, more numerous globular inclusions (Fig. 3B), and in the case of thin shells, was markedly reduced in thickness.

An egg which collapsed on laying showed little development of the palisade layer, and consisted primarily of mammillae which were barely fused together (Fig. 4A). The shell showed normal pigmentation and thus was probably not extruded prematurely. The contents of this egg were severely desiccated 3 days after laying. Another egg, the apex of which was dented inwards

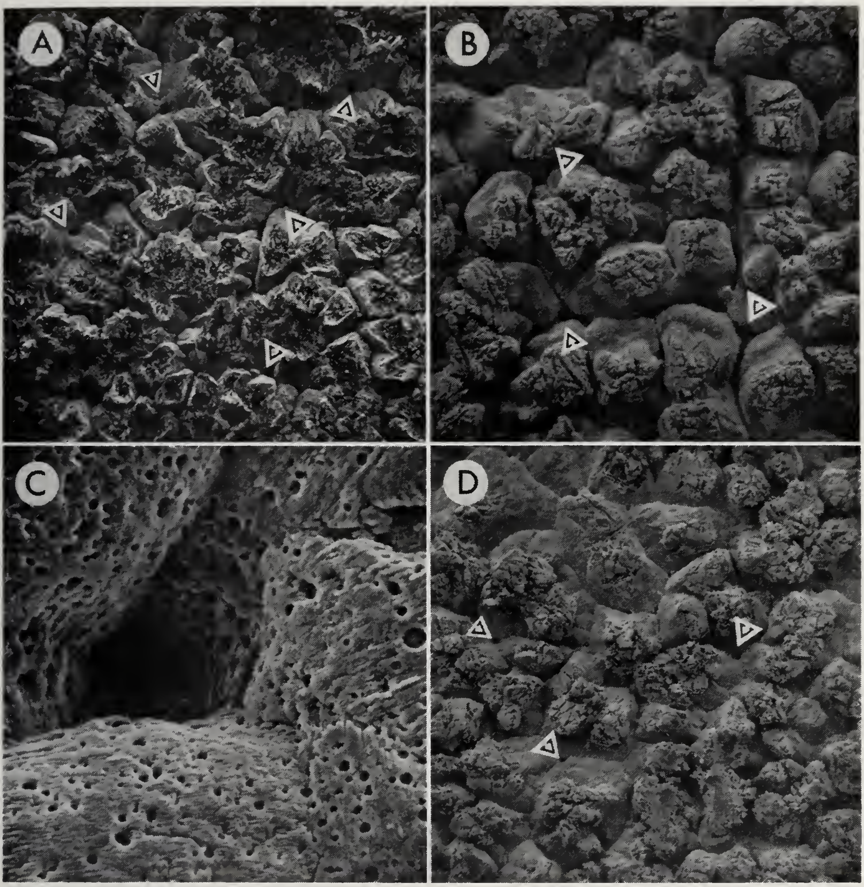

FIG. 2. Structure of Common Tern eggshells collected during this study. A, Inner surface of a viable egg with membranes removed (168×). Note the densely packed, evenly distributed mammillae and prominent pores (arrows). B and D, Inner surface of a non-viable egg with membrane removed (168×). Mammillae are larger, unevenly distributed, and less densely packed. Pores are fewer and less prominent. C, Outer surface of a viable egg with cuticle removed showing a normal pore (1690×).

upon laying, was also deficient in the palisade layer but complete fusion was attained (Fig. 4B). Fusion was attained rather close to the surface making the shell inherently weak. The number and distribution of mammillae was normal as was the external surface. Several eggs collected in this study showed globular projections on the outer surface (Figs. 4C and D), similar to those associated with chlorinated hydrocarbon contamination (Erben and Krampitz 1971, McFarland et al. 1971, Peakall et al. 1973).

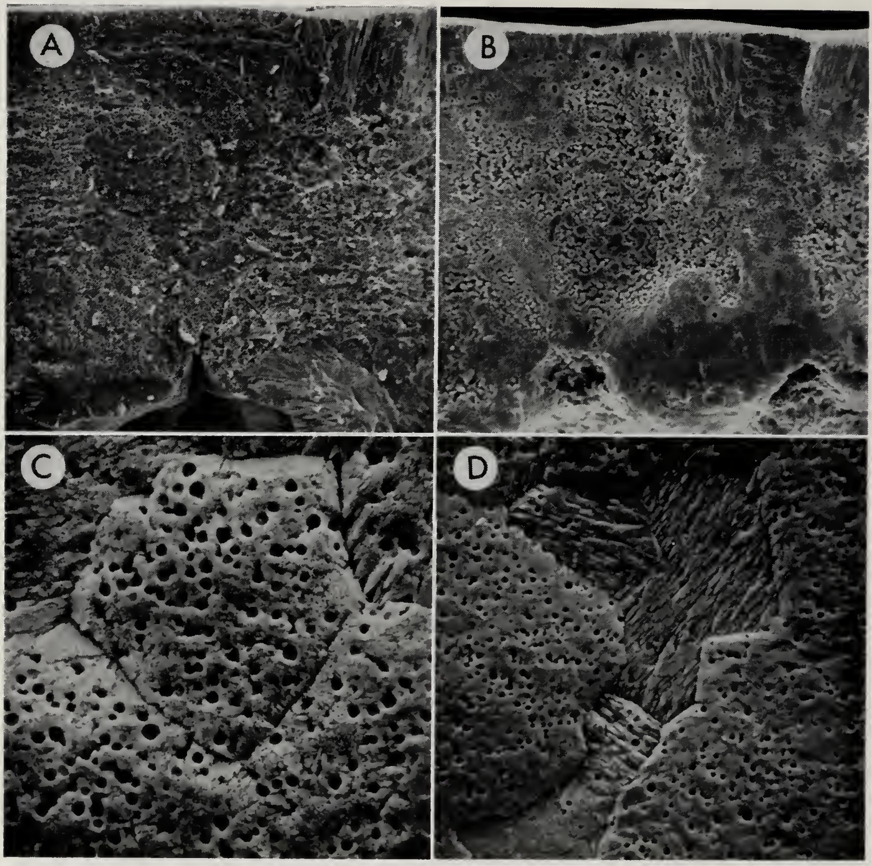

FIG. 3. Structure of Common Tern eggshells collected during this study. A, Radial view of broken edge of a viable egg (770×). Note tightly packed mammillae and even, spongy appearance. B, Same view of a non-viable egg (420×). The mammillae are less densely packed, and the palisade layer is disorganized and cavitated. C, Tangential view of the outer surface of a viable egg with cuticle removed (1680×). Note the close-fitting, regular-shaped junctions between columns. D, Same view of a non-viable egg (840×). Junctions between columns are irregular in shape and widely separated with prominent "plugs" of material showing varied crystalline orientation.

A reduction in number, irregular distribution, and increases in the size of mammillae or number of globular inclusions in the palisade layer are accompanied by reduced shell strength (Robinson and King 1970, Simons 1971). Peakall et al. (1973) induced changes in structure and breaking strength in Pekin ducks (*Anas platyrhynchos*) by feeding DDE. Longcore et al. (1971a) fed DDE to Black Ducks and observed an increase in the Mg:Ca ratio and

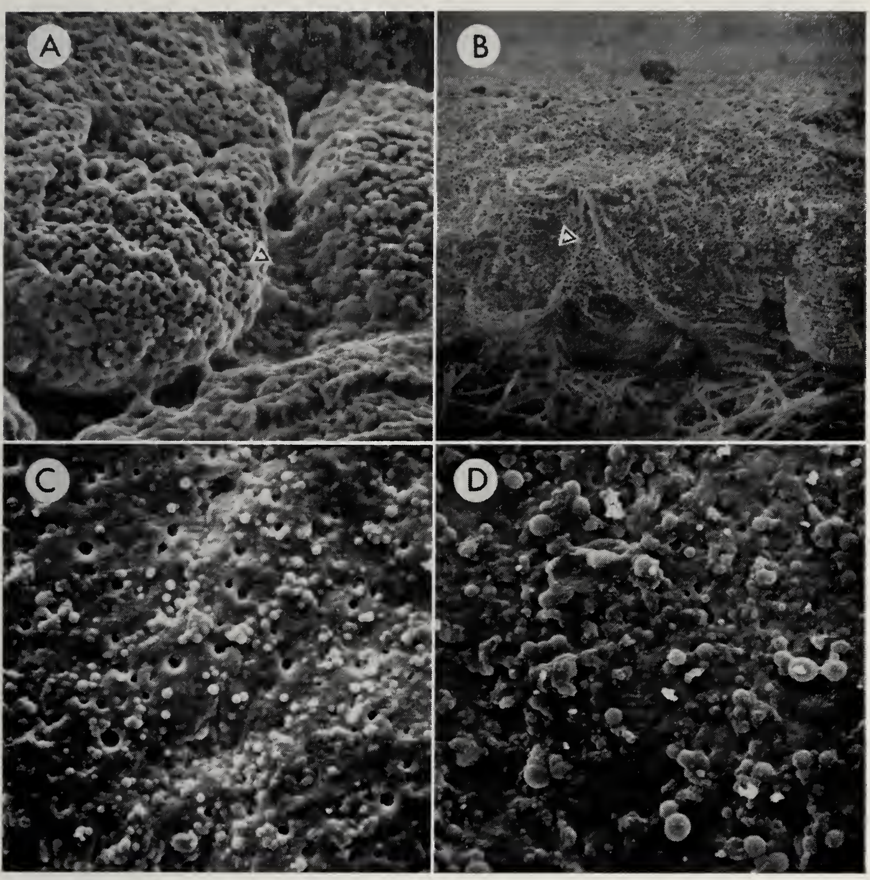

FIG. 4. Structural abnormalities in Common Tern eggshells collected during this study. A, Oblique view of outer surface of a shell which collapsed on laying (1680×). Note the prominent fissures between mammillae and absence of palisade layer. B, Oblique view of outer surface of a shell whose apex dented inward upon laying (840×). Note the poorly developed palisade layer, disorganized structure, and poor fusion. C and D, Views of the outer surface of two non-viable eggs (1680×) showing abundant globular projections which have been associated by other authors with organochlorine contamination.

a marked incidence of cracking of the eggshells. Erben and Krampitz (1971) concluded that the obvious abnormalities in recent Brown Pelican (*Pelecanus occidentalis*) eggshells were an increase in the number of globular inclusions and changes in the amino acid composition of the matrix substance, while Gould (1972) detected changes in the calcite:vaterite ratio. The matrix composition may determine what "morph" of calcium carbonate is deposited during biomineralization (Watabe and Wilbur 1960). Changes in amino acid composition of the matrix substance, which alter the net charge, could alter the number and distribution of nucleation sites, hence altering the number and distribution of mammillae.

Pore area and gaseous exchange.—Continuous water loss by the egg depends on the relative humidity of the microenvironment and the permeability of the eggshell to water vapor which is determined by the pore area (Wangensteen et al. 1970/71). The measurement of evaporative water loss during normal incubation can be used as a measure of pore area and gaseous exchange (Ar et al. 1974). The mean evaporative water loss of 26 eggs which were incubated but failed to hatch was 2.3 mg/cm^2 per day. This is significantly ($P < 0.0003$, Mann-Whitney U test) less than the mean of 3.8 mg/cm^2 per day attained by 15 eggs which hatched. This 39% difference implies a decrease in total pore area. Examination with the scanning electron microscope confirmed a marked decrease in pore numbers. Reductions in pore area or atmospheric oxygen concentration markedly reduce the hatchability of chicken (*Gallus gallus*) eggs (Taylor et al. 1956, Tazawa 1972, Wangensteen et al. 1974). Peakall et al. (1973) observed marked decreases in pore area of eggshells of DDT-fed American Kestrels (*Falco sparverius*), Ringed Turtle Doves (*Streptopelia risoria*), and Pekin ducks.

ORGANOCHLORINE RESIDUES

Forty-four eggs were analysed for organochlorine residues. Thirteen eggs were selected at random from the total available and were analysed individually. The remaining 31 were analysed in 5 pools of 5, and 2 pools of 3; each pool containing eggs with a common chemical or physical shell characteristic. This sample represents about 10% of the eggs laid and is biased towards eggs which failed to hatch or which were obviously abnormal. DDE and PCB's were present in all samples, dieldrin was present at trace levels. PCB's were present at approximately 1/10 the concentration of DDE but were not quantified. The mean DDE content of these 44 eggs was 3.98 ppm wet weight. A range of 0.05 to 11.08 ppm was encountered in the 13 individual eggs (geo. mean = 1.54 ppm). A pool composed of 5 eggs with dented shells, whose mean thickness index was 17% less than the pre-1945 mean, contained 6.67 ppm DDE (wet weight basis). almost twice the mean value of 3.42 ppm detected in the other 39 eggs ($P < 0.01$, modified t-test).

B. Switzer and colleagues (pers. comm.) found a highly significant negative correlation between shell thickness and DDE residues of 40 randomly collected eggs from a nearby colony. The mean DDE content of their random sample was 4.42 ppm wet weight, in contrast to 7.72 ppm in 13 eggs with dented shells ($P < 0.01$). The dented shells were 12% thinner than the random sample ($P < 0.01$). A DDE:PCB ratio of 9:1 was found in these eggs.

A pool of 10 food items collected from those brought to the colony, and constructed to represent the relative proportion each species contributed to the diet of the terns while present on Buffalo Lake, contained 0.02 ppm DDE. PCB's and dieldrin were absent. It is apparent that the body burden of DDE and PCB which is reflected in the eggs of Buffalo Lake terns is not accumulated on the breeding grounds. Recoveries of 8 terns banded in Alberta colonies indicate that they winter and spend the first 2 years of their life along the coast of Southern California (5), Mexico (1), El Salvador (1), and Peru (1). The coast of southern California is heavily contaminated with organochlorines (Burnett 1971, Risebrough et al. 1967). DDE:PCB ratios as high as 9:1 have been associated only with the Gulf of California. Hence it is likely that this is the site of contamination of the Alberta population.

Five eggs collected from the highly successful Coquet Island colony in 1965 contained a mean of 0.04 ppm DDE and food fish contained 0.03 to 0.08 ppm (Robinson et al. 1967). Thus, Buffalo Lake tern eggs contained 95 times more DDE than those of Coquet Island terns, whereas the levels in food fish in the areas of the 2 colonies were similar.

Eggshell thinning, increased egg breakage and/or disappearance, increased embryonic mortality, and decreased hatchability have been observed in controlled laboratory studies of American Kestrels (Porter and Wiemeyer 1969), Black Ducks (Longcore et al. 1971b), and Bengalese Finches (*Lonchura striata*, Jefferies 1971) fed low dietary levels of DDE. Studies of American Kestrels and Pekin ducks have shown that carbonic anhydrase levels in the shell glands vary inversely with dietary DDE and directly with shell thickness (Lincer 1972, Pritchard et al. 1972). Field studies of European Sparrowhawks (Newton and Bogan 1974) clearly show the relationship of shell thinning and organochlorine contamination to egg breakage, embryonic mortality, and hatching success.

SHELL QUALITY AND ITS RELATIONSHIP TO BEHAVIOR

No difference was detected in the tendency to retrieve an egg from the nest rim between parents who produced eggs with high and low quality shells. This is an indication that no difference in the intensity of incubation instinct accompanied the variation in shell quality observed. Enderson et al. (1973) detected no abnormalities in films of parental behavior of unsuccessful tundra Peregrines (*Falco peregrinus*). Peakall and Peakall (1973) present evidence that altered incubation rhythm resulted in increased embryonic mortality in PCB-fed Ringed Turtle Doves.

Seventeen tern chicks, 3 to 8 days of age, representing eggs from 17 clutches with high shell quality (BBS classes 5, 6, and 7) were tested on a visual cliff. Fourteen (82%) reacted to the visual situation, 13 (93%) of them chose the shallow side. In contrast, of 14 chicks of similar age representing 14 clutches with low shell quality (BBS classes 1 and 2), only 6 (43%) reacted to the visual situation and only 4 (66%) chose the visually shallow side. This behavioral difference was independent of fresh egg weight and weight or age of the chick at testing. The difference in the proportion of chicks reacting to the visual situation is marginally significant ($0.10 < P > 0.05$, χ^2), and indicates a difference in motivation. The difference in the proportion of chicks choosing the visually shallow side is significant ($P < 0.05$, Fisher test) and is indicative of altered depth perception. Nisbet (pers. comm.) tested 150 chicks in the Massachusetts colonies in 1973, using identical equipment, and found 93% of those which responded chose the shallow side. The majority of his chicks reacted to the stimuli. The normal feeding pattern of tern chicks requires that they recognize the presence of a fish in the parent's beak and accurately and actively peck at the head rather than the tail of the fish (Quine and Cullen 1964). Hence good visual and depth perception are necessary. No differences in chick survival or growth could be associated with visual cliff performance. Survival and growth of *C*-chicks of Common Terns were positively correlated with the feeding performance of the male parent (Nisbet 1973). Terns are sight-oriented, plunge-diving predators and as such require high acuity and good depth perception (Dunn 1972b, Salt and Willard 1971). Hence altered visual perception, if it persists, could reduce an individual's feeding efficiency and thus reduce its chances of survival and lower its performance as a parent.

The feeding of dieldrin (Baxter et al. 1971) and PCB (Dalgren and Linder 1971) to penned pheasants (*Phasianus colchicus*) altered the visual cliff performance of their chicks. Revzin (1966) found that endrin, another organochlorine, selectively affects the avian ectostriatum, the visual projection area of the telencephalon. Levels required to produce perceptual deficits are much lower than those needed to produce overt behavioral disturbances. Altered visual perception of tern chicks in this study is likely the result of the presence of a toxicant in the egg contents, a toxicant which is capable of altering shell quality.

CONCLUSION

Although the rigidity, calcium content, and antimicrobial properties of the shells of the majority of eggs which failed to hatch did not differ from those of viable eggs, abnormalities in shell structure and composition were responsible for shell damage, which resulted in egg disappearance, and for embryonic death through hypoxia. Reduced pore area was not associated with any significant thinning.

Various chemical and structural abnormalities similar to those observed

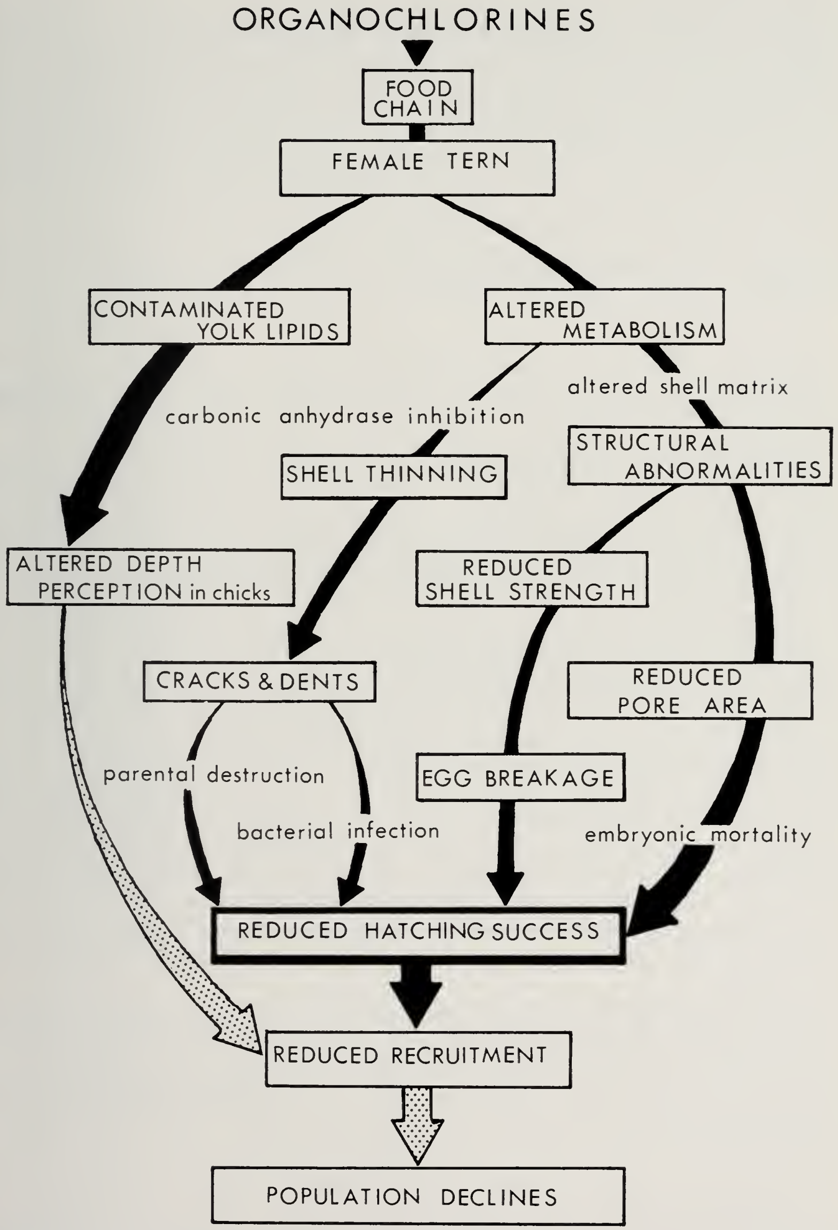

Fig. 5. The mechanisms and interrelationships by which organochlorines are thought to affect reproductive success in the Common Tern. Solid arrows indicate mechanisms which were observed in this study and shaded arrows represent postulated outcomes.

in this study have been induced in several species by incorporating DDE into their diet. Thus, there are several ways that organochlorines, and in particular DDE, can affect eggshells to induce embryonic mortality independent of shell thinning. In the Common Tern these mechanisms are operative at residue levels lower than those associated with marked shell thinning and are probably far more effective in reducing hatching success. Figure 5 is an attempt to indicate the mechanisms and relationships among factors involved in the "reduced hatchability syndrome" as we know them at the present time and as they are seen in the Common Tern. Whether they are functional in all species remains to be determined.

SUMMARY

A portable beta-backscatter gauge was used to measure the shell quality of 416 eggs laid in a colony of Common Terns located on Buffalo Lake, Alberta, Canada (52° 20′ N, 112° 50′ W) in 1972.

Eggshell quality as measured by beta-backscatter (a composite response to thickness, chemical composition and ultrastructure) was an important determinant of hatching success. Abnormalities in shell structure and chemical composition were responsible for shell damage, which resulted in egg disappearance, and for death through hypoxia. There were also indications that low levels of DDE contamination had detrimental effects on the visual perception of chicks. No difference in intensity of incubation instinct could be detected between parents who produced eggs with high and low quality shells.

Eggshells had a mean thickness index which was 3.8% lower than the pre-1945 mean for this geographical population. Denting of shells accompanied a 13.3% decrease in the thickness index which was not accompanied by a significant decrease in calcium content, but by increased molar Mg:Ca ratio. Both dented shells and shells of eggs in which the embryo died had significantly increased phosphorus contents when compared to shells surrounding viable embryos. Although small size of the pre-1945 sample prevented statistical comparisons, the chemical and physical characteristics of shells surrounding viable embryos were very similar to pre-1945 shells. Scanning electron microscopy revealed that shells of eggs in which embryos died had 44% fewer pores, and 21% fewer mammillae which were larger and more irregular in their distribution than those of shells of eggs which hatched. Evaporative water loss from eggs which were incubated but failed to hatch was 39% less than that from eggs which hatched, reflecting the reduction in pore numbers.

The mean DDE content of 39 eggs with nondented shells was 3.42 ppm wet weight, while 5 eggs with dented shells contained a mean of 6.77 ppm. PCB's were present at about $\frac{1}{10}$ the concentration of DDE. Food fish from Buffalo Lake contained a mean DDE content of 0.02 ppm wet weight basis. Hence, contamination is assumed to occur on the wintering grounds.

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LITERATURE CITED

Ar, A., C. V. Paganelli, R. B. Reeves, D. G. Greene, and H. Rahn. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. Condor 76: 153–158.

Baerends, G. P. 1969. The ethological analysis of incubation behavior. Ibis 101:357–368.

Baxter, W. L., R. L. Linder, and R. B. Dalgren. 1969. Dieldrin effects in two generations of penned hen pheasants. J. Wildl. Manage. 33:96–102.

Becking, J. H. 1975. The ultrastructure of the avian eggshell. Ibis 117:143–151.

Brooks, J. and H. P. Hale. 1955. Strength of the shell of the hen's egg. Nature 175: 848–849.

Burnett, R. 1971. DDT residues: Distribution and concentrations in *Emerita analoga* (Stimpson) along coastal California. Science 174:606–608.

Cooke, A. S. 1973. Shell thinning in avian eggs by environmental pollutants. Environ. Pollut. 4:85–152.

Dalgren, R. B. and R. L. Linder. 1971. Effects of polychlorinated biphenyls on pheasant reproduction, behavior, and survival. J. Wildl. Manage. 35:315–319.

Dunn, E. K. 1972a. Studies on terns with particular reference to feeding ecology. Ph.D. thesis, Durham Univ., Durham, England.

———. 1972b. Effect of age on the fishing ability of Sandwich Terns *Sterna sandvicencis.* Ibis 114:360–366.

Emlen, J. T. 1963. Determinants of the cliff edge and escape responses in Herring Gull chicks in nature. Behavior 22:1–15.

Enderson, J. H., S. A. Temple, and L. G. Swartz. 1973. Time-lapse photographic records of nesting Peregrine Falcons. Living Bird 11:113–118.

Erben, H. K. and G. Krampitz. 1971. Eischalen DDT-verseuchter Vögel: Ultrastruktur und organische Substanze. Akad. Wiss. Lit. Abh. Math-Naturwiss Kl. (Mainz) 1971: 31–64.

Fox, F. A., F. W. Anderka, V. Lewin, and W. C. MacKay. 1975. Field assessment of eggshell quality by beta-backscatter. J. Wildl. Manage. 39:528–534.

Gould, R. W. 1972. Brown Pelican eggshells: X-ray diffraction studies. Bull. Environ. Contam. Toxicol. 8:84–88.

Hailman, J. P. 1968. Visual cliff response of newly-hatched chicks of the Laughing Gull *Larus atricilla.* Ibis 110:197–200.

Harwood, J. E., R. A. van Steenderen, and A. L. Kuhn. 1968. A rapid method of orthophosphate analysis at high concentrations in water. Water Res. 3:417–423.

Hawksley, O. 1957. Ecology of a breeding population of Arctic Terns. Bird-Banding 28:57–92.

Heyn, A. N. J. 1963. The crystaline structure of calcium carbonate in the avian eggshell. An electron microscopic study. J. Ultrastruct. Res. 8:176–188.

James, P. E. and H. J. Retzer. 1967. Measuring egg shell strength by beta-backscatter technique. Poult. Sci. 46:1200–1203.

Jefferies, D. J. 1971. Some sublethal effects of pp′-DDT and its metabolite pp′-DDE on breeding passerine birds. Meded. Fac. Landbouwwet. Rijksuniv. Gent. 36:34–42.

———. 1973. The effects of organochlorine insecticides and their metabolites on breeding birds. J. Reprod. Fertil. Suppl. 19:337–352.

Langham, N. P. E. 1968. The comparative biology of terns, *Sterna* spp. Ph.D. thesis, Durham Univ., Durham, England.

Lincer, J. L. 1972. The effects of organochlorines on the American Kestrel (*Falco sparverius* Linn.). Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Longcore, J. R., F. B. Samson, J. F. Kreitzer, and J. W. Spann. 1971a. Changes in mineral composition of eggshells from Black Ducks and Mallards fed DDE in the diet. Bull. Environ. Contam. Toxicol. 6:345–350.

———, F. B. Samson, and T. W. Whittendale, Jr. 1971b. DDE thins eggshells and lowers reproductive success of captive Black Ducks. Bull. Environ. Contam. Toxicol. 6:485–490.

——— and F. B. Samson. 1973. Eggshell breakage by incubating Black Ducks fed DDE. J. Wildl. Manage. 37:390–394.

McFarland, L. Z., R. L. Garrett, and J. A. Nowell. 1971. Normal eggshells and thin eggshells caused by organochlorine insecticides viewed by the scanning electron microscope. Proc. Annu. Scan. Elect. Micro. Symp. 4:377–384.

Newton, I. 1973. Success of Sparrowhawks in an area of pesticide usage. Bird Study 20:1–8.

——— and J. Bogan. 1974. Organochlorine residues, eggshell thinning, and hatching success in British Sparrowhawks. Nature 249:582–583.

Nicolet, M-A., J. W. Mayer, and I. V. Mitchell. 1972. Microanalysis of materials by backscattering spectrophotometry. Science 177:841–849.

Nisbet, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. Nature 241:141–142.

Paganelli, C. V., A. Olszowka, and A. Ar. 1974. The avian egg: Surface area, volume, and density. Condor 76:319–325.

Peakall, D. B., J. L. Lincer, R. W. Risebrough, J. B. Pritchard, and W. B. Kinter. 1973. DDE-induced egg-shell thinning: Structural and physiological effects in three species. Comp. Gen. Pharmacol. 4:305–313.

——— and L. M. Peakall. 1973. Effect of a polychlorinated biphenyl on the reproduction of artificially and naturally incubated dove eggs. J. Appl. Ecol. 10:863–868.

Pettingill, O. S., Jr. 1939. History of one hundred nests of Arctic Tern. Auk 56: 420–428.

Porter, R. D. and S. N. Wiemeyer. 1969. Dieldrin and DDT: effects on Sparrow Hawk eggshells and reproduction. Science 165:199–200.

Pritchard, J. B., D. B. Peakall, R. W. Risebrough, and W. B. Kinter. 1972. DDE-induced eggshell thinning in White Pekin Ducks *Anas platyrhynchos*: structural, physiological, and biochemical studies. Bull. Mount Desert Island Biol. Lab. 12: 77–79.

Quine, D. A. and J. M. Cullen. 1964. The pecking response of young Arctic Terns *Sterna macrura* and the adaptiveness of the "releasing mechanism." Ibis 106:145–173.

Ratcliffe, D. A. 1967. Decrease in eggshell weight in certain birds of prey. Nature 215:208–210.

Revzin, A. M. 1966. Effects of endrin on telencephalic function in the pigeon. Toxicol. Appl. Pharmacol. 9:75–83.

Risebrough, R. W., D. B. Menzel, D. J. Martin, Jr., and H. S. Olcott. 1967. DDT residues in Pacific sea birds: a persistent insecticide in marine food chains. Nature 216:589–590.

Robinson, D. S. and N. R. King. 1970. The structure of the organic mammillary cones in some weak egg shells. Br. Poult. Sci. 11:39–44.

Robinson, J., A. Richardson, A. N. Crabtree, J. C. Coulson, and G. R. Potts. 1967. Organochlorine residues in marine organisms. Nature 214:1307–1311.

Salt, G. W. and D. E. Willard. 1971. The hunting behavior and success of Forster's Tern. Ecology 52:989–998.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

Simkiss, K. 1964. Phosphates as crystal poisons of calcification. Biol. Rev. 39:487–505.

——— and T. G. Taylor. 1971. Shell formation. Pp. 1331–1343. *In* Physiology and biochemistry of the domestic fowl (D. J. Bell and B. M. Freeman, eds.), Academic Press, London.

Simons, P. C. M. 1971. Ultrastructure of the hen eggshell and its physiological interpretation. D. Phil. thesis, Landbouwhogeschool, Wageningen, Netherlands.

Soikkeli, M. 1973. Breeding success of the Caspian Tern in Finland. Bird-Banding 44:196–204.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.

Taylor, L. W., R. A. Sjodin, and C. A. Gunns. 1956. The gaseous environment of the chick embryo in relation to its development and hatchability. II. Effect of carbon dioxide and oxygen levels during the first four days of incubation upon hatchability. Poult. Sci. 35:1206–1215.

Tazawa, H. 1972. Gas exchange in the chicken embryo. Res. Inst. Appl. Electricity 20:1–15.

Voisey, P. W., J. R. Hunt, and P. E. James. 1969. A comparison of the beta-backscatter and quasi-static compression methods of measuring eggshell strength. Can. J. Anim. Sci. 49:157–168.

Walk, R. D. and E. J. Gibson. 1961. A comparative and analytical study of visual depth perception. Psychol. Monogr. (Gen. Appl.) 75:1–14.

Wangensteen, O. D., D. Wilson, and H. Rahn. 1970/71. Diffusion of gases across the shell of the hen's egg. Respir. Physiol. 11:16–30.

———, H. Rahn, R. R. Burton, and A. H. Smith. 1974. Respiratory gas exchange of high altitude adapted chick embryos. Respir. Physiol. 21:61–70.

Watabe, N. and K. M. Wilbur. 1960. Influence of the organic matrix on crystal type in molluscs. Nature 188:334.

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THE RELATIONSHIP BETWEEN BROOD SIZE AND AGE OF EFFECTIVE HOMEOTHERMY IN NESTLING HOUSE WRENS

Erica H. Dunn

Altricial birds when hatched are not able to maintain a constant body temperature, and the ability to thermoregulate develops gradually during the first weeks of life (Dawson and Evans 1957). Many authors have investigated this developmental pattern of thermoregulation by studying the abilities of individual nestlings outside the nest. The age at which a single nestling can thermoregulate at ambient temperatures below normal body temperature could be termed the age of "physiological" endothermy, and has been determined for at least 22 species (Dunn 1975).

In nature, the pattern of thermoregulatory development might be quite different than that studied in the past in laboratories, because nest and siblings would provide insulation for the individual nestling. There is some evidence that this is true (Mertens 1969, Yarbrough 1970, M. J. Hamas pers. comm.), although no systematic study has been made to date. If insulation of nest and sibling is substantial, the age at which wild birds can thermoregulate would be advanced over the age of physiological endothermy. A lowered age of "effective" endothermy could be important to adult birds in allowing them to stop continuous brooding sooner than if the nest provided no insulation.

The following data for the House Wren (*Troglodytes aedon*) were taken to test the idea of a difference in ages of physiological and effective endothermy and to see if such a difference varied with brood size. Previous work on this species (Kendeigh and Baldwin 1928, Kendeigh 1939) provide extensive data on physiological development with which to compare my work done under natural conditions.

MATERIALS AND METHODS

The study was carried out in June and early July 1974, near London Grove, Chester Co., Pennsylvania. Nest boxes with internal dimensions of 15 × 15 × 30 cm were placed in old fields. Wrens half filled boxes with sticks, and made a small nest cup in one corner of the box, about 5–6 cm wide and equally deep. The cup was usually lined, often with feathers and occasionally with bits of plastic bag or snake skin.

I followed growth in 8 broods. Nestlings were weighed to the nearest 0.1 g with a spring balance, and measurements to the nearest mm were made on the 7th primary (both sheath and distance from skin to tip of erupted feather) and 2 or 3 feathers each on the flank and back.

Temperature studies took place only on cool mornings (between 14 and 23°C), to avoid using boxes heated by solar radiation. Box interiors were usually only 1–2°C above ambient temperatures (T_a). A given nest was not investigated more than once a day.

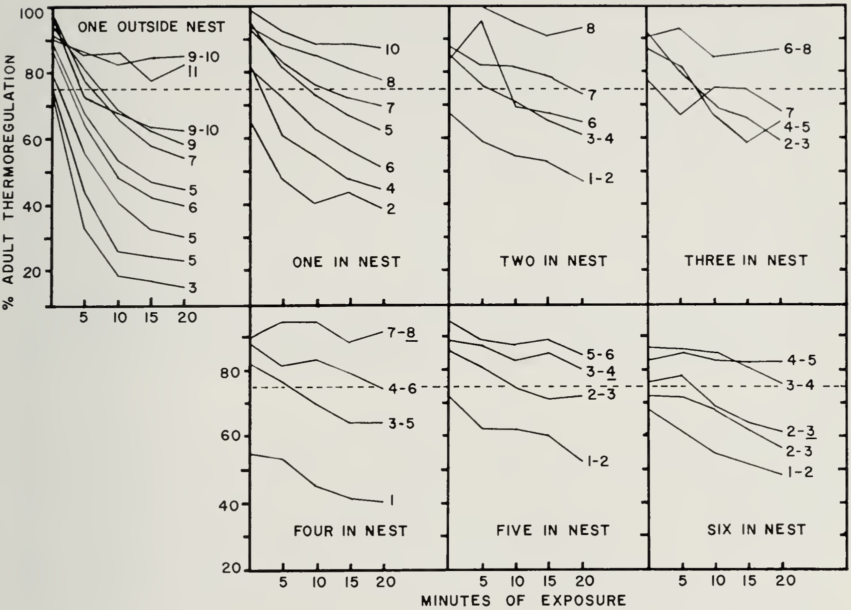

FIG. 1. Body temperature of nestlings after 5, 10, 15, and 20 min without brooding, expressed as percent of adult thermoregulation (see text). Each line represents one series of measurements on one brood. The age of nestlings involved is given at the end of each cooling curve, with the predominant age underlined where appropriate. The dotted line indicates the level of effective endothermy, defined as 75% of adult thermoregulatory abilities.

On my arrival at the nest, 3 Yellow Springs Instrument Co. telethermometer probes were immediately set up to simultaneously measure T_a, temperature in the nest box (at the surface of the sticks but away from the nest cup), and degrees body temperature of the nestlings (T_b). Readings were taken at 5 min intervals for 20 min. In most cases, initial T_b's were higher than T_b's after 20 min, indicating that an adult had been brooding prior to my arrival at the nest. In at least some cases, I must have arrived towards the end of the adult's inattentive period; thus, many of the periods of exposure to ambient conditions must have been longer than the 20 min of temperature readings.

Body temperature was measured by removing the nestling from the box and inserting the probe down its gullet. Although it would have been preferable to leave the nestling with inserted probe in the box throughout the measurement period, this proved impossible with the equipment at hand. Cooling through removal from the nest box was minimized, however, as I opened the box only to remove and replace the nestling, T_b measurement took less than a min, and a different nestling was used each 5 min when possible.

The easiest way to present the data would be to plot cooling rate against time. However, T_a differed from day to day, making thermoregulatory performances of nestlings on warm days appear to be better than they would be on cool days. Thermoregulatory

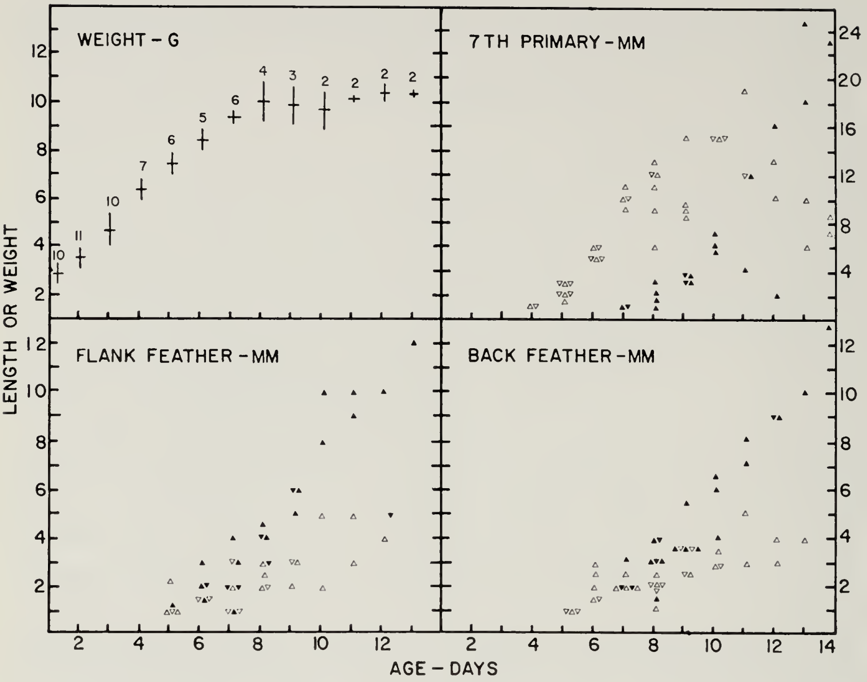

FIG. 2. Weight and feather development of House Wren nestlings. Weight data include mean (horizontal line), S.D. (vertical line), and sample size for each age. Feather lengths are shown for all individuals measured. The solid symbols show the amount of feather out of the sheath, while open symbols represent sheath length.

performance of the young was therefore standardized by expressing the difference in degrees between T_a and T_b as a percentage of the degrees between T_a and normal adult T_b (40.4°C, Baldwin and Kendeigh 1932). For example, if T_a was 20.4°, and nestling T_b was 30.4°, the nestling was thermoregulating 50% as well as an adult. Age of effective thermoregulation was arbitrarily defined as the age at which nestlings thermoregulated 75% as well as adults, after at least 20 min of exposure to T_a's below 23°C.

RESULTS

Figure 1 shows the results of nestling T_b measurements for different ages and brood sizes. Individual nestlings outside the nest cooled rapidly for 10 min, then more slowly, with physiological endothermy occurring at about 9–10 days. These data agree well with those of Kendeigh and Baldwin (1928), giving the age of physiological endothermy as 9 days. Also in agreement with Baldwin and Kendeigh was the noticeable rise in initial T_b (of young which presumably had been recently brooded) as the nestlings grew older.

TABLE 1

AGE AND WEIGHT OF HOUSE WREN NESTLINGS FROM BROODS OF DIFFERENT SIZES AT AGE OF EFFECTIVE ENDOTHERMY[a]

	out of nest	inside nest and nest box					
Brood size	1	1	2	3	4	5	6
Age-days	9–10[b]	7.5	7.5	7.5	5–6	3–4	3–4
Ave. weight (g)/nestling[c]	9.9	9.5	7.8–8.0	7.3–7.7	6.3	3.3–4.0	3.3–4.1

[a] See methods for definition.

[b] Age of these nestlings was not known any closer. In all other cases, a range indicates that no additional measurements were taken to pinpoint the exact age of effective endothermy.

[c] Weights taken from actual broods whose T_b's were measured, instead of from Fig. 2.

When a single nestling was left in the nest box, it was able to thermoregulate at 8 days, indicating a one day difference between ages of physiological and effective endothermy due to insulation of the nest and nest box. Although the 8- and 9-day-old young had both reached asymptotic weight, 8-day-old young had less complete feather development (Fig. 2).

When 2 or 3 nestlings were in a nest, the age of effective endothermy did not decline further (Fig. 1). Younger birds cooled more slowly in the larger brood sizes, however, and average weight per nestling was lower (Table 1). This suggests that insulation does increase with brood size, although too little to have an effect on age of effective endothermy.

Broods of 4 can effectively thermoregulate at about 5 days, when pin feathers are just beginning to appear and body weight is about ⅔ of asymptotic weight (Fig. 2). Broods of 5 and 6 thermoregulate at about 3–4 days, before feathers have even begun to appear and when body weight is only about a third of that at age of physiological endothermy.

That the age of effective endothermy does not drop progressively with the addition of each nestling may depend on the fact that nestlings in broods of 4 or more tend to lie heaped up in the nest cup in at least 2 layers, while 3 or fewer have room to lie next to each other. Surface exposure per nestling is thus much reduced in the larger broods.

DISCUSSION

Although both parents of House Wrens feed the nestlings, only the female broods. In the first 2 days after hatching, this takes about 50% of her time during daylight hours (Kendeigh 1952), and some brooding may occur as late as 10 days after hatching. Assuming that females stop brooding once their young can effectively thermoregulate, then the mother of a brood of 6 could spend about half the number of days on the nest as a mother of 3.

This would clearly be of an advantage in freeing her to do more foraging for her larger brood. In addition, each nestling would spend less energy on keeping warm, and would require less food (Mertens 1969), lending support to Royama's (1969) ideas on the advantages of larger clutches in cold climates.

The relationship between insulation, number of young, and timing of the end of brooding is not simple. As mentioned, 2 layers of nestlings thermoregulate sooner than one layer, so the thermoregulatory advantages of adding one nestling to the brood are not the same for all brood sizes. Also, my work was done at ambient temperatures below 23°C, and nestlings were likely faced with overheating on occasion. Measurements made under these conditions might show thermal advantages for smaller broods.

Other species of birds have nests with different insulative properties and location, and have nestlings with different patterns of feather and behavioral development. There are probably numerous patterns of thermoregulatory development in the wild, adapted to different ecological conditions in each case. The subject would be well worth pursuing.

ACKNOWLEDGMENTS

This work was done while I was a Research Associate at the Philadelphia Academy of Sciences. I appreciate the loan of equipment and criticism given by R. E. Ricklefs, as well as support from his N.S.F. grant (#GB 31554X).

LITERATURE CITED

Baldwin, S. P. and S. C. Kendeigh. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 3:1–196.

Dawson, W. R. and F. C. Evans. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. Physiol. Zool. 30:315–327.

Dunn, E. H. 1975. The timing of endothermy in the development of altricial birds. Condor 77:288–293.

Kendeigh, S. C. 1939. The relation of metabolism to the development of temperature regulation in birds. J. Exp. Zool. 82:419–438.

———. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22(1–3). Univ. Ill. Press, Urbana.

——— and S. P. Baldwin. 1928. Development of temperature control in nestling House Wrens. Am. Nat. 62:249–278.

Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits, *Parus major major.* Ibis 111:11–16.

Royama, T. 1969. A model for the global variation of clutch size in birds. Oikos 20: 562–567.

Yarbrough, C. G. 1970. The development of endothermy in nestling Gray-crowned Rosy Finches (*Leucosticte tephrocotis griseonucha*). Comp. Biochem. Physiol. 34: 917–925.

LONG POINT BIRD OBSERVATORY, BOX 160, PORT ROWAN, ONTARIO N0E 1M0.
ACCEPTED 23 JULY 1975.

GENERAL NOTES

Winter abundance patterns of North American kinglets.—The Golden-crowned (*Regulus satrapa*) and Ruby-crowned kinglets (*R. calendula*) are morphologically similar, small, insectivorous birds. They are widely sympatric in the nesting season in northern coniferous forests, although the Ruby-crowned Kinglet breeds considerably farther north. They winter together across much of the United States (Am. Ornithol. Union, Checklist, 1957). An interesting aspect of their distributions is that the Ruby-crowned Kinglet breeds farther north but winters farther south (to Guatemala) than the Golden-crowned Kinglet.

In this study, winter abundance patterns for the species were obtained from Audubon Society Christmas count data, and the correlations of these patterns with climatic variables were examined. From these we attempted to determine what factors of climate and (by inference) habitat were important to each species in the United States and southern Canada.

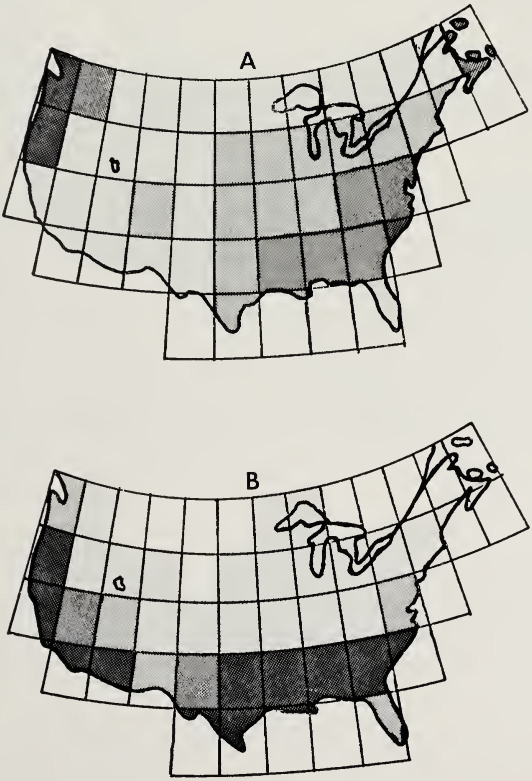

Fig. 1. Winter abundance patterns of (A) Golden-crowned and (B) Ruby-crowned kinglets, based upon Christmas count data for 1969, 1970, and 1971. Open blocks = no birds observed; four degrees of shading represent ⩽1, >1–3, >3–7, and >7 birds per 10 party-hours, respectively.

TABLE 1

CORRELATION COEFFICIENTS BETWEEN WINTER DENSITIES OF KINGLETS AND 50-YEAR MEANS OF CERTAIN CLIMATIC VARIABLES[1]

Variable	Correlation coefficients Golden-crowned Kinglet	Ruby-crowned Kinglet
Mean annual temperature	.215	.677**
Minimum temperature	.309*	.659**
Mean January temperature	.255	.681**
Number of frost-free days	.283*	.688**
Annual precipitation	.642**	.216
Winter precipitation	.801**	.216
Golden-crowned Kinglet	1.000	.327*

[1] Data are from 47 latitude-longitude blocks at least partially in the U.S.
* $P < .05$.
** $P < .01$.

Details of computerized data storage, retrieval, and analysis have been described elsewhere (Bock and Lepthien, Am. Birds 28:556–562, 1974). In this case we analyzed those Christmas counts which occurred south of 50° N latitude in 1969, 1970, and 1971 ($n = 2680$), published in *American Birds* (vols. 24–26). Counts were grouped by geographic blocks of 5 degrees of latitude and longitude, and the mean number of birds observed per party-hour of count effort was computed for each block (Fig. 1). The number of censuses falling in each block was highly variable, ranging from 3 to 280. However, 46 of the 51 blocks had 10 or more counts. Measures of climatic variables were adapted from maps published by the U.S. Dept. Agriculture (Climate and Man, Washington, D.C., 1941). The statistics program BMD 02R was used to determine the correlations of all the variables in a pairwise manner (Dixon, Univ. Calif. Publ. in Automatic Computations no. 2, 1971). Stepwise regressions also were run in an attempt to explain variation in the kinglet abundance patterns as they correlated with combinations of the climatic variables; see Bock and Lepthien (op. cit.) for a description of this technique.

Figures 1a and 1b show the winter abundance patterns of the Golden-crowned and Ruby-crowned kinglets based upon Christmas count data. It is apparent that the Ruby-crowned Kinglet predominated in the southern 2 tiers of blocks, in parts of the Great Basin, and in central California. The Golden-crowned Kinglet was more widely distributed, but centers of abundance were the northwest and southeast.

The table of correlations of kinglet densities with climatic variables (Table 1) shows a rather striking contrast between the species. Golden-crowned densities were more highly correlated with precipitation variables, particularly winter precipitation, while Ruby-crowned densities were related more to temperature variables, especially winter temperature regime. It also is interesting to note that the species' abundance patterns were not complementary; in fact, there was a slight but significant ($p < .05$) positive correlation between them. Stepwise regression was not especially illuminating, as there were no significant increases in the multiple *R* value after step 1 for the Golden-crowned Kinglet or after step 2 for the Ruby-crowned Kinglet. For the Golden-crowned Kinglet winter precipitation alone resulted in an *R* of .80 (see Table 1), while for the Ruby-crowned Kinglet number of frost-free days and mean January temperature gave a multiple *R* of .70.

The results of this study indicate that in spite of extensive sympatry, there is a major difference in selection of winter climate regime by the 2 kinglet species. Golden-crowned Kinglets evidently prefer areas with significant levels of winter precipitation (Table 1); from Fig. 1 it can be seen that these areas are the moist forests of the Pacific Northwest and the mixed hardwood-pine communities of the coastal plain in the southeast. By contrast, the Ruby-crowned Kinglet winters most abundantly in areas with warm winter temperatures (Table 1), regardless of the amount of precipitation; the habitats involved appear more variable than those where the Golden-crowned Kinglet is common. Ruby-crowned Kinglets occupy forest understory, open or "edge" situations, desert scrub, xeric oak woodland, and chaparral (e.g., Jewett et al., Birds of Washington State, Univ. Wash. Press, Seattle, 1953; Burleigh, Georgia birds, Univ. Okla. Press, Norman, 1958; Miller and Stebbins, The lives of desert animals in Joshua Tree National Monument, Univ. Calif. Press, Berkeley, 1964).

These species provide an interesting example of the ways in which migratory birds may respond to suitable habitats. During the breeding season the Golden-crowned Kinglet usually is associated with dense and substantial conifer forests—especially of spruce (*Picea*)—and it breeds north only to the limits of the closed boreal forest (Bent, U.S. Natl. Mus. Bull. 196:382–418, 1949). In winter it migrates to warmer, moist, conifer forests, or less frequently (Fig. 1) to hardwood forests. The structural configurations of breeding and preferred winter habitats therefore are generally similar. The Ruby-crowned Kinglet also breeds across boreal Canada in conifers, but unlike the Golden-crowned Kinglet it occurs north to the very edge of the taiga (Bent, op. cit.), revealing a tolerance of, or perhaps even a preference for, open or edge habitats. This tolerance or preference also manifests itself in winter, when Ruby-crowned Kinglets are common in such habitats as desert scrub and chaparral.

This project was supported by grant GB 36860 from the National Science Foundation. Frances James and Chandler Robbins kindly reviewed an earlier draft.—LARRY W. LEPTHIEN AND CARL E. BOCK, *Dept. of Environmental, Population, and Organismic Biology, Univ. of Colorado, Boulder, 80302.* *Accepted 15 Aug. 1975.*

Vocal mimicry in the Thick-billed Euphonia.—Snow (Wilson Bull. 86:179, 1974) recently discussed vocal mimicry in the Violaceous Euphonia (*Euphonia violacea*) on Trinidad. In this species only males are known to mimic and they have their own song in addition to imitations. The imitations are probably learned from models living nearby, and nearly all the calls imitated are unmusical and staccato. Many of them are alarm or contact calls (Snow, op. cit.).

Here I report on mimicking in the Thick-billed Euphonia (*Euphonia laniirostris*), a species largely allopatric to the Violaceous, which occurs from southern Costa Rica to northern Bolivia and the western Amazon basin in Brazil (De Schauensee, Birds of South America, Livingston Publ. Co., Narbeth, Pa., 1966:465). My observations are from the Panama Canal Zone and were made in 1970, 1971, and January and March, 1974.

Both sexes of the Thick-bill use an imitation as a call note when they are inactive, usually solitary, and sitting high up in a tree crown. One female was collected to make

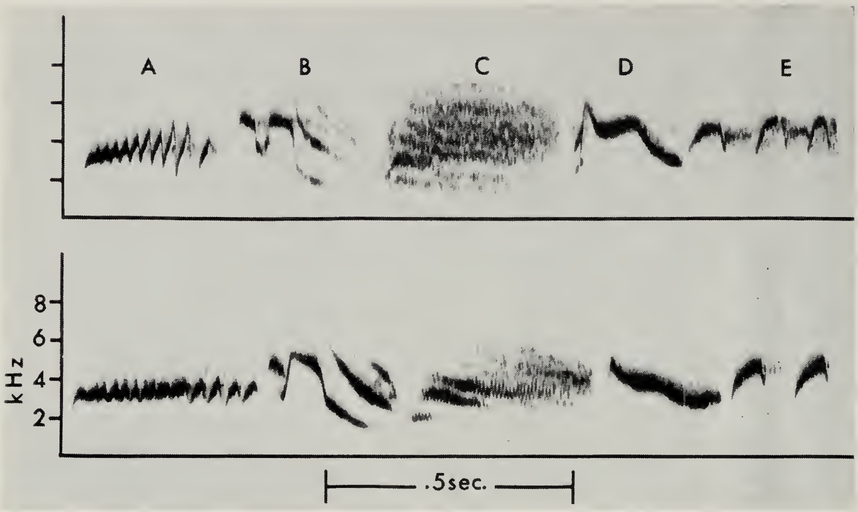

FIG. 1. Spectrograms (wide band filter setting) of calls mimicked by Thick-billed Euphonia (top) with the euphonia's imitation (bottom). A. Tropical Wood Pewee, *Contopus cinereus*; B. Social Flycatcher, *Myiozetetes similis*; C. Yellow-green Vireo, *Vireo flavoviridis*; D. Variable Seedeater, *Sporophila aurita*; E. Tropical Kingbird, *Tyrannus melanocholicus*. The spectrograms were positioned artificially, thus the time scale (horizontal axis) is indicated as a 0.5 sec interval, not continuous time.

certain that an immature male was not involved. The initial discovery that the Thick-bill imitates came in 1970 when, at Summit Gardens, Madden Lake Boy Scout Camp, and near Gamboa, I consistently heard them rendering the *peeayik* call characteristic of the common Paltry Tyrannulet (*Tyranniscus vilissimus*). In 1971, I called this note to the attention of E. Eisenmann, who thought *Tyranniscus* was calling until he saw the euphonia. In 1974 this same population was using the *peear* call note of the Variable Seedeater (*Sporophila aurita*) in the same context—none were heard imitating the Tyrannulet!

A second form of mimicking was discovered at Summit Gardens, Canal Zone, where I found 7 nests of the Thick-bill. The females, when frightened from the nest during incubation, or either sex when I was near a nest with young, would immediately begin imitating the calls of common birds nesting nearby. In every case where I knew the species being mimicked, it was the sound that the species would give if it were being frightened near its own nest (Fig. 1). The euphonia used the alarm calls of other species in their correct context and only imitated species nesting concurrently. In 2 instances euphonias evoked mobbing of me by Yellow-green Vireos (*Vireo flavoviridis*) by imitating the vireo's *nyaaah* alarm note. The euphonia remained still and continued mimicking when the vireos approached me.

The use of vocal mimicry to provoke mobbing may be the reason why many of the sounds imitated by the Thick-bill and the Violaceous Euphonias are "alarm" notes even when the birds use them in a social context. It is possible that mimicking to provoke mobbing was the origin of the mimicking habit but that it has since been incorporated into the euphonias' intraspecific social behavior as well.

Interestingly, although Snow (op. cit.) lists 2 thrush (*Turdus*) species as imitated by the Violaceous Euphonia, I never heard the Thick-bills mimic a thrush even though the Clay-colored Robin (*T. grayi*) was an abundant breeding species at Summit Gardens (Morton, Science 171:920, 1971). This robin's normal nest "defense," however, is to leave, so the euphonias may be selective in their choice of species to imitate, mimicking those that mob.

It should be clear that this report leaves more questions than it answers and I hope that this note stimulates studies of the ontogeny of mimicry in this genus.

I am grateful to Eugene Eisenmann for his stimulating discussions of tropical birds, to W. John Smith for making some of the recordings, and to the Smithsonian Tropical Research Institute and the National Geographic Society for providing funds for the study.
—Eugene S. Morton, *National Zoological Park, Smithsonian Institution, Washington, D.C. 20009.* *Accepted 16 May 1975.*

Observations of vocal mimicry in the Thick-billed Euphonia.—Snow (Wilson Bull. 86:179–180, 1974) noted 17 species imitated by the Violaceous Euphonia, *Euphonia violacea*, in Trinidad. During 8 months on Isla de Santa Sofia II, an island in the Amazon River about 32 km northwest of Leticia, Amazonas, Colombia, I noted the Thick-billed Euphonia, *Euphonia laniirostris*, incorporating the call notes of many species into its song on numerous occasions. Table 1 presents a list of 25 species imitated on 9 separate singing bouts for which I have detailed notes. All observations were from either the island in wet second-growth forest or from the adjacent mainland in swampy or flooded (varzea) forest, usually in edge situations. All model species occurred in the same vicinity as the euphonia as noted by Snow, 1974 for *E. violacea* in Trinidad. Robinson (Emu 74:9–10, 1974) found that lyrebirds (*Menura*) do most of their imitating at a time of year when the models are not breeding and presumably the imitated sounds have reduced significance for the models; unfortunately, I have no data on either the breeding seasons of the models or the euphonia. All euphonias I observed imitating were solitary, adult males.

This species imitates a remarkable variety of sound types from harsh screams to soft call notes. The imitations themselves are excellent and would be indistinguishable to my ear from the models if heard by themselves. This was also noted for *E. violacea* by Snow. In contrast to *E. violacea*, however, *E. laniirostris* gave songs which were either "pure" *E. laniirostris* notes or pure imitations. The imitation sequences consisted of 15–20 notes in quick succession, involving about 10 different species; thus models' calls may be repeated within a sequence but seldom in succession. Individuals used both pure sequences and imitation sequences in the same singing bout, these often following each other after only a pause of a second or so.

Four other species of euphonia (*E. minuta*, *E. xanthogaster*, *E. chlorotica*, and *E. rufiventris*) were seen regularly in the same habitat as (and, except *E. rufiventris*, often in the same flocks with) *E. laniirostris*, but none was ever heard to mimic other species. As Snow (op. cit.) reports, there are no published accounts of vocal mimicry in other species of euphonias. This, in addition to plumage and morphologic similarities and basically allopatric ranges, strengthens the position that *E. laniirostris* and *E. violacea* are very closely related.

TABLE 1

SPECIES IMITATED BY *EUPHONIA LANIIROSTRIS* IN AMAZONAS

Species imitated	Call imitated
Accipitridae	
Buteo magnirostris	"*peeéeeuuuuur*"
Helicolestes hamatus	"*whéeeaah*"
Cuculidae	
Crotophaga ani	"*foi?*"
Galbulidae	
Galbalcyrhynchus leucotis	"*kyew*"
Ramphastidae	
Pteroglossus castanotis	"*wheeep*" yelp
Picidae	
Melanerpes cruentatus	"*ttttt-huhuhu*"
Dendrocolaptidae	
Nasica longirostris	one note from the "whoooah" sequence
Sittasomus griseicapillus	portion of rising note sequence
Furnariidae	
Synallaxis albogularis	"*chéep-dududu*" antiphonal song
Formicariidae	
Myrmoborus lugubris	"*jeep*" alarm call
Tyrannidae	
Megarhynchus pitangus	"*jea-lelele*"
Myiozetetes similis	"*chi-chi-chi-chéw*"
Pitangus sulphuratus	"*kyew*" and "*kiskadée*"
Pitangus lictor	"*vweeeeee, vwee-vwee-vwee*"
Attila cinnamomeus	"*ka-whéeeoooo*"
Myiarchus ferox	"descending trill"
Myiarchus tuberculifer	mournful whistle
Camptostoma obsoletum	"*wheeeée-tututu*"
Tyranniscus gracilipes	"*what?*"
Tyrannulus elatus	"*pá-whéeeooo*"
Vireonidae	
Vireo olivaceus	alarm scold
Thraupidae	
Thraupis episcopus	"*vweet*"
Ramphocelus nigrogularis	"*chi*" and "*veet*" calls
Icteridae	
Icterus icterus croconotus	"*wha-wheeeeeeeeee?*"
Fringillidae	
Saltator coerulescens	"*cheenk*"

My research was supported by a National Science Foundation Doctoral Dissertation Grant and by the Frank M. Chapman Memorial Fund. I would like to thank David S. Dobkin and Frank A. Pitelka for useful comments on this note.—J. V. REMSEN, JR., *Museum of Vertebrate Zoology, Univ. of California, Berkeley 94720. Accepted 3 Jan. 1976. Page costs paid.*

Crop contents of Rock Doves in Virginia.—Little information has been published concerning the ecology and food habits of the Rock Dove (*Columba livia*) in the United States. This study describes contents of Rock Dove crops obtained in December 1972 at Blacksburg, Virginia.

Rock Doves were collected by shooting at roosts (i.e. building roofs and other structures) on the campus of Virginia Polytechnic Institute and State University. The crop contents of 144 Rock Doves were analyzed by identifying food species and volume. The *Seed Identification Manual* by Martin and Barkley (1961, Univ. Calif. Press, Berkeley) was used to identify seeds. Food items were separated and then volume was determined by displacement in a graduated cylinder that contained a known amount of water.

Data presented in Table 1 show the food items used by Rock Doves and the relative importance (% frequency) of each. Rock Doves examined in this study were heavily dependent upon local agricultural activities. Much corn is planted each year on the University farms, and grain and chopped corn silos are located 1–2 km from campus. Corn was found in 141 (97.9%) of all crops and accounted for 91.7% of the total volume of the contents of all 144 crops examined.

Gompertz (1957, Bird Study 4:2–13) noted that Rock Doves in London frequented areas where 4 species of wild food plants, including knotweed, were consistently found,

TABLE 1

MATERIALS FOUND IN ROCK DOVE CROPS, COLLECTED AT BLACKSBURG, VIRGINIA (N = 144)

Material	Number of crops	% occurrence	Volume	% of total volume
Corn, *Zea mays*	141	97.9	2439.0	91.7
Oat, *Avena* sp.	72	50.0	85.0	3.2
Knotweed, *Polygonum aviculare*[a]	38	26.4		
Cherry, *Prunus* spp.	33	22.9	97.0	3.7
Grit	27	18.7	2.5	0.1
Wheat, *Triticum* sp.	19	13.2	11.0	0.4
Barley, *Hordeum* sp.	18	12.5	14.3	0.5
Plant debris[a]	18	12.5		
Goosegrass, *Eleusine indica*[a]	12	8.3		
Pokeberry, *Phytolaca americana*[a]	6	4.2		
Crabgrass, *Digitaria ischaemum*[a]	6	4.2		
Millet (species undetermined)[a]	3	2.1		
Black locust, *Robinia pseudoacacia*[a]	2	1.4		
Sorghum, *Sorghum vulgare*[a]	2	1.4		
American elm, *Ulmus americana*[a]	2	1.4		
Poison ivy, *Rhus radicans*[a]	2	1.4		
Pigweed, *Amaranthus* sp.[a]	1	0.7		
Acorn, *Quercus* sp.[a]	1	0.7		
TOTAL			2648.8	99.6

[a] These materials combined yield 10.5 cc volume and 0.4% of total volume.

but he did not study crop contents of the Rock Doves. While we found wild seeds in a substantial proportion of crops, they contributed little in terms of total volume of food consumed by the Rock Doves.

It is interesting to note that the doves studied apparently did not frequent bird feeders, for only 1 crop contained seed that apparently came from such a source. We report crop contents of Rock Doves in a semi-rural environment; it would be valuable to compare data from a truly urban population with ours. Goodwin (1970, Pigeons and Doves of the World, The British Museum, London) states that in both urban and rural areas Rock Doves depend directly or indirectly on man for food sources. Our observations tend to support this conclusion.—THOMAS A. PIERSON, ROBERT G. COBB, AND PATRICK F. SCANLON. *Dept. of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State Univ., Blacksburg 24061. Accepted 19 Jan. 1976. Page costs paid.*

A probable Mourning × MacGillivray's Warbler hybrid.—Cox (Auk, 90:190–191, 1973) first reported and qualitatively described probable hybrid individuals between the Mourning Warbler, *Oporornis philadelphia*, and MacGillivray's Warbler, *O. tolmiei*. Cox's study was made in SW Alberta, Canada, in an area in which the species' breeding ranges contact each other at occasional points (Cox 1973). No measurements were presented.

On 22 May 1975, a male Oporornis was mist-netted in Johnson County, (eastern) Kansas. The bird was photographed (Fig. 1), carefully measured, banded, and released. Both the plumage characteristics and the measurements of this individual strongly suggest that the bird was a hybrid.

Phillips (Auk, 64:296–300, 1947) first stressed the importance of the wing minus tail ratio in MacGillivray's. Lanyon and Bull (Bird-Banding, 38:187–194, 1967) stressed this same characteristic in separating the Mourning from MacGillivray's.

In their study of *Oporornis*, Lanyon and Bull presented the following pertinent data (mm): For 65 male Mournings, the mean wing (flat) measurement was 62.3 ± 0.22; the mean tail measurement was 48.8 ± 0.19. For 87 male MacGillivray's, the mean wing (flat) measurement was 60.8 ± 0.19; the mean tail measurement was 54.3 ± 0.30. A wing minus tail ratio of 9 to 11 mm was considered to be within the "region of possible overlap" between the species (Lanyon and Bull 1967).

The individual which we netted had a wing (flat) measuring 62 mm and a tail measuring 52 mm, yielding a wing minus tail ratio of 10 mm. This measurement falls squarely between the species.

The adult spring male MacGillivray's is characterized by conspicuous white eyelid spots, blackened lores, and the absence of a black apron on the breast. Conversely, adult spring male Mourning lacks the white eyelid spots and blackened lores of MacGillivray's, and has a black apron on the upper breast (see generally Griscom and Sprunt, The warblers of America, Devin-Adair, New York, 1957).

The individual which we netted had only moderate, but quite noticeable, development of the white eyelid markings, heavily blackened lores, and less extensive black on the upper breast than in most typical spring male Mournings. Moreover, the black lores and the measurements show that this bird was not merely an unusual Mourning Warbler, a common migrant species in eastern Kansas (Allan R. Phillips, pers. comm.).

FIG. 1. A probable Mourning × MacGillivray's Warbler Hybrid.

Many authors have commented on the obvious similarity of these species. See, for example, Phillips (1947) and Lanyon and Bull (1967). Yet surprisingly little research has been done in a comparative sense. While this is apparently only the second report of probable hybrids of these species, more intermediates may be found with careful museum searches. Clearly, more field work in contiguous breeding areas is needed to better define the relationship of these species.

We wish to thank Dr. Allan R. Phillips for his most helpful correspondence, and Drs. Wesley E. Lanyon and George A. Hall for their helpful comments.—SEBASTIAN T. PATTI AND MARY LOUISE MYERS, *6528 Wenonga Terrace, Shawnee Mission, KS 66208.* *Accepted 21 Apr. 1976. Page costs paid.*

Change in status of Red-cockaded Woodpecker colonies.—A survey of Red-cockaded woodpecker (*Dendrocopos borealis*) colonies in 10 southeastern states was made in 1969–70 (Thompson and Baker, pp. 170–186 *in* The Ecology and Management of the Red-cockaded Woodpecker, R. L. Thompson, ed., Bureau of Sport Fisheries and Wildlife, U. S. Department of the Interior, and Tall Timbers Research Station, 1971, Tallahassee, Florida). During the fall and winter of 1973–74, 312 of these colonies were resurveyed by various observers and evaluated as to status by the presence of birds or by the amount and freshness of pine gum around cavities or resin wells on cavity trees. For those colonies judged inactive, the probable causative factor (timber management, land development, road construction, etc.) was noted whenever possible. The regional

TABLE 1
THE 1973–74 STATUS OF 312 RED-COCKADED WOODPECKER COLONIES WHICH WERE ACTIVE IN 1969–70

	LAND OWNERSHIP			
	Federal	State	Private	Total
ACTIVE	199	8	64	271
INACTIVE	19	3	19	41
CAUSATIVE FACTOR				
Timber harvest	11	2	7	20
Residential development	0	0	2	2
Commercial development	1	1	3	5
Road construction	0	0	1	1
Unknown	7	0	6	13

distribution of the colonies was: Alabama, 4; Arkansas, 16; Florida, 130; Georgia, 34; Louisiana, 20; Mississippi, 33; North Carolina, 9; South Carolina, 43; Texas, 20; and Virginia, 3.

The results of the survey are summarized in Table 1. The number of active colonies decreased by 13.1% during this 4 year period. The relative losses on federal, state, and private lands were 8.7, 27.3 and 22.9%, respectively. This 3.5% annual loss in the number of active colonies indicates that populations of this endangered species are still being subjected to considerable environmental stress.

The author gratefully acknowledges the efforts of those individuals who made the survey in their respective state and without whose concern this study would not have been possible. I thank Robert McFarlane for his comments on the manuscript.—RICHARD L. THOMPSON, *U. S. Fish and Wildlife Service, Department of the Interior, Tallahassee, FL 32301.* *Accepted 7 Apr. 1976. Page costs paid.*

Notes on two species of Bolivian birds.—In 1966 the Louisiana State University Museum of Zoology received a collection of Bolivian birds from Mr. Franz Steinbach. Among this material is a specimen of an adult female Rufous-thighed Kite, *Harpagus diodon,* in moderately worn plumage but showing no signs of molt. According to Meyer de Schauensee (The species of birds of South America and their distribution, Livingston Publ. Co., Wynnewood, Pa., 1970:40) this species has not previously been reported from Bolivia. The specimen, LSUMZ 37050, was collected by Steinbach at Buena Vista, Provincia de Ichilo, Departamento de Santa Cruz, on 30 May 1946. The LSUMZ also received in this same collection 3 specimens of the Double-toothed Kite, *H. bidentatus,* taken at the same locality, one of these having been collected on the same date as the *H. diodon.*

Also among this material are 2 specimens of the Unicolored Thrush, *Turdus haplochrous,* known in the literature only from the holotype, an adult female taken by Steinbach on 25 May 1918 at Palmarito on the Río San Julián, Provincia de Chiquitos, in the Departamento de Santa Cruz, and described by Todd in 1931 (Critical notes on the Neotropical thrushes, Proc. Biol. Soc. Washington 44:54). The 2 LSUMZ specimens, both of which are males, were also collected by Steinbach, but on the Río Mamoré, Provincia de Marbán, in the Departamento de Beni, 250–275 km northwest of the type locality. LSUMZ 36465 was collected on 4 April 1944 and LSUMZ 38084 was taken on 12 March 1944. Kenneth C. Parkes (in litt.) informed me that the Carnegie Museum received an additional specimen of this thrush (adult male, CM 119459) 15 years after having received the holotype. This specimen was obtained at the same place and on the same date as the holotype, but it was, for some reason, retained by Steinbach for inclusion in the second collection that he sent to the Carnegie Museum. Both of these birds are in quite fresh plumage and show no signs of the last of the molt. Parkes found that even though the 2 LSUMZ specimens were in exceedingly worn plumage, they did not differ significantly from the pair at Carnegie. I thank Kenneth C. Parkes for supplying information on the 2 specimens in his care and for comparing them to the 2 LSUMZ examples.—JOHN P. O'NEILL, *Museum of Zoology, Louisiana State Univ., Baton Rouge 70893.* *Accepted 9 Apr. 1976. Page costs paid.*

Breeding chronology and interspecific relations of Pied-billed Grebes in northern Minnesota.—I investigated waterfowl use of 10 beaver (*Castor canadensis*) flowages on the Chippewa National Forest in north central Minnesota during 1970 and 1971 in order to form a base line for later comparison of man-made impoundments with these natural areas (Kirby, M.A. thesis, S. Ill. Univ., 1973). The Pied-billed Grebe (*Podilymbus podiceps*) is common on the Chippewa Forest, but I observed only one grebe brood successfully reared on the beaver flowages studied in 1971. I here provide data on nesting chronology for northern Minnesota and some previously unrecorded observations of interspecific relationships of Pied-billed Grebes collected during the period from first open water in early April through the departure of grebes from the study areas in late summer.

Pied-billed Grebes arrive on the Chippewa shortly after open water first appears in the spring. In 1971 these birds were first observed 6 April on the Mississippi River below the Lake Winnibigoshish dam. Pied-bills were on smaller lakes by 12 April and were first seen on a beaver flowage 17 April, 2 days after first open water on the pond. Flowage 300, where the following observations were made, became ice-free early in the third week of April.

On 23 April, 4 adult grebes were observed feeding quietly together in the center of the flowage main pool. The number of Pied-bills on the flowage was reduced to one pair by 3 May, at which time the total area of available breeding habitat for grebes (open water and emergent vegetation) was only slightly more than 4.4 ha. Four young grebes were first seen on 30 June. Based upon the first record of a single pair on the flowage, literature records of hatching times ranging from a minimum of a clutch of 6 in 2 days (Glover, Wilson Bull. 65:32–39, 1953) to at the same rate as laying (various authors), the recorded incubation time of approximately 23 days (Bent, U.S. Natl. Mus. Bull. 107, 1919; Deusing, Auk 56:367–373, 1939), and the last date the pair without a brood was observed, nest initiation for this pair was approximately 21 May and hatch was approximately 21 June. Since the young seen 30 June were still quite small but not downy, their age could be estimated as 1 week, leading to similar estimates of nest initiation and hatch dates. The adult grebes stayed with the young approximately 25 days. The young grebes (the brood of 4 was reduced to 2 by 2 August) departed the natal area after approximately 44 days.

No data are available in the literature on either growth rates or age at independence of Pied-billed Grebe young. Palmer (Handbook of North American Birds, vol. 1:112, 1962) suggested that independence and first flight may occur in less than 3 weeks. My data from 1971 suggest that these times are not synonymous. Even if the first observation of the brood is taken as day 1 after hatching, time to first flight was still 35 days. Age at departure of the adults, 25 days, was within Palmer's estimation.

Between 30 June and mid-July, waterfowl were present on flowage 300 in various numbers on every occasion that the area was visited. By 30 June there were a female and a brood of 8 Common Goldeneyes (*Bucephala clangula*), 2 broods of Mallards (*Anas platyrhynchos*) and 3 Wood Duck (*Aix sponsa*) broods. A hen Mallard and 9 ducklings, and a hen Blue-winged Teal (*Anas discors*) and brood of 11 ducklings, which entered the flowage during the third week of July made a total of 8 different waterfowl broods which used the flowage in company with the grebes between 31 May and early August.

Aggression by Pied-bills against goldeneye ducklings was observed from 30 June until late July when the adult grebes left the flowage. A typical example is illustrated by my first observation of this behavior 30 June. One of the adult grebes flew to 3 of the goldeneye ducklings from a distance of approximately 15 m, landed approximately 2 m short of the young birds, and then chased them by running across the water while flapping with its wings. The goldeneyes were driven off the open water area into a flooded alder (*Alnus* spp.) bay. Thereafter, on no occasion did I observe the grebes to allow the young goldeneyes to move any farther than 3 m from the vegetation edge into open water. The adult Pied-bill always pecked at the ducklings, but was able to strike the goldeneyes only during the first week of these attacks. The goldeneye young escaped the grebes on all later occasions by outrunning the Pied-bills in a flapping chase across the water. Nevertheless, the goldeneyes were always forced into the emergent border of the flowage. On 2 occasions, after a short chase, the adult grebe dove, then surfaced beneath the goldeneyes causing them to flee across the pond. The other waterfowl on the flowage did not spend as much time in the open water areas of the flowage as did the goldeneyes, but even when near the Pied-bills they elicited no agonistic behavior from the grebes.

Munro (J. Wildl. Manage. 3:339–344, 1939) and Ryder (Auk 76:424–442, 1959) did not believe that interspecific attacks by water birds seriously affected other species. Glover (1953) based sex discrimination on the size of the bird and found that the area defended by the male Pied-billed Grebe usually was included within an arc of about 46 m around the nest, with the total area used being approximately twice the size of the defended area. Palmer (1962) reports that territorial defense is usually accomplished by the male and that such behavior may be directed at other Pied-billed Grebes, Coots (*Fulica americana*) and several duck species. Kilham (Wilson Bull. 66:265–267, 1954) documented territorial attacks by a Pied-bill on a female Ring-necked Duck (*Aythya collaris*), a female Hooded Merganser (*Lophodytes cucullatus*), and an immature Pied-bill, but observed no attacks upon Blue-winged Teal, Wood Ducks, or Coots on the same water area. Kilham's hypothesis that the attacked species bore enough resemblances to adult Pied-billed Grebes to elicit defensive behavior from the male grebe may apply to the behavior observed on the Chippewa also. The goldeneyes superficially resembled grebes (brown above, white below) and were the only birds on the flowage "acting" like grebes, i.e. diving, shaking feathers with the breast raised above the water, and using the open water areas instead of the emergent vegetation. However, I believe that this behavior is adaptive. All reports of Pied-bill interspecific agonistic behavior in the literature concern species that, at least partially, overlap the grebes in requirements for food and nesting and brood-rearing habitat. The larger area of available wetland in the spring allowed the grebes and ducks to use flowage 300 without conflict. The reduced midsummer flowage area and the presence of the brood apparently were responsible for the initiation of attacks against the goldeneyes.

Whatever the releasers for the grebe attacks, the effects upon the goldeneye ducklings were profound. The young birds were denied access to the deeper water portions of the flowage whenever the grebes were active. This goldeneye brood, unlike many others observed, became scattered along the shoreline and often mixed with other broods after being harassed by the Pied-bills. Some portion of the goldeneye brood loss observed (4 ducklings) may have been indirectly attributable to the interspecific conflict. Although Pied-billed Grebes can rear broods on even very small water areas, their presence may, at times, be detrimental to some other species.

This work was supported by the Max McGraw Wildlife Foundation, Dundee, Illinois, and the U.S. Forest Service through the Chippewa National Forest and The North Central Forest Experiment Station, St. Paul. Assistance of many kinds was offered by several people as acknowledged in Kirby (1973). This note benefited from the comments of S. R. Derrickson, M. R. Fuller, and J. R. Tester.—Ronald E. Kirby, *Coop. Wildl. Res. Lab., S. Ill. Univ., Carbondale, Ill.* (Present address: *Migratory Bird and Habitat Research Laboratory, Laurel, MD 20811*). *Accepted 30 May 1975.*

Growth rate in the Monk Parakeet.—The Monk Parakeet (*Myiopsitta monachus*) has aroused considerable interest since its introduction into the U.S. Studies on the basic biology of this species have focused in particular upon their potential for establishment in this country. There is good evidence that physiologically this species is well adapted to invade many of the climatic regions of North America (Weathers and Caccamise, Oecologia 18:329–342, 1975), and based on the numerous breeding records it would appear that other aspects of their niche requirements are met at least in certain geographic areas.

One way of evaluating the potential for an exotic species to become established in a new area is to evaluate its breeding success. One important component of breeding success is the ability of parents to maintain the growth rates of young within those acceptable limits determined by the physiological capabilities of the species. The purpose of this study was to determine the growth rates of nestling Monk Parakeets in both caged and wild situations in order to provide a basis for comparative studies.

Subjects for this study consisted of 3 nestlings reared in an outdoor flight cage (4 × 3 × 2 m) by 2 pairs of adults using 2 separate nests. These birds were all live-trapped as adults in New Jersey and maintained in the cage for about 7 months before breeding began. In addition, data were collected on 3 nestlings reared by a pair of free-living birds nesting in Franklin Township, New Jersey. This nest was located near the top of an eastern hemlock (*Tsuga canadensis*) at a height of about 10 m.

The wild birds were part of a flock of 6 individuals of which only 1 pair bred at the nest under observation. This nest had been active for at least 3 years prior to 22 May–13 June 1974 when these observations were made. Local residents stated that this nest was constructed initially by only 2 birds, however, in the succeeding 3 years the flock grew to 6 individuals. Whether this increase was due to reproduction or to recruitment is not known.

Age-dependent weights are presented in Fig. 1. Since the free living birds deserted their nest about midway through the nest cycle none of their nestlings survived to fledge.

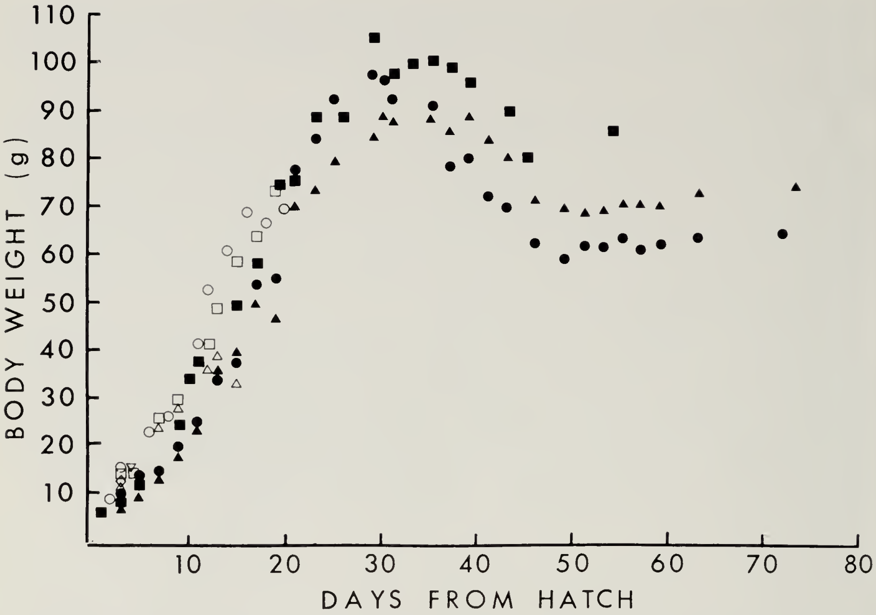

FIG. 1. Time dependent weights of nestling Monk Parakeets. Open symbols are free-living nestlings and solid symbols are nestlings reared in the cage.

However the growth rate of these nestlings was similar to that of the caged birds during the coincident periods of development.

In order to compare growth rates of Monk Parakeets with other species, the growth rate constants described by Ricklefs (Ecology 48:978–983, 1967) were calculated using his logistic equation. The resulting growth rate constants are expressed in both forms described by Ricklefs ($K = 0.1624$, $t_{10\text{-}90} = 26.98$). These are intermediate in value (Ricklefs, Ibis 110:419–451, 1968; Ibis 115:177–201, 1973), characteristic of birds generally much larger than Monk Parakeets. From the list of species presented by Ricklefs those with growth rates most similar to the Monk Parakeet include the Double-crested Cormorant (*Phalacrocorax auritus*) (1900 g), female Cooper's Hawk (*Accipiter cooperi*) (290 g) and the Common Crow (*Corvus brachyrynchos*) (450 g). A regression of maximum nestling size versus growth rate for temperate zone passerines and raptors resulted in an inverse relationship (Ricklefs 1968). Therefore, based on this regression the relatively low growth rate in Monk Parakeets would be expected for nestlings attaining a maximum size of about 1000 g. This is far greater than the 95–105 g maximum weight observed in the Monk Parakeet nestlings. Examples of growth rates for birds with weights similar to Monk Parakeets would include *Taxostoma curvirostre* (wt. = 79.3 g; K = 0.384) and *Xanthocephalus xanthocephalus* (wt. = 91.0 g; K = 0.540). The growth rate of Monk Parakeets is only 42.4% of the first species and 30.1% of the second.

Beyond day 35 there is a weight remission from about 97 g to as low as 60 g. Such a remission is not uncommon in altricial birds (Ricklefs 1968), however the magnitude of the weight loss is impressive, particularly since these caged birds had access to a superabundant food supply.

Ricklefs (1968) analyzed the relationship between maximum nestling weight and average adult weight for individual species. For this he constructed a ratio (R) of the asymptote from the growth curve to the average adult weight. Ratios greater than 1.10 were most common in aerial feeders, while ratios less than 0.90 were most common for ground feeders. Also, species with high R values tended to have long nestling periods. The ratio for Monk Parakeets was 1.28. This was somewhat higher than the intermediate levels that might be expected of an arboreal and ground feeder such as this species. However, the high R value of Monk Parakeets is in accord with what would be expected in species with similarly long nestling periods.

Since the energy requirements for nestlings is the sum of maintenance energy and energy for growth, a low growth rate would tend to decrease the rate of energy demand for a nestling. If the number of surviving offspring is limited by the rate at which the parents can deliver energy to the young, then changes in the factors tending to lower the rate of energy demand of the nestlings could increase the number of potential offspring reared by the parents. One way to effect such a change is to lower the growth rate. However a low growth rate also increases the chances for predation and other nest losses by increasing the time in the nest. Monk Parakeets lay large clutches (5–9 eggs) and with their sizable stick-nests which are often built in clusters, this species would seemingly have a relatively secure nest environment. Thus it would seem that this safe nest environment could allow for the extended period of incubation (31 days) and the very low growth rate without a substantial increase in mortality. Therefore the low rate of development may be an adaptation for maximizing the production of young by maximizing clutch size.—Donald F. Caccamise, *Dept. of Entomology and Economic Zoology*, and Peter J. Alexandro, *Dept. of Zoology, Rutgers, State Univ. of New Jersey, New Brunswick, 08903.* *Accepted 1 July 1975.*

Foraging methods of the Song Thrush.—A recent review by Clark (Wilson Bull. 83:66–73, 1971) of bill sweeping in foraging behavior includes his personal observations on the Wood Thrush (*Hylocichla mustelina*), the American Robin (*Turdus migratorius*) and the European Blackbird (*Turdus merula*). Some time ago I was able to make incidental observations at close range of foraging behavior in the Song Thrush (*Turdus philomelos*) and these add some detail and expand the context of Clark's observations. These notes concern the coordination of bill sweeping and foot movements, the occurrence of a distinct form of foraging also using the bill, intra- and inter-individual differences, and the relative use of the 2 types of behavior on different substrates.

All my observations were made between August 1960 and June 1962 on hand-reared birds kept in a large aviary (15 × 5 m). Up to 7 birds lived in one-half of the aviary and were tested singly or in pairs in experiments on camouflage that were set up in the other half. This section contained 3 circular experimental plots about 150 cm in diameter. Two plots were formed from woodwool (a commonly used animal bedding material similar or identical to excelsior) which had been torn up into shorter pieces averaging 5 cm long by 0.2 cm wide. The third plot was formed from wood shavings, each about 1.5 × 0.75 cm, to simulate leaf litter. Each substrate was 2 to 4 cm in depth over a concrete floor. Also in the aviary was a large stack of untorn woodwool and a shallow gutter filled with a wind-blown loose detritus of decayed leaves, dust, small pieces from the experimental plots, etc. The birds regularly found maggots and mealworms in all substrates and also snails in the experimental plots.

TABLE 1

RELATIVE USE OF BILL SWEEPING AND PULLING IN DIFFERENT SUBSTRATES

	Woodwool stacks	Woodwool plots	Floor detritus	Shavings plots
% bill sweeps	25	59	95	100
% lateral pulling	75	41	5	0
Total responses	245	155	519	694
Number of individuals	4	7	10	7

The constant feature of bill sweeping by the Song Thrush is a rapid and usually repeated lateral sweep of the head; at the start the bill is partly buried in the substrate so that typically the movement results in substrate material being thrown to one side. Usually there are 3 to 8 sweeps in quick succession before the bird switches to another activity but occasionally almost continuous sweeping occupies up to 1½ min, as, e.g., when 88 sweeps occurred with the bird pausing only briefly and moving only a few steps during this period.

Sometimes there is a simultaneous scratching movement of one foot acting close to where the bill is sweeping so that both actions disturb the substrate. This foot movement is very rapid and of small amplitude and can only be seen with a close and completely unobscured view. Thus, even though the aviary gave excellent observation conditions, on only a few of the occasions when bill sweeping was observed could the presence or absence of a foot scratch component be determined. I have never noted a foot scratch in the absence of a simultaneous bill sweep and, as I recall it, a scratch of the left foot occurs with a bill sweep to the left and vice versa.

During 12 observation sessions involving 5 birds, sequences of bill sweeping were observed closely enough to examine the bill and foot coordination in a semi-quantitative way. Only 1 bird regularly used the foot scratch. In 3 tests about 75% of 228 sweeps coincided with a foot scratch; in another test (15 sweeps) the foot scratch occurred in fewer than half the responses. A second bird produced foot scratches in 1 out of 2 tests that gave a total of 28 bill sweeps whilst the final 3 birds demonstrated in 6 tests only 2 scratches in 190 bill sweeps.

Variation also occurs in the general incidence of bill sweeping. The length of an observation session depended on the success of a bird in snail hunting and hence was usually between 10 and 20 min. The probability of recording any sweeping during a test varied among individual birds from 0.13 to 0.60. On a sample of 6 birds this variation is highly significant (chi-square; $p < 0.01$). The variation is not simply due to different test lengths since the 3 birds with the lowest probabilities of sweeping were observed over more and longer tests.

Quite often my Song Thrushes showed a distinct additional foraging behavior; a bird would grasp material firmly in the bill and pull it backwards and laterally with a combined head and body movement with the overall position of the bird shifting little or not at all. The use of this pulling response is strongly connected with the type of substrate. Table 1 shows that pulling is a common response when a bird forages at the edge of a stack of tangled. untorn woodwool and fairly common on the plots of torn-up woodwool. Bill sweeping is the dominant response on the plots of wood shavings and in floor detritus; in both these cases long fibers are scarce. The pulling behavior is very similar to that shown by recently fledged birds that grip and pull back the paper lining of a cage floor but in that context the lateral component is absent.

The overall frequency of sweeping plus pulling varies among birds by a factor of × 5. The relative frequency of pulling (out of the 2 foraging behaviors combined) varies among birds from 0 to 35% due to different frequencies of foraging in different substrates and to differences in behavior on a single substrate. These data are distributed rather erratically among birds and substrates so that an overall formal analysis is not possible.

The sweeping behavior of Song Thrushes in aviaries seems similar to that of the species in the wild and to that of the closely related European Blackbird. Thus Snow (A Study of Blackbirds, George Allen and Unwin, London, 1958) writes of *Turdus merula*: "as the bill comes down to flick, . . . , one foot comes forward to the level of the head and scratches vigorously backward." I have also observed this species pick up and throw aside individual leaves of Sycamore (*Acer pseudoplatanus*) which besides being large had become sodden and heavy. It would be interesting to examine other species of *Turdus* to determine if they share the range of foraging behaviors reported here and whether species of different body size use different behaviors in the same substrate.

In my aviary situation Song Thrushes found most of their food without sweeping and pulling and in many observation sessions these behaviors did not occur. Inspection of my original notes suggests that, when they did occur, sweeping and pulling could not be correlated with any change in environmental stimuli or placed at particular times in a sequence of hunting and resting. It is possible that field observations would reveal a more systematic organization of foraging and a lesser degree of individual variation. It would be of interest to examine in controlled operant situations how the frequency of these natural patterns of foraging behavior could be influenced by making the discovery of food more or less contingent on performance.

These observations were made during the course of work for a D. Phil. supervised by Professor N. Tinbergen and using the facilities of the Department of Zoology, University of Oxford, by permission of Professor Sir A. C. Hardy.—C. J. HENTY, *Dept. of Psychology, Univ. of Stirling, Stirling, Scotland. Accepted 18 July 1975.*

A late nesting attempt by Clark's Nutcracker.—On 1 June 1974 I observed a pair of Clark's Nutcrackers (*Nucifraga columbiana*) during an early stage of nest construction. The nest platform had patches of sky showing through and resembled the first-day structure described by Mewaldt (Condor 58:3–23, 1956). Placed approximately two-thirds up in a 20 m lodgepole pine (*Pinus murrayana*), the nest was located on an east-facing slope above Tioga Lake, elevation 2970 m, latitude 38°, in Inyo National Forest, Mono Co., California.

Between 12:40 and 13:30, the birds made 9 trips to the nest. Twigs were brought and set in place on 3 visits. Forty-five min after the last nest visit both nutcrackers returned to the vicinity of the nesting tree, one bird landing near the nest and the other perching in an adjacent lodgepole pine, each giving the soft, "musical" nesting call described by Mewaldt (1956). Although the intensity of nest-building activity did not match the rate observed by Mewaldt (1956) of one trip with nesting material per bird every 3 or 4 min, the use of territorial perches and nesting calls followed his description.

I observed the nest again on 20 June, 12:00, at which time the structure was a complete bowl with no holes in the bottom. After two hours of observation, there were no signs of an incubating nutcracker on the nest, nor were any nutcrackers seen in the vicinity. Again on 26 June, I saw no nutcrackers; and, I assume the nesting attempt was aborted.

Nutcracker nesting and egg dates from the literature—adjusted using Mewaldt's breeding chronology data (1956)—indicate that from British Columbia to California first-day nest construction dates range from 1 February to 18 May. Although the available nesting records support the premise that the nutcracker is an early nesting strategist, I suggest here that in some years nesting continues later into the season in response to local conditions. The onset and duration of the nesting season for this species probably varies regionally and from year to year. Local factors such as weather conditions and cone crop production the previous fall are probably the ultimate controls of nutcracker nesting.

I am grateful to Stephen I. Rothstein and L. Richard Mewaldt for reading the manuscript critically. Field work was supported by a Sigma Xi Grant-in-aid of Research.—Diana F. Tomback, *Dept. of Biological Sciences, Univ. of California, Santa Barbara, 93106.* *Accepted 18 July 1975.*

Lek behavior of the Buff-breasted Sandpiper.—In the early part of June 1972 we observed a lek-like mating system of Buff-breasted Sandpipers (*Tryngites subruficollis*) at the Firth River, Yukon Territory (69° 23′ N, 139° 25′ W). Our observations were opportunistic, as time from other work permitted. While incomplete, they substantiate the developing picture of *Tryngites*' social behavior and add new details.

Study area and methods.—Most observations were made in an area approximately 3 km^2 adjacent to the Firth River and about 15 km from the coast of the Beaufort Sea. The topography was rolling tundra. Habitat varied from low marshy areas with many small ponds to higher drier slopes and knolls. During the display period Buff-breasts were found mainly in the better drained locations. Closely-spaced sedge tussocks approximately 20 cm high and 25 to 50 cm in diameter characterized these areas.

Although male Buff-breasts are larger than females (Oring, Auk 81:83–86, 1964), the sexes are not always evident in the field (cf. Pitelka et al., Am. Zool. 14:183–202, 1974). We called birds engaging in active wing-lifting display, males, and those that did not display in this manner, females. That this is not always correct is indicated by observations of females displaying while on migration (Oring, 1964) and occasionally on the breeding ground (R. T. Holmes, pers. comm.).

Breeding chronology.—We noted the first displaying Buff-breasted Sandpipers on 1 June, although display could have begun 1 or 2 days earlier when observers were absent from the area. On 3 June birds were displaying actively but by 7 June display had nearly ceased.

Males apparently left the breeding area soon after the courtship period. There was a marked decline in sightings of Buff-breasts after 7 June when display was last noted. Virtually all sightings after 7 June were of single birds, and few were observed on the display grounds. Those seen were usually in wetter, marshy areas and may have been birds away from nests.

We discovered the first of 8 nests on 10 June. All nests were on fairly dry slopes with numerous sedge tussocks; they appeared to be well scattered over suitable habitat. As Pitelka et al. (1974) and Parmelee et al. (Bull. Natl. Mus. Canada 222:1–229, 1967) also noted, there was no tendency for nests to be concentrated near display grounds. Each time an incubating bird flushed it flew off silently. We never saw 2 Buff-breasts in the vicinity of a nest. The presence of just one adult at nests and with broods (found to be a female in the 3 cases that the adult was collected) led Sutton (Arctic 20:3–7, 1967) to conclude that Buff-breasted Sandpipers were probably polygamous and that males deserted the females on termination of egg-laying. Bailey (Birds of Arctic Alaska. Colorado Mus. Nat. Hist., Popular Series No. 8, 1948) had previously reported that male Buff-breasts

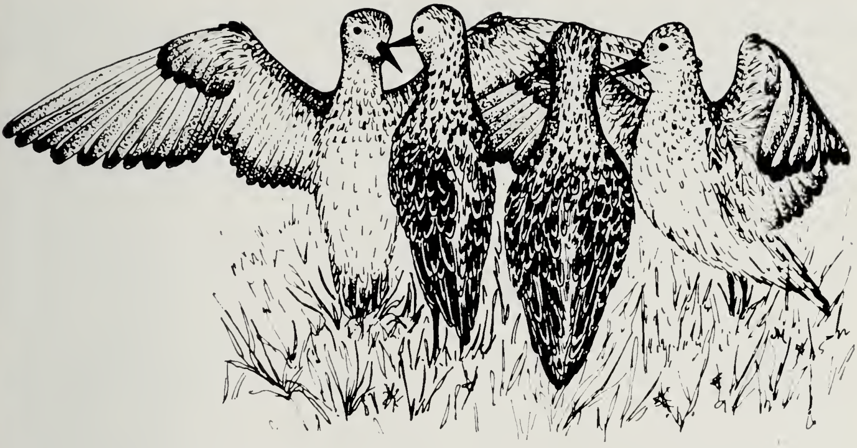

FIG. 1. Two male Buff-breasted Sandpipers displaying to two females (corresponding to 2D of Oring 1964). Evidently of a higher intensity than 2C, this display often occurred when a neighboring male attempted to display on a rival's territory.

do not have brood patches. Pitelka et al. (1974) affirmed that *Tryngites* is polygamous and that males do not incubate. Our observations strongly support the presence of polygamy in this species.

Territorial behavior of males.—Males were distributed in small groups, numbering from 3 to perhaps 10 at several different locations. Within each group individual males were spaced at intervals of approximately 25–50 m.

Males actively chased intruders from their territories. Chases frequently occurred when a male with no females on his territory went to a territory where females were present. The encroaching male normally attempted to display to these females but was always driven off by the "resident" male whereupon it flew back to its own territory. Since birds could not be recognized individually, we could not be sure that individual males consistently defended the same area.

Display behavior.—On 3, 4 June a group of approximately 8 presumed males were observed displaying between 21:00 and 02:30, providing most of our observations of behavior on the lek. It was our impression over the subsequent 3 days that displays were most vigorous in the soft light of the night hours when the sun was low in the sky.

Displays of the Buff-breasted Sandpiper have been described during spring migration (Rowan, Br. Birds 20:186–192; Oring, 1964) and from breeding areas (Parmelee et al., 1967). All display postures noted at the Firth River were described at least in part in those papers but we did not observe all the displays listed therein. The numbering system used by Oring (1964) is retained here.

Males displayed more or less constantly while under observation, but were particularly vigorous when females were nearby. By far the most common display on the breeding ground involved the lifting of a spread wing to a nearly vertical position from which it was "waved" (display 1A), revealing the contrasting light underwing with its delicate and precise markings. Transitory variations and other movements observed by Oring (1964) with this display were noted (1B, 1C, 2A), with the addition that the displaying bird might also jump up and down (termed "flutter jumping" by Pitelka et al. 1974). Oring (1964) twice observed females displaying in this manner in Oklahoma. Although we could not be positive of sexes, all displays appeared to be given exclusively by territory-holders (considered here to be males).

Two-wing displays were evidently of a more intense nature. While one-wing displays were commonly given by lone males, two-wing displays were only noted when other birds were present on a territory. Oring (1964) saw display 2C (both wings extended laterally, primaries pointed above the horizontal) only by lone males; when females were present 2C was replaced by 2D (both wings spread, primaries below the horizontal). At the Firth River, both of these displays were performed while females were present on territories but if a displaying rival encroached on a territory, the 2 males seemed most often to perform 2D. In several instances resident males continued this high intensity courtship display while an intruding male also displayed within 0.5 m (Fig. 1).

If neighboring males intruded during less intense displays (e.g. 2C), the resident usually immediately broke off displaying and chased the intruder. Males would occasionally fight while displaying at close quarters as described by Parmelee et al. (1967). Sometimes 2 males displaying close together would fly up vertically together to a height of 5 to 10 m, their legs trailing (similar to 2F of Oring 1964, except that it occurred between males and was agonistic in nature). This display was also noted by Parmelee et al. (1967) and by Murdoch (pp. 71–72 *in* Bent, U.S. Natl. Mus. Bull. 146, 1929). The intruder would usually break away, landing some distance away, presumably on his territory. A "vertical flight" could also ensue after an interloper landed near a territory-holder giving the single-wing display.

Behavior of females.—Females were seen near displaying males in parties of 3 to 8 birds. Certain males seemed to be more attractive than others since it was common to find several females in one territory and none in others; however, our inability to distinguish individual birds prevented us from determining whether the same males were consistently favored and whether individual females were always attracted to the same male.

It seemed unusual for just one female to be present on a male's territory. Females in loose groups wandered through territories, often making feeding movements. They responded to both two-wing displays. Periodically, females would assume an upright posture and walk on "tip toes" towards a displaying male (cf. Oring 1964). Suddenly, all females in the territory would hurriedly approach the male as a group and make pecking motions at the base of his bill or cheek. Occasionally, a male was backed up against a tussock by the advancing females. The male's outstretched wings seemed to "embrace" them at times. Up to 5 females were seen in these compact, closely-spaced display groups. Rapid "tik" notes were heard at this time. It was during such high intensity displays that neighboring males were most apt to fly in and attempt to posture near the females. The situation is not always so straightforward as described here, however, since males have been collected among birds in these compact groups near a displaying individual at Barrow, Alaska (R. T. Holmes, pers. comm.). Copulation was not observed.

Discussion.—Pitelka et al. (1974) have recently discussed the evolution of social organization in calidridine sandpipers. Most species have stable pair bonds and maintain large territories which are used for feeding as well as display; this is the conservative pattern. Other species have progressively more specialized breeding behavior, exhibiting forms of "serial" polygamy. The array culminates in promiscuity in the Pectoral Sandpiper (*Calidris melanotos*), the Ruff (*Philomachus pugnax*) and *Tryngites.* In these species territories are small and serve mainly for display and mating. Males do not incubate or care for the young. The Buff-breasted Sandpiper and the Ruff show an "exploded lek" and a lek mating system respectively. *Tryngites* departs from the classical lek situation in that territories tend to be larger and the locations of display grounds may change between years. Our observations support this interpretation of *Tryngites*' breeding behavior.

Parmelee et al. (1967) reported that display areas were abandoned on Jenny Lind Island, N.W.T., and that displaying males would suddenly appear in new locations. It is possible that such shifts could explain the short display period observed at the Firth River. However, since we did not find displaying males in other locations after 7 June, despite visits by several observers over a wide area of similar habitat, we conclude that the display period was very brief in 1972. The early departure of males from breeding habitat is probably adaptive in that it would increase food resources available for the female and young and reduce activity near nests which might attract predators (cf. Pitelka, Condor 61:233–264, 1959).

The conspicuous light flash from the waving exposed underwing surface has been remarked upon by others (Parmelee et al. 1967, Pitelka et al. 1974). This feature was particularly striking during the twilight hours typical of the latitude at Firth River in early June. The flashing was visible at long distances and, as Parmelee et al. (1967) pointed out, drew attention to birds that otherwise would have been overlooked. Pitelka et al. (1974) suggested that the wing flashing might serve an important locator function to females since display grounds change location from year to year. If the display period is normally as short as indicated by our observations, this function would assume added importance.

The occurrence of display associated with pairing, both in flocks on migration and leks on the breeding ground, invites further speculation. An important function of lek behavior apparently is to ensure that a few particularly "fit" males fertilize most females (Tinbergen, pp. 375–378 *in* D. A. Bannerman, The birds of the British Isles, Vol. 9. Oliver and Boyd, London, 1960). The less than two weeks of display of Buff-breasted Sandpipers at the Firth River in 1972 is much shorter than the display period of the Ruff and other lek species (Tinbergen 1960). Although the spring of 1972 was abnormally delayed, short summers at this latitude would preclude long periods for display on the leks even in normal years; this time conceivably could be too brief to permit the establishment of stable relationships among males and to ensure the fertilization of females. If this is so, the same groups of birds might maintain their association throughout spring migration to the breeding ground, constituting a "moving lek." The desirability of more systematic study of the breeding behavior and ecology of the Buff-breasted Sandpiper is obvious.

Observations were made while the authors were employed by L.G.L. Ltd. We thank Northern Engineering Services Ltd. and Canadian Arctic Gas Study Ltd., for permission to publish this communication. Several people kindly read and offered helpful comments on the manuscript; we particularly thank Harry Lumsden for his suggestions. We are grateful to John Black and Michael Dyer for their observations. Special thanks go to June Mullins for preparing the figure.—J. P. Prevett, *Zoology Dept., Univ. of Western Ontario, London 72 Ontario and* J. F. Barr, *Zoology Dept., Univ. of Guelph, Guelph, Ontario.* Present addresses: (JPP) *Ministry of Natural Resources, Moosonee, Ontario*; (JFB) *91 Forest Street, Guelph, Ontario.* *Accepted 21 July 1975.*

Sandhill Cranes feeding on ducklings.—On 8 July 1972 while watching a pair of Sandhill Cranes (*Grus canadensis*) at Malheur National Wildlife Refuge, Harney Co., Oregon, I saw an adult male crane kill and eat a 1- to 5-day-old Gadwall (*Anas strepera*) duckling.

I first saw the cranes at 17:40 sitting near the north shore of Boca Lake. At 18:36

the male stood and watched a brood of Gadwalls about 50 m offshore. At 18:37 he flew directly to the brood, landed among the young, and instantly grabbed a duckling. He shook and speared the young bird into several pieces. As the male crane ate the pieces, the female walked over and ate with him. All the remains were eaten by 18:45. The male drank briefly, then the pair walked to the shore.

In July 1962 a member of the refuge staff watched a male catch and eat a young Mallard (*Anas platyrhynchos*). The crane approached the brood from the rear, caught one young, violently shook it 2 or 3 times, and swallowed it intact. This incident occurred in a meadow in about 5 to 7 cm of water. R. C. Drewien (pers. comm.) has seen Sandhill Cranes consume young Mallards and Green-winged Teal (*Anas crecca*) near Grays Lake, Bonneville Co., Idaho.

Mullins (M.S. thesis, Univ. Idaho, 1974) collected 20 Greater Sandhill Cranes in southeastern Idaho and reported on their stomach contents. Plant material comprised 73% of the diet, and insects and earthworms accounted for 27%. No remains of eggs or young birds were found. Harvey et al. (Wilson Bull. 80:421–425, 1968) found that Lesser Sandhill Cranes (*G. c. canadensis*) readily fed on Snow Goose (*Anser hyperborea*) eggs and Willow Ptarmigan (*Lagopus lagopus*) chicks. Walkinshaw (The Sandhill Cranes, Cranbrook Inst. Sci. Bull. 29, 1949) also reported on the food habits of Sandhill Cranes, but none of these reports mention ducklings in their diet.

The importance of young ducks as a food source for cranes is unknown, but crane predation on ducklings would normally go undetected because vegetation height restricts visibility and prevents close observation at the time of duck hatching.—CARROLL D. LITTLEFIELD, *U.S. Fish & Widllife Service, Box 671, Burns, OR 97720. Accepted 25 July 1975.*

Successful parasitism of the Gray Catbird by the Brown-headed Cowbird.—The Gray Catbird (*Dumetella carolinensis*) is considered a poor host species for the Brown-headed Cowbird (*Molothrus ater*) because it normally ejects cowbird eggs from its nest (Rothstein, Auk 91:796–807, 1974). Thus the following record is of interest. On 12 June 1971 I found a catbird incubating 3 catbird eggs and 1 cowbird egg. On 15 June the nest contained a down-covered cowbird and 3 catbird eggs. On 19 June there was a large cowbird nestling and a small, nearly naked young catbird; the other 2 catbird eggs had disappeared. On 23 June the feathered cowbird was sitting on the dead catbird nestling. On 29 June the nest was empty, and the adult catbirds were scolding vigorously, as they had on all visits, suggesting that the young cowbird was in the vicinity.

The nest was 1.2 m above the ground in a clump of mountain laurel (*Kalmia latifolia*) located in a 0.8–1.2 ha wood lot in a residential area near Takoma Park, Montgomery Co., Maryland. Canopy trees were mainly white oak (*Quercus alba*). There was little herbaceous understory but many clumps of 1.5–1.8 m mountain laurel shrubs.

Two previous reports give specific information on young cowbirds in catbird nests. Nickell (Wilson Bull. 70:286–287, 1958) found a nest in Ontario that contained two 6- to 7-day-old catbirds and a cowbird 1 or 2 days older. The second report (Auk 79:116–117, 1962) concerned a Michigan catbird nest containing 4 catbird eggs and 1 cowbird egg. That cowbird egg hatched, but the nest was subsequently destroyed by a predator. Later in the same vicinity, catbirds were seen feeding a young cowbird and 3 fledgling catbirds. Another record appears erroneous. Elder (Bird Lore 23:185–191, 1921) states that catbirds frequently rear 1 or 2 of their own young in addition to 1 or more cowbirds. A careful reading of Elder's paper indicates that this statement probably refers to the Wood Thrush (*Hylocichla mustelina*).—JOAN C. WOODWARD, *2433 Southgate Square, Reston, VA 22091. Accepted 30 May 1975.*

Avian tuberculosis in a Saw-whet Owl.—On 3 Nov. 1974, I collected a road-killed Saw-whet Owl (*Aegolius acadicus*) 9.7 km S. of Hill City, Itasca Co., Minnesota. Initial examination showed a deposit of dried blood, 15 × 8 × 4 mm, built up over the base of the beak in the feathers surrounding the nostrils. In preparing the bird as a study skin (placed in the vertebrate collection at Wayne State College, Wayne, Nebraska), I noted 2 yellowish lumps, 2 × 3 mm, at the ventral base of the tongue and in the ventral surface of the pharynx. Further dissection revealed several more nodules of a similar type beneath the skin on the back of the neck and numerous lumps up to 15 mm in diameter in the liver, stomach, mesenteries, and intestines. The lumps made up about 25% of the viscera, by weight. The bird had no fat but was not thin and appeared healthy. The stomach contained a pellet of hair, probably of *Microtus sp.*

The gastro-intestinal tract, along with the liver, was preserved in formalin and later sectioned, mounted on slides and stained. Slides were stained with Harris' hematoxylin stain, Brown-Brenn stain and Kinyoun carbolfuchsin acid-fast stain. Drs. F. D. Kapps and R. Villella, Clinical Pathologists at Mercy Medical Center, Coon Rapids, Minnesota, examined the tissue and slides and diagnosed it as avian tuberculosis, stating that they had never seen such a high concentration of acid-fast organisms in a tissue specimen. An attempt to isolate the organism on Lowenstein media was unsuccessful, probably due to the desiccation of the study skin. It was felt that the causative agent was probably of the *Mycobacterium avium*-Battey bacillus group since they are most frequently involved in tuberculosis among poultry.

I have examined about 200 road-killed birds of various species and have never before seen a blood deposit on the beak similar to that noted here. Frequently there will be some oral or nasal bleeding but it will be recognizable as such; this deposit was obviously built up over a period of time before the bird's death and is probably symptomatic of the disease. Such a deposit might serve as a warning to the uninitiated that a diseased state is indicated. This may be of some importance from a medical standpoint since cases of avian tuberculosis have been reported in humans, even though rarely, and the disease has been traced to exposure to diseased animals; also, this form of tuberculosis responds poorly to drugs (Bailey and Scott, Diagnostic Microbiology, The C. V. Mosby Co., St. Louis, 1974).

Acknowledgments go to Rita Nelson for specimen preparation and staining and to Dr. F. Donald Kapps, M.D., and Dr. Ronald Villella, M.D., for examination and diagnosis.—WAYNE J. MOLLHOFF, *907 Queen's Lane, Anoka, MN 55303.* *Accepted 27 June 1975.*

Observations at a cavity nest of the Common Grackle and an analysis of grackle nest sites.—A 16-apartment martin house, located at Rice Creek Biological Field Station, Oswego College, Oswego, N.Y., normally inhabited by Tree Swallows (*Iridoprocne bicolor*) was used exclusively by a Common Grackle (*Quiscalus quiscula*) pair in May 1974. The apartment used was 3.6 m above ground and had a western exposure which overlooked a 10.5 ha pond. Nest temperatures were monitored continuously and recorded by a Leeds and Northrup Speedomax thermocouple recorder. The thermocouple was secured under the 4 eggs at the bottom of the nest. Supplementary data on Common Grackle nesting locations were obtained from 2601 cards on file at the Nest Record Card Program at Cornell University's Laboratory of Ornithology, Ithaca, New York.

TABLE 1
SUBSTRATE TYPES* AND PERCENT OF TOTAL COMMON GRACKLE NESTS** FOUND IN EACH

Coniferous		Deciduous		Shrub		Other	
Substrate	% of Total	Substrate	% of Total	Substrate	% of Total	Substrate	% of Total
red cedar	23.7	osage orange	2.4	honeysuckle	1.9	bridge	2.4
scotch pine	3.3	willow	1.8	buttonbush	1.3	cattails	1.5
yew	3.1	elm	1.5	lilac	0.8	nest box	0.6
Norway pine	2.5	crabapple	1.5	bayberry	0.7	building	0.5
juniper	2.3	bayberry	0.9	dogwood	0.1	tower	0.2
blue spruce	1.4	hedge	0.5	not given	3.0	cavity-conifer	0.2
white pine	1.3	apple	0.3			snag	0.2
white cedar	1.0	mulberry	0.3			stump	0.2
Norway spruce	0.2	thornapple	0.2			vine	0.2
not given	23.7	oak	0.2			cavity-deciduous tree	0.04
		poplar	0.1			channel marker	0.04
		not given	13.7			under pail	0.04
						power pole	0.04
						cliff	0.04
						cornbinder support	0.04
						railroad bed	0.04

* Scientific names are not given for the substrates listed since the substrates were noted only by common names and by many different observers. Assignment of species designations might introduce some error.

** Data from 2601 Nest Record Cards at the Laboratory of Ornithology, Cornell University, Ithaca, New York.

The nest was constructed in the week immediately prior to egg-laying (May 8–15). One egg was laid each day from 16 through 19 May. The first egg laid did not hatch, the second 2 eggs hatched on 31 May, the last on 1 June. The diurnal (05:00–21:00) mean incubation constancy (Skutch, Wilson Bull. 74:115–152, 1962) during the 13-day incubation period was 68.8%, slightly lower than the 76% reported for 5 pair in northern Ohio (Maxwell, Auk 89:349–359, 1972) nesting in red cedar (*Juniperus virginiana*). The nocturnal (21:00–05:00) mean incubation constancy was 98.5%. There were nest-cooling periods of from 5 to 55 min duration on 6 different nights during the incubation period which indicated that some nocturnal activity of the incubating adult probably occurred away from the nest. During the diurnal period, the incubation constancy increased to a peak of 79% mid way through the incubation period and declined to a low of 50% on the final day of incubation. Nest temperatures during the diurnal incubation period ranged from a mean maximum of 29.5°C to a mean minimum of 21.3°C and the mean maximum-minimum environmental temperatures during the same period were 19.0°C and 9.2°C. The mean maximum-minimum nest temperatures during the nocturnal portion of the incubation period were 26.4°C and 23.9°C and the mean maximum-minimum environmental temperatures during the same period were 12.1°C and 10.0°C.

Hole-nesting grackles account for only 21 (0.8%) of 2601 nests recorded in the Nest Record Card Program. Of the 2601 nests, 62.5% were located in coniferous trees, 23.4% in deciduous trees, 7.8% in shrubs and 6.3% in other nest sites which included the hole-nesters. The mean height of 1621 nests in coniferous trees was 2.3 m, of 610 nests in deciduous trees 3.3 m, and of 211 nests in shrubs 1.8 m. The types of substrates recorded on the Nest Record Cards are summarized in Table 1.

These data show that coniferous trees, and especially the red cedar, are the most commonly used support trees. The red cedar supported at least 23.7% of all nests recorded; 8 other species of conifers, 11 deciduous species, 5 species of shrub, and 16 unusual nest support sites accounted for 35.9% of all Common Grackle nests reported on the 2601 cards analysed. The discovery of records of nests in 4 cavities in conifers, 1 cavity in a deciduous tree, and 16 nest boxes confirms our opinion that the Common Grackle is a plastic species capable of increasing its numbers by changing its nesting behavior in order to use marginal habitats and nest sites.

We wish to thank David Peakall, former Director of Cornell University's Nest Record Card Program, for his assistance to us during our visits to the lab. Thanks also to Carol Wernick for help with manuscript preparation.—George R. Maxwell II, Jean M. Nocilly, and Robert I. Shearer, *Rice Creek Biological Field Station, State Univ. College, Oswego, NY 13126.* *Accepted 1 July 1975.*

Unusual intensity of fighting in Ring-necked Ducks.—At 10:07 CST on 22 May 1969, we observed vigorous aggressive interactions between 2 male Ring-necked Ducks (*Aythya collaris*) on the open water of a 1.1 ha pothole south of Minnedosa, Manitoba. An interaction was already in progress when the birds were first perceived. The males were clutching each other's breast feathers just below the neck with their bills and hitting each other with their wings which were partly or wholly submerged. One male achieved an advantage and kept the other wholly under water. At this point, a coot (*Fulica americana*) interrupted and chased the 2 males. The male which had had the advantage in turn chased the coot for 2 to 5 sec. Meanwhile, 2 female Ring-necks within 10 m of the males did not interact with each other or with the males.

Following the brief interlude with the coot, the fight between the males resumed, initiated by the male which had earlier dominated, and lasted 3 min more. The males then separated and joined the females. The 4 birds remained close together and each male associated with one female, suggesting that they were paired. Then one male left his female and swam head to head at the other male. They pushed against, and grabbed at each other's breasts before resuming the wing-beating. As the males fought the females moved away and never displayed aggression. This interaction lasted 60 sec and ended when a pair of Pied-billed Grebes (*Podilymbus podiceps*) chased the males apart. The males rejoined the females and one grebe chased all 4 ducks from the pond. The pairs separated and flew from sight.

The wing-beating was unusual in that the wings were frequently submerged as the birds struck at each other. We are not aware of a description of wing-beating by Ring-necks, but in Mallards (*Anas platyrhynchos*) this fighting posture generally occurs above the water surface (Weidmann Z. Tierpsychol. 13:208–271, 1956.).

Ring-necks were occasionally observed in the region during the preceding 2 weeks but no nests were found on an adjacent 280 ha study area and only 3 observations of single pairs were made on this area throughout the breeding season. In the 1969 breeding season Ring-necks were not subsequently observed on the pothole where the fight occurred and the species appeared to be transient in the Minnedosa area.

Mendall (1958, The Ring-necked Duck in the Northeast. Univ. of Maine Studies, 2nd Ser., no. 73) observed fights among male Ring-necks on rare occasions during nuptial courtship. He noted that the male defends the female only when she is in immediate danger of being molested and also that spacing of breeding pairs appeared to occur without defense. Although the fighting had been in progress when we first observed it, aggressive behavior directed toward a female was not detected. It appears unlikely that these were courting birds or that either of the pairs was defending a nesting site. It still seems most probable that the fight arose in defense of the mate (Koskimies and Routamo, Zur Fortpflanzungsbiologie der Samtente *Melanitta f. fusca* (L). I. Allgemeine Nistokologie. Papers on Game Research 10, 1953).

These interactions appeared to constitute an unusually overt expression of aggression by a species which Mendall (1958) records as seldom displaying aggression. The lack of involvement by the females is interesting considering that males are believed less aggressive and females more aggressive in the genus *Aythya* than in the genus *Anas* (Delacour, The Waterfowl of the World, Vol. 4, Country Life Ltd., London, 1964).

We are grateful to John P. Ryder, Lakehead University, Thunder Bay, Ontario for his suggestions. Financial support for our studies in the Minnedosa area were provided by the Delta Waterfowl Research Station, Manitoba.—RODGER D. TITMAN AND NORMAN R. SEYMOUR, *Dept. of Renewable Resources, Macdonald College of McGill Univ., Ste. Anne de Bellevue, Québec H0A 1C0.* *Accepted 21 July 1975.*

Cedar Waxwings and Eastern Bluebirds feeding on winter stoneflies.—Aquatic insects such as stoneflies (Plecoptera) are seldom considered a principal food of passerines. Bent (U.S. Natl. Mus. Bull. 197, 1950) reported that stoneflies are a noteworthy item in the diet of the Cedar Waxwing (*Bombycilla cedrorum*), and Chapin (U.S. Dep. Agric. Bull. 1355, 1925) found an unidentified stonefly in the stomach of a Solitary Vireo (*Vireo solitarius*). Hamilton (Auk 49:352, 1932) observed a pair of Blue Jays (*Cyanocitta cristata*) feeding on stoneflies in late winter, but I could find no other records of passerines exploiting Plecoptera prey. Although this paucity of records involving songbird predation of Plecoptera is surprising, the lack of reports of predation on the "winter stoneflies" which emerge during winter when few other insects are available is also noteworthy.

The Cedar Waxwing and the Eastern Bluebird (*Sialia sialis*) winter in varying numbers at northern latitudes; both are largely frugivorous during the winter months. From 1200–1600 on 15 and 16 March 1975 I observed several small flocks of these 2 species feeding in a wooded area near Washington, Macomb Co., Michigan. The birds were preying on small insects later identified as the stoneflies *Allocapnia granulata* and *Taeniopteryx nivalis* which belong to the winter stonefly families Capniidae and Taeniopterygidae, respectively. The insects were emerging from two small, swift-flowing streams that contained numerous riffles, a gravel-sand bottom, some leaf detritus, and logs, rocks, and other objects that stoneflies crawl onto when undergoing ecdysis (Finni, Ann. Entomol. Soc. Am. 66:1243–1248, 1973). Snow covered the ground although the streams were essentially free of ice. Air temperatures were 4–5°C and the water temperature was 1.0°C.

The manner of capture differed for the 2 bird species. The waxwings obtained most of their prey by flycatching; short dashes from a conspicuous perch were more common than longer flights. The bluebirds gleaned most of their prey from tree limbs and branches, although some stoneflies (mostly adults, but undoubtedly a few naiads that had not yet molted into adults) were obtained on the ground; flycatching was infrequent. Both species fed almost entirely on the emerging stoneflies during the 2 observation periods as well as on several occasions during the following week.

Future observations should indicate that other birds (e.g. the Eastern Phoebe, *Sayornis phoebe*, and the Tree Swallow, *Iridoprocne bicolor*) that arrive at northern latitudes during March or earlier and regularly feed near streams also prey on winter stoneflies during periods of peak emergence.

I wish to thank Richard P. Narf for identifying the specimens.—BENEDICT C. PINKOWSKI, *15738 Millar, Fraser, MI 48026.* *Accepted 29 July 1975.*

An incident of Blue Jay predation on a Yellow-rumped Warbler.—Although the propensity of Blue Jays (*Cyanocitta cristata*) to raid the nests of small birds for eggs and nestlings is well-known, there are no reports of predation on mature birds. Carothers et al. (Wilson Bull. 8:204, 1972) reported several incidents of predation on small birds by Steller's Jay (*C. stelleri*). Roth (Condor 73:113, 1971) described an attack on a sparrow by a Mexican Jay (*Aphelacoma ultramarina*). Inclement weather and food stress were common factors in those reports. Blue Jay predation on red bats (*Lasiurus borealis*) was reported by Hoffmeister and Downes (Southwest. Nat. 9:102, 1964).

On 16 March 1975 we watched a Blue Jay attack and kill a Yellow-rumped Warbler (*Dendroica coronata*) in a residential area in Temple, Bell Co., Texas. The dive of the jay capturing the warbler drew our attention. Whether the warbler was on the ground when attacked, or was forced down by the jay is unknown. The warbler broke free briefly, but had scarcely left the ground when it was recaptured. The jay apparently killed the warbler with a series of pecks, picked it up by the head in its bill, and flew into a tree directly above us. After a few seconds it flew out of sight still carrying the limp warbler in its bill.

The weather was warm and typical of a central Texas spring. Food or climatic stress were probably not factors in the incident described here.—KENNETH W. JOHNSON, *Dept. of Biology, Mary Hardin-Baylor College, Belton, TX 76513, and* JOYE E. JOHNSON, *St. Francis Episcopal School, Temple, TX 76501.* *Accepted 1 July 1975.*

ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in The Wilson Ornithological Society are available because of funds generously donated in the memory of Aaron M. Bagg, a former president of the Society. Application forms for the awards to be granted in 1977 may be obtained from Douglas James, Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701. The deadline for applying is 1 November 1976. An Aaron M. Bagg Student Membership Award provides a 1-year gratis new membership in The Wilson Ornithological Society for selected exceptional students in the field of ornithology.—Douglas James, Chairman, Student Membership Committee.

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge. Although grantees are not required to publish their studies in The Wilson Bulletin, it is hoped that they will submit their manuscripts to the editor of The Wilson Bulletin for consideration.

Most statements applicable to the Fuertes Awards also are applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the colleges. High school students are eligible.

In some years two Fuertes Awards have been made, in some years, one. Amounts have been between $200 and $100. One Nice Award is made annually, in the amount of $100.

Interested persons may write to Jared Verner, PSW Forest Range Experiment Station, 1130 "O" St., Fresno, CA 93721. Completed applications must be received by April 1, 1977. Final decisions will be made by the Council at the annual meeting of the Society, 18–21 May 1977.

PACIFIC SEABIRD GROUP MEETING

The Pacific Seabird Group will hold its next annual meeting on 6–9 January 1977, at Asilomar, Pacific Grove, California. Announcement of the meeting and a call for papers will be mailed to members in early fall. Those not members and wishing to receive this information may write to the Secretary, Kees Vermeer, Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2, Canada. The Chairman of the Local Committee is L. Richard Mewaldt, Avian Biology Laboratory, California State University, San Jose, Calif. 95192.

The meeting will include a symposium on shorebirds in marine environments, to be held Friday 7 January. It is being arranged by Frank A. Pitelka, Museum of Vertebrate Zoology, University of California, Berkeley, Calif. 94720. Persons interested in the symposium may write to him for information.

Additional details regarding the annual meeting will also appear in the fall issue of the Pacific Seabird Group Bulletin (Editor, Dr. Daniel W. Anderson, Division of Wildlife and Fisheries Biology, University of California, Davis, CA 95616).

WANTED INFORMATION ON COLOR-MARKED BIRDS OF PREY

Color-coded vinyl wing markers were placed on Golden Eagles, Prairie Falcons, Red-tailed Hawks, and Ravens in the Snake River Birds of Prey Natural Areas to study movements and migration. Information needed: species sighted, wing(s) marked, color, location of sighting, and date. Please send information to: Bird Banding Laboratory, Office of Migratory Bird Management, Laurel, MD 20811.

REQUESTS FOR COLOR-MARKED BIRD SIGHTING REPORTS

An increasing number of banders advertise that reports of color-marked birds should be reported directly to them. Many of these observations concern individual birds that can be identified or related to a standard U.S. Fish and Wildlife Service band. The banding office is losing certain recoveries because researchers fail to notify them once they have their own information. All reports that can be identified to F & WS band numbers and any color-marking sightings that are not of your own birds should be sent to the bird banding laboratory. If you advertise for reports, please request that all sighting reports be made directly to the Bird Banding Laboratory, Office of Migratory Bird Management, Laurel, MD 20811. They will report back to the banders involved as rapidly as possible.

THE ROBERT F. AND JUDY H. MASON MEMORIAL FUND

The Wilson Ornithological Society is delighted to announce that Mr. and Mrs. Mason have expressed their intention of making a bequest to the Society. The income from this endowment would be awarded annually to support field studies of living birds of the Nearctic region (south to Central Mexico), especially of rare and endangered species or those whose populations are known, or thought, to be declining. Examples of appropriate topics for study would include behavior, vocalization, reproductive biology, feeding behavior, ecology, population dynamics, distribution, and migration; collecting of specimens should be avoided if possible. Applications would be accepted from citizens of the United States and Canada. The recipient of a grant would agree to submit any papers resulting from the study to the Editor of *The Wilson Bulletin* for consideration for publication.

The Officers of the Wilson Ornithological Society wish to express their appreciation to the Masons for their generosity in thinking about the future welfare of the Society and of future students of the living bird.

NOTICE OF FUMIGATION SCHEDULE AT THE U.S. NATIONAL MUSEUM

In order to comply with EPA safety requirements for fumigation with DOWFUME 75, the bird collection of the National Museum of Natural History, Smithsonian Institution will be closed to all investigators without exception twice annually from Thursday through Tuesday of the first weeks of April and October.

ERRATUM

The correct citation to the work of Sutton in Mengel's note in the last issue of the Wilson Bulletin (88:351–353) should be: Bull. Oklahoma Ornithol. Soc. 2:9, 1969.

ORNITHOLOGICAL LITERATURE

Birds in Japan: A Field Guide. 2nd printing (actually 2nd edition). By Yoshimaro Yamashina. Tokyo News Service, Tokyo, Japan, 1974: vii + 266 pp., 147 color figures, 3 black and white plates, 23 black and white photos, 22 figs. $29.50.—A useful guide to the more common Japanese birds (314 out of 480+ species) as well as a good guide for planning a birding itinerary. The bulk of the book is carried over from the first edition and is composed of ⅓ page color paintings of one or two species (with background), the rest of each page containing descriptive material under three headings: Recognition, Range and Habitat, and Habit. The 1st edition covered somewhat less than 200 species. In the 2nd edition, the additional 115 species are grouped into 15 new plates, without background, with abbreviated textual material on adjacent pages. The new plates have been inserted at appropriate places in the text, but a few species are separated from the rest of the family. The Wetmorean order of families has been followed.

The color plates are accurate and attractive, but only 10 species are illustrated in flight. Descriptions are good and contain pointers for distinguishing similar species. However, no mention is made of species not covered in this guide. The Range and Habitat, and Habit sections tell where and when a bird is likely to be found as well as some of its distinctive habits.

The introductory chapter provides enough information about climate, distribution and habitat of birds, migration and good birding areas to enable the user to plan his travel and birding in Japan. This chapter is far more extensive than most (if not all) field guides and provides a useful overview of avian distribution and its dynamics in Japan. Some 29 main birding areas, plus many supplemental places throughout Japan are discussed, including the dominant or most interesting birds and vegetation.

Unfortunately the binding of both copies I examined was beginning to come apart; the cover will soon separate from the book. There is a number of unimportant typographical errors.

The high price of this guide will restrict its sale appeal. Color figures on most pages and the heavy glossy paper are a bit lavish for a field guide with a limited market. Although this book has a complete list of Japanese birds in an appendix (those treated are not indicated), the traveller to Japan may also want the "Check-list of Japanese Birds" (1974, Ornithological Society of Japan, $29.00) for its description of the range, occurrence and habitat of all species, and "Birds of Japan in Natural Colors" (K. Kobayashi, text in Japanese, with English and scientific names, about $10.00) for its excellent color plates of all Japanese birds. This adds up to nearly $70.00 for three books, whereas the whole of North America is covered with two Peterson guides and the Robbins guide for only $20.00. The English speaking birder in Japan will find Dr. Yamashina's guide indispensable as well as attractive.—Ben King.

Fundamentals of Ornithology, 2nd edition. By Josselyn Van Tyne & Andrew J. Berger. John Wiley & Sons, New York, 1976:xviii + 808 pp. $22.50.—Andrew J. Berger has prepared a new edition of this popular ornithological textbook first published in 1959. There are nearly 200 additional pages with reduced type size, resulting from considerable new text material, but much of the expansion is due to the increase in illustrations from 254 to 528. Although these are generally good, many of the photographs are somewhat blurred, lacking in contrast, or only vaguely related to the text.

The chapter contents have been somewhat reorganized, and cover the following topics: paleontology, structure and function, plumage and molt, senses and behavior, voice and sound production, bird distribution, migration, flight and flightlessness, food and feeding habits, courtship and nest building, eggs and young, taxonomy and nomenclature, and the classification of world birds by families. All of the chapters have been extensively revised and include much recent material with numerous references to current research literature. The references are listed at the ends of the chapters, and give the student an excellent introduction to the literature for further investigation. The method of extensive in-text citations gives the book a sense of immediacy and authority often lacking in textbooks where the original sources are not cited.

One of the highlights of the original edition was the final chapter on the families of birds of the world, and this has been revised for the second edition. Each family is covered on a single page, with a standardized format covering physical characteristics, range, habits, food, breeding, and the original literature sources for its technical diagnosis and classification, as well as a small selection of important general references. Each family is also illustrated by a drawing of a representative species by George M. Sutton. Unfortunately the quality of reproduction of these attractive line drawings is much reduced in the new edition. This section is an invaluable summary of information on avian classification. The system used has been slightly modified from the first edition, but is still relatively conservative. The ratites are retained in separate orders, the Opisthocomidae are kept in the Galliformes, and the Pteroclidae in the Columbiformes. The passerine suborders Eurylaimi and Menurae are retained, as is the separate familial status of the Cyclarhidae, Vireolaniidae, Tersinidae, and Catamblyrhynchidae. However the Spheniscidae are now placed beside the Procellariiformes, a suborder Furnarii is introduced, and the families Rhabdornithidae and Climacteridae are now recognized.

Two useful sections of the first edition, the list of ornithological sources and the glossary, have been deleted. The loss of the latter is particularly unfortunate; where else can one go for a ready definition of antipericoelous, cultirostral, dertrotheca, elaeodochon, grypanium, nomopelmous, paradactylum, or ultraexaspidean? What other convenient source is there when one needs a quick distinction between homoeomeri and heteromeri? The loss of the glossary is also unfortunate because it is attributed to space limitations, yet many of the new photographs could have been more easily sacrificed.

The general trend of declining quality in book production is evident here: the paper and printing are inferior to the first edition, and the construction is weaker. My review copy already has a cracked binding, while my frequently-used, decade-old first edition is still intact.

On the whole this remains an outstanding textbook of ornithology, being thorough and detailed in its coverage of most aspects of avian biology, and especially good in its coverage of structure, function, and systematics.—ROBERT J. RAIKOW.

BREEDING BIOLOGY AND BEHAVIOR OF THE OLDSQUAW (CLANGULA HYEMALIS L.) By Robert M. Alison. Ornithological Monographs No. 18, American Ornithologists' Union, 1975: 52 pp., 7 B & W Illus., 3 photos. $3.50. ($2.50 to A.O.U. members). Obtainable from Glen E. Woolfenden, Dept. of Biology, University of South Florida, Tampa, FL 33620.—The author set about to determine: (1) Oldsquaw population levels and breeding pair distribution, (2) nest site tenacity and homing, (3) nest distribution and location, nesting success, and the effect of weather upon nesting and renesting, (4) territorial behavior, and (5) species-specific displays of this species in sufficient detail to permit comparison with those of other species.

Forty-three to 47 pairs of Oldsquaws were studied 1968–71 on a 4000 ha area 5 km east of Churchill, Manitoba. Supplemental behavioral observations were made in Toronto in winter. Alison's data on age and sex distribution in the population, arrival, mortality, productivity, predation, nest site selection, homing, etc. will be standard references for anyone interested in Oldsquaw breeding biology. Predation relative to nest site is extensively covered. Behavioral descriptions are far more complete than were available previously. They are adequate for comparison to other species with regard to sequence of displays and seasonal variation in display frequency. Display morphology and vocalizations are not described quantitatively.

At times, interesting facts are skimmed over with essentially no discussion. For example, Alison states that females spend no time searching for or preparing nest sites in advance of time for the first egg to be laid. This is an unusual situation for waterfowl and deserves discussion. Likewise, his finding that Oldsquaws did not nest at ponds with Common Eider (*Somateria mollisima*) colonies deserves further comment. Alison did not review reports of Oldsquaws avoiding King Eiders (*S. spectabilis*).

The weakest aspect of this monograph is its failure to draw clear and logical conclusions. Discussions and explanation of territoriality are hard to follow and lack conclusions. The design of experiments aimed at testing territorial defense was poor and did not allow the formation of firm conclusions. The high rate of inviability which Alison reports is inadequately discussed. Alison found that all three females returning a second year to the same nest site had been successful the previous year, yet he concludes "Success or failure of a previous nest clearly does not determine the nest site chosen in any given breeding season."

This paper is handicapped by cumbersome and careless writing. In many cases, poor choice of words interrupts a reader's train of thought. References to figures in the text are, in several cases, misleading relative to what the figures actually portray. Certainly Fig. 4 does not illustrate individual variability of plumage! Discussions of nest site fidelity, weather, and predation are duplicated to an unnecessary extent. Illustrations are of poor quality.

Overall, this monograph represents a significant advance in our understanding of Oldsquaw biology. It is unfortunate that the author missed an opportunity for an extensive comparison of Oldsquaws to other arctic waterfowl. It is equally unfortunate that he failed to relate his work to relevant biological concepts. Without such comparative and theoretical material, this work should have been published as two average length papers.—Lewis W. Oring.

Population Ecology of the Mallard. I. A Review of Previous Studies and the Distribution and Migration from Breeding Areas. By D. R. Anderson and C. J. Henny. U.S. Dept. of the Interior, Bureau of Sport Fisheries and Wildlife Resource Publication 105. 1972: 166 pp., 61 figures, 16 tables. $1.50.—This is the first in a series of reports aimed at compiling data on mallards gathered by the Bureau over the last 20 years. This report reviews the history of waterfowl management, summarizes previous studies, and reports, summarizes and discusses the distribution of band recoveries throughout the breeding range of the mallard. A review is presented of waterfowl management from 1850 to the present. The mallard is the most abundant wild duck in North America. Its population in late summer has ranged from 13–30 million birds (mean = 19½ million), with an annual "harvest" of from 1.3 to 5.7 million (mean = 3.5 million) since 1955. Waterfowl conservation practices have gradually developed from the first game legislation in the 1870's, through the establishment of the Migratory Bird Conservation Act of 1929 (creation of wildlife refuges), the Duck Stamp Act, the Migratory Bird treaty with Mexico, the establishment of research areas, and a National Flyway Council and the institution of banding programs and aerial surveys, to the development of the Migratory Bird Population Station (Patuxent) and other research centers. Today there are numerous data gathering programs which provide a basis for making management decisions.

A brief section on research studies on mallards provides an overview of the information available on sex ratios, mortality, population size, influence of habitat, behavior and pesticide research. Although this whole section is only 6 pages, it provides a starting point for any student of mallard biology.

The bulk of this report deals with banding data. Banding terms are carefully defined. It is difficult to deal with banding data from all of North America, and so the authors designated 16 major "reference areas." A major reference area is the sum of all the preseason banding stations located in the same general area and having similar recovery distribution patterns. Large reference areas were subdivided where necessary. Each major reference area is described with a brief summary of the quantity and quality of information available, including research, surveys and banding data. The percentage of the continental mallard population nesting in each reference area is estimated. Voluminous information is presented on the banding recoveries from each reference area including figures of the distribution of band recoveries. Tables present data subdivided by age and sex, and by direct, indirect and total recoveries. The information in this section is detailed and very useful for biologists interested in any subsection of mallard breeding range. Conclusions are drawn in each section relative to the number of mallards harvested, the location of the harvest, migration routes, and possible reasons for differences between areas. This section ends with a discussion of the general patterns of band recovery distribution by flyways, and as a function of wet versus dry years.

POPULATION ECOLOGY OF THE MALLARD II. BREEDING HABITAT CONDITIONS, SIZE OF THE BREEDING POPULATIONS AND PRODUCTION INDICES. By R. S. Pospahala, D. R. Anderson and C. J. Henny. U.S. Dept. of the Interior, Bureau of Sport Fisheries and Wildlife Resource Publication 115, 1974: 73 pp., 25 figures, 18 tables. $1.60.—This is the second in a series of reports on the comprehensive analysis of population data on the mallard at the continental level. This report provides information on mallard breeding habitat, the size and distribution of breeding populations, and indices to production. It is largely based on large-scale aerial surveys conducted during May and July 1955–1973. May surveys were used to estimate habitat conditions and the number of breeding birds, and July surveys were used to estimate variables related to midsummer habitat conditions and waterfowl production. Climatic conditions have a considerable effect on the quality and quantity of waterfowl breeding habitat which in turn influences waterfowl production and the distribution of birds on the breeding grounds.

There were 127 million acres of natural wetlands in the United States at the time of settlement; by 1953 only 82 million acres remained. Since then this has decreased to

75 million acres. Programs dealing with North American wetlands have simultaneously promoted wetland drainage and wetland preservation. Federal support of wetlands has only partially offset the acreage drained in the Northern Great Plains for wheat production. This loss of wetlands has been the major cause of declines in waterfowl populations. Similar decreases have occurred in the Canadian wetlands.

The number of ponds present in the Prairie-Parkland area during the breeding season and the midsummer periods, and the effects of precipitation and temperature on the number of ponds are analyzed in detail. Pond numbers in a given year were a function of the number of ponds present in the previous year and the amount of precipitation during the previous 10 to 12 months. The number of July ponds was a function of the number of May ponds that year and the precipitation received during the May 1–July 31 period. Precipitation in any individual month is only weakly correlated with the number of ponds in a given year. An analysis of 33 years of monthly precipitation data from the Prairie-Parkland area failed to reveal any significant precipitation cycles. Precipitation appeared to be strongly influenced by substantial seasonal and random components. Although precipitation appears to change from one extreme to another in successive years, the number of ponds did not vary to this degree. Since the number of ponds in a given year is related to the number the previous year, pond numbers are unlikely to change drastically from one year to the next. I found the presentation of the wetlands and pond data especially useful for anyone interested in marsh and prairie ecosystems. This data base may well prove useful in understanding population levels of other avian species in these habitats.

Aerial surveys sampled 84% of the estimated breeding population of mallards. The estimated size of the May population ranged from 14.4 million (1958) to 7.1 million (1965). Generally, the mallard population declined from 1958 to 1962, and remained below 10 million birds until 1970. The center of mallard abundance during the breeding season is the Prairie Parkland area in south-central Canada where 51.5% (range of 37.7 to 68.5%) of the population breeds. An average of 29% of the mallards was found in northern Canada and the Northwest Territories, 16% were found in the north-central United States, and 4% were in the Alaska-Yukon area. Mallards represent 28% of the breeding duck population in all surveyed areas except the far North. The distribution of mallards tends to parallel the distribution of total breeding ducks.

Estimates of midsummer habitat conditions and indices to production from the July surveys were studied and described. Several indices showed declines from west to east in the Prairie Pothole region. These indices are 1) density of mallards, 2) brood density, 3) average brood size, and 4) brood survival. Late nesting and renesting efforts were highest during years when midsummer water conditions were good.

An interesting discussion of production rates as a function of density-dependent and density-independent factors is presented. They suggest that spacing of birds is the key factor in density-dependent population regulation. The spacing mechanism along with habitat conditions influences some birds to overfly the primary breeding grounds into less favorable habitats to the north where production rates are lower. Emigration from prime habitat (Prairie-Parkland area) is thus density dependent. Breeding populations remaining in these prime breeding habitats appear to produce young at a rate independent of density. The number of young produced appears to be a linear function of the breeding ducks in the area. This is perhaps the first study of a continent-wide nature having sufficient data to substantiate densities on the broad scale necessary to show this density-dependent effect.

This report presents much valuable data for all avian biologists and I recommend it to anyone interested in behavior, populations, reproduction indices, ducks, mallards, marshes and wetlands.

Population Ecology of the Mallard III. Bibliography of Published Research and Management Findings. By D. R. Anderson, P. A. Skaptason, K. G. Fahey and C. J. Henny. U.S. Dept. of the Interior, Bureau of Sport Fisheries and Wildlife Resource Publication 119. 46 pp., $1.30.—This third report in a series on population data on the mallard is a bibliography of references. It was prepared primarily to aid waterfowl management and research personnel but will be helpful to all biologists interested in mallards. It is arranged under the following topics: population ecology, behavior and social interactions, genetics-evolution, food and food habits, habitat-wetlands, censuses and surveys, pesticide research, lead poisoning, disease and unclassified. The authors selected 900 of the approximately 3,000 references examined for inclusion in this bibliography. The report also includes an author index.—Joanna Burger.

Comparative Behavior of the American Avocet and the Black-necked Stilt (Recurvirostridae). By Robert Bruce Hamilton. Ornithological Monographs No. 17, American Ornithologists' Union, 1975: vi + 98 pp., 18 text figs., paper cover. $7.50 ($6.00 to A.O.U. members). Obtainable from Glen E. Woolfenden, Dept. of Biology, Univ. of South Florida, Tampa, Fla. 33620.—The principal purposes of this study are given by the author on p. 1: "Because of the insufficiency of detailed information about the North American avocet and stilt, I studied the behavior of these species, as related to their morphology and ecology, to determine if their supposedly close relationship can be supported on other than superficial morphological grounds." Most of the study was conducted at salt evaporation ponds in Alameda County, California (in the San Francisco Bay area), and one trip was made to natural ponds near the Oregon-California border from 21–26 June 1968. The study was completed in 1969, which explains why there are no literature references later than 1968.

There is a brief review, with maps, of the geographic distribution of recurvirostrids with particular attention to North America, but no discussion of the taxonomic problems involving species limits within the family. A section on morphology deals with standard measurements of tail, wing, tarsometatarsus, and body weight. Special measurements were devised to represent the recurved bill of the avocet, and the absence or extent of sexual dimorphism in all the above dimensions is given particular attention. The morphology section does not include osteology, myology, other internal anatomy, pterylosis, or molt. Avocets show no sexual dimorphism in color but differ in bill configuration; stilts differ in color (pp. 6–7), but the nature of the differences was inadvertently omitted (females have duller, brownish backs, males have glossy black backs). There are other slight differences and an important one in tarsometatarsus length, which is significantly longer in the male in both species.

Habitat differences are discussed in one page, with literature references cited to show that avocets usually inhabit more saline waters and stilts prefer fresh water habitats.

The long section on Maintenance Behavior (pp. 15–57) is made up largely of detailed descriptions of each posture or series of movements involved in maintenance activities, and various exceptions to the usual picture are described. The narrative style is very objective and complete—for example, drinking (p. 48): "When the bill is just above the water surface, it is placed in the water by movement of the entire body, which is accomplished by bending the ankle joint. The neck and body are then raised with the neck bent somewhat and the head resting along the axis of the back, but with the body angled so that the bill is higher than the back. Because of gravitational influence, water then flows into the mouth where it is swallowed." Sometimes cautious objectivity is carried to an extreme (p. 43): "Resting is a comfort movement which is difficult to define. The basic characteristic of resting is a lack or minimizing of activity, which probably results in minimal expenditures of energy."

Tables and chi-square statistical analyses treat the associations of different activities with each other and with disturbance or non-disturbance. Various differences between species and sexes are described. Observations during one week at one locality in northern California showed that male stilts forage more frequently in deeper water than do females. No such difference was noted in avocets, and there was considerable overlap between the two species in the water depth at which foraging was most frequent. Avocets tended to forage more often by plunging the head under water than did stilts, and male avocets did so more often than females.

A section on locomotion describes the postures and movements of flight, walking, running, wading, and swimming. Aerodynamics and the energy cost of these activities are not discussed.

The section on social behavior consists largely of descriptions of postures and actions and the circumstances under which they occur. There is a similar treatment of sexual interactions, with some discussion of pair formation and the possible means of sex recognition. The author suggests that plumage dimorphism in stilts and bill shape in avocets are the most important clues. Remarkably, there seems to be no noticeable difference in pairing, precopulatory display, copulation, and postcopulatory display in the two species, but only one copulation of stilts was observed. The nesting behavior section includes accounts of nest locations along the dikes of the salt ponds, nest building, incubation behavior, hatching, brooding, care of young, and distraction displays. Hamilton observed nest building only in avocets, and believes that the scrape is made altogether by rotation of the breast feathers against the substrate. The incubation period was not precisely determined for either species but it seems to be 23 to 25 days in both. The sexes appear to share incubation duties and brooding and care of the young more or less equally. The young seem quite precocial and leave the nest scrape on the day of hatching, but parents may brood their own young and sometimes mixed groups during the first post-hatching week. Avocets and stilts have a variety of distraction displays and most of these differ between the two species. The displays are most intense away from the vicinity of the nest and are probably effective in misleading potential predators about its location.

The final section consists of three pages of summary and conclusions; there is no separate discussion section. The author concludes that *Recurvirostra* and *Himantopus* are correctly included in the same family, that *Cladorhynchus* of Australia should tentatively be maintained as a separate genus, and that *Ibidorhyncha* probably does not belong in the Recurvirostridae.

In a field of research in which overinterpretation is a principal hazard it may seem churlish for a reviewer to complain of underinterpretation, but this is my chief criticism. The other complaint is the limited scope of the study. I have already listed a number of things that might have been included but were not, and among additional ones the absence of any discussion or analysis of vocalizations is most regrettable. The author gives us descriptions of postures and movements in virtually unlimited detail but is extremely restrained in giving us his ideas on their significance. The monograph does provide a useful catalog of avocet and stilt behavior, and its value is greatly enhanced by Gene Christman's excellent drawings that depict most of the activities described. I just wish that the author had concentrated less on descriptive material and given more analysis, interpretation, and insight.—THOMAS R. HOWELL.

THE GREAT BOOK OF BIRDS. By John Gooders. Dial Press, New York, 1975: 351 pp., 386 photographs (all but 1 in color), 19 color paintings. $24.95.—For the past two Christmas seasons, the bookstore displays have included so many of the ponderous, gaudily illustrated bird books collectively known as "coffee-table books" that it is getting harder and harder to remember which book is which. This profusion may have impelled Dial Press to rechristen Gooders' book "The Great Book of Birds" to catch the eye of the American purchaser; the British edition is more modestly entitled "Birds: an Illustrated Survey of the Bird Families of the World." Gooders states that he accepted the commission to write this book to fill an "obviously vacant niche." By this he meant a family by family survey illustrated by color photographs as opposed to paintings (". . . to illustrate a bird book, other than a field guide, without photographs is virtually unthinkable," a dictum that might come as a surprise to, among others, Leslie Brown and Dean Amadon). Gooders specifically contrasts his book with that of Oliver L. Austin, Jr., with its well-known paintings by Arthur Singer. Incredibly, he does not mention or list in his bibliography E. Thomas Gilliard's "Living Birds of the World," which was wholly illustrated with photographs, and with which Gooders' book ought more properly to be compared. Gooders states that "our knowledge of birds and their lives has changed remarkably since [Austin's book] appeared in 1961." Perhaps so, but one must search diligently through the pages of Gooders' book to find information that could not have been published in 1961, and most of the "remarkably changed" knowledge I found dealt with recent censuses of endangered birds or range changes in Britain.

The publisher's blurb on the dust jacket (at least of the English edition, which I have) describes John Gooders as "an ornithologist of international repute." An ornithologist (whether "professional" or "amateur") is, or should be, a scientist, characterized by a commitment to care and accuracy. Traveling around the world to look at birds does not make one an ornithologist, merely a more experienced bird-watcher. Before obtaining this book, my only knowledge of John Gooders was through his finding guide "Where to Watch Birds," which I attempted to use during a driving trip through Britain in October 1975. I soon learned that Gooders is no Pettingill, and the present book indicates that he is also neither an Austin nor a Gilliard.

The text, in general, is an undistinguished rehash of information much the same as that available in other surveys of birds of the world. The family chapters are excessively brief for such a large book; the amount of space available for the text has been severely diminished by reproduction of many photographs far larger than either necessary or desirable. Often the largest photographs are among the poorest. The nadir is perhaps the double-page spread on pp. 138–139, a 17¾″ × 11⅝″ reproduction of an out-of-focus photograph of *Rostratula benghalensis*. The bird occupies an area of about 3½″ × 2½″, and the rest of the picture consists of a blurred image of singularly unattractive looking mud. This kind of infringement on text space has meant that, for most families, information is given on fewer species and in much less detail than in either the Gilliard or Austin books. Inevitably, some family accounts are lopsided.

Of approximately one page of text on the parrots (versus 2½ in Austin and almost 5 in Gilliard), discussion of the entire New World radiation of this family is confined to one sentence about the Carolina Parakeet and five sentences about macaws in general and *Ara ararauna* in particular. The only indication that the Jacanidae inhabit the New World is the statement that "the name jacana is derived from the South American [!] and is Portuguese in origin," although five of the six Old World species are mentioned and described. Gooders' slighting of the work of the late E. T. Gilliard extends to the family accounts of the bowerbirds and birds of paradise; we are told that "most of our knowledge of the behaviour of birds of paradise has been gleaned from the study of birds in captivity." In the account of the Tetraonidae, one paragraph is devoted to the grouse-shooting and drinking habits of the British aristocracy, while the Ruffed Grouse is not even mentioned—in fact, *all* of the North American grouse are said to boom and to have inflatable air sacs on the sides of the neck.

The writing style is plebeian, and the text abounds with sloppy generalizations (like that on the grouse) and irritating errors. On the same page (65), Gooders uses the expression "one of the most unique . . ." and describes Central America as a continent. The New World range of the Cattle Egret is given as Central America, the West Indies, and eastern United States; South America, where the first immigrants of this species appeared, is not mentioned. "Bitterns" are characterized by a description of the voice and habits of the European *Botaurus stellaris*, written as if the generalizations applied to all species. Females and immature males of the American Redstart are described as "uniformly grey with white patches in the tail."

Gooders indulges in slangy British vernacularisms that I, at any rate, found irritating, although I am anything but an anglophobe. On p. 10, "a new generation of bird photographers has hit the unphotographed list for six . . ." (a cricketing term, not a number of species). On p. 327, "Starlings are the wide boys of the bird world." Numerous species are described as the "odd bird out" of their respective families. And Gooders occasionally permits himself subjective value judgments that also annoyed me. For example, in describing the Little Egret, he writes ". . . only yellow feet on black legs jar the sense of beauty." Most writers consider this color contrast one of the most strikingly attractive attributes of the small egrets. On p. 89, "Pride of place among swans goes to the three northern species." In a word, why? On p. 338 Gooders states that crows, characterized as "the most advanced and intelligent of birds," are "placed at the end of the list by most modern systematists." I wonder whether he has taken a poll.

It almost goes without saying that this book has its share of typographical errors and misspellings, usually in scientific, proper and geographic names (*baralli* for *baraui*, Gambell for Gambel, Lake Janin for Lake Junin), but in general the proofreading was more successful in this than in many recent error-plagued books.

It seems almost a waste of time to dwell on the multiple inadequacies of the text of this book, as most people will probably make their purchase decision on the basis of the illustrations. Here we have indeed seen great progress since 1958, when Gilliard's book (with its vastly superior text) was published. Gilliard had to use many black and white photographs; there is only one (of a cave painting) in Gooders' book, and color reproduction has also improved in the past 26 years. One or more color photographs are presented for most living families of birds. Most (but by no means all) have been well chosen, although as mentioned above, many are reproduced far too large. I dislike seeing a Stonechat portrayed at the body size of a Bobwhite, and a Hawfinch as big as a Peregrine. The ten-inch Quelea on p. 324 is an excellent photograph abominably presented. Certain photographs of well-known birds are disappointingly mediocre. That of the House Sparrow shows only females (and is printed too yellow in my copy); the incubating Red-eyed Vireo has been washed out by a strong flash; hundreds of better photographs than that used of the Cardinal must have been available; the Boat-billed Heron is a scruffy-looking, probably captive juvenile accompanied by an error-filled caption; the Herring Gull photograph chosen is a blurred, off-color, confused shot of a dozen immature birds, apparently swimming toward a food handout.

But, given these disappointments, let us rejoice at the array of truly magnificent photographs of birds little known to many of us. I mention only a few of my favorites: the Squacco Heron feeding young; twelve male Harlequin Ducks on wave-pounded rocks; the superb white Gyrfalcon clutching a ptarmigan; the perky group of Crested Auklets; the facing pages with a flying Boobook Owl and an incubating Ural Owl; the Carmine Bee-eater swooping from its perch on the back of a Kori Bustard; wonder of wonders, a close-up of a Rufous Scrub-bird. There are many others that I enjoyed, assembled from the files of an international list of fine photographers. I assume that Gooders was responsible for the captions, and these are largely unworthy of the photographs. Scientific names are not given, which is a handicap because the figured species is not uncommonly omitted from the text. And in some instances neither a scientific nor an English name is provided for the species photographed. We are not told, to list some examples, *which* tinamou, cassowary, kiwi, darter, diving-petrel, or frigate bird is portrayed. In several cases a second species is visible in the photograph, but these are almost never identified. The Hottentot Teal among the wintering Garganeys is not mentioned, for example, nor are the terns among the Crab-plovers or the second species of gull in the Grey Gull photograph.

In addition to the photographs, there are several paintings reproduced in color. Most are rather amateurish, the worst being a grotesque rendition of five species of guans. At the opposite extreme are three attractive plates by the always reliable Robert Gillmor, portraying the Pelecanidae, Sulidae and Fregatidae of the world.

Any avid collector of bird photographs who simply *must* have this book would be poorly advised to spend twenty-five dollars for it. Like many other coffee-table books, it will probably appear eventually at a discounted price on the clearance house lists. Alternatively, one could send for the British edition, published by Hamlyn at £6.95. At this writing, the exchange rate for the Pound Sterling is such that the book would cost only a bit more than $14.00 plus overseas postage. Apply the money saved toward a copy of Gilliard's "Living Birds of the World" (now back in print at $19.95) for its much more thorough and reliable text.—KENNETH C. PARKES.

ATLAS OF EASTERN CANADIAN SEABIRDS. By R. G. B. Brown, D. N. Nettleship, P. Germain, C. E. Tull, and T. Davis. Canadian Wildlife Service, Ottawa, 1975: 220 pp., 108 pelagic and 23 breeding distribution maps. Order from Information Canada, Ottawa K1A 0S9. $6.75 in Canada, $8.10 elsewhere.—This atlas, measuring 8½ by 11 inches and printed on quite heavy coated stock, records pelagic distribution and colonial breeding distribution in the northwestern Atlantic region—from 40°W (near southern tip of Greenland, hence includes western Greenland) westward to 95°W (includes waters around Boothia Peninsula, Somerset Island, etc.) and from about 40°N (New England and Maritimes) northward to 80°N (beyond which few species occur). The pelagic data were gathered in all seasons, March 31, 1969–March 31, 1973. The seabird colony data are not limited to this period but sometimes extend back much earlier.

After the introduction, there is a discussion of how pelagic distributional data were gathered, a section on oceanographic features (temperature, salinity, etc.), one on factors influencing seabird breeding ranges (mainly terrestrial conditions), and a most useful and timely exposition of where and when seabird concentrations occur—where the birds are most vulnerable to oil spills.

The bulk of the atlas consists of the maps, plus brief but important accompanying text, for Fulmar, shearwaters, petrels, Gannet, cormorants, phalaropes, jaegers, gulls, terns, and Alcidae. Quantitative maps show average numbers of birds recorded per 10-minute watch; "rarebird" maps naturally have less to show; and colony maps are supplemented by tables giving named locations, geographical coordinates, colony size, census year, and authority. Much work went into this project; it seems natural for the authors to refer to mapping "effort" by month.

What can one learn from this atlas? Location of colonies and other breeding distribution, migration, dispersal, distribution at sea, relation of species to zonation of water temperature, and so on. The text by no means elucidates everything. Example: it is obvious from the maps that there is a northward postbreeding dispersal of *Larus marinus.* Thus the atlas invites a lot of use and some interpretation, but first one must learn that the circular symbols are "Type I" data (full-time observations) and square ones are "Type II" (part-time)—as explained on page 14—and with keys to symbols on page 13 and repeated on page 220. All through the atlas, either by adjusting arrangement of the maps slightly, or often not at all, the key(s) could have been repeated on one or the other of facing pages. Just from preliminary use, the review copy already is loose at the spine; the pages will have to be kept in a looseleaf notebook. This is a nuisance, especially for a document that will get hard use by everyone concerned in any way with boreal seabirds. It is possible that the uninformed person might, perhaps, assume that pelagic distributions as shown are quite constant, i.e. will be essentially repeated over many years. But ocean currents, hence temperature of water and composition of marine fauna on which birds feed, do shift with time and the birds must adjust accordingly. Vibe (Arctic animals in relation to climatic fluctuations, *Medd. om Grønland* 170(5):1–227, 1967) treated this subject at length and for a major portion of area within that encompassed by this important atlas.—RALPH S. PALMER.

ANOTHER PENGUIN SUMMER. By Olin Sewall Pettingill, Jr. Charles Scribner's Sons, New York, 1975: 80 pp., 36 color and 70 black-and-white photographs. $10.00.—This book is a popular introduction to the penguins of the Falkland Islands—"intended to entertain as well as to inform." Its 24 pages of text include a general discussion of penguin biology and more detailed sections on Gentoos, Rockhoppers, Magellanic, King, and Macaroni penguins. The narrative describes the behavior of these species on the Falklands and provides much interesting detail. Many questions that came to my mind as I read were answered, either in the text or in the photograph captions. The photographs present an excellent record of arrival at the shore, landing, the inland trek, and breeding. One shows a Magellanic Penguin skittering on its toes and flippers. In others the Rockhopper's moods, as expressed by its head plumes, are well-illustrated. Distant shots of several colonies give a good feeling for their size, relation to topographic features and the shore, and in some cases show the well-worn traffic routes.

This book is attractive and well-produced. Its text meets the author's intent, at least for the young student and the adult layman, and the pictures will interest many ornithologists as well.—Richard L. Zusi.

Golden Eagle Country. By Richard R. Olendorff, illus. by Robert Katona. Alfred A. Knopf, Inc., New York, N. Y. 1975: xvi + 202 pp., 39 black-and-white drawings, 1 map. Foreword by Dean Amadon. $12.95.—This large volume presents an anecdotal account of the daily experiences of a keen raptor biologist (and, later, two associates) as he conducted intensive field studies in 1971 and 1972 on breeding Golden Eagles and other raptors on a 1,000 square mile area of shortgrass prairie on the western Great Plains. The details presented are factual and concern "specific places, birds, and observations," but the setting, a place called Eagle Breaks, is fictitious to protect the birds.

Raptor biologists will find many fascinating nuggets of information scattered throughout the book. For example, the author concludes that there are far more Golden Eagles, and presumably other raptors, in North America than currently recognized. I found this conclusion of considerable interest because I independently suggested a similar conclusion elsewhere based upon studies of migrating hawks. Dr. Olendorff makes a plea for programs of active management of raptors. I agree that raptor management can aid these birds in many instances, but I would hasten to add that one method of management is to *do nothing.* There is a danger in working with wildlife as glamorous as birds of prey that management programs could become sophisticated professional toys. Hence objective, professional judgment must be the basis for developing raptor management programs.

Most of Robert Katona's drawings illustrating this book are excellent. They add a good deal of charm to the volume.

My main criticism with this book is the fact that the author is sympathetic toward falconry. This is extremely disappointing because I consider this activity to be totally ill-advised and unnecessary—one out of place with astute modern conservation goals.

In all, this is an interesting book which gives readers an excellent insight into the amount of work required to conduct field studies of raptors. It will be of primary interest to raptor enthusiasts.—Donald S. Heintzelman.

Summer of a Million Wings. Arctic Quest for the Sea Eagle. By Hugh Brandon-Cox. Taplinger Pub. Co., N.Y., 1974: 184 pp., 21 text figures, 25 black-and-white photos. $8.95.—Although I started reading this fascinating book with the view that I would be reading mostly about the White-tailed Sea-eagle, I soon discovered that Brandon-Cox's approach to the eagle was a total environmental account, an account of the sudden Arctic break from winter to summer, and seemingly an almost total picture and feel for the perhaps indescribable transition beginning the first week in May, in Arctic latitudes. An account that is partly narrative, partly a detailed chronological portrayal of happenings from the bloom of marine algae to the constant roar at night of millions of guillemots, auks, puffins, gulls, all thronging to the cliffs of Vaeroy in the Lofoten Islands off northern Norway. And above all this, the great wings of one of the largest sea-eagles. This is not a detailed biology of the eagle . . . one should turn to Wilgoth's monograph for that . . . but this book seemingly brings to the reader the total ecosystem which unfolds beneath the wide wings of the soaring eagle.

For all who have felt the lure of the Arctic, the lure of great sea cliffs alive with marine life, the intimate, intricate lure of even a square yard of tundra, the almost magic of untold millions of seabirds thronging to the astonishingly large but very temporary photosynthetic yield of marine phytoplankton supporting a zooplankton that defies quantitative estimate, for those who love the lure of almost total seclusion from human encumbrances of everyday life, this book is a must.—WALTER R. SPOFFORD.

THE NESTING POPULATION OF LESSER SNOW GEESE IN THE CANADIAN ARCTIC: A PHOTOGRAPHIC INVENTORY OF JUNE 1973. By Richard H. Kerbes. Canadian Wildlife Service Report Series No. 35, 1975:47 pp., 19 figs., 9 tables, paper cover. $3.25 in Canada, $3.90 in other countries.—Order from Information Canada, Ottawa K1A 0S9, Canada.—R.J.R.

BIRDS OF THE ROSETOWN-BIGGAR DISTRICT, SASKATCHEWAN. By Wayne E. Renaud and Don H. Renaud. Special Publication No. 9, Saskatchewan Natural History Society, Box 1121, Regina, Saskatchewan, Canada, 1975: 121 pp. $4.00.—This unusually complete and attractively printed paperback guide lists the occurrence, breeding status, abundance, and local distribution of 236 species in an area of 1512 square miles in central Saskatchewan. In addition to the species accounts there are brief discussions of the geography and habitats of the region, and a guide to birding areas.—R.J.R.

NON-GAME BIRDS OF THE WEST: AN ANNOTATED BIBLIOGRAPHY. By Steve Trimble. U.S. Dept. of the Interior, Bureau of Land Management, Technical Note, 1975: 320 pp., paper cover. Free on request from the Wildlife Staff, Denver Service Center, Bureau of Land Management, Denver Federal Center, Bldg. 50, Denver, CO 80225.—This bibliography covers the Cuculiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes of Alaska, Washington, Oregon, California, Montana, Idaho, Nevada, Wyoming, Utah, Arizona, Colorado, and New Mexico. References are grouped according to the biome in which the species predominantly occurs, and in addition there are sections on general biology, research techniques, associates of man, and state surveys. Within each division the birds are arranged by family. A Master Species List and Index is arranged taxonomically, so that one can quickly look up a given species and find the locations in the book where papers are listed. The papers are from many sources, including unpublished theses, but the Wilson Bulletin, Auk, and Condor are heavily referenced. Shorter papers are mainly listed by title only, but for many papers a brief summary or abstract of the contents is given. This is a very useful compilation of literature on the ecology, life history, habitat, and behavior of western birds, and should be especially valuable in helping students to quickly survey the literature at the beginning of a research project.—ROBERT J. RAIKOW.

BIRDS OF CENTRAL PENNSYLVANIA. 2nd ed. By Merril Wood, 54 pages, maps, paper covers. $1.50 (by mail $2.00 from State College Bird Club, Inc., 626 West Nittany Ave., State College, PA 16801).—This is a compilation of records of the State College

Bird Club, and gives species, relative abundance, and habitats of birds recorded in a 25-mile radius of State College.—R.J.R.

THE BIRDS OF MANITOBA. By Ernest S. Thompson. Proc. U.S. Natl. Mus., XIII, pp. 457–643, with plate XXXVII. 1891. Reprint edition published by Premium Ventures Ltd., Winnipeg, Manitoba, Canada, 1975: 187 pp. Paper Cover. $5.00. Order from the publisher at 235 Garry St., Winnipeg, Manitoba, Canada, R3C 1H2.—The author is better known as Ernest Thompson Seton. This is an early work, containing 266 species accounts with distributional data and some rather anecdotal accounts of habits.—R.J.R.

VOICES OF NEOTROPICAL BIRDS. Record # Ara–1. Written and narrated by John William Hardy. Most recordings by Hardy. Published privately by John William Hardy and Carol K. Hardy, Gainesville, Florida, 1975: One LP record in jacket. $6.00 postpaid. Add $1.00 for Canadian and $1.50 for other foreign mailing.—In spite of the great increase in travel to the neotropics by both ornithologists and birders, published records of the voices of neotropical birds are still few and far between, and the present work is thus a welcome newcomer to the scene. Forty-five species are presented in systematic order, with others heard on the background bringing the total to over 50. Most of the birds were recorded in Mexico, Nicaragua, and Costa Rica, only two being from South America. The recordings themselves are of good but not surpassing quality, not up to the standard we are used to from professionals like William Gunn and J-C. Roché, but nonetheless adequate for both listening pleasure and learning purposes. The most brilliant recording and also aesthetically the most pleasing is that of the Sinaloa Wren, *Thryothorus sinaloa.* Many recordings are "firsts," of particular note being the three rare jays, *Aphelocoma mirabilis*, *A. nana*, and *Cyanocorax dickeyi.*

Although the record has definite use as an identification aid and will give pleasure to those who simply enjoy listening to bird voices, these are not Hardy's primary purposes. His main thrust is to provide a biologically oriented commentary to the recordings so that the listener may be instructed at the same time as he is being entertained. To this end there is an introduction on the back of the jacket, together with a list of species and details of the recordings, also a definition of terms used in the narration. The bulk of the instructional commentary is contained in the narration on the record, and herein lies one of the major defects of the publication. So much space is used up by the spoken commentary that there is often little time left for the birds themselves. Had the commentary been in printed form, many more bird vocalizations could have been presented, increasing the usefulness of the record. And whereas one can listen indefinitely to the bird songs, the human voice begins to pall on the third or fourth repetition. Further, information retrieval is difficult with this type of presentation. Hardy has many interesting things to say, but in order to refer to them you have to play over the record until you reach the right spot.

There is much of ornithological interest on this record. Hardy's intention is to depart from the rather bald presentation of many conventional identification records and attach some scientific point to the recordings he presents. This is a laudable aim, and while the connection between some of the vocalizations on this record and biological theory is often somewhat tenuous, the commentary providing little beyond the circumstances of the recording, this is more than made up for by the meat in the other examples. Of particular interest is the illustration of the songs and calls of two species pairs, *Catharus frantzii/occidentalis* and *Vireo griseus/pallens*, each of which was formerly thought to consist of a single species. Equally fascinating are the vocalizations of the complex of *Agelaius phoeniceus* subspp. living in central Mexico, including those of a hybrid swarm of *A. p. gubernator* × *nelsoni.*

While the record itself is technically free of flaws, whoever proofread the jacket was asleep on the job. My editorial eye spotted speces, esthetic, tratining (training), concensus, Violaceus Jay, Ciccadas, *Cacciculus*, *Ara aruana*, *Megarhynchus pitangus*, and Matto with no Grosso, among others. But just as these were overlooked by the proofreader, so we too can overlook them, since this record makes a valuable contribution and is recommended for purchase.—G. STUART KEITH.

MY ORPHANS OF THE WILD. By Rosemary K. Collett with Charlie Briggs. J. B. Lippincott Co., Philadelphia & New York, 1974: 288 pp., B & W photos. $8.95.—Subtitled "Rescue and home care of native wildlife," this book has resulted from the author's many years of caring for young, injured, or diseased birds and mammals at her home in Florida.

Less than a third of the book is devoted to mammals, such as raccoons, armadillos, and rabbits. The majority of the chapters concern birds, grouped by types that require similar care and diet: song and garden birds (sparrows, jays, cardinals, mockingbirds, etc.); insectivores (woodpeckers, caprimulgids, swifts, martins, flycatchers, etc.); piscivorous marsh birds (herons, egrets, and bitterns); two groupings of raptors; etc. Although the accounts are limited to Florida species that the author has had experience with, much of her information can be extrapolated by the reader to include northern birds (e.g., robins, probably the most common "orphans" wherever that species breeds). The only major groups omitted are shorebirds and hummingbirds, apparently because the author has never been brought a Killdeer chick or exhausted Ruby-throated Hummingbird—which is surprising.

Each chapter contains a brief description of the included species, a section on infant diet and care, another on adult diet and care, a discussion of how to house the birds (with pen and cage designs in an appendix), and notes on special problems of the species under discussion: force-feeding piscivores; incubating eggs; diseases and common injuries; capture (as of a pelican bristling with rusty fishhooks); avoiding injury or contagious diseases; and general do's and don'ts. Each chapter ends with advice on releasing the birds as soon as they are able to care for themselves, and commendable stress is placed on not releasing exotic species into the wild. The last sections of the book contain general discussions of first aid and an excellent practical account of cleaning and caring for oiled birds. Appendices include a veterinary reference section (the author's long-experienced veterinarian served as consultant for the book) with a list of medicines (with uses and doses), surgical equipment, and special diets (often brand names). Another appendix is a sparse and misleading list of the natural diets of common birds. Although not so stated, the list is limited to adult foods, whereas many species differ strongly in nestling vs. adult diets (e.g., under "sparrow" the only food listed is "seed"). The book concludes with a short discussion of the legalities involved in caring for wild birds, a bibliography of suggested reading, and a good index.

A reviewer might quibble about some of the book's shortcomings, such as the lack of concern for readers who do not live in a warm climate and would have to provide warmer and more protective housing, a few small mistakes on ornithological facts, the degree of repetition (too much for general reading but not enough for quick reference use), and occasional slips into the cute (e.g., her three *Gavia immer* named "Claire de," "Panta," and "the Loon Ranger"). On the other hand, Mrs. Collett has included many details not only useful to a person caring for a bird, but also that can be transmitted to a veterinarian who (as is so often true) has had little experience with non-domestic birds. My only serious complaint is the lack of practical emergency diets and of diets based on easily obtained ingredients, at least for some groups of birds. The emergency recipe given for infant garden birds consists of Zymadrops vitamin supplement, a 25 mg vitamin B_1 tablet, and Gaines Meal dry dog food (the consistent recommendation for Gaines products is not explained). The author also occasionally forgets that people suddenly burdened with a baby robin might not be willing to invest in an expensive supply of exotic ingredients. The basic diet for infant garden birds simply replaces the Gaines Meal with medicated turkey starter (which even Mrs. Collett has to special-order, and it only comes in 50 lb. bags). A more practical list of ingredients should have been tried out while the book was in preparation, so the author could have recommended substitutions from her own experience. I can suggest high-protein baby cereal instead of the turkey starter—it comes in small boxes and is often on hand in households with children who bring home baby birds.

These objections aside, the book is extremely useful and a generally practical guide to bird care. It is a refreshing change from others on the subject, which tend to be overly emotional, to include too much second-hand information, or to require a veterinarian/aviculturist to use.—Mary H. Clench.

The Endangered Ones. By James A. Cox. Crown Publishers, Inc., New York, 1975: 224 pp., 250 + color and black and white photographs, line drawings and engravings. Hard cover. $14.95.—Over the last 10 years we have witnessed a surfeit of works dealing with one aspect or another of "ecology." Some are more eloquently written than others and scientific content varies widely. Cox has directed his volume at the general reader. His message is clear: the wildlife of the world (notably vertebrates) are in serious trouble and the problem will only become more pronounced unless conservation measures are increased. A book with this noble aim in mind cannot be judged harshly. Cox's text is exceedingly basic and gives a quick rundown of the environmental crisis and some of its causes, and a brief review of the history of various conservation efforts. As with any book, nits can be picked: the reasons for the supposed correlation between declining populations of big cats and the subsequent increase of domestic rats are not readily evident to me (p. 17); 88 m.p.h. seems a bit fast, even for a cheetah (p. 137); etc. They are only minor problems, in any case.

The major thrust of the book is a continent by continent pictorial review of almost all of the endangered vertebrates of the world. Each species is briefly discussed, ecologically, along with the reasons for its being placed in the IUCN's *Red Data Book* (the primary source for Cox's material). Species are illustrated by drawings or photographs. Quality of artwork varies from rather poor (the Kaibab squirrel, p. 37; Attwater's Greater Prairie Chicken, p. 41) to spectacular (Red Uakari, p. 78). By and large the illustrations are excellent; many were taken in zoos, underscoring the rarity of some species. Interspersed among the accounts are some detailed case histories of conservation efforts (or their absence) on selected species, ranging from the Great Auk (lost) to the Vicuña (saved). These accounts are poignant at times and well written. Cox's book can scarcely fail to impress. *Life* magazine once published an issue with pictures of over 200 U.S.

servicemen killed in battle during the preceding week. One could hardly glance over the pages and not be impressed with the futility of the war, or at least its terrible human toll. Reading this book, one realizes the ephemeral natures of species and their singularity. My work in South America has brought me into contact with a number of animals described in the volume. Seeing the Andean Condor included in this book is like finding a friend's name in the obituary column of the daily paper. One thinks, "I didn't know," or "I didn't realize." Perhaps. More probably I just didn't think about it. Cox makes me do that, and in that he has succeeded. As Tennyson wrote, "Brutes, the brutes are not your wrongers . . . Sweet Saint Francis of Assisi, would that he were here again."—Michael A. Mares.

Waterfowl Populations in Denmark 1965–1973. Danish Review of Game Biology, 9(1). By Anders Holm Joensen. 1974: 206 pp., many maps, charts, and graphs. Paper cover. $9.00. Order from Game Biology Station, Kalø, 8410 Rønde, Denmark.—A survey of non-breeding waterfowl populations based on ground and aerial censusing and hunting records. The distribution, age, and sex composition of populations in relation to hunting pressure is analyzed.—R. J. R.

Emperor Penguin, Bird of the Antarctic. By Jean-Claude Deguine. The Stephen Greene Press, Brattleboro, Vt., 1974: 30 pp., 38 color photos. Hard cover. $6.50.—This attractive but overpriced little book contains excellent color photos of the life of the Emperor Penguin and other Antarctic animals. The brief text merely comments on the photographs.—R. J. R.

The Sequence of Plumages and Moults of the Passerine Birds of New York. By Jonathan Dwight, Jr. Annals N.Y. Acad. Sci., XIII (2):73–360, 1900 (reprint, 1975). Order from The New York Academy of Sciences, 2 East 63 Street, New York, N.Y. 10021. —The classic study of passerine plumages has been reprinted with a new introduction by Kenneth C. Parkes that places the work in its historical context and discusses changes in terminology since the book was written. The reprint would have been more useful if an index and cross-reference to modern scientific names had been added.—R. J. R.

Supplement to The Birds of Chile. By A. W. Johnson. Platt Establecimientos Gráficos S.A., Buenos Aires, 1972: 116 pp., black-and-white and color photos. $10.00. Order from Pierce Book Co., Winthrop, Iowa.

Man and Birds. By R. K. Murton. Taplinger Publishing Co., New York, 1974: xx + 364 pp., many charts, graphs, and black-and-white photos. $8.95.—This is a popular but well-documented account of the economic effects of birds on various human activities, especially agriculture and wildlife management. The examples discussed are mainly from England, but similar problems exists elsewhere.—R. J. R.

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SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

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THE WILSON ORNITHOLOGICAL SOCIETY

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Yucatan Jay *(Cyanocorax yucatanica)*. Upper left, adult (4 years or older); upper right, juvenile; lower left, 2-year-old; lower right, yearling. The 2-year-old bird is in the Up-fluffing display. Painting by Nancy Halliday, Florida State Museum.

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BEHAVIORAL ECOLOGY OF THE YUCATAN JAY

RALPH J. RAITT AND JOHN WILLIAM HARDY

Prominent among bird groups possessing highly developed cooperative social systems are the New World jays (Brown 1974). Recent studies by Brown (1972) of *Aphelocoma ultramarina* and Woolfenden (1973, 1975) of *Aphelocoma coerulescens coerulescens* have revealed a high degree of sociality in those forms. Cooperative breeding also occurs among the black-and-blue jays of the subgenus *Cissilopha* (genus *Cyanocorax*, fide Hardy 1969), as recently shown by Hardy (1976) for the northern form of the San Blas Jay, *Cyanocorax sanblasiana nelsoni*, of western Mexico and Bushy-crested Jay, *C. melanocyanea*, of Central American highlands. As our results presented here will demonstrate, the Yucatan Jay, *C. yucatanica*, is also highly social and a cooperative breeder.

METHODS

Preliminary field work in the vicinity of Xpujil and Zoh Laguna, Campeche, Mexico (18°35′N, 89°26′W), by Hardy in April 1968 gave indications of the social nature of Yucatan Jays. Intensive studies were undertaken of the species in the same area in the breeding seasons of 1972 and 1973 and in the intervening winter. A field party of 5 persons studied nesting from 7 June to 2 July 1972, and a group of 4 studied winter behavior from 7 to 13 January 1973. Nesting was again studied in 1973, by 1 field worker on a part-time basis beginning 22 May and by 5 additional workers beginning on 3 July; the entire party departed from the study area by 30 July. Jorge E. Orejuela, a member of the field party, also collected specimens for stomach analysis in 1974.

The field work was concentrated in a strip of apparently highly favorable jay habitat along the 9.5 km of narrow unpaved road from Xpujil (on Mexico Highway 186) north to Zoh Laguna, a small lumbermill town. During the breeding season the primary effort was to locate as many nests as possible along the road and to observe behavior at the nests. Special attention was given to determining the number of individuals attending the nests, their sex and age, and their relative contribution to the several phases of nest attendance. We noted behavioral interaction among birds whenever they were observed and attempted to determine something of the movements and foraging behavior of the flocks (once it became apparent that the breeding social unit in this species is, indeed, a flock).

In pursuing these approaches, frequent and extended periods were spent observing nests and recording activity; locations of nests and of flocks were noted and mapped, and as many birds as possible were captured, marked, and released. Capture of the birds proved to be difficult. We failed in attempts to use wire ground traps; all birds marked were captured in mist nets: a few near nests in the breeding season, and 9 adjacent to foraging sites at edges of milpas in January. Each captured bird was marked with a distinctive combination of colored plastic (Saflag) flags about 1.5 cm wide and 5.0 cm long, 1 attached by a metal eyelet to each leg. Sex of birds captured in January was determined by laparotomy; in the breeding season this procedure was avoided because of the risk.

Data on age differences in behavior and age composition of groups were based on differences in phenotype of several age classes, as described by Hardy (1973). The color plate preceding this paper depicts the 4 prominent age classes, juvenile, first year, second year, and adult (3-year-olds, here called adults, differ from older birds in having whitish inner bill surfaces).

In January 1973 we concentrated on capturing jays and observing the sizes, age composition, and locations of flocks. Additional details of methods are discussed below.

RANGE AND HABITAT

General description from literature.—The Yucatan Jay occurs throughout the Yucatan Peninsula (Paynter 1955), in the adjacent Mexican state of Tabasco (Miller et al. 1957: 119–120), in the northern half of Belize (Russell 1964:134), and in the Peten district of Guatemala (Land 1970:243). Our study area is approximately in the geographical center of this range.

Literature reports of habitat occurrence and abundance give scant information but do indicate only slight variation except in Belize. For the Peninsula generally, Paynter (1955) says that the race *C. y. yucatanica* is "most common in the region of deciduous forest" but that it occurs occasionally in coastal scrub; for the southwestern race, *C. y. rivularis*, he gives rain forest as the habitat. Judging from his vegetation map and accompanying descriptions it seems that the species occurs in virtually all forested areas of the Peninsula. Edwards (1972:167) reports it as "very common" and occurring "in dense scrubby woodland." In the Peten it is reported by both Land (1970) and Smithe (1966:232) as occurring in "tintal" forest (see beyond for a description of this forest type). Of its occurrence in Belize, Russell (1964) reports that it is uncommon and that "Densely overgrown 'broken pine ridge' and the swampy regions that sometimes border these pinelands are its usual habitat. One specimen was taken several miles from pinelands in dense second growth."

Study area.—The climate of our study area is relatively warm, with rather slight variation in temperature. Freezing temperatures occur rarely if ever. Annual rainfall averages 1025 mm, of which about 80% falls in the months May–October. Monthly mean temperatures (°C) and rainfall (mm), January through December, based on the years 1965–1972 were: 20.8, 57; 21.5, 32; 24.0, 22; 25.7, 22; 27.2, 140; 26.3, 154; 25.4, 97; 25.3, 125; 25.9, 185; 24.7, 100; 22.1, 46; 21.8, 32. These data for Zoh Laguna, are from the Oficina de Climatológia, Secretaría de Recursos Hidráulicos, República de México. Precipitation falls in 2 distinct modes: typical afternoon tropical thunderstorms and prolonged drizzle and downpour acompanying fronts or cyclonic storms, with shifting winds and fog. The latter sometimes last 2 days and bring substantial moisture to the area. During our field work in June 1972 the relative humidity was between 90 and 100% for most of each day but dropped to around 80% in mid-day. The elevation of the area is approximately 250

m. The topography is relatively flat, with occasional low ridges. Apparently because of the nature of the underlying limestone substrate, there is very little surface drainage, and there are no streams or canyons of any significance in the immediate vicinity. In the rainy season standing water accumulates in numerous scattered small depressions.

The vegetation of the region is a mosaic of dense forest, cultivated fields (milpas), and old fields in various stages of secondary succession. The vegetation of the Yucatan Peninsula, including the forests of eastern Campeche, has been variously classified and generally described in several earlier works (Paynter 1955, and others cited therein). More recently Pennington and Sarukhan (1968) gave useful descriptions of the forest types. From them it appears as if the forests of our study area are of 1 or a mixture of 2 types: "selva mediana subperennifolia" and "selva baja subperennifolia." *Brosimium alicastrum*, *Manilkara zapota*, *Chrysophila argentea*, and *Swietania macrophylla* are all listed as principal species of the former type and all occur in our area. Of the similarly abundant tree species of the selva baja, *Bucida buceras*, *Coccoloba cozumelensis*, *Croton reflexifolius*, and *Metopium brownei* were all identified on our study area. On the basis of the generally low stature (approximately 10 m) of the trees and of the numerous areas of poorly drained, inundated substrate, the Xpujil-Zoh Laguna forests are more nearly the selva baja type. We did not identify the main species of that forest type, the tintal, *Haematoxylum campechianum*, but our study of the vegetation did not stress species occurrence and it could have been common and still have escaped our identification. It is also possible that the species has been decimated by selective cutting.

We measured vegetation structure using methods modified from James and Shugart (1970). Data collected include density and basal area (at breast height) of trees, canopy cover, and density of woody stems of shrubs and vines (also at breast height) on 5 circular plots of 100 m^2. In order to sample the forest most heavily used by the jays we located the plots as close to nest trees as possible while including only intact forest. All trees (woody stems 2.0 cm dbh or greater) were measured, but species were not differentiated. Cover was estimated by sighting through a vertical tube with crosshairs, held at eye height, on 20 points at 1-m intervals on 2 randomly selected diameters of each plot. Woody stems of vines and shrubs (less than 2.0 cm dbh) were counted in each of two 2-m wide transects along randomly selected diameters of each plot.

The mean number of trees per m^2 was 1.0 (range 0.8–1.2). The basal area (cm^2) of trees per m^2 was 26.5 (range 19.8–40.9). The percent cover was 73 (range 45–90) and the number of shrubs and vines per m^2 was 1.9 (range 1.5–2.5). Most of the trees were small; over 50% of them in each plot were less than 4.0 cm dbh. Our impressions of high density were confirmed by the heavy canopy cover and by the occurrence of an average of nearly 3 woody stems per m^2. This structure of the forest is a reflection of its secondary character. For centuries it has been subject to milpa agriculture. This type of agriculture continues to the present, with an additional disturbance due to selective logging. Turner (1974) describes the similar nature of classical Mayan agriculture in the area centering about Xpujil.

The forests of the area were fully leafed out during all of our stay in July 1973 and by the end of June 1972. In April 1968 most of the trees were almost completely bare (Fig. 1D), and many were bare or partly so at the time of our arrival in early June 1972, leafing out only after the onset of frequent rains (Fig. 1C). In January 1973, during a relatively wet winter, full foliage was general. From these observations and from the use of the word "subperennifolia" to classify forests of the region by Pennington and Sarukhan (1968), it seems likely that most of the trees are facultatively deciduous, normally dropping their leaves in the autumn and growing them again after the onset of

FIG. 1. Photographs of the main study area showing: A, newly cleared milpa in 1973, where forest like that in background existed in 1972; B, interior of the forest, with quadrat being laid out; C, Xpujil-Zoh Laguna road, with Yucatan Jay nesting habitat on both sides; D, dry season aspect of the jay habitat.

rains in the early summer, but retaining them for longer periods when soil moisture remains high.

ANNUAL CYCLE

The social organization and other activity of the Yucatan Jay vary seasonally, with an orderly progression of changes. Our central interests in this study were the events of the breeding season: nest-building, incubation, and care of nestlings and fledglings. Social organization and ecology in the non-breeding period were also of some interest and importance in facilitating our understanding of the significance of characteristics of the breeding biology of Yucatan Jays. Our approach in this major section is to consider in turn the various phases of the annual cycle, beginning arbitrarily with behavior in the pre-reproductive season, then considering several consecutive aspects of breeding, and ending with a brief description of jay social structure in winter.

Pre-reproductive Period

Our studies do not include work at the time of the transformation of large winter aggregations of jays (see p. 547) into the smaller ones typical of pre-reproductive and reproductive periods. This breakup occurred prior to early April in 1968, a year characterized by a fairly dry winter season, no rain in March or April, and a virtually complete leaf fall in the study area. The period 3–13 April was clear and windy, with temperatures daily reaching the low 30's C. Yucatan Jays were studied almost daily, mainly in the woodland within 1 km of the north edge of Zoh Laguna. Two flocks of fewer than 10 birds (usually counted as "6 or 7" in field notes) inhabited this woodland. They usually occupied discrete areas. A count of about 20 unmarked birds, presumably the total of these flocks, was seen on one occasion attending a swarm of army ants (species unknown) from just after dawn to late morning (see Hardy 1974a). Each of the 2 smaller flocks contained first-year individuals. A flock of about 10 birds was watched twice 9.5 km NW of Zoh Laguna. It also contained at least 2 first-year birds.

Until 16–18 April no observations made of these birds suggested the onset of reproductive behavior; that is, except for group size, behavior was seemingly random wandering within a consistent area, foraging, and resting, at which times allopreening and social "Up-fluffing" displays were evident (Hardy 1974b).

Testes of 3 males taken in this period were enlarged to the size we found in the breeding season in 1972. Those of 2 adults taken by Hardy on 4 and 8 April, respectively (MLZ 65835, JWH 614, not preserved), measured 16 × 10 and 14 × 10 mm and a third adult taken by Kenneth C. Parkes on 6 April (Carnegie Museum 143272) measured 14 × 7 mm. Yet ovaries of 4 females taken in this same period were small. An adult and a yearling female collected 11 km E Ciudad Campeche on 31 March had a slightly enlarged ovary with ova to 2 mm and a small ovary with ova to 1 mm, respectively. An adult female (CM 143292) taken by Parkes on 8 April also had ova to 2 mm. In Hardy's captive flock a 4-year-old female had ova 0.25–0.50 mm on 9 April 1971 and laid an egg in the first week of May, and a 4-year-old male had 10 × 5 mm testes on 5 April 1971. Two other adult males in this group had testes 9 × 5 and 11 × 5 mm, respectively, on 13 April. The data thus suggest that in mid-April 1968 in Campeche, males were coming into breeding condition and that females were on the verge of doing so. This may account for the fact that the groups usually encountered were of breeding flock size, i.e., fewer than 10 birds.

The probable proximity of the breeding season, given appropriate environmental stimuli, was further suggested by behavior of some adult birds from 16 to 18 April. In the woodland by Zoh Laguna, in that period, pairs of adults away from the regular flock were seen several times. In Hardy's study of the captive flock of 6 Yucatan Jays from 1968 to 1972, the 2 oldest birds (a male and a female), especially at the time of onset of reproduction, showed a tendency to stay together away from other group members. In each year from 1969 to 1971, this was in April. Thus the pair behavior of the adults in the wild in mid-April 1968 is probably significant with respect to onset of breeding.

Breeding Flocks

Size, composition, number.—The social unit during the breeding season invariably was a flock; that is, birds in the breeding season were not members of simple male-female pairs but of groups of more than 2 adults and, usually, yearlings and 2-year-olds. Table 1 shows the sizes and makeup of the flocks regularly observed from the Xpujil-Zoh Laguna road in the breeding season in 1972 and 1973. Our field work was not at perfectly comparable times in the 2 years. June 1972 was a period primarily of laying and incubation in what were apparently the first nestings of the season, whereas in July 1973 the breeding season was well along, with fewer active nests and many nests having already fledged young. Thus, the largest of the 1973 flocks may have been composite groups, of the order of winter flocks (see beyond), formed by the amalgamation of 2 or more breeding flocks. Arguing for that interpretation is the fact that we recognized 10 distinct flocks in 1972 but only 9 in 1973. In our analysis of the size and composition of the breeding flocks we follow a conservative interpretation by assuming the 2 largest 1973 flocks to be atypical, perhaps composite, and therefore exclude them. On that assumption it may be seen in Table 1 that the flocks consisted of 4 to 15 individuals of adult phenotype: the mean was 6.4 per flock in 1972 and 8.7 in 1973, but differences between years were not significant ($p > .05$, Mann-Whitney U-test). A few flocks contained 2-year-old birds in 1972 but none was seen in 1973. Several flocks in 1972 contained 1 or 2 yearling birds; in 1973 all flocks contained at least 2 yearlings and 2 contained 6. The 1972 year-class was large relative to that of 1971, and the presence of additional yearlings in 1973 was largely responsible for the larger size of flocks in that year. The sizeable number of juveniles already fledged in July 1973 indicated that that year-class potentially was also relatively large.

Members of at least some discrete flocks apparently had more than 1 nest. In 1972 nests 1, 11, and 12 all seemed to be within the range of a single flock, as did nests 5, 8, and 9 (Table 1). All 3 nests in each group were close together, well within the normal radius of movements of flocks in the breeding season (see subsequent section on flock movements), and we could detect no dividing lines between them in the movements of birds. Nests 5, 8, and

TABLE 1

COMPOSITION OF BREEDING SEASON FLOCKS OF YUCATAN JAYS NEAR XPUJIL, CAMPECHE, 1972, 1973

Flock Location[1]	Number of:				Total Birds
	Adults	2-year-olds	Yearlings	Juveniles	
1972					
Nests, 1, 11, 12	10	3	0	0	13
Nest 2	5	0	1	0	7[2]
Nest 3	4	0	0	0	4
Nest 4	9	0	0	0	9
Nests 5, 8, 9	6	0	2	0	8
Nest 6	7	1	2	0	10
Nest 7	6	1	0	0	7
Nest 10	5	0	1	0	6
0.5 km	6	0	0	0	6
2.4 km	6	1	0	0	7
TOTAL	64	6	6	0	77
1973					
0.8 km	6	0	2	4	12
Nest 1	6	0	6	8	20
3.9 km	9	0	4	4	17
Nest 4	10	0	2	5	30[2]
Nest 9	5	0	2	2	9
6.9 km	15	0	4	5	24
Nest 8[3]	28	0	3	11	42
7.8 km[4]	24	0	3	5	32
8.6 km	10	0	6	4	20
TOTAL	113	0	32	48	206

[1] Locations of flocks given either as the nest site(s) of the flock or as road km north of Xpujil.
[2] Total flock size known but ages of some individuals unknown.
[3] "Flock B."
[4] "Flock C."

9 were active simultaneously, and separate small groups of birds seemed involved in activities of incubating and feeding young at them. Other interpretations are possible, but the observations seem to suggest that the situation involved division of labor within 1 communal flock with 3 concurrent nests. In the other group, nests 1 and 12 were at about the same stage; nest 11 was a later effort, built after the other 2 had reached the nestling stage. Otherwise, the situation appeared similar to that with nests 5, 8, and 9. In 1973 the presence of fledged juveniles in the flocks tending nests 1, 4, and 8 (Table 1) seemed strong evidence that members of at least those flocks

nested more than once. The large numbers of such juveniles in the vicinity of nests 1 and 8 suggest the possibility of more than 2 nests by those groups. We cannot say how much overlap in time there was between these putative multiple nestings in 1973, but clearly overlap was little since juveniles from early nestings tended nestlings of later ones.

Distribution and movements.—The flocks were unevenly distributed along the study transect in both years. Each year there were 4 flocks along the northern ⅓ of the road where there was the most varied mixture of milpas and forest. The southern ⅓, near Xpujil, where milpa clearings are also common, contained 4 flocks in 1972 but only 2 in 1973. The middle ⅓ of the transect, where milpas are uncommon and unbroken forest the rule, contained only 2 flocks in 1972 but 3 in 1973. The ranges of all flocks included either small clearings along the road or isolated milpas. From this pattern and from observations elsewhere in Campeche and Quintana Roo, it appears that the breeding flocks prefer forest edge and that optimal habitat is a mixture of clearings and patches of forest.

Important questions concerning the ecology of the social system of these birds center around territoriality or home range. Two major difficulties hampered our study of the use of area by the flocks. While they were in the forest they were usually impossible to follow. The second problem was the difficulty in capturing birds alive for color-marking. Too few were marked late in June 1972 to be of much help in the study of flock movements in that year. In many instances it was impossible to be confident of the identity of a given flock, especially near boundaries of ranges of 2 flocks. The greater, but still modest, trapping success in January 1973 provided a group of marked individuals that were of considerable assistance in ascertaining the movements of 2 flocks: 1, which we called flock B, "owned" nest 8 and contained 2 marked birds; the other, flock C, was located north of the other, centering at 7.8 km N Xpujil, and contained 4 marked birds. Locations of members of these flocks and some of their prominent movements are shown in Fig. 2. The 2 flocks appeared to occupy ranges roughly comparable in size: in both cases the maximum distance between sightings was about 400 m. Both were highly mobile within their range, moving distances on the order of 100–200 m and then back in the opposite direction within a few minutes. Both flocks were extraordinarily large (Table 1); as suggested earlier they perhaps were comprised of more than 1 breeding flock. It is possible that their ranges were larger than those of smaller flocks, but they did not appear to behave differently from known simple breeding flocks. At times they moved as tight, complete groups, especially at dusk. At other times they were spread out in looser units; occasionally the flocks were fragmented into small somewhat independent sub-flocks.

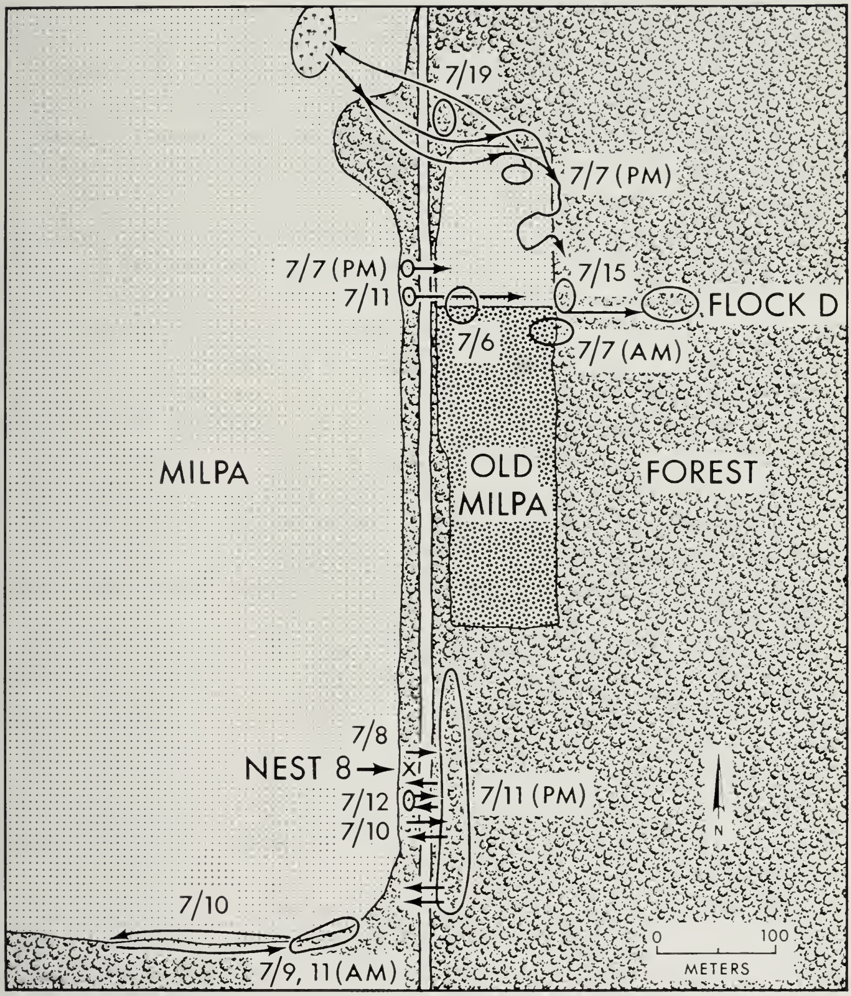

FIG. 2. Map of a portion of study area showing dates and locations of sightings of Yucatan Jay flock B (at southern edge) and flock C (at northern edge), and location of single sighting of flock D, all in July 1973. Lines with arrows indicate movements. Different patterned area at northern edge visited by flock C on 7 and 19 July was site of cluster of small papaya trees.

The 2 flocks apparently did not interact. The shortest distance between observed locations of the 2 was approximately 300 m. A possible third flock (flock D, Fig. 2) approached and overlapped the range of flock C. We followed this group of about 20 birds about 100 m east into the forest from the eastern edge of the milpa where flock C was frequently observed. We observed the birds at close range as they approached us in the forest in response to broadcast of recorded calls but saw no marked individuals. Because of the absence of marked birds, 1 or more of which were conspicious on nearly all observations of flock C, we believed this group to constitute a separate flock. We never saw interactions that would indicate interflock hostility.

In summary, our observations of flocks B and C indicate that each flock occupies a separate home range within which the flocks or segments thereof are at times highly mobile. The size of this area ranges up to 400 m in diameter. Much foraging and other activity appears to take place at or near forest-field edges. Observations of other flocks in both years are consistent with the above summary. Whether the group ranges are territories defended against other flocks is unknown. The dispersion of flocks in both years, at intervals of several hundred meters along the road, in a transect of what appeared to be continuous favorable habitat, suggests that some spacing mechanism exists. If this mechanism is territorial-type aggression between flocks, it probably occurs in the spring when large winter flocks split into the smaller breeding units; it seems absent among the usually well-separated breeding flocks.

Social behavior.—Yucatan Jays within both breeding and nonbreeding flocks engage in ritualized displays and postures, as described by Hardy (1974b). The most common of these are "Up-fluffing" and "Peck-preening," the typical action and reaction of 2 or 3 closely spaced individuals. This behavior serves in greeting and appeasement; fighting is rare, as are threat and more extreme appeasement in response to aggression. The rarity of such behavior is probably due to the development of the "Up-fluffing-Peck-preening" ritual, and allofeeding.

In the wild Up-fluffing and Peck-preening were a prominent feature of group behavior when the flock had paused to rest when foraging or when the birds were sunning or preening in early morning hours in the top of a tall tree or after a rain. Among Hardy's captives such activity was not clearly correlated with sex, age, or social dominance. The 2-year-old in the color plate is beginning the Up-fluffing display.

Social feeding of one bird by another was less common but still frequently observed. It appeared that any individual of any age class might pass food to any other bird. Often food was passed back and forth or through the bills of several birds before being eaten.

We recorded no instances of fighting in the wild; in captives Hardy induced overt aggression by removing a bird from a flock for several days and then reintroducing it. In the few minutes after this reintroduction, the newly arrived individual was chased and pecked on the tarsi and head. It responded by extreme appeasement gaping. Such treatment ceased within a few minutes. Hardy's unpublished data on the closely related San Blas Jay, of which he had many more captives from different family groups and different locations, show that the reaction of a communal group to a stranger is the same as just described, but that it continues and the new individual is never accepted, and is sometimes injured or killed. Spontaneous occurrences of such activity were extremely uncommon in the Yucatan Jay and seen not more than 5 or 6 times between 1968 and 1972 in the captive flock. Our failure to see fighting in the wild probably indicates that individuals rarely if ever become separated from the flock for sufficient time to invoke the reentry pecking and chasing behavior.

Nests and Nest-building

Nearly all of the active nests found were within 5 m of the edge of the forest. Two were deeper into the forest and one was in one of a narrow row of trees isolated from the forest itself. Of course, edge nests are easier to find than others and there is thus bias in our sample, but it seemed unlikely that there were enough unknown nests deep in the forest to offset the apparent preponderance of ones at the edge.

Most nests were near the lower edge of the upper canopy, from 4.3 m to 9.1 m up (mean 6.2, $N = 10$). The top of the forest canopy was 2–5 m above the nests.

As with all species of *Cissilopha*, the nest was a flimsy platform with shallow cup and composed mostly of a collection of sticks inlaid with a few finer twigs or coarse plant fibers. The lining was never dense, often permitting the clutch or nestlings to be viewed from below. We noted no instances in which the nest failed to remain intact beyond fledging of the young.

Nest-building in the captive flock was preceded by a period in which the birds carried material around but dropped it or deposited it at the nest site without visible constructive effect. In 1969 the first carrying of material was observed in January when, before nest material was provided, the birds began pulling pine needles through the wire mesh of the outdoor aviary to carry them about. Hardy immediately provided sticks and coarse grasses, but this did not stimulate any increase in this earliest manifestation of building. Between 15 and 23 April there was a marked increase in the carrying of nest-building material. The adult male carried 1 stick around, placing it here and there in crevices, and the cage wire mesh. His mate also carried sticks and was observed presenting a stick to him. On 5 May nest-building actually began.

In this captive flock, the female (at least 4 years old) was principally responsible for the nest in 1969 and 1971, but in the same flock in 1970 her mate (also at least 4 years old) seemed largely responsible for its construction. In 1969, the male carried many sticks to the nest but usually left them with the female, who built the nest. In 1970, the roles were reversed and the female seemed of less help to the male than he had been to her. Other birds in the flock (2 two-year-olds and 2 yearlings in 1969, that became 2 three-year-olds and 2 two-year-olds in 1970) made no constructive efforts toward the nest's construction, although each time in the early stages they were busy carrying about sticks, visiting and perching on the nest, pulling sticks from it, or moving them about. Rarely, they were chased from the nest by the building pair and usually they were ignored or "tolerated." Concerted nest-building in 1969 lasted from 5 May to 17 May. In 1970 the nest was completed in 1 week, 7–13 April.

We have information on building of only one nest in our field studies. A half-completed nest was found on 23 June 1972 (nest 11). At least 3 birds, 2 adults and one 2-year-old (with almost completely black bill and partial yellow eye-ring), were nest-builders. One of the adults and the 2-year-old brought nest material and sat in the nest. The other adult was seen carrying material but because none of the birds was color-marked we do not know that 2 adults actually built. This sub-flock included at least 2 adults, 2 two-year-olds, and 1 yearling. (The yearling as indicated in Table 1 was otherwise undetected in our studies of the whole flock in this part of the study area.) By 30 June an adult was sitting on the completed nest for protracted periods.

Eggs and Laying

Eggs of all 4 species of *Cissilopha* are colored similarly and are unlike those of other New World jays. The base color is mottled pale to medium pinkish-buff, speckled with reddish-buff.

We obtained no data on laying in the wild. In Hardy's captive flock the oldest female laid several clutches or parts thereof in 1969, 1970, and 1971. On 12 May 1971 she laid a first egg prior to 09:15. On each successive day through 15 May an additional egg was in the nest when checked before noon. Four eggs were probably the full clutch. This same female laid 2 eggs on successive days on several other occasions, but we have no other full record for a complete clutch.

Of 8 study area clutches, 6 were of 5 eggs and 1 each was of 4 and 6 eggs. Hardy (1976) reported a clutch size of 3 or 4 based upon limited data for both Bushy-crested and San Blas jays.

Incubation

We have data on incubation from 9 nests observed in 1972. Of 4047 min of observation 1110 min were at 1 nest. We concentrated on the activities of

Table 2

Incubation and Feeding of Incubating Yucatan Jays

Nest	Minutes (days) of Observation	% of Time Clutch Covered	No. of Absences (With Guard)	No. of Feedings (By Yearlings)	Minimum No. of Feeders (Yearlings)
1	688(6)	96	3(3)	25(0)	2(0)
3	1110(8)	95	12(0)	20(0)	1(0)
5	450(5)	92	2(2)	7(0)	1(0)
6	435(3)	95	4(3)	10(0)	1(0)
7	30(1)	93	1(0)	2(0)	1(0)
8	465(3)	—	—	11(2)	2(1)
9	230(3)	100	0	1(0)	1(0)
Total	3408	95	22(8)	76(2)	

fully grown attendants at the nest. It appeared as if 1 bird did all of the incubating at each nest. Our evidence for this statement is all indirect, because of unmarked birds. We observed no instance of 1 bird replacing another in incubation, though on several occasions an incubating bird departed immediately after being fed by another bird which remained at or near the nest. All incubating birds were adults, and probably were females. On 19 April 1974 Jorge E. Orejuela collected an incubating adult female from a nest. In Hardy's captive flock practically all of the incubating was done by the adult female parent; the male parent once sat on the eggs briefly. If our surmise is correct that incubation is done nearly exclusively by the female parent, then *C. yucatanica* differs in this respect from *C. melanocyanea* and *C. sanblasiana nelsoni*, in which Hardy (1976) has shown that more than 1 individual incubates.

Data on attentiveness and feeding of the incubator are summarized in Table 2. Data from 2 nests are omitted because of the probability that the presence of the observer caused abnormal behavior. In nearly all of the observation periods at all nests, regardless of the stage, the incubating bird remained on the eggs for over 90% of the time. Absences of the sitter averaged 5.4 min; 10 of 22 absences were for less than 3 min and only 2 were for longer than 10. Often another bird was present near the nest, especially when the sitter was absent. These "guardian" birds usually remained silent and relatively motionless, perched from as close as the nest rim to 5 m away, but usually in the nest tree. At nest 3 guarding was never observed.

Sitting birds were fed at the nest by other birds at irregular intervals averaging about 45 min. Two of these feedings were by yellow-billed yearlings; the rest were by adults; 2-year-olds were not observed to bring food. We know that at least 2 adults participated at nest 1 and at least 1 adult and 1 yearling at nest 8. Probably greater numbers participated, as we occasionally saw several birds near nests containing eggs. For example, on 21 June 1972 an adult that had just fed the sitter joined a group of 5 other adults in a tree 30 m from the nest; 4 members of the group were carrying food. At times the delivery of food to the incubator was preceded and/or accompanied by begging by that bird. Wings were spread and fluttered, tail and head were raised with open gape, and, in some instances, distinctive calls were given. This begging was more common at some nests than at others; it apparently did not increase in frequency with advancement of incubation as in *C. melanocyanea* (Hardy 1976). In no other obvious respect did feeding of the incubator differ between the Yucatan Jay and either the Bushy-crested or Nelson San Blas jays studied by Hardy.

We refrained from frequently disturbing incubation to check nest contents. As a consequence, we have little information on incubation periods or on losses of eggs. The incubation period of a clutch of eggs in captivity was 17 days and our field observations are consistent with such a period.

Hatching through Fledging

Hatching.—In 1972 the earliest date of hatching in one of the nests under study was 24 June; hatching was underway on that date in nests 4, 5, and 7, and within 2 days of 24 June in nests 3 and 6. Hatching occurred on 30 June in nest 1. That few if any successful clutches hatched appreciably earlier than late June in that year is indicated by our failure to observe any fledged juveniles before our departure on 1 July. By contrast, Orejuela observed young being fed in a nest as early as 22 May in 1973, and fledged white juveniles were common in that year on 4 July when we arrived at the study area. Those juveniles must have hatched at least by early June.

Hatching within a clutch must be nearly synchronous. The week-old nestlings collected from 2 nests in 1972 closely resembled their nestmates in size and stage of development except for a "runt" that fell out of one nest about 5 days after hatching.

Brooding and nest sanitation.—Immediately after hatching the young were brooded almost continuously. The percentage of time devoted to brooding declined gradually during the first half of the nestling period. This pattern is best illustrated by the percentage of our observation periods during which young were brooded at nest 4 in 1973, as follows: day 0 (day of hatching), 91% of 242 min; day 1, 83% of 498 min; day 2, 78% of 265 min; day 3, 83% of 295 min; day 4, 95% of 328 min; day 5, 87% of 172 min; day 6, 62% of 108 min; and day 7, 62% of 311 min. We have no data for the middle portion of the nestling period, but the percentage of brooding time must decline rapidly, for no brooding was observed in the 9 days prior to fledging at nest 1 in 1973.

Usually when the brooding bird left the nest, it was replaced by another bird that remained at or near the nest. On several occasions at nest 4 (1973) the replacement settled on the nest as if brooding. In all instances birds that actually sat on nestlings were black-billed adults. Since such birds were not individually marked we know only that at least 2 adults participated in brooding.

Fecal sacs were removed from nests by adults, at times by the brooding bird, at times by others. Fecal sacs were either eaten quickly, or carried away; they were never dropped to the ground within view of an observer.

Attendant birds spent substantial amounts of time in caring for the nest. Often a bird appeared to closely examine the undersurface of the nest, occasionally picking at it and probing into it with its bill; this behavior gave rise to our shorthand term "inspecting." Less often a bird spent 20–30 min scanning the entire nest, pecking at or into it frequently, apparently consuming small items. These were presumably larvae of a fly (*Mydaea* sp., Muscidae) that parasitizes nestlings; most nestlings examined had several subcutaneous cysts containing these larvae. Only adults performed this behavior and there probably was a division of labor among attending adults. A green-tagged adult at nest 1 (1973) fed nestlings but apparently did not participate in nest care. We seldom saw a bird alternate directly between brooding and inspecting. Inspecting was seen only after hatching and it seemed to be more common in more advanced nests, which lends credence to the hypothesis that nestling parasites are involved in it. Hardy (1975) reported similar behavior by Bushy-crested, San Blas, and Mexican jays. So much time (approximately 60% of one 30 min observation period) is devoted by Yucatan Jays to this form of nest care that it must be important to nest success.

Feeding of nestlings.—Data on frequency of feeding of nestlings and on the number and ages of feeders are given in Table 3. Feeding rates accelerated as the nestling period advanced.

At all of the nests but 2 it was certain that more than 2 birds participated in feeding. We were unable in most cases to recognize individuals, so the numbers of feeders may have been considerably higher than those listed in Table 3. It is, however, clear that feeding of the nestlings in the Yucatan Jay is, in at least a limited sense, a communal effort. In respect to communality *C. yucatanica* resembles its close relatives *C. melanocyanea* and *C. sanblasiana* (Hardy 1976) and other New World jays such as *Aphelocoma ultramarina* (Brown 1970, 1972) and *A. c. coerulescens* (Woolfenden 1975). (Detailed comparisons among these species will be discussed below.)

TABLE 3

FEEDING OF NESTLING YUCATAN JAYS

Nest	Days	Min Obs.	Min per feeding	Total feedings	No. of Feedings by:[1] Adults	1-yr. olds	Juvs.	No. of Feeders Adults	1-yr. olds	Juvs.
1972										
4	4	484	54	9	9	0	0	3	0	0
5	3	590	37	16	16	0	0	2	0	0
9	1	180	45	4	4	0	0	1	0	0
Totals		1254	43	29	29	0	0			
1973										
1	9	2181	15	141	138	3	0	3	2	0
4	10	2832	20	142	131	5	6	3	3	2
8	3	327	33	10	9	1	0	3	1	0
Totals		5340	18	293	278	9	6			
Grand Totals		6594	20	322	307	9	6			

[1] No. 2-year-olds fed nestlings.

The 2-year-old age group is the only one for which we have no evidence of feeding of nestlings. The lack of data in this case is almost certainly a sampling error, a result of the scarcity of birds of this age in both years of our study (see Table 1). Even though birds of all ages probably participated in feeding, it is nevertheless clear that birds of adult age contributed most of the food. Data on 2 marked birds give conflicting indications of the division of the labor of feeding nestlings among adults. At nest 5, 1972, the marked adult, "Orange," made 15 of the 16 feeding visits recorded; the other feeding was by an adult that spent most of the period brooding the nestlings. "Green," the marked adult at nest 1, 1973, fed nestlings 27 times after it was marked. In that same period we recorded 56 additional feedings, of which adults contributed 55. We know that there were (at least) 2 feeding adults in addition to "Green." It appeared that the division of labor at nest 1 was more nearly equal than at nest 5. This difference may have been related to the different stages of the 2 nests; the observations at nest 1 were made in the last few days of the nestling period, with no brooding, while those at nest 5 were in the initial days, with brooding during a high percentage of time. For the Bushy-crested Jay, Hardy (1976) found 8 adults feeding nestlings at 1 nest, with numbers of visits per individual as follows: 38, 22, 22, 17, 12, 10, 8, and 2. At a nest of the San Blas Jay, Hardy observed the following numbers of visits per respective adult feeder: 63, 61, 50, 26, and 6. Large numbers of birds (as many as 16) fed young in the nests of the Mexican Jay studied by Brown (1972); birds older than 1 year did a large percentage of the feeding; the visits otherwise were divided according to no obvious pattern.

The manner of delivery of food varied at nests in early stages of the nestling period. When a feeder arrived at a nest with a brooder present it often delivered food to the brooder, which then fed the young. When another bird was present but not brooding, it likewise often acted as an intermediary. At other times the bearer of food fed the young directly or delivered some of its food to the other bird before both of them fed the nestlings. Even white-feathered, fledged young-of-the-year acted as intermediaries in feeding nestlings. On 21 July 1973 at 17:10 three juveniles came to nest 4; 5 min later a 4th came and fed the adult brooder, which in turn fed the nestlings; 4 min later another adult came to the nest, fed 1 of the fledged juveniles, which then fed another juvenile; the latter delivered food to the brooder and then both fed the nestlings!

Many visits were made to nests with nestlings without the delivery of food. The nest with nestlings often appeared to be a focus of activity by the flock. At 09:50 on 19 July 1973 an adult arrived at nest 4 and delivered food via the brooder; it then began inspecting the bottom of the nest; 5 min later the 2 adults on the nest were joined by a 3rd and a group of 10–15 adults, 2 yearlings, and 3 juveniles; all came within 1 m of the nest; after about 10 min all but 2 adults left.

Fledging and post-fledging care.—We have no field data on length of the nestling period. A male Yucatan and female Nelson San Blas jay that paired in captivity reared 1 nestling to age 26 days, at which time the nestling seemed grown and feathered to a stage comparable to fledgings we observed in the field. We did observe the final days of activity at 2 nests in 1973. On the morning of 9 July (the 6th day of intensive observation) the 2 surviving young of nest 1 remained in the nest as usual. In the afternoon they climbed out of the nest onto supporting limbs, venturing as far as .5 m, but they returned both times. The next day they behaved similarly, but by 17:34 both were out of the nest, perched in different locations, each about .5 m from the nest. On 11 July they were in similar positions at 06:10. Later in the morning they became increasingly active, moving from limb to limb, farther away from the nest; one returned to the nest at 06:46 and departed again at 07:26, after which we saw neither in the nest again. By 12 July they were heard begging loudly about 30 m away but were mobile enough to evade our search and we did not see them again to recognize them. Similar events occurred at nest 9, which we discovered on 5 July just as the 2 young had apparently begun to fledge.

Throughout the period of field work in 1973, when the strikingly white-feathered juveniles were much in evidence, we frequently saw and heard them begging and being fed by other members of their flocks. Much of their food in the initial weeks following fledging must have been provided by older birds, even though juveniles soon reach full size and can move with the flock.

Nest Losses and Breeding Success

All but 2 of the 16 nests whose histories we followed at all in either year suffered losses of either eggs or nestlings, or both. Five nests were complete losses; 4 had contained eggs and 1 had nestlings before being found empty and abandoned. At the most advanced stage for which we obtained data, 8 nests contained nestlings. Numbers of nestlings per nest were as follows: 4, 4, 3, 2, 2, 1, 1, and 1. Comparison of these numbers with the most common clutch size of 5 further indicates the magnitude and commonness of losses. Assuming that all 16 nests originally contained 5 eggs (a reasonable assumption) and that all of the nests suffered no losses after our most advanced observation (a very optimistic assumption), then 80 eggs laid gave rise to 33 fledged young, a success rate of 41% or 2.1 young fledged per nesting attempt. These figures are indices of maximal success. It is likely that additional nests were preyed upon or otherwise lost after our last observations.

Predation was probably the predominate cause of the nest losses. Tree squirrels (*Sciurus*) were common in the forest. One was circumstantially implicated in the overnight disappearance of a set of young nestlings, having been seen in the nest tree on the previous day. Another squirrel appeared very close to a nest with a young being brooded. The brooding bird gave a social alarm call and within 2 sec another adult jay appeared and flew directly at the squirrel, striking it bodily and knocking it off the limb. The squirrel fell about 3 m before it regained its footing and fled; the attacking bird soon flew away. Two of 4 nestlings in another nest were killed by a snake in spite of the prompt arrival of an adult jay, that pecked vigorously at it and called loudly. The 2 remaining nestlings fledged 5 days later. The preceding accounts indicate the sort of predation to which the jay nest contents were subjected; they also indicate that nest attendants defend the contents, with some success. Predation was not the only cause of nest losses; on 29 June 1972 one of the 4 5-day-old nestlings in nest 4 was helplessly hanging by its neck from the vegetation, apparently ignored by the other jays. We retrieved and kept it alive for a few days; it proved to have been the runt of the brood —which, incidentally, had earlier been reduced from 5 to 4 by unknown cause.

The overall breeding success rates calculated above appear to be rather low, especially as the estimates are conservative on the optimistic side. Yet the numbers of yearlings (32) and of fledged juveniles (48) in the population in July 1973 indicate that the reproductive effort in both 1972 and 1973 was moderately successful (Table 1). Assuming that the population studied included 10–12 breeding flocks, then in 1972 the breeding effort produced at least 2.7–3.2 young per flock. Similarly, in 1973 each flock had fledged, on the average, 4–5 juveniles even before the breeding season had ended. It is apparent from the discrepancy between the nest-specific success rate and the flock-specific success rates that flocks must have made multiple nesting attempts. As has already been described, and as is indicated in Table 1, we know that members of 2 different flocks each made at least 3 nesting attempts in 1972.

The few yearlings in June 1972 (Table 1) suggests low breeding success in 1971. This may have been related to lack of rain. Rainfall in the early months of 1971 was minimal. The 9-year mean cumulative rainfall at the Zoh Laguna station for January–May was 274 mm, whereas the total for those months in 1971 was 78 mm. The severe defoliation of the forest under these dry conditions probably results in lowered insect populations. Nesting in bare trees would increase susceptibility to predator detection; lowered food supply should also lead to increased mortality of young and perhaps to reduction in breeding attempts.

Winter Flocks

The social order in winter was very large flocks. Our information on these flocks is based on a brief study, 7–12 January 1973. In that period we concentrated on netting and marking birds and on determining locations, sizes, and composition of flocks. Although the high mobility of the flocks and the usual shyness of the birds made study difficult, it was clear that they were grouped into a small number of large flocks. There were at least 3 of these in the study area, and we obtained counts of 45, 45, and 53 birds in what we were almost certain were distinct groups. Another count of 51 was made of 1 of these, but we were uncertain as to which flock it was. These counts represented the minimum sizes of the respective flocks. We were unable to make accurate counts of the 3 age classes within these groups. We estimated that roughly 40–50% of each was composed of first-year birds. Of 9 birds netted, 4 were adults, 3 were first-year, and 2 were second-year birds.

As in the breeding season, the birds were concentrated in the vicinity of the northern ⅓ of the Xpujil-Zoh Laguna road (2 flocks, at least), with a secondary concentration (1 flock) near the southern end. The high mobility of the flocks is attested to by the number and distribution of sightings and by direct observation of movements. Virtually all groups seen were on the move; we watched 1 flock of at least 53 birds move about 500 m from within the forest, across the road, and across a large milpa, in perhaps 20–30 min. At times over 50 m separated the vanguard from stragglers. Portions of the group stopped to forage briefly on or near the ground while others moved ahead. Another group flushed from a milpa near the road as our vehicle approached, flew across the road into the forest, then moved south through the forest, recrossed into the milpa, and moved out of sight deep into it, all within 15–20 min. Maximum distances between sightings of what we felt confident were the same flocks were on the order of 1 km.

We could not determine how cohesive these winter flocks were. It seems likely that they were formed by the simple joining together of neighboring breeding flocks. Observations the following July seem to suggest this, as described in the section on breeding flocks. Subsequently, at or prior to the onset of the breeding season, the flocks might well have resegregated. Unfortunately we have few data on the important question of whether the integrity of the breeding flocks was maintained between breeding seasons. Most of the birds marked in either June 1972 or January 1973 that were observed in a subsequent season had remained within the range of a single winter flock, but there were 2 exceptional birds. One was marked in June and was glimpsed briefly the following January at a point about 7 km from the point of capture: it was in the winter flock most distant from the bird's breeding season locality. One of the birds marked in January was repeatedly seen with flock C in the following July; the range of flock C was within the range of a different winter flock and other marked birds in flock C had been captured at a January station, over 1 km north of where the bird in question was captured. The movement of those 2 birds across ranges of other flocks raises questions crucial to the understanding of seasonal and annual changes in social organization; answers to these questions must await further study.

FOOD AND FORAGING

Information on the diet of the jays was obtained from direct observation of birds foraging and carrying food and from the analysis of the contents of 29 stomachs. Of these, 9 were collected in April 1968, 3 in June 1972, and 17 in the spring of 1974. Apart from rocks and soil, contents were about equally divided between plant and animal material. Seeds accounted for at least 68% by volume of the vegetable material: corn was the most important, occurring in 12 of the stomachs and comprising more than 43% of the volume of vegetable material. Arthropods were the primary animal food. Beetles (Coleoptera) were most common, occurring in 13 stomachs and accounting for 19% of the volume of animal food. Families identified included Scarabeidae, Elateridae, Carabidae, Chrysomelidae, and Curculionidae, in roughly decreasing order of importance. Orthopterans were also important among animal items, occurring in 8 of 29 stomachs and having a volume of 30% of the animal material. Lepidopteran larvae were found in only 3 stomachs but comprised 17% of the volume of animal food. Spiders, ants, dipterans, and a mollusk (slug) were also found among the contents. Rocks and soil accounted for about 22% of the total volume of contents. In several stomachs the soil was inseparably mixed with material of animal origin, perhaps of soft-bodied forms such as earthworms.

The above sample of stomach contents is biased in its emphasis on the spring season. Our field observations to a degree remedy that bias as regards summer foods. In June 1972, caterpillars of several species (and perhaps of more than 1 family) were very abundant, mainly on the vegetation. In all but 1 of the several instances when we were able to identify food being delivered to incubating birds or nestlings in 1972, the items were caterpillars. Caterpillars comprised 40 and 60%, respectively of the contents of 2 of the 3 stomachs collected in that period. Corn was probably not important, as there was little in the stomachs or milpas, but berries were once fed to an incubating bird, and stomachs contained small seeds that probably were from berries.

In July 1973 caterpillars were uncommon and we had no evidence of their being eaten. On the other hand, fruit was abundant. We especially noted the abundance of a kind of berry, of about the size, shape, and color of coffee berries. Jays were seen a number of times eating them and bringing them to nests. On 4 occasions birds brought these berries to nests with nestlings, but each time they failed to deliver them to the young. Other types of fruit were also eaten in that period. On 2 dates, members of the large flock C (Fig. 2) made numerous trips to a milpa containing a clump of small papaya trees (escapes?) and brought back small (2–4 cm in diameter), green fruits. A member of another flock was seen in a forest tree extracting material from a larger (5 ± cm), brown fruit.

This analysis presents a picture of a population of omnivorous, opportunistic birds. Their diet was variable from season to season and from year to year, with a wide range of items even within a season. Apparently they were able to capitalize upon temporary, and perhaps spatially localized, abundance of items as different as caterpillars and berries.

Foraging behavior by birds with such a variable diet was found to be variable and generalized. Obviously much of their food came from or near the ground. We frequently saw birds fly to low positions, apparently to forage, and flushed birds from such positions, but their shyness and the vegetative cover precluded actual observation of their foraging. In 1968, 1973, and 1974, jays were observed to forage at swarms of army ants (Hardy 1974a). From perches about 1–5 m above the columns of ants they appeared to capture invertebrates flushed by the ants. Other observations of foraging were primarily of jays in arboreal situations. Usually they moved along near the forest edge in loose groups, flying or hopping between perches, at various levels from the lowest strata to the top of the canopy. Most of the time they moved slowly and deliberately, examining foliage and branches of varied sizes, apparently thoroughly but not particularly systematically. In 1973, when fruit was so abundant, they concentrated on heavily laden trees and flew longer distances between bouts of foraging. Long flights to and from the small papayas were mentioned above and are illustrated in Fig. 2.

DISCUSSION

Control of Timing of Annual Cycle

Rain and resulting foliation may accelerate onset of reproduction, but nesting begins by May regardless of these factors, indicating an internal rhythm or photoperiodic control. Further evidence of this is provided by captive birds in California (in a rainfall regime exactly opposite that of Campeche) which began reproductive activities in April. On the other hand, in 1973 when little defoliation occurred at our study site, much successful fledging had resulted by June. In 1972, a dry year with 75% defoliation, no fledging had occurred by the end of June and all nests in early June contained eggs; no hatching occurred until late June.

Evolution of Communal Behavior

Comparison within Cissilopha.—We have demonstrated that the Yucatan Jay is social at all seasons and communally reproductive in groups of 4 to over 15 post-juvenal birds. The larger groups may have 2 or more simultaneous nests attended by separate units of the flock, and there seem to be 2 sequential or partially overlapping nesting phases in a breeding season. In all these respects the system is like that of Bushy-crested and Nelson San Blas jays (Hardy 1976). There are minor differences. In the Yucatan Jay only the putative parent female seems to incubate, while in the other forms incubation is by 2 birds. Attendants at a single nest were never known to include more than 6 post-juvenal birds in the Yucatan Jay, but in the Bushy-crested Jay at least 11 adults were known to feed young in 1 nest. There are suggestions of other differences as regards number and sex of participants in incubation and brooding, but these remain to be verified. (Certainly 2 birds incubate and 2 females brood in both the Bushy-crested and San Blas jays.)

Environmental correlates of the communal habits.—Are there similar environmental factors shared by these 3 jays that could explain their similar social systems? Certainly rainfall regimes, seasonal fluctuations in food supply, and foliage structure and dynamics are not similar in their ranges. The remaining prominent factor that the species share is a proclivity for forest edge and disturbed forest. Hardy (1976) tentatively concluded that such disturbed habitats had prevailed in the ranges of the Yucatan and Nelson San Blas jays but that montane forest habitat of the Bushy-crested Jay might well have only recently been dissected. Further reflection leads us to suggest that edge might well have prevailed in all 3 places for thousands of years. It seems certain that accelerated clearing by man has caused the spread and increase of the Yucatan Jay and its relatives. In other words, the present-day association with disturbance may be a recent artifact, and the original habitat of the jays was limited but stable forest edge. This pattern would conform to Brown's (1974) postulate of stable, isolated habitats as favorable for the origin and evolution of communal breeding.

Communality and population characteristics.—Yucatan Jays are generally sedentary. Eight of 10 marked birds were not seen farther than 0.5 km from the place where they were marked. As pointed out previously, 1 bird was seen in winter 7 km south of the place where it was marked in the previous summer. Another bird, marked in winter, was seen over 1 km north the following summer, having traversed the home ranges of 2 communal flocks. More data are needed to determine the frequency of such long movements. In this study we have not demonstrated that kinship is involved in membership of communal groups, but the likelihood of this is certainly increased by the sedentary character of the birds.

Brown's (1974) list of kin-selection correlates includes 2 known features of Yucatan Jays "that reduce and formalize intra-flock conflict. . . ." These are well developed display (Up-fluffing/Peck-preening) and conspicuous age difference in soft parts and plumage. The latter is most strikingly seen in the snow-white head and body plumage of juveniles.

Brown (1974) hypothesizes that kinship promotes successful communality by permitting altruistic acts to retain selective advantage without invoking group selection. This advantage is a relatively K-selected one. The correlates of K-selection, according to Brown, are delayed maturity, low reproductive rate, low dispersal, non-migratory habits, occupation of stable versus transitional habitat, and density-dependent mortality. Delayed maturity in the Yucatan Jay is certain. Full adult phenotype is reached in the 4th year of life (Hardy 1973), and active reproductive status may be delayed even longer by age-related social dominance (Hardy and Raitt 1974). Reproductive rate, as discussed earlier, was generally low in this study. Low dispersal, non-migratory habits, and habitat stability have already been discussed; though our data are few on these factors, they seem to provide no strong contradictions. The only mortality we detected was through predation of nests, and predation is usually considered to be density-dependent.

In summary, of the several correlates of K- and kin-selection listed by Brown we have no data on some and incomplete data on others. But all data that we have are consistent with the mode of evolution of communal reproduction he suggests.

SUMMARY

We studied communal behavior of the Yucatan Jay (*Cyanocorax yucatanica*) mainly in 1972–73 in Campeche, Mexico, mostly in a strip of dense forest and cultivated clearings along 9.5 km of an unpaved road. Nesting, flock age-composition, movements, behavior, foods, weights, gonadal condition, and age characteristics were studied. Study of a captive flock in California provided some information.

The climate of the study area is warm, humid tropical. A dry season from November through April and a rainy season from May through October are irregular in onset and severity, effecting irregularity in foliation and defoliation.

Pre-breeding (April 1968) flocks of fewer than 10 individuals, moved about in discrete areas with some separation of pairs. Gonadal development suggested (as was experimentally supported) that due to internal rhythm or photoperiod, prior to rains, birds (especially males) were coming into breeding condition. Breeding was early in 1973 relative to 1972.

The typical reproductive unit consists of a pair of adults plus other adults, 2-year-olds, and yearlings. Breeding season flocks averaged 7.7 in 1972, 12.4 in 1973.

Some flocks had 2 or probably 3 overlapping nests per breeding season, with division of labor among flock members, including juveniles.

Breeding season flocks seemed to occupy separate areas, up to 400 m in diameter, with preference for patchy environments of forest and milpa. Dispersion of flocks suggested a spacing mechanism such as territoriality. Intraflock behavior was usually benign, even among captives, consisting primarily of ritualized displays, postures, and social allofeeding.

The flimsy twig nests seemed concentrated near the road, generally were 2–5 m beneath the crown of the upper canopy, and ranged in height from 4.3 to 9.0 m. Nest-building is communal but primarily by an adult male or female.

Eggs in all *Cissilopha* are pinkish-buff speckled with reddish-buff. Seemingly the clutch of 4–6 eggs was laid and incubated by 1 female, who spent over 90% of her time on the nest; she was fed there by 2 or probably more other birds. Eggs are apparently laid at 1-day intervals and the incubation period is about 17 days. Hatching seemed synchronous.

Brooding of young was almost continuous at first (90%), dropping to 62% by day 7, and to none in late nestling stage. A brooder off the nest was usually replaced by a guard that perched on the rim and occasionally appeared to brood. Some attendant birds spent much time "inspecting" and probing with the beak at the nest's interstices.

At all but 2 nests it was certain that more than 2 adults fed the young. Adults brought most food; fledglings contributed the least but sometimes were conspicuous visitors. Young probably fledge in about 26 days.

Flying juveniles beg for food and probably are largely dependent for it on the communal flock. Enterprise and opportunism characterize this species' diet.

Maximum reproductive success of all nests studied based upon probable number of eggs laid to young fledged was 41% or 2.1 young fledged per nest. Predation was the likely predominant cause of losses. Jays defended against predators with some success. Although fledging rates appeared low, our census of the population suggested 2.7 to 3.2 young per flock in 1972 and 4 to 5 juveniles per flock midway through the breeding season in 1973. Discrepancy here we attribute to multiple nestings. Low breeding success seemingly occurred in 1971, with low rainfall in early months of the breeding season probably a factor.

Winter flocks consisted of 45 to 53 birds, with roughly 40–50% being first-year birds. Winter flocks ranged up to 1 km. Most birds marked in June 1972 or January 1973 were observed the next breeding season within the range of a single winter flock; only 2 birds moved across flock boundaries.

A preference for forest edge and disturbed forest is shared by all *Cissilopha* jays. Probably the now common Yucatan Jay, like its relatives, was rare and restricted to natural edge and clearings prior to man's appearance. Kinship of breeding flock members seems likely based on their sedentary character. The species has certain behavior and ontogenetic changes that reduce and formalize intra-flock conflict. Correlates of K-selection (that promote values of kin-selection and altruistic communality) shown by the Yucatan Jay are delayed maturity, low reproductive rate, low dispersal, and nonmigratory habits.

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LITERATURE CITED

Brown, J. L. 1970. Cooperative breeding and altruistic behavior in the Mexican Jay, *Aphelocoma ultramarina.* Anim. Behav. 18:366–378.

———. 1972. Communal feeding of nestlings in the Mexican Jay (*Aphelocoma ultramarina*): interflock comparisons. Anim. Behav. 20:395–403.

———. 1974. Alternate routes to sociality in jays—with a theory for the evolution of altruism and communal breeding. Am. Zool. 14:63–80.

EDWARDS, E. P. 1972. A field guide to the birds of Mexico. Sweet Briar, Virginia, publ. privately by author.

HARDY, J. W. 1969. A taxonomic revision of the New World jays. Condor 71:360–375.

———. 1973. Age and sex differences in the black-and-blue jays of Middle America. Bird-Banding 44:81–90.

———. 1974a. Jays as army ant followers. Condor 76:102–103.

———. 1974b. Behavior and its evolution in Neotropical jays (*Cissilopha*). Bird-Banding 45:253–268.

———. 1976. Comparative breeding behavior and ecology of the Bushy-crested and Nelson San Blas jays. Wilson Bull. 89:96–120.

——— AND R. J. RAITT. 1974. Ecology and evolution of communal habits in the black-and-blue jays (*Cyanocorax, Cissilopha*). 16th Int. Ornithol. Congr., Canberra, Australia, Abstracts, p. 105.

JAMES, F. C. AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

LAND, H. 1970. Birds of Guatemala. Lancaster, Pa., Livingston Publ. Co.

MILLER, A. H., H. FRIEDMANN, L. GRISCOM, AND R. T. MOORE (eds.). 1957. Distributional check-list of the birds of Mexico. Part 2. Pac. Coast Avif., No. 33.

PAYNTER, R. A., JR. 1955. The ornithogeography of the Yucatan Peninsula. Peabody Mus. Nat. Hist. Yale Univ. Bull. 9.

PENNINGTON, T. D., AND J. SARUKHAN. 1968. Manual para la identificación de campo de los principales árboles tropicales de México. Instituto Nacional de Investigaciones Forestales, México, and United Nations, FAO, Rome.

RUSSELL, S. 1964. A distributional study of the birds of British Honduras. Ornithol. Monogr., No. 1.

SMITHE, F. B. 1966. The birds of Tikal (Guatemala). Natural History Press, N. Y.

TURNER, B. L., II. 1974. Prehistoric intensive agriculture in the Mayan lowlands. Science 185:118–124.

WOOLFENDEN, G. E. 1973. Nesting and survival in a population of Florida Scrub Jays. Living Bird 12:25–49.

———. 1975. The effect and source of Florida Scrub Jay helpers. Auk 92:1–15.

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HOST-PARASITE RELATIONSHIPS OF THE BROWN-HEADED COWBIRD IN A PRAIRIE HABITAT OF WEST-CENTRAL KANSAS

Richard A. Hill

The parasitic nature of the Brown-headed Cowbird (*Molothrus ater*) is believed to have developed as a result of its association with the bison (*Bison bison*). Cowbirds subsisted on insects flushed by herds of bison, however, the nomadic nature of the bison made it impossible for cowbirds to remain with the herd and simultaneously perform nesting activities. Theoretically the evolution of parasitic habits allowed the cowbird to achieve reproductive success and concurrently maintain the established feeding relationship with the bison. Thus the distribution of the cowbird was similar to that of the bison or as Friedmann (1929) states, "the home of the cowbird was the open grasslands of the midcontinent." Therefore the reproductive success of the cowbird was determined by the establishment of a functional equilibrium of a host-parasite relationship in a prairie habitat.

In this regard, Sutton (1967) states that possible ground-nesting hosts in open grassland in Oklahoma are not heavily parasitized. Mayfield (1965) states that host species of the cowbird in western grassland have had long ancestral experience with parasitism and are much less receptive than host species of the eastern forest which have little experience with the social parasite.

Data from breeding bird surveys, Van Velzen (1972) show that the center of abundance of the cowbird is still within the central plains of the United States. This suggests that species nesting in these predominantly grassland states are receptive hosts. The purpose of this paper is to present data on the extent of cowbird parasitism and to discuss adaptations to parasitism of hosts nesting in a predominantly prairie habitat.

MATERIALS AND METHODS

The study was conducted in Ellis County, in west-central Kansas in 1973 and 1974. The county is composed of 62% cropland, 38% pastureland, and 0.4% woodland (U.S.D.C. 1969). In 1973 efforts were made to study nests of all passerine species nesting in Ellis County, and in 1974 efforts were concentrated on finding nests of likely host species of the cowbird. Data from all available Ellis County nesting records were used to determine the frequency of parasitism of each species (Tables 1 and 2).

The term "grassland species" refers to the following 6 species listed by Shelford (1963) as characteristic of a grassland habitat: Horned Lark, Western Meadowlark, Dickcissel, Lark Bunting, Grasshopper Sparrow, and Lark Sparrow. The young of grassland species are prone to leave the nest at an early age. The young of Horned Larks,

TABLE 1

FREQUENCY OF PARASITISM OF HOST SPECIES IN ELLIS COUNTY, KANSAS

Species	Nests Investigated	Number Parasitized	Percent Parasitized
Cardinal *(Cardinalis cardinalis)*	3	3	100.0
Lark Sparrow *(Chondestes grammacus)*	11	9	81.8
Pine Siskin *(Spinus pinus)*	51	28	54.9
Orchard Oriole *(Icterus spurius)*	15	8	53.3
Dickcissel *(Spiza americana)*	28	14	50.0
Bell's Vireo *(Vireo belli)*	2	1	50.0
Horned Lark *(Eremophila alpestris)*	31	14	45.2
Grasshopper Sparrow *(Ammodramus savannarum)*	18	4	22.2
Red-winged Blackbird *(Agelaius phoeniceus)*	228	50	21.9
Lark Bunting *(Calamospiza melanocorys)*	142	22	15.5
Eastern Phoebe *(Sayornis phoebe)*	68	7	10.1
Western Meadowlark *(Sturnella neglecta)*	29	2	6.9
Brown Thrasher *(Toxostoma rufum)*	49	3	6.1
Say's Phoebe *(Sayornis saya)*	37	1	2.7

Brown-headed Cowbirds, Dickcissels, and Grasshopper Sparrows were each observed to leave the nest at an estimated age of 6 to 7 days. Nests of grassland species were approached from different directions each time the nest was checked in an attempt to reduce predation, but still 44% were destroyed by predators. Consequently a category of "presumed fledged" was established to aid in the interpretation of fledging success due to the high rate of predation and the tendency of the young to leave the nest early. It is obvious that the "presumed fledged" category cannot be accurate, but it is probably nearer to the actual rate of fledging success than is the number actually known to fledge. Thus references here to fledging success of grassland species refer to the number presumed to have fledged. Young birds surviving at least 4 days would probably fledge, barring predation; thus the young of grassland species which were at least 4 days old were presumed to have fledged.

TABLE 2

NUMBER OF NESTS OF NON-PARASITIZED SPECIES INVESTIGATED IN ELLIS COUNTY

Species	Nests Investigated
Mourning Dove (*Zenaida macroura*)	1023
Barn Swallow (*Hirundo rustica*)	284
Common Grackle (*Quiscalus quiscula*)	79
Western Kingbird (*Tyrannus verticalis*)	51
American Robin (*Turdus migratorius*)	32
House Sparrow (*Passer domesticus*)	26
Eastern Kingbird (*Tyrannus tyrannus*)	16
Common Nighthawk (*Chordeiles minor*)	14
Mockingbird (*Mimus polyglottos*)	12
Loggerhead Shrike (*Lanius ludovicianus*)	9
Scissor-tailed Flycatcher (*Muscivora forficata*)	7
Black-billed Magpie (*Pica pica*)	6
Northern Oriole (*Icterus galbula*)	6
Killdeer (*Charadrius vociferus*)	5
Yellow-billed Cuckoo (*Coccyzus americanus*)	4
Blue Jay (*Cyanocitta cristata*)	3
Catbird (*Dumatella carolinensis*)	1

The predation rate appeared to increase with the frequency of nest visits by researchers so visits were reduced to 5-day intervals until the young reached an age of 4 or 5 days. After this time nests were checked at 3-day intervals when possible.

Species described as common, or uncommon to common summer residents in Ellis County (Ely 1971) are collectively referred to as common species while those described as uncommon or low-density are referred to as uncommon species.

I have used the criteria established by Mayfield (1965) for evaluating frequency of parasitism—less than 10% light; 10–30% moderate; over 30% heavy.

RESULTS AND DISCUSSION

Cowbird parasitism occurred from 21 April until 16 July with the greatest intensity of egg-laying occurring between 25 April and 1 July (Fig. 1). Six of the 14 species parasitized are grassland species. The overall frequency of parasitism ranged from 100% for the Cardinal to 2.7% for Say's Phoebe. The range for the grassland species was 81.8% (Lark Sparrow) to 6.9% (Western Meadowlark).

The small number of nests investigated for each species, the high rate of nest predation among grassland species, and the tendency of grassland species to leave the nest early have made the interpretation of the effect of cowbird parasitism difficult. Although the relatively small number of parasitized

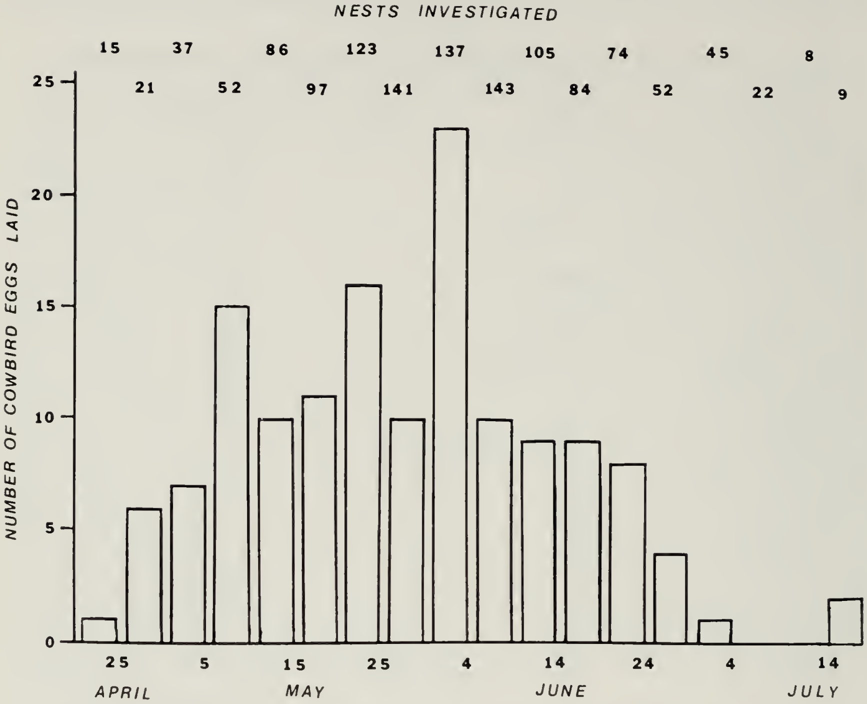

FIG. 1. Number of cowbird eggs laid per 5 day interval in Ellis County, Kansas, 1973–1974.

nests investigated may be inconclusive evidence of the role played by each host species, a substantial amount of parasitism seems to occur among grassland species.

The measure of the success of cowbird parasitism is determined by the number of cowbirds raised by each host species. Mayfield (1965) has defined "tolerance" to cowbird parasitism as the ratio of cowbirds fledged to the number of cowbird eggs laid in the nest of the host. He regarded a fledging rate from cowbird eggs of more than 20% as an indication of a tolerant host. By this measure, 3 of the 6 grassland species are tolerant hosts: Lark Sparrow, Grasshopper Sparrow, and Horned Lark. The situation for the Dickcissel and Lark Bunting is uncertain. Nine of 13 parasitized Dickcissel nests (69%) were destroyed by predators or human activities and 5 of 13 parasitized Lark Bunting nests were destroyed by predators. Consequently, very few eggs laid by the cowbird in nests of these species had an opportunity to fledge. Since I observed Dickcissels to rear 2 cowbirds to at

TABLE 3

COWBIRD NESTING SUCCESS IN ELLIS COUNTY, KANSAS 1973–1974

Species	Parasitized Nests	Cowbird Eggs	Number Fledged	Percent of Success
Lark Sparrow	9	16	11	69
Grasshopper Sparrow	4	5	3	60
Eastern Phoebe	7	10	4	40
Orchard Oriole	2	3	1	33
Horned Lark	14	24	7	25
Dickcissel	13	14	2	14
Red-winged Blackbird	18	19	2	11
Lark Bunting	13	15	1	7
Pine Siskin	16	20	1	5
Say's Phoebe	1	1	0	0
Brown Thrasher	1	3	0	0
Bell's Vireo	1	1	0	0
Western Meadowlark	1	1	0	0

least 6 days of age and a pair of Lark Buntings raised a cowbird for at least 5 days, it is possible that only the Western Meadowlark, among the grassland species, is intolerant to cowbird parasitism (Table 3).

All of the species in which no cowbird parasitism was observed are among

TABLE 4

NUMBER OF COWBIRD EGGS LAID PER NEST FOR EACH OF 13 SPECIES IN ELLIS COUNTY, KANSAS

Host Species	Nests Investigated	1 Egg	2 Eggs	3 Eggs	Number of Eggs per Parasitized Nest	Number of Eggs for all Nests
Lark Sparrow	9	4	3	2	1.78	1.78
Pine Siskin	23	12	4	0	1.25	.87
Horned Lark	30	6	6	2	1.71	.80
Orchard Oriole	5	1	1	0	1.50	.60
Dickcissel	26	12	1	0	1.08	.54
Bell's Vireo	2	1	0	0	1.00	.50
Grasshopper Sparrow	15	3	1	0	1.25	.33
Red-winged Blackbird	90	17	1	0	1.05	.21
Lark Bunting	135	19	3	0	1.32	.19
Brown Thrasher	20	0	0	1	3.00	.15
Eastern Phoebe	68	5	1	1	1.43	.14
Western Meadowlark	22	1	0	0	1.00	.05
Say's Phoebe	37	1	0	0	1.00	.03
Total	520	84	21	6	1.41	.48

TABLE 5

FLEDGING SUCCESS OF 13 COWBIRD HOST SPECIES AT NON-PARASITIZED NESTS, ELLIS COUNTY, KANSAS

Species	Number of Nests	Number Fledged	Number Fledged per Nest	Presumed Fledged	Number Presumed Fledged per Nest
Eastern Phoebe	61	137	2.3		
Say's Phoebe	36	51	1.4		
Horned Lark	16	4	0.3	22	1.4
Brown Thrasher	14	7	0.5		
Bell's Vireo	1	0	0.0		
Western Meadowlark	16	11	0.7	34	2.1
Red-winged Blackbird	63	6	0.1		
Orchard Oriole	3	9	3.0		
Dickcissel	12	5	0.4	18	1.5
Pine Siskin	7	14	2.0		
Lark Bunting	49	19	0.4	71	1.5
Grasshopper Sparrow	8	4	0.5	20	2.5
Lark Sparrow	0	0	0.0		

those regarded by Friedmann (1963) as uncommon, rare, or accidental victims of cowbird parasitism.

The number of cowbird eggs found in each parasitized nest varied from 1 to 3 eggs. Twenty-five percent of 110 parasitized nests contained more than 1 cowbird egg per nest, yet the percentage of multiple parasitism was lower than the 40% reported by Friedmann (1963). He also stated that in more recent and more carefully made studies, nests with multiple eggs slightly outnumber nests with single cowbird eggs.

The frequency of parasitism and the number of cowbird eggs laid per nest of each host species should reflect the use of each host by the cowbird. The host species with the greatest frequency of parasitism and the highest number of cowbird eggs per nest should be an indication of a preferred host. On this assumption 4 of the 7 most "preferred" hosts are grassland species (Table 4).

Cowbird parasitism decreased the number of host fledglings, as an average of 1.54 young fledged from each non-parasitized nest while only 0.53 young of the host species fledged from each parasitized nest. Cowbirds were less successful than their nest-mates as only 0.32 cowbirds fledged per parasitized nest (Tables 5 and 6).

The relatively greater abundance of Brown-headed Cowbirds in Kansas (Van Velzen 1972) is also indicated by the high frequency of cowbird parasitism found in several species nesting in Ellis County. Breeding-bird surveys

TABLE 6

FLEDGING SUCCESS OF 13 COWBIRD HOST SPECIES AT PARASITIZED NESTS, ELLIS COUNTY, KANSAS

	Host Species					Cowbird			
Species	Number of Nests	Number Fledged	Fledged per Nest	Presumed Fledged	Presumed Fledged per Nest	Number Fledged	Fledged per Nest	Presumed Fledged	Presumed Fledged per Nest
Eastern Phoebe	7	1	0.1			4	0.6		
Say's Phoebe	1	0	0.0			0	0.0		
Horned Lark	14	0	0.0	10	0.7	7	0.5	7	0.5
Brown Thrasher	1	0	0.0			0	0.0		
Bell's Vireo	1	0	0.0			0	0.0		
Western Meadowlark	1	0	0.0	0	0.0	0	0.0	0	0.0
Red-winged Blackbird	17	6	0.4			2	0.1		
Orchard Oriole	2	3	1.5			1	0.5		
Dickcissel	13	0	0.0	9	0.7	0	0.0	2	0.2
Pine Siskin	16	3	0.2			1	0.1		
Lark Bunting	13	0	0.0	7	0.5	0	0.0	1	0.1
Grasshopper Sparrow	4	2	0.5	8	2.0	2	0.5	3	0.8
Lark Sparrow	9	2	0.2	5	0.6	8	0.9	11	1.2

show the greatest abundance of cowbirds to be in the north-central part of Kansas (Fig. 2) and it is possible that an even greater intensity of parasitic activity may occur there.

The high relative abundance of cowbirds in the plains states and my findings of relatively heavy parasitic activities among most grassland species suggests that grassland species do contribute greatly to the success of the cowbird.

SPECIES ACCOUNTS

Eastern Phoebe.—Friedmann (1963) reports that the Eastern Phoebe is a very common victim of cowbird parasitism, but the degree to which the phoebe is affected varies locally. In this study 7 of 68 nests investigated were parasitized and the phoebe was a tolerant host: 40% of the cowbird eggs laid, fledged young. Five of 7 instances of parasitism occurred in the first half of the breeding season. The phoebe is an uncommon summer resident of Ellis County, and considering the relatively low frequency of parasitism, the Eastern Phoebe does not play a major role as a host.

Say's Phoebe.—Only 6 instances of cowbird parasitism of Say's Phoebe were reported by Friedmann (1963), 5 of them from Kansas. The only parasitized nest I found held 4 phoebe eggs and 1 cowbird egg, but 3 days later held only 5 phoebe eggs. Fried-

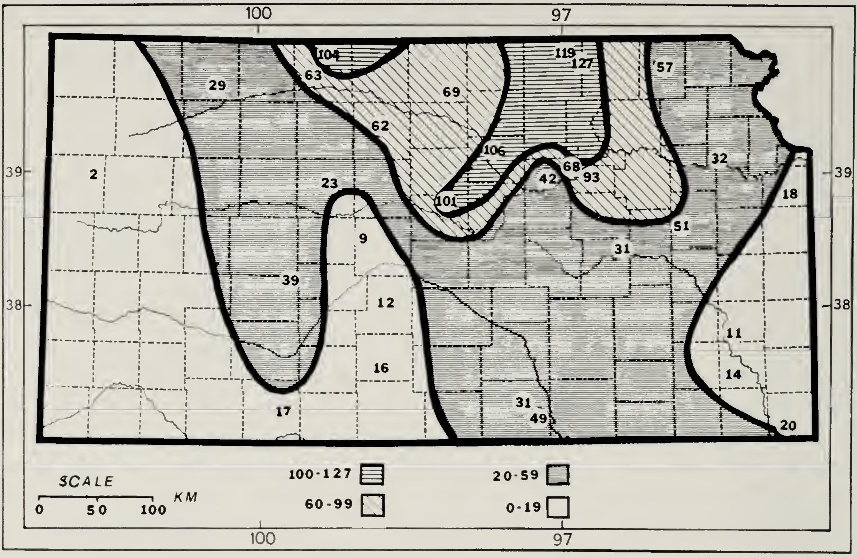

FIG. 2. Relative abundance of the Brown-headed Cowbird in Kansas during the breeding season.

mann suggests that Say's Phoebe is not of much importance to the cowbird and the latter in turn is not an important factor in the economy of the phoebe. My finding of only 1 parasitized nest out of 37 studied supports Friedmann's belief.

Horned Lark.—Horned Larks characteristically laid 2 clutches, the first between 20 March and 14 April, the second between 15 May and 15 June. I observed no parasitism in the first clutch (8 nests) but 14 of 22 (63.3%) of second clutches were parasitized. Three nests fledged 2 cowbirds each and 2 other Horned Lark nests each contained two 9-day-old cowbirds. Friedmann (1963) regards the Horned Lark as a generally infrequent victim of the cowbird, although in some places it is a fairly frequent host. If the frequency of parasitism of the second clutch (63.3%) is considered, it seems to be more than just a fairly frequent host in Ellis County. The Horned Lark is a common summer resident, is heavily parasitized, and is a tolerant host. Consequently it appears to play a major part in the reproductive success of the cowbird. It is also possible that the Horned Lark has adapted to a heavy frequency of parasitism by laying its first clutch of eggs prior to the breeding season of the cowbird.

Brown Thrasher.—Friedmann (1963) states that the Brown Thrasher is occasionally parasitized. This is supported by a 6.1% parasitism rate of the nests I investigated. The low frequency of parasitism appears to exclude the Brown Thrasher as a host of any major importance.

Bell's Vireo.—Friedmann (1963) lists Bell's Vireo as a frequent victim of the cowbird within an area that includes Kansas. The single parasitized nest of only 2 investigated is insufficient evidence for speculation on the role of Bell's Vireo as a host. Barlow's work in Kansas (1962) revealed that 24 of 35 occupied nests (68%) were parasitized. Since Bell's Vireo is a fairly common summer resident of Ellis County and since a high rate of parasitism was observed by Barlow it is possible that Bell's Vireo is an important host of the cowbird in Ellis County.

Western Meadowlark.—Friedmann (1963) states that the Western Meadowlark like the Eastern Meadowlark is an uncommon host and is parasitized even less. The Western Meadowlark was the only grassland species in which a low frequency of parasitism was observed (6.9%). Hergenrader (1962) noted several instances of cowbird eggs near meadowlark nests in Nebraska which suggested to him that the meadowlark is sometimes successful in expelling the eggs from the nest. I recorded no instances of cowbird eggs that had been removed from meadowlark nests. No adaptations that would explain the low frequency of parasitism were evident.

Red-winged Blackbird.—Friedmann (1963) stated that the Red-winged Blackbird is a common victim in some areas but is almost unmolested by the cowbird in other localities. In Ellis County nests of Red-wings were moderately parasitized (21.9%). Fledging success was relatively low, apparently due in large part to predators following paths to nests checked too frequently at the beginning of this study. The extremely high proportion of Red-wing nests destroyed by predators makes the Red-wing appear as an intolerant host, but since 2 cowbirds were known to have fledged from Red-wing nests, it is possible that the Red-wing actually is a tolerant host. Since the Red-wing is a common summer resident, is moderately parasitized, and possibly is a tolerant host, it probably is of some importance to the reproductive success of the cowbird.

Orchard Oriole.—Friedmann (1963) regarded the Orchard Oriole as a fairly frequent host although actual records are few. Though an uncommon summer resident it was heavily parasitized (53.3%) in this study. Although fledging success could be assessed for only 2 parasitized nests, it appears that the Orchard Oriole is a tolerant host and produces a few cowbirds from the limited number of nests occurring in Ellis County.

Cardinal.—Friedmann (1963) states that the status of the Cardinal as a cowbird fosterer varies in different parts of its range. Cardinals are uncommon in Ellis County and although all 3 nests investigated were parasitized, the Cardinal probably plays an insignificant role as a host species.

Dickcissel.—Friedmann (1963) states that the Dickcissel is a common victim and it appears to be parasitized more often in Texas, Oklahoma, Nebraska, and Kansas than elsewhere. I found a 50% parasitism rate for the Dickcissel, though Zimmerman (1966) found a 78% rate of parasitism in eastern Kansas. A high rate of nest predation obscured a determination of tolerance, but since 2 cowbirds were raised by Dickcissels to an age of 6 days it is probable that the Dickcissel is a tolerant host. Since it is a fairly common summer resident, heavily parasitized, and possibly a tolerant host, it is probably one of the more important host species in Ellis County.

Pine Siskin.—The Pine Siskin is generally allopatric with the cowbird; however, wherever the 2 species do overlap, the Pine Siskin occasionally is imposed upon (Friedmann 1963). Nesting records of the Pine Siskin are rare, but in Ellis County it is subject to heavy cowbird parasitism (54.9%). Tolerance of parasitism is low (5%) and the effect of parasitism on the siskin is detrimental. Irregular nesting of the Pine Siskin in Ellis County and a low tolerance of parasitism eliminate it as a productive host species. The Pine Siskin appears to be an example of a receptive host that has had little exposure to nest parasitism (see Mayfield 1965).

Lark Bunting.—The Lark Bunting is a common local victim of northwestern cowbird populations but overall it is a rather infrequent victim (see Friedmann 1963). In my study it was subject to moderate parasitism (15.5%). The most frequent nesting habitat appeared to be milo stubble. Consequently 52% of the nests were destroyed by farming activity and these are omitted from calculation of fledging success. The tolerance of the Lark Bunting is questionable because of a high rate of predation and nest desertion. Seven of the 13 parasitized nests were destroyed by predators and 5 were deserted. Since 1 cowbird was raised to an age of 5 days it is possible that the Lark Bunting is a tolerant host. Because of a relatively low frequency of parasitism and the high proportion of nests destroyed by farming practices, the Lark Bunting appears to be a species of little value to the cowbird as a host. One possible adaptation of the bunting to cowbird parasitism may be the removal of cowbird eggs from the nest. The color contrast of the blue bunting egg and the brown speckled egg of the cowbird is greater than that of all other grassland species except the Dickcissel. Thus, if any grassland species is capable of distinguishing between eggs of their own and those of the cowbird it would be the Lark Bunting. The recognition and subsequent removal of a foreign egg is suggested by 5 separate observations of cowbird eggs found outside of bunting nests. The removal of cowbird eggs would help explain the relatively low frequency of parasitism in comparison to other grassland species. Nest desertion may be another adaptation to parasitism as 5 out of 13 parasitized nests were deserted. However, at least one was a direct result of human interference. Only 3 of 49 non-parasitized nests were deserted.

Grasshopper Sparrow.—Instances of parasitism of the Grasshopper Sparrow are few, but Friedmann (1971) reports one case in which a young nestling cowbird was ready to leave the nest. Two 8-day-old and one 4-day-old cowbird I observed in separate nests of Grasshopper Sparrows further reinforce the evidence that the sparrow is a true host. Although the frequency of parasitism was relatively low (22.2%) I found the Grasshopper Sparrow to be a very tolerant host (60%). Considering that it is one of the most abundant summer residents in Ellis County, a significant portion of the cowbirds produced in Ellis County may fledge from Grasshopper Sparrow nests.

Lark Sparrow.—Friedmann (1963) lists the Lark Sparrow as a relatively uncommon host, but this was not the case in Ellis County where 81.8% of the nests investigated were parasitized. In my study the Lark Sparrow had the highest tolerance to parasitism of all host species (69%). Even though it is an uncommon summer resident in Ellis County, the high frequency of parasitism and the high level of tolerance to parasitism suggests that the Lark Sparrow is an important host of the cowbird.

SUMMARY

Of 520 nests of 14 host species, 111 (21%) were parasitized. The frequency of parasitism varied from 2.7% (Say's Phoebe) to 100% for 3 Cardinal nests. All but 1 grassland host species received moderate to heavy parasitism. Parasitized nests fledged 1 less host (0.5 per nest) than non-parasitized nests (1.5 per nest). Only 0.3 cowbirds fledged per nest.

Probable adaptations to parasitism were nesting prior to the cowbirds breeding season by Horned Larks and nest desertion and removal of cowbird eggs by Lark Buntings.

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LITERATURE CITED

BARLOW, J. C. 1962. Natural history of the Bell Vireo, *Vireo bellii* Audubon. Univ. of Kansas Publ. Mus. Nat. Hist. 55:241–296.

ELY, C. A. 1971. A history and distributional list of Ellis County, Kansas birds. Fort Hays Studies (N.S.), Sci. Ser. 9:vii + 1–115.

FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. Charles C. Thomas, Springfield, Illinois.

———. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

———. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88:239–255.

HERGENRADER, G. L. 1962. The incidence of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) on roadside nesting birds in Nebraska. Auk 79:85–88.

MAYFIELD, H. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13–28.

SHELFORD, V. E. 1963. The ecology of North America. Univ. of Illinois Press, Urbana.

SUTTON, G. M. 1967. Oklahoma birds. Univ. Oklahoma Press, Norman.

U.S. DEPT. OF COMMERCE. 1969. Census of Agriculture. Vol. 1. Part 21, p. 209.

VAN VELZEN, W. T. 1972. Distribution and abundance of the Brown-headed Cowbird. Jack Pine Warbler 50:110–113.

ZIMMERMAN, J. L. 1966. Polygyny in the Dickcissel. Auk 83:534–546.

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BREEDING BIOLOGY AND PARASITISM IN THE RUDDY DUCK

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There is little published information on the breeding biology of the Ruddy Duck (*Oxyura jamaicensis*). Ruddy Duck eggs have been found in the nests of other waterfowl, and this form of parasitism has been intraspecific as well as interspecific (Weller 1959, Joyner 1973). This paper is concerned with aspects of the breeding biology of the Ruddy Duck, and the species' parasitism.

METHODS

I studied Ruddy Ducks in the pothole region near Minnedosa, Manitoba, during May–August 1971. Descriptions of this area and its use by waterfowl appear in Evans et al. (1952), Bird (1961) and Dzubin (1969).

I recorded all Ruddy Ducks on ponds within a 580 ha study area. All emergent cover in 203 ponds was searched for duck nests. Nest-searches and censuses of Ruddy Ducks were performed at bi-weekly intervals. The "beat-out" technique (Evans and Black 1956) was used in censusing adults and broods. Ruddy Ducks were collected periodically from ponds outside the confines of the 580 ha census area. Each duck was weighed to the nearest gram and standard physical characteristics measured as in Baldwin et al. (1931).

RESULTS

Breeding chronology.—Migratory Ruddy Ducks began arriving in Manitoba during the last week of April and the majority of the population was present in mid-May 1971, which is normal (Hochbaum 1944, Dzubin 1969).

Ruddy Ducks collected in May and early June generally were fat. Subcutaneous fat deposits carefully dissected from the bodies of 2 pre-laying females collected in May amounted to 150 and 200 g or 18 and 27% respectively of the females' body weights. Later in the season, brood-accompanying females had exhausted their subcutaneous and visceral fat reserves and were much lighter (Table 1). Early in the season females generally were heavier than males, although males and females are very similar in body size (cf. Tables 1 and 2). The difference in body weight can be attributed to the females' relatively greater fat reserves. The gonads of both sexes were well developed in May (Table 1). For 2 of the laying females collected in June, I determined, through examination of their ovaries and nests, that they were in the process of completing clutches of 7 eggs each.

In the Minnedosa area a sharp peak in egg-laying occurred in the last half of June (Table 3). Thus, most females began nesting about 4 weeks after their arrival on the breeding grounds.

TABLE 1

MEAN BODY AND GONAD WEIGHTS (G) OF RUDDY DUCKS IN RELATION TO CHRONOLOGY OF BREEDING

Dates specimens collected	Body weight[1]			Gonad weight[2]			Status
	x̄	range	*n*	x̄	range	*n*	
Females							
May 25–31	688	620–789	4	55.0	50–65	4	Pre-laying
June 15–25	732	690–765	5	31.0	8–55	5	Laying
July 28–31	490	460–525	6	0.9	0.4–1.4	6	With broods 1–2 weeks old
Males							
May 25–31	656	619–705	6	2.4	1.3–5.3	6	
June 15–25	653	627–680	5	3.3	1.7–4.8	5	
July 28–31	625	594–660	4	0.5	0.1–1.7	4	

[1] Does not include weight of gonads, oviducal eggs, and contents of esophagus and gizzard.
[2] Includes both testes of each male.

In a sample of 40 egg-sets, ducklings hatched successfully from 28, a nesting success of 70%. Of the 12 clutches which failed to hatch ducklings, 3 were depredated, 3 flooded, 3 deserted, and 2 lost to unknown causes. I suspect that re-nesting attempts comprised a small proportion of all nests found during the course of the season. Relatively few clutches were started after July, and I found no new clutches in August. Some of the late clutches may have been produced by females, possibly first-year individuals, which had

TABLE 2

MEAN MENSURAL DIMENSIONS (MM) ± S.D. OF ADULT RUDDY DUCKS. ALL DATA DERIVED FROM SHOT OR TRAPPED BIRDS MEASURED IN THE FIELD

Dimension	Males				Females			
	n	x̄	SD	range	*n*	x̄	SD	range
Culmen length	37	41.5	± 1.3	(38– 44)	27	41.5	± 1.2	(38– 43)
Culmen width	36	25.7	± 0.8	(24– 27)	26	25.9	± 0.7	(24– 27)
Tarsus	38	32.9	± 0.8	(31– 34)	28	32.2	± 0.8	(30– 34)
Middle toe	37	54.9	± 1.9	(50– 58)	27	54.6	± 1.8	(51– 58)
Wing	32	147.7	± 2.5	(143–153)	23	143.9	± 2.1	(140–148)
Primary 10	30	86.3	± 1.7	(82– 89)	27	83.3	± 1.9	(80– 87)
Tail	34	73.8	± 3.0	(67– 81)	27	71.4	± 3.2	(65– 78)

TABLE 3

BREEDING SEASON OF THE RUDDY DUCK IN MANITOBA, BASED ON NUMBER OF CLUTCHES AND BROODS OBSERVED IN 1971. ALL RECORDS ADJUSTED TO DATES WHEN EGGS WERE LAID

May		June		July		August	
1–15	16–31	1–15	16–30	1–15	16–31	1–15	16–31
0	3	41	77	36	12	0	0

molted their remiges after arrival on the breeding grounds (Siegfried 1973a). Hochbaum (1944) states that at Delta a small number of ducklings are not yet able to fly when ice closes the bays in late October or early November. Clearly, the Ruddy Duck is not double-brooded in Manitoba.

Nesting habitat.—I found 40 Ruddy Duck nests in 36 of the 203 ponds during the course of the breeding season. This represents a high density of breeding Ruddy Ducks (cf. Dzubin 1969). A comparison of the mean number of females (50) counted with the maximum number of nests found (40) indicated that most females initiated clutches. The mean sex ratio (70:50) was biased in favor of males, which is normal (Dzubin 1969).

Nests usually were spaced far apart. Only 4 ponds supported as many as 2 nests at the same time, and 2 occupied nests less than 10 m apart were found only once. In this case the 2 females were observed copulating with the same male. I was not able to determine the precise nature (polygyny or promiscuity) of the sexual association among these birds. However, within the Ruddy Duck population breeding in Manitoba, monogamous pair bonds of varying stability were usual; some individuals of both sexes essentially lacked bonds (Siegfried 1976). Quantitative data on these phenomena are lacking.

TABLE 4

NUMBER OF RUDDY DUCK NESTS LOCATED IN PONDS CLASSIFIED ACCORDING TO DOMINANT EMERGENT VEGETATION

Period in which clutch completed	> 50% *Scolochloa festucacea* and *Carex atherodes*	> 50% *Typha latifolia* and *Scirpus acutus*
1–15 June	29	9
16–30 June	35	28
1–15 July	11	15
16–31 July	2	6

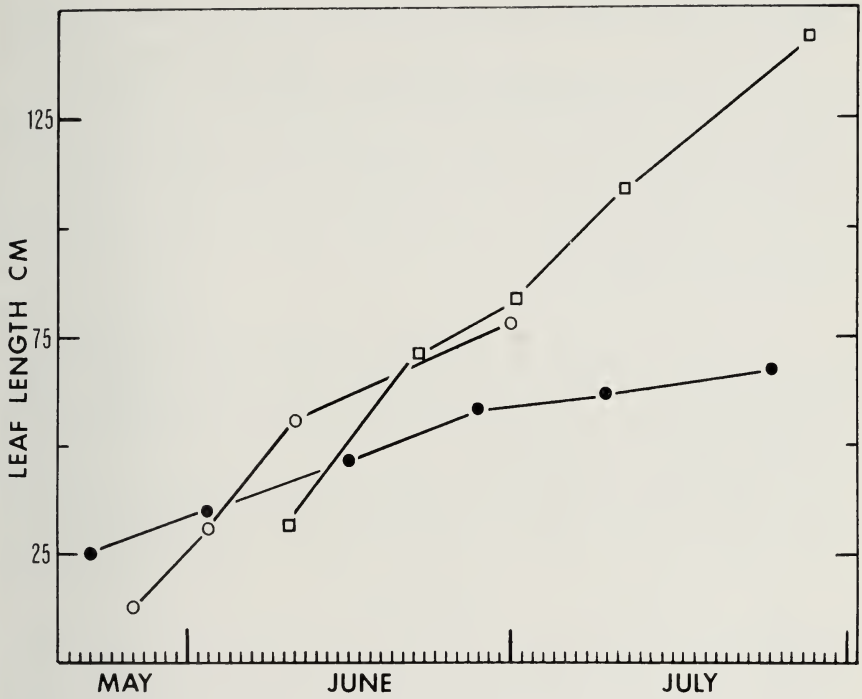

Fig. 1. Growth in length of longest leaf in *Scolochloa festucacea* (solid circles), *Scirpus acutus* (open circles) and *Typha latifolia* (squares). Each data point represents a mean value derived from measurements of five plants.

Most June nests were found in ponds supporting primarily *Scolochloa* and *Carex* as emergent vegetation, whereas July nests were found more often in ponds containing predominantly *Typha* and *Scirpus* (Table 4, $\chi^2 = 6.5$, $p \leqslant .05$). *Scolochloa* started growing earlier in the season than *Typha* and *Scirpus*, and remained ahead until after the first week in June (Fig. 1). Most

Table 5

Number of Ruddy Duck Nests Located in Stands of *Scolochloa*, *Carex*, *Typha* and *Scirpus*

Month in which clutch completed	*Scolochloa festucacea*	*Carex atherodes*	*Typha latifolia*	*Scirpus acutus*
June	33	6	4	4
July	7	2	8	5

TABLE 6

MEAN DEPTH (CM) OF WATER UNDER RUDDY DUCK NESTS BUILT IN *SCOLOCHLOA*, *SCIRPUS* AND *TYPHA*

Scolochloa festucacea (A)				*Scirpus acutus* (B)				*Typha latifolia* (C)			
$\bar{x}$	± S.D.	range	*n*	$\bar{x}$	± S.D.	range	*n*	$\bar{x}$	± S.D.	range	*n*
42	11	30–75	24	57	18	35–90	11	61	21	30–90	10

A > B ($t = 2.47, P < 0.02 > 0.01$.
A > C ($t = 2.70, P < 0.02 > 0.01$.

early nests were constructed in *Scolochloa* and late nests were located relatively more often in *Typha* and *Scirpus* (Table 5, $\chi^2 = 12.8$, $p \leqslant .01$). Nests in *Typha* and *Scirpus* were built over slightly deeper water than those in *Scolochloa* and *Carex* (Table 6).

Clutch size and nest parasitism.—Slightly more than half of all clutches contained 7 or 8 eggs (Table 7). Although the clutches averaged slightly larger in June than in July, the difference was not significant statistically (7.65 ± 1.96 S.D. versus 7.26 ± 1.65 S.D., *df* 48 $t = 0.72$). Only one clutch (13 eggs) exceeding 10 eggs was completed in July, the remaining 7 containing 10 or more eggs were completed in June. The frequency distribution of clutches in Table 7 is skewed to the right. Plotted on arithmetic probability paper, the frequency distribution showed a deviation from normal at a clutch of 10 eggs which may be the maximum clutch possible for one female.

I was able to observe 3 individual females (2 marked with nasal-saddles) throughout the egg-laying phase of their reproductive cycle. Two produced 7 eggs each and the 3rd a 9-egg clutch. Each female deposited one egg daily. I suspect that clutches of more than 10 eggs are the result of more than one female laying in the same nest. Direct evidence for this supposition is, however, meager and results on 2 clutches (11 and 13 eggs) for which I established clearly that extra eggs had been deposited subsequent to onset of

TABLE 7

CLUTCH SIZE OF THE RUDDY DUCK

No. eggs in clutch									
4	5	6	7	8	9	10	11	12	13
1	3	10	16	17	5	3	2	1	2

incubation. Of 8 clutches containing 10 or more eggs, only one (10 eggs) successfully hatched all eggs.

I examined 53 nests and 61 broods of 9 other duck species. I found no Ruddy Duck eggs or ducklings in 15 nests and 21 broods of the Redhead (*Aythya americana*). Only 2 of 42 Canvasback (*Aythya valisineria*) clutches had been parasitized by Ruddy Ducks. One Canvasback nest contained 5 of its own eggs and 1 egg of the parasite. A Canvasback brood included 2 Redhead, 4 Ruddy Duck, and 3 Canvasback ducklings. These 2 clutches were completed in late May and early June respectively. I found no Ruddy Duck eggs in 234 American Coot (*Fulica americana*) nests. These data indicate a low incidence of interspecific parasitism by the Ruddy Duck.

The incidence of intraspecific parasitism is much more difficult to assess. However, assuming that clutches of 11 eggs and more represented the product of intraspecific parasitism, then a minimum of 8% of all clutches had been parasitized. During the period 25 May–8 June I found 6 Ruddy Duck eggs which had been dropped on the ground, each at different places and at least 50 m from the nearest nest. Isolated, dropped eggs were not subsequently encountered.

DISCUSSION

This paper reports data gathered during the course of a single breeding season. Hence, caution is needed when interpreting results and in comparing findings with those made by other workers.

The Ruddy Duck breeds later in the year than most duck species and onset of nesting is delayed for about 4 weeks after the bird's arrival on the Manitoba breeding grounds. Low (1941) found that first nests were built in May, about 7 weeks after arrival of Ruddy Ducks in Iowa. The timing of nesting may be correlated with the availability of nesting cover, though other factors influencing onset of breeding will be involved as well. Ruddy Ducks usually use fresh, green plant material in constructing nests, unlike the Canvasbacks and to a lesser extent the Redheads which often construct nests in old, dead vegetation. These species normally nest about 3 weeks ahead of the Ruddy Duck (Hochbaum 1944, Weller 1959). The peak of Ruddy Duck nesting occurred during 1–15 June in 3 years (1938–1940) in Iowa, and nests built after 1 June were predominantly of green plant materials (Low 1941).

Fresh, green emergent plant growth, tall and dense enough to provide cover suitable for the Ruddy Duck's nesting requirements, is generally unavailable before June. It is unlikely that shortage of food limits onset of nesting, since most birds examined soon after arrival in Minnedosa had well developed gonads, and extensive deposits of body fat and had fed on protein-rich food (Siegfried 1973b). Thus, females presumably were not short of the energy and protein necessary for forming eggs. Indeed, pre-laying females were observed to spend most of their time loafing and not feeding (Siegfried 1973c).

The length of the delay in onset of nesting and the sharp peak in initiation of clutches in June should be viewed in relation to the species' temporally limited opportunity for breeding successfully in regions as far north as Manitoba. Drought and freeze-up imminent in fall means that Ruddy Ducks initiating clutches after July have little chance of producing flying young. There is thus a premium on nesting as early as possible after arrival in Manitoba. Consequently, nests are constructed as soon as the first green emergent cover becomes available. An arrival time earlier than the start of May would, however, appear to be disadvantageous, since it appears that the almost exclusively aquatic Ruddy Duck does not tolerate cold water (Siegfried 1973c). Like all other *Oxyura* species, the Ruddy Duck is essentially warm temparate in its area of geographical distribution, and members of the genus are warm season breeders generally nesting in stands of newly grown, emergent vegetation, mainly rushes and sedges (Siegfried 1976).

Weller (1959), in commenting on the Ruddy Duck's tendency to drop eggs on the ground and in nests of other birds, says that this occurs most often early in the breeding season and that it presumably results from variation in synchrony of nesting and laying behavior. The data available now suggest tentatively a relationship between incidence of dropped eggs and parasitism and the chronology of nesting concomitant with the quantity and quality of available nesting cover. I have suggested that some females are physiologically ready to lay soon after their arrival on the nesting grounds, and that a lack of coordination between a female's readiness to breed (in particular the nest-construction "drive") and the availability of suitable nesting cover provides the motivation for "abnormal" nest-building behavior (Siegfried 1973c). It seems likely that one explanation for the Ruddy Duck's parasitic laying, resorts fundamentally in a degree of asynchrony between physiological and behavioral responses to environmental cues. Dropped eggs and parasitic laying may be regarded as responses caused by lack of attunement of egg-laying and nesting. A female physiologically ready to lay, but lacking the environmental stimuli for constructing her own nest, conceivably might be stimulated by the sight of an already complete nest, containing eggs, to lay parasitically in that nest.

Weller (1959) considered the influence of both environmental and genetic factors in reviewing several causes for parasitism in waterfowl. He concluded that cover quality did not affect the number of eggs laid parasitically, and thought it likely that the parasitic tendencies of the Redhead and Ruddy Duck are inherent and not subject to measurable modification by the physical environment. In the case of the Ruddy Duck in Manitoba, I suggest that the incidence of parasitism is expressed as a consequence of variation in the response of phenotypes to environmental factors.

The apparently low incidence of interspecific parasitism by the Ruddy Duck in Minnedosa, contrasts with Joyner's (1973) finding that 11% of 305 duck nests of 5 species at Farmington, in Utah, were parasitized by the Ruddy Duck. Clearly geographical and perhaps also annual differences attend the species' parasitism, and the factors promoting the behavior in one region may be different in other areas.

SUMMARY

The breeding phenology of the Ruddy Duck (*Oxyura jamaicensis*) in Manitoba, Canada, is described. Most females began nesting about 4 weeks after their arrival on the breeding grounds. The delay in onset of nesting may be correlated with the availability of suitable cover. The incidence of interspecific nest parasitism by the Ruddy Duck was low. A relationship is indicated between degree of parasitism and the chronology of nesting concomitant with the quantity and quality of available nesting cover. Parasitic laying apparently results from a lack of attunement of a female's physiological and behavioral responses to environmental cues.

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LITERATURE CITED

Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 2:1–165.

Bird, R. D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Can. Dep. Agric. Res. Branch, Res. Station Contrib., 27.

Dzubin, A. 1969. Assessing breeding populations of ducks by ground counts. Pp. 178–230, *in* Saskatoon wetlands seminar. Can. Wildl. Serv. Rep. Ser., No. 6.

Evans, C. D., A. S. Hawkins, and W. H. Marshall. 1952. Movements of waterfowl broods in Manitoba. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl., No. 16.

Evans, C. D., and K. E. Black. 1956. Duck production studies on the prairie potholes of South Dakota. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Wildl., No. 32.

Hochbaum, H. A. 1944. The Canvasback on a prairie marsh. Stackpole Co., Harrisburg, Pa.

Joyner, D. E. 1973. Interspecific nest parasitism by ducks and coots in Utah. Auk 90:692–693.

Low, J. B. 1941. Nesting of the Ruddy Duck in Iowa. Auk 58:506–517.

Siegfried, W. R. 1973a. Wing moult of Ruddy Ducks in Manitoba. Bull. Br. Ornithol. Club 93:98–99.

———. 1973b. Summer food and feeding of the Ruddy Duck in Manitoba. Can. J. Zool. 51:1293–1297.

———. 1973c. Platform-building by male and female Ruddy Ducks. Wildfowl 24: 150–153.

———. 1976. Social organization in Ruddy and Maccoa ducks. Auk 93:560–570.

WELLER, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. Ecol. Monogr. 29:333–365.

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WOODPECKER DEPENDENCE ON TREES INFECTED BY FUNGAL HEART ROTS

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A considerable expenditure of energy is necessary for woodpeckers to excavate a nest cavity. Factors that would soften the wood in the nest tree prior to excavation would decrease the energy requirements needed to make a suitable nest cavity.

Studies of the Red-cockaded Woodpecker (*Dendrocopos borealis*) by Steirly (1957), Ligon (1970) and Jackson (in press) indicate that this woodpecker selects mainly pines (*Pinus* spp.) that are infected by *Fomes pini* (red heart disease) for nest and roost trees. (Authorities and synonyms for names of fungi are found in Miller and Farr 1975.) Dennis (1969) thought that Common Flickers (*Colaptes auratus*) in Massachusetts were dependent on decayed trees for nest sites. Although he mentions several species of fungi that infected the trees he examined, he unfortunately did not report how the fungi were identified. Kilham (1971) reported that Yellow-bellied Sapsuckers (*Sphyrapicus varius*) in New Hampshire showed a preference to excavate nests in trees infected by *Fomes igniarius*. Jackson (1976) found mushrooms (species unknown) growing inside a nest cavity made by a Red-bellied Woodpecker (*Centurus carolinus*) 4 days after the nestlings had fledged.

The above studies of woodpecker-fungi association apparently used examinations of the fungal fruiting bodies that were on the exteriors of the nest trees or, in the case of *Fomes pini*, red-colored corings with pockets of decay taken from decayed pines as evidence indicating infection.

We tried to culture fungi from the heartwood of woodpecker nest trees in addition to identifying the species that fruited on the exteriors of the trees. Our primary objective was to determine if the Downy (*Dendrocopos pubescens*), Hairy (*D. villosus*), and Pileated (*Dryocopus pileatus*) woodpeckers, and the Common Flicker of the oak—hickory forests of southwestern Virginia, preferred to nest in trees infected by heart rots or whether they excavated nest cavities in trees with firm, undecayed wood. Our secondary objective was to determine what fungi were involved if indeed the decayed trees were preferred.

METHODS

During the springs of 1972, ’73, and ’74 we searched the upper drainages of Craig and Poverty creeks on Jefferson National Forest in southwest Virginia and the college farm and campus of Virginia Polytechnic Institute and State University for woodpecker nest trees.

Nesting territories of the woodpeckers were located by listening to drumming and vocalizations of the birds. Locations of nest trees were pinpointed by listening for vocalizations and observing movements of the woodpeckers. Chips of wood from the freshly excavated cavities were examined to see if they had been softened by hyphal growth prior to excavation.

After the nesting season we cut down the nest trees and cut out the sections that contained the nest cavity. In addition to the nest cavities we removed sections of the nest tree that appeared to contain the transition zone where recently decayed portions of the tree met undecayed portions. We assumed that the primary wood decay fungus would be found in the newly decayed wood and that isolations from this zone would result in a culture of the primary rot that had infected the tree.

Although we collected 24 nest trees, 10 were so advanced with decay that it was impossible to obtain pure cultures from them. Six Pileated, 4 Downy, 2 Hairy woodpecker, and 2 Common Flicker nest trees were at stages of decay suitable to obtain cultures.

The heartwood from the nest trees was dissected aseptically from 4 to 5 predetermined locations below the nest cavity (Fig. 1) so as to detect, if present, successive invasions of different species of fungi. The chips of wood that were dissected were placed on malt agar. Sixteen to 20 plates were cultured for each nest tree. The actual position from which chips were dissected varied from tree to tree depending on how advanced the fungal infection was. Four additional malt agar plates were inoculated for each nest tree with chips from the zone where decayed wood met firm, undecayed wood.

Isolates were cultured on malt agar in the dark for 8 weeks at 25°C. They were examined every 7 days for growth rate, appearance and color of the mycelium, and odor. At the end of weeks 1, 2, 3, 6, and 8, the cultures were examined microscopically to see if hyphal differentiation had formed special structures as described by Davidson et al. (1942). The agar in each culture was also examined to determine if it were discolored, bleached, or unchanged. At the end of the 6th and 8th week, the cultures were checked for the initiation and development of fruiting bodies.

The presence or absence of extra-cellular oxidases and clamp connections at septa were key factors in the identification. Isolates were cultured on gallic acid agar for 2 weeks and tested with gum guaiac to determine if extra-cellular oxidases were present. Identifications of the fungi were made by comparing observed characteristics with those described by Davidson et al. (1942) and Nobles (1965).

The data obtained from cultural examination of the isolates and cultures of the fungi were sent to Mrs. Frances Lombard at the Center for Forest Mycology Research, Madison, Wisconsin for further cultural examination and confirmation of our identifications. Mating compatibility tests (Buller phenomenon) were conducted to confirm tentative identifications of 10 of the isolates (Buller 1930, 1931, Quintanilha 1937).

In addition to culturing fungi from chips of heartwood, we collected and identified fruiting bodies found on the exterior of the nest trees.

RESULTS AND DISCUSSION

The 14 nest trees examined were infected by a heart rot that had softened the core of the nest tree. The primary rot in most cases was *Spongipellis pachyodon* (syn: = *Irpex mollis*) (Fig. 2). This species is a top rot of hardwood trees and not found in conifers.

Spongipellis pachyodon was the primary rot in 5 of the 6 Pileated Woodpecker nest trees (*Quercus alba*, *Q. rubra*, *Q. prinus*, *Acer saccharum*, and

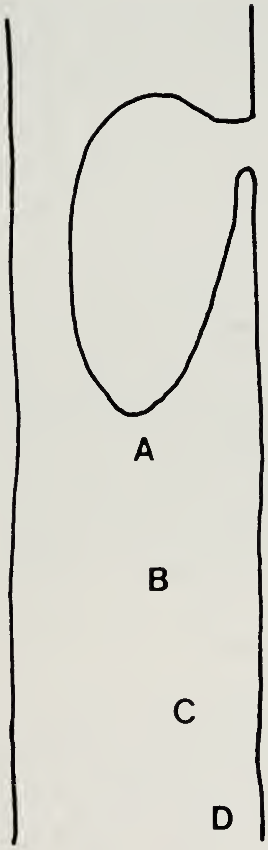

FIG. 1. Relative positions in the nest tree from which chips of wood were taken to culture. Positions were relative depending on how advanced the decay was.

Carya tomentosa) examined. The 6th tree, a table mountain pine (*Pinus pungens*), was primarily infected by a species of fungus that we were unable to identify. Half of the Pileated nest trees were infected by additional Basidiomycetes: *Phellinus spiculosus*, *Corticium alutaceum*, *Polyporus dichrous*, *P. gilvus*, *P. pargamenus*, *P. velutinus*, and *P. abietinus*. We did not detect secondary Basidiomycetes in 3 of the nest trees. All the Pileated nest trees were infected secondarily with imperfect fungi (e.g. *Penicillium* spp. and others) and bacteria.

Spongipellis pachyodon was the primary rot in 2 of 4 Downy Woodpecker nest trees, all of which were hardwoods. The other 2 trees, a mimosa (*Albizzia julibrissin*) and a black haw (*Viburnum prunifolium*) were primarily

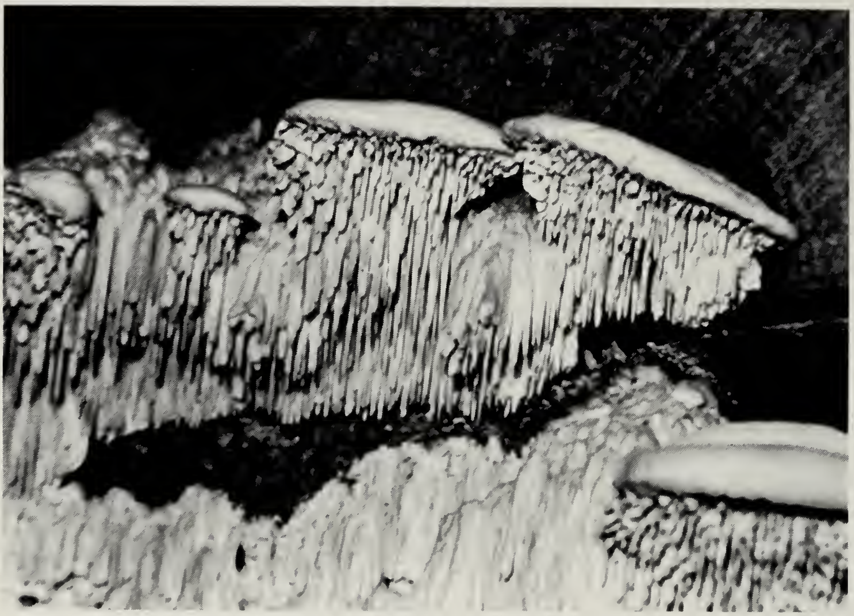

FIG. 2. *Spongipellis pachyodon*, the fungus responsible for the primary rot in 10 of the 12 hardwood nest trees examined.

infected by *Polyporus versicolor* and *Phellinus igniarius* (syn: = *Fomes igniarius*) respectively. Half of the Downy Woodpecker nest trees examined were infected secondarily by Basidiomycetes: *Polyporus versicolor*, *P. pargamenus*, and *P. velutinus*. We were able to detect imperfect fungi in 3 of the 4 Downy Woodpecker nest trees. All the trees were infected by bacteria.

Spongipellis pachyodon was the primary rot in both of the Hairy Woodpecker nest trees (*Quercus coccinea* and *Acer saccharum*) examined. One of the trees was infected secondarily by other Basidiomycetes: *Pleurotus sapidus* and *Stereum complicatum*. Both trees were secondarily infected by imperfect fungi and bacteria.

One Common Flicker nest tree we examined, a chestnut oak (*Quercus prinus*), was infected primarily by *Spongipellis pachyodon*. We were unable to identify the primary rot in the 2nd flicker nest tree which was a table mountain pine. Both Common Flicker nest trees were infected secondarily with other Basidiomycetes (*Stereum hirsutum* and *Poria candidissima*), imperfect fungi, and bacteria.

We superficially examined 7 other Common Flicker nest trees, 6 of which were black locusts (*Robinia pseudoacacia*) and the remaining 1 a yellow birch (*Betula alleghaniensis*). *Phellinus rimosus* was the only fungus ever observed to fruit on the black locust nest trees and probably was the primary rot in all 6 cases. *Daedalea unicolor* was the rot associated with the yellow birch nest tree.

Decay of the nest trees appeared to be a series of infections commencing with a Basidiomycete; in most cases in our study the fungus was *Spongipellis pachyodon.* Other Basidiomycetes (8 out of 14 cases), imperfect fungi (13 out of 14 cases), and bacteria (all cases) invaded the nest trees following the primary rot.

Although *Spongipellis pachyodon* was the primary rot in 10 of the 12 hardwood nest trees from which isolates were cultured, it had not fruited on the surface of any at the time sections of the tree were collected. Species of fungi that fruited on the exteriors of the nest tree were typically secondary rots (11 of 13 instances). *Spongipellis pachyodon* did fruit on the inside of 2 Pileated Woodpecker nest cavities, but this was after the trees had been cut down and stored indoors under damp conditions for a month. One Red-bellied Woodpecker nest tree that was visually examined after the 1975 nesting season had 3 different places, all near the nest cavity, where *Spongipellis pachyodon* had fruited.

As we examined the nest trees a pattern began to emerge which revealed the initial sequence of invasion of the primary rots in most instances. The fungi appeared to obtain access to the heartwood of the tree via a broken, dead branch. Subsequent hyphal growth proceeded into the core of the main trunk and started a pocket of decay in the heartwood that gradually decayed the core of the tree upward and downward from the initial site of infection. This is probably the reason why many of the nest cavities we examined were immediately below an old stub of a dead, broken branch. Baumgartner (1939) described a similar invasion sequence during the formation of fox squirrel (*Sciurus niger*) dens.

If only a heartwood rot is present, the sapwood of the nest tree remains healthy and firm. This condition appears to be the optimum for a woodpecker nest cavity as it would be difficult for a predator such as a raccoon (*Procyon lotor*) to chew its way into the nest cavity. Kilham (1971) made a similar observation of Yellow-bellied Sapsucker nest trees.

Often following or concurrent with heart rots were sap rots which destroy the living xylem and phloem tissue of the sapwood and thus kill the tree. Sap rots were noticed in most of the nest trees we examined with sometimes several different species of fungi involved. All but 2 of the Pileated Woodpecker nest trees we examined were infected by both a heart rot and a sap rot at the level of the nest cavity. The decay, coupled with the excavation of nest cavities, greatly weakens the nest trees and as a result many were broken off at the topmost cavity in the tree (Conner, et al. 1975).

Some nest trees had been subjected to fungal decay for a very short period of time. These trees appeared completely healthy on the outside. However, when cut down and sectioned a small pocket of rot was discovered. Somehow, probably by sounding the tree with their bills, the woodpeckers had been able to detect the decay and subsequently excavate through several centimeters of healthy oak before hitting the decayed pocket out of which the nest cavity was chiseled.

We examined freshly excavated chips of wood from 78 other nest trees of the 4 species of woodpeckers. All had been softened by fungal decay. We saw on several occasions for each woodpecker species, aborted nest excavation attempts after only 2–5 cm of penetration. In all instances, the woodpeckers subsequently excavated a cavity either in another tree or in a different place on the same tree. These observations may indicate that woodpeckers occasionally err in detecting suitably rotted nest sites.

There are many species of fungi that cause heart rots in southeastern hardwoods. *Spongipellis pachyodon* is considered an infrequent species in our geographical area, yet was found in our isolates as the primary rot in more than 80% of the hardwood trees we examined. This imbalanced association suggests several possible explanations. The woodpeckers may be preferentially selecting trees infected by *Spongipellis pachyodon.* Another explanation is perhaps more feasible. Since *Spongipellis pachyodon* is a top rot that fruits infrequently, its detection by forest pathologists would be very difficult. Other species of heart rots that fruit frequently and infect portions of the trees closer to the ground would be easier to detect and thus might seem to occur at a greater frequency than *Spongipellis pachyodon.*

It is possible that the presence of a particular fungal flora in woodpecker nest trees may impart a hitherto undetermined benefit to the well being of the developing fledgling. Investigations are needed to determine if respiration of the fungal flora produces enough heat to decrease the incubation and brooding requirements of the adult woodpeckers.

SUMMARY

Four species of woodpeckers used trees with heartwood softened by fungal heart rots prior to cavity excavation. The woodpeckers were apparently able to detect the presence of the heart rots and select suitably infected trees for nest excavations, thus reducing the energy expenditure necessary to excavate nest cavities. *Spongipellis pachyodon* was the primary rot in most of the trees we examined. Nest trees were usually infected secondarily by other Basidiomycetes, imperfect fungi, and bacteria.

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LITERATURE CITED

BAUMGARTNER, L. L. 1939. Fox squirrel dens. J. Mammal. 20:456–465.

BULLER, A. H. R. 1930. The biological significance of conjugate nuclei in *Coprinus lagopus* and other hymenomycetes. Nature 126:686–689.

———. 1931. Researches on Fungi. Vol. 5. Hafner Publ. Co., New York.

CONNER, R. N., R. G. HOOPER, H. S. CRAWFORD, AND H. S. MOSBY. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39:144–150.

DAVIDSON, R. W. AND W. A. CAMPBELL. 1942. Fungi causing decay of living oaks in the eastern United States and their cultural identification. U.S. Dep. Agric. Tech. Bull. 785.

DENNIS, J. V. 1969. The Yellow-shafter Flicker (*Colaptes auratus*) on Nantucket Island, Massachusetts. Bird-Banding 40:290–308.

JACKSON, J. A. 1976. A comparison of some aspects of the breeding biology of Red-headed and Red-bellied woodpeckers in Kansas. Condor 78:67–76.

———. Red-cockaded Woodpeckers and red heart disease of pines. Auk. In press.

KILHAM, L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers. I. Preference for nesting in *Fomes*-infected aspens and nest hole interrelations with flying squirrels, raccoons, and other animals. Wilson Bull. 83:159–171.

LIGON, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. Auk 87:255–278.

MILLER, O. K., JR. AND D. F. FARR. 1975. An Index of the common fungi of North America (synonymy and common names) Bibliotheca Mycologica 44, J. Cramer, W. Germany.

NOBLES, M. K. 1965. Identification of cultures of wood-inhabiting Hymenomycetes. Can. J. Bot. 43:1097–1139.

QUINTANILHA, A. 1937. Contribution a l'etude genetique du phenomene de Buller. C. R. Acad. Sci., Paris 205:745–747.

STEIRLY, C. C. 1957. Nesting ecology of the Red-cockaded Woodpecker in Virginia. Atl. Nat. 12:280–292.

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THE BREEDING DISTRIBUTION OF NORTH AMERICAN MIGRANT BIRDS: A CRITIQUE OF MacARTHUR (1959)

Mary F. Willson

MacArthur (1959) claimed that the eastern deciduous forest has more neotropical migrants than northern coniferous forests or grasslands, and concluded that "the density of breeding individuals of species migrating to the Neotropics seems to correlate with the contrast between winter and summer food supply in the given habitat." A reanalysis of data covering part of the area dealt with by MacArthur suggests that the basis for his conclusion deserves reassessment. We certainly expect to find some association of migratoriness with temporal stability of the food supply (Fretwell 1972), but the nature of the "correlation" reported by MacArthur (1959) can be reinterpreted.

For simplicity, the reanalysis deals only with the eastern two-thirds of North America, and only with 3 major habitat types: grassland, northeastern deciduous forest, and northern coniferous forest. Each of these categories clearly encompasses a variety of specific habitats, but in order to compare my results with MacArthur's, and attempt to discern large-scale contrasts, major habitat categories are useful. Summaries of the census data (excluding nocturnal species) are presented in Table 1. The locations of wintering grounds were determined mainly from the Peterson field guides (1947, 1961, 1973), and the range maps of Robbins et al. (1966). Two-tailed Mann-Whitney U tests ($p \leqslant .05$) were used to test for statistically significant differences between habitat types.

MacArthur (1959) depended greatly on breeding bird censuses found in *Audubon Field Notes (American Birds)*, and I have done the same in order to make possible comparisons with MacArthur's paper. These censuses are notoriously open to criticism, perhaps especially regarding estimates of population sizes, but nevertheless are adequate for criticism of MacArthur's interpretation and statement of a reassessment that suggests alternative hypotheses. All the censuses used by MacArthur (1959) for the 3 habitat categories analyzed here were included in the present study (except those in Audubon Field Notes, Vols. 1 and 2, which were not readily available) and the sample sizes were increased considerably. In choosing censuses to be included, an effort was made to use those from relatively homogeneous study plots.

The discussion is necessarily speculative. The purpose of this note is to *restate* an old hypothesis about seasonal variation of food resources in different habitats; testing of the hypothesis must come later.

TABLE 1

SUMMARY OF PROPORTION OF MIGRANTS IN BREEDING BIRD CENSUSES FOR 3 HABITAT TYPES

		% total migrants		% neotropical migrants	
Location	Reference	Spp.	Individ.	Spp.	Individ.
GRASSLAND					
Manitoba	Jones 1972	100	100	18	33
Minnesota	Hibbard 1972	88	93	38	53
N. Dakota	Johnson 1973	82	99	44	32
N. Dakota	Johnson 1972	100	100	38	31
Wisconsin	Bailey & Ellis 1968	89	90	33	16
S. Dakota	Springer 1965	100	100	56	59
Wyoming	Mickey 1939	67	88	0	0
Iowa	Kendeigh 1941	75	73	25	31
Colorado	Porter 1973	75	43	0	0
Kansas	Zimmerman 1965	55	82	22	41
Kansas	Walker 1965	50	49	0	0
Oklahoma	Howell 1941	60	60	40	50
Texas	Allen & Sime 1939	50	57	0	0
	x̄	76	73	24	27
NORTHEASTERN DECIDUOUS FOREST					
New York	Kendeigh 1946	67	91	67	91
Connecticut	Palmer 1973	68	74	57	64
Michigan	Irish et al. 1973	59	61	38	42
Ohio	Williams 1947	59	83	53	81
Indiana	Webster & Adams 1971	47	64	45	62
Indiana	Mannon & Webster 1973	71	68	56	58
Indiana	Adams & Webster 1971a	52	63	46	59
Indiana	Adams & Webster 1971b	59	76	55	72
W. Virginia	Katholi 1973	63	85	56	79
West Virginia	DeGarmo 1948	86	98	71	91
Maryland	Criswell et al. 1973	56	51	47	50
Maryland	Stewart & Robbins 1947	57	80	50	79
	x̄	62	75	53	69
NORTHERN CONIFEROUS FOREST					
Northwest Territory	Stewart 1955	53	85	35	58
Northwest Territory	Stewart 1955	63	84	36	44
Saskatchewan	Erskine 1973	79	97	47	76
Manitoba	Erskine 1972a	82	97	44	55
Manitoba	Erskine 1972b	90	99	60	52
New Brunswick	Tull 1973	100	100	76	79

TABLE 1. (*Continued*)

		% total migrants		% neotropical migrants	
Location	Reference	Spp.	Individ.	Spp.	Individ.
Maine	Cadbury & Cruickshank 1941	87	94	63	65
Maine	Stewart & Aldrich 1952	76	93	53	79
Quebec	Erskine 1970	100	100	64	48
Ontario	Kendeigh 1947	68	90	46	81
Ontario	Nakashima 1973	80	90	53	42
West Virginia	Bush et al. 1973	77	94	48	72
	x̄	80	94	52	62

Deciduous forests have, on the average, the same percentage (53% of spp., 69% of individuals) of neotropical migrants as coniferous forests (52%, 62% respectively), and the percentage in grassland (24%, 27%) is significantly lower than either of the forests. In contrast, MacArthur stated that the proportion of neotropical migrants was greater in deciduous forest, less in coniferous forest, and least in grassland, but he apparently did no statistical tests on his data. MacArthur called a species a "neotropical migrant" if most of the area of its winter range, as determined from the 1957 A.O.U. checklist, fell within the tropical zone. The major reason for the difference between MacArthur's results and mine is that I included any species that commonly winters in the tropics, whether or not most of its winter range was tropical, for lack of any obvious biological reason to exclude them. Had I used MacArthur's criteria, the results resemble his more closely, but with no difference of statistical significance between forest types. The relative paucity of neotropical migrants from North American grasslands is perhaps not surprising in view of the rather small area occupied by neotropical grasslands. Coniferous forest breeders obviously change vegetation types on the wintering grounds, but this may be a relatively smaller behavioral change than for a grassland breeding bird to shift to a forested winter habitat.

However, there is no apparent reason why seasonal change in food supply should be reflected by the proportion of the avifauna that includes *neotropical* migrants only. *Any* species that commonly leaves its breeding habitat in the non-breeding season probably does so because of seasonal habitat changes, or conversely, seasonality in habitat characteristics is evidenced by any species moving to its breeding grounds, no matter where it comes from. Many North American breeding birds leave their breeding habitat to winter in the southern U.S. or nontropical Mexico. Considering *all* migrants (and sometime migrants such as the Red-headed Woodpecker, *Melanerpes erythrocephalus*) in the major habitat types, the percent of species in the avifauna that are migrants is rather similar in grasslands (76%) and in coniferous forest (80%), and these percentages are marginally ($.10 > p > .05$) higher than in deciduous forest (62%). The average percent of migrant individuals is about the same in grasslands (73%) and in deciduous forests (75%), and is significantly less in those habitat types than in coniferous forest (94%). Thus, relatively more species in deciduous forest are year-round residents than in the other 2 habitats, and more individuals may be permanent in deciduous forest (and grasslands) than in coniferous forest.

Despite the conspicuous seasonal change in foliage in deciduous forests, any effect on the migratory avifauna is apparently less than in coniferous forests with relatively small seasonal changes in foliage. Seasonal "blooms" of insects in these forests may be more a function of climate (e.g., length of summer) than of foliage type. Very short summers may produce large insect blooms and provide resources for many migrants. Latitudinal differences within a habitat type in the proportion of migrants might be used to test this suggestion. The grassland data presented here suggest such a trend (increasing migratoriness with increasing latitude), but the forest data do not. A larger sample is required to explore this possibility adequately.

Resident populations exploit chiefly bark-dwelling arthropods and fruits or seeds as winter food resources (c.f. Morse 1971). It is possible that the variety of fruits and seeds available in deciduous forest throughout the winter is greater than in coniferous forest. Furthermore, the form of deciduous trees may provide a greater variety of foraging sites than does the form of coniferous trees, even in winter. Woodpeckers partition deciduous tree bark surfaces in part by branch size (Willson 1970 and others). They are relatively rare residents of most kinds of coniferous forest (in the censuses used here, about 1% of the avifauna, compared with almost 10% for deciduous forests), and account for part of the difference between the forest types. Other bark gleaners such as chickadees and nuthatches also contribute to the difference. In sum, the contrast between winter and summer food supply in deciduous forests (total amount and/or accessibility) actually may be *less* than in the other habitats, which is a suggestion directly opposite to MacArthur's. In addition, deciduous forests may provide more roosting holes as shelter from the most severe weather. And winter weather may be slightly milder in the region of deciduous forest: longer times without snowcover on the ground than in coniferous forest and less wind than in grassland, for instance. As a result, demands on the food resources might be reduced.

The situation can also be viewed in terms of just the neotropical migrants to these 3 major habitats. The neotropical migrants in the census data were categorized as much as possible by their primary nesting habitat (a few species that primarily use open shrubby habitats but occurred in the censuses were not included). Fifty-seven percent (34 spp.) of the neotropical migrants breed primarily in deciduous forest, 37% (22 spp.) nest most frequently in coniferous forest, and the remainder in grassland. More species migrating from the neotropics to the nearctic have exploited the deciduous forest than the coniferous forest or grassland. The advantages of the deciduous forest might include a somewhat shorter distance from the wintering grounds, possibly a greater similarity of leaf shape and spatial distribution to wintering habitat, a greater diversity of nesting sites, and perhaps a wider variety of small, soft fruits as alternate dietary items.

Nevertheless, a significant number of neotropical migrants are adapted to exploit primarily the coniferous forest. Over half of these are warblers (Parulidae, 15 spp.). In comparison, only about ⅓ (11 spp.) of the neotropical migrant, deciduous-forest nesters are parulids. Purely historical explanations for the predominance of parulids as coniferous forest migrants are insufficient; some ecological basis for their prevalence must be involved. Perhaps their small size and slender bills facilitate foraging among the narrow leaves and flexible branch tips of most northern conifers. Some may use deciduous enclaves within the coniferous forest, but more precise census reporting would be needed to ascertain this.

SUMMARY

A partial reanalysis of MacArthur (1959) has shown that (1) North American neotropical migrants are less prevalent in grasslands than in forests (as MacArthur also showed) but that there is no significant difference in the proportion of neotropical migrants in deciduous and coniferous forest (unlike MacArthur's results); (2) coniferous forests have relatively fewer year-round resident individuals than grasslands or deciduous forest, and grasslands and coniferous forests have slightly fewer resident species than deciduous forests; (3) most neotropical migrant birds breed primarily in deciduous forest and most of those that breed in coniferous forest are parulids.

The results suggest that seasonal changes in available food resources may be effectively less in deciduous forest than in coniferous forest (in contrast to MacArthur's conclusion). Possible ecological bases for the habitat differences are suggested, but remain to be demonstrated.

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LITERATURE CITED

Adams, D. L. and J. D. Webster. 1971a. Census 23. Am. Birds 25:978–979.

———. 1971b. Census 26. Am. Birds 26:982–983.

Bailey, S. F. and T. Ellis. 1968. Census 56. Audubon Field Notes 22:706.

Bush, K. et al. 1973. Census 50. Am. Birds 27:981.

Criswell, J. H. et al. 1973. Census 13. Am. Birds 27:964–965.
Erskine, A. J. 1970. Census 20. Audubon Field Notes 24:753–754.
———. 1972a. Census 78. Am. Birds 26:990.
———. 1972b. Census 79. Am. Birds 26:990–991.
———. 1973. Census 107. Am. Birds 27:1009–1010.
Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, N. J.
Hibbard, E. A. 1972. Census 98. Am. Birds 26:1004–1105.
Irish, J. et al. 1973. Census 24. Am. Birds 27:969.
Johnson, D. H. 1972. Census 49. Am. Birds 26:973.
———. 1973. Census 66. Am. Birds 27:989.
Jones, R. E. 1972. Census 82. Am. Birds 26:993–994.
Katholi, C. B. 1973. Census 8. Am. Birds 27:962.
MacArthur, R. H. 1959. On the breeding distribution pattern of North American migrant birds. Auk 76:318–325.
Mannon, B. and J. D. Webster. 1973. Census 27. Am. Birds 27:970.
Morse, D. H. 1971. The insectivorous bird as an adaptive strategy. Annu. Rev. Ecol. Syst. 2:177–200.
Palmer, G. E. 1973. Census 3. Am. Birds 27:959–960.
Peterson, R. T. 1947. A Field Guide to Birds. Houghton Mifflin, Boston.
———. 1961. A Field Guide to Western Birds. Houghton Mifflin, Boston.
——— and E. L. Chalif. 1973. A Field Guide to Mexican Birds. Houghton Mifflin, Boston.
Porter, D. K. 1973. Census 74. Am. Birds 27:991.
Robbins, C. S., B. Bruun, H. S. Zim. 1966. A Guide to Field Identification: Birds of North America. Golden Press, N. Y.
Springer, P. F. 1965. Census 51. Audubon Field Notes 19:618–619.
Tull, C. E. 1973. Census 106. Am. Birds 27:1008–1009.
Walker, B. 1965. Census 50. Audubon Field Notes 19:618.
Webster, N. D. and D. L. Adams. 1971. Census 25. Am. Birds 25:981–982.
Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169–174.
Zimmerman, J. C. 1965. Census 43. Audubon Field Notes 19:614.

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VARIATION IN CADENCE OF FIELD SPARROW SONGS

DONALD B. HECKENLIVELY

Over 10 years ago, Reynard (1963) showed that different species of song birds sing at different rates. Since that time singing rates have received little attention, although they have occasionally been used as one measure of the response of birds to playback of recorded songs (e.g., Goldman 1973). The purpose of this study was to examine intra-population variation in singing rates of Field Sparrows (*Spizella pusilla*) in a variety of contexts, taking an initial hypothesis that rate of singing reflects male responsiveness to exogenous conditions. Consideration of population variation in song morphology has also been included in the report, since previous descriptions (Saunders 1922, Brand 1938) antedated the development of sound spectrography.

METHODS

Breeding populations of Field Sparrows were studied in the summers of 1967–1971, inclusive, at the University of Michigan, Matthaei Botanical Gardens, Dixboro, Washtenaw Co., Michigan. Additional observations were made in 1971 at Island Lake State Recreation Area, Livingston Co., Michigan. Field work started in late May in 1967, in mid-June in 1968 and 1969, and in early April in 1970 and 1971.

Territorial limits of the males were estimated from the areas encompassed by their singing sites. Males were identified by their songs, which were generally unique within populations (Saunders 1922, pers. observ.). Recordings were made in the field with a Uher 4000 Report-L tape recorder at 19.05 cm/sec. A 61 cm aluminum parabola was used in the first several years; in 1971 a 30.5 cm parabola with pistol grip, fashioned from a photoflood reflector, was used interchangably with the larger reflector. While obtaining recordings, I often induced the birds to continue singing by playback of their own songs; this was done using the Uher speaker.

Singing rate was measured as the cadence, i.e., the time interval between successive songs in a bout. The average cadence was then calculated for each bout, except for the data in Table 5, which involved comparisons of rates within bouts. It should be noted that this criterion of singing rate does not include the number of bouts of singing in which an individual bird might engage, which could also be a key factor in the overall daily rate of singing. Cadences were measured both directly in the field and from tape recordings. Timing was done with the second hand of a watch, to an estimated accuracy of ± 0.5 sec. Cadences were measured simultaneously from adjacent birds whenever possible.

About 500 songs were recorded from the 8 birds on the study area in 1967, averaging 62 songs (range 6–263) from each. About 110 songs from the 1967 population were chosen for sound spectrography, forming the basis for most of the analysis of population characteristics. In subsequent years an additional 400 songs were recorded, primarily for identification of individuals. Sound spectrograms were done on a Kay Elemetric Corp. Vibralyzer, using a wide-band filter setting; a Sony TC-106A recorder was used for laboratory playback.

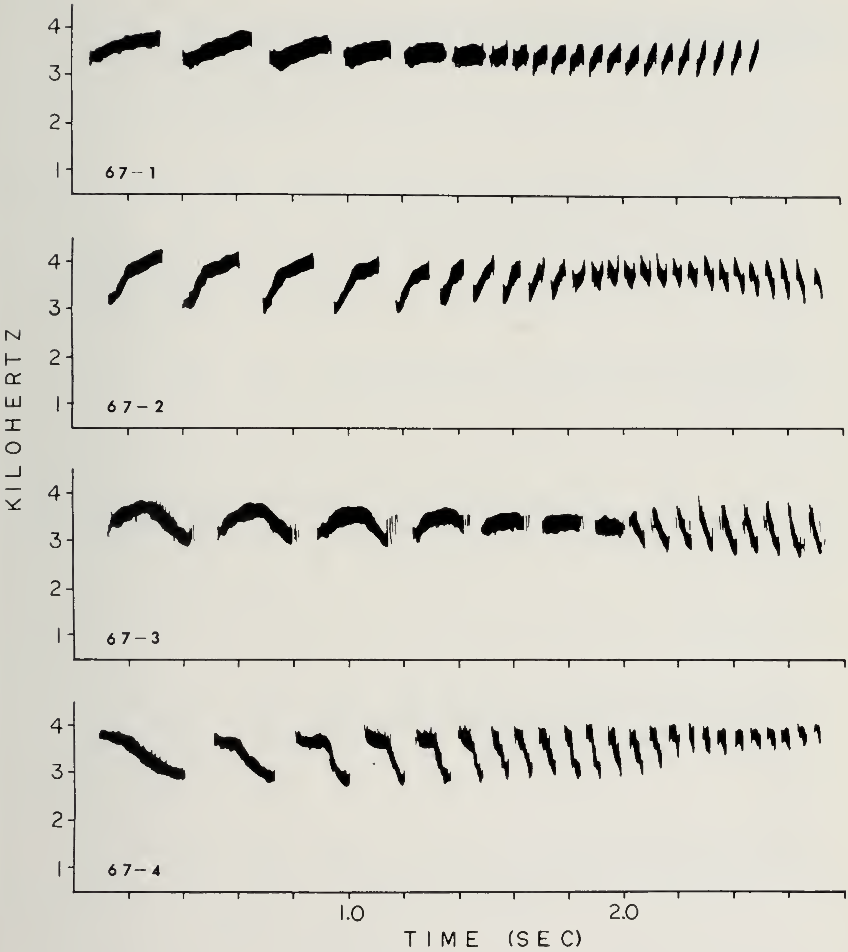

FIG. 1. Typical songs from four individuals in the 1967 population of Field Sparrows at Matthaei Botanical Gardens.

Unless otherwise stated, parameter estimates are given as the mean ± 1 standard deviation. Statistical notation generally follows Simpson, et al. (1960).

SONG MORPHOLOGY

Each male in the 1967 population had 1 distinctive song-type, unique within the population. Typical songs of 6 individuals are shown in Fig. 1 and Fig. 2. These differences were readily distinguishable by ear and formed the basis by which I identified individuals. Characteristically, Field Sparrow

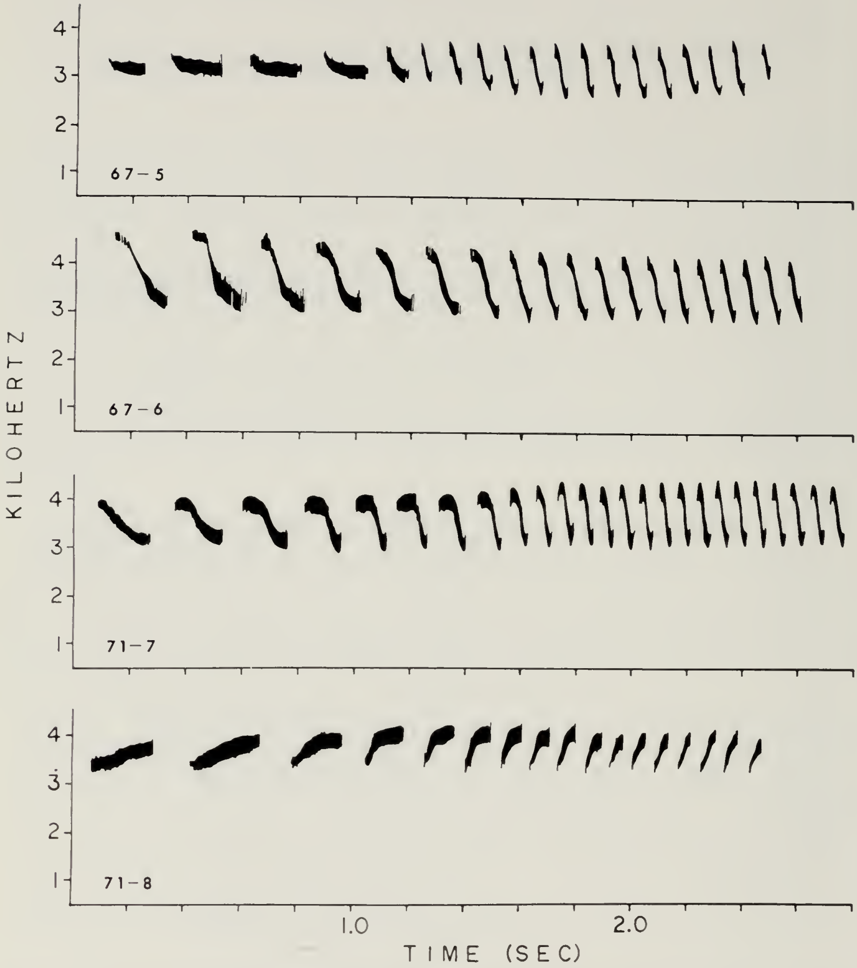

FIG. 2. Typical songs from four individuals in the 1967 population of Field Sparrows at Matthaei Botanical Gardens (67-5 and 67-6) and the 1971 population at Island Lake State Recreation Area (71-7 and 71-8).

song starts with several notes of relatively long duration, with subsequent notes of progressively shorter duration to form a final trill, so that the overall effect is one of acceleration of the notes in the song. The initial notes may be of rising pitch (Fig. 1, 67-1, 67-2), dropping pitch (Fig. 1, 67-4), straight pitch (Fig. 2, 67-5), or a rising then falling pitch (Fig. 1, 67-3). Similarly, the more rapid notes in the final trill may be either of rising or falling pitch. In some song-types notes in the final trill continued the rising or falling pat-

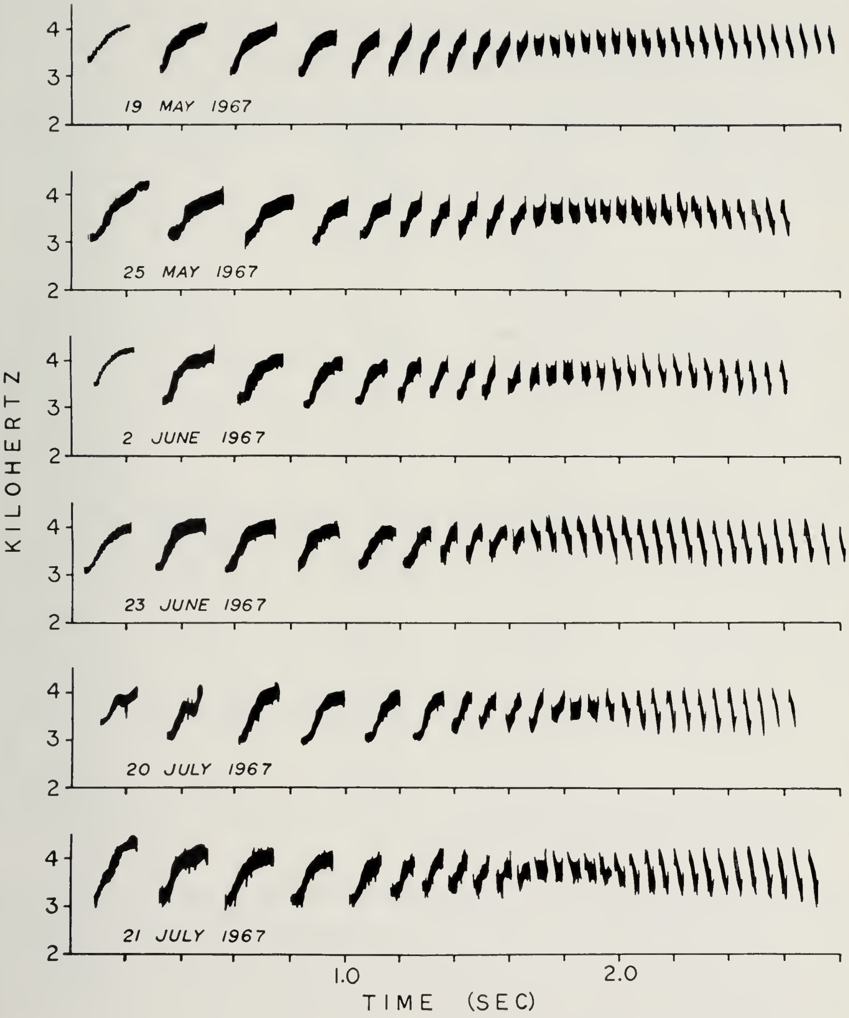

FIG. 3. Songs of individual 67-2, over the 1967 season.

tern of the earlier part of the song (e.g., Fig. 2, 67-6); in others the notes in the final trill took a form distinct from the opening notes (e.g., Fig. 1, 67-3).

Variation within individuals primarily took the form of adding or omitting notes, resulting in variation in the overall duration of the song as well. Notes were omitted both from the early portion of the song and from the final trill. Nonetheless, the basic, overall pattern of any one individual's song-type remained essentially the same throughout the season. Fig. 3 shows samples

TABLE 1

CHARACTERISTICS OF THE SONGS OF 8 FIELD SPARROWS

Birds	Sample Size (*N*)	No. of Notes Mean ± SD	Song Duration (sec) Mean ± SD	Max. Frequency (kHz) Mean ± SD	Min. Frequency (kHz) Mean ± SD
67-1	4	22.25 ± 1.89	2.55 ± 0.16	4.06 ± 0.06	3.01 ± 0.08
67-2	4	30.25 ± 3.10	2.74 ± 0.12	4.25 ± 0.07	2.96 ± 0.08
67-3	2	19.00 ± 4.24	2.79 ± 0.28	3.98 ± 0.04	2.72 ± 0.04
67-4	4	23.00 ± 0.82	2.75 ± 0.12	4.08 ± 0.10	2.60 ± 0.08
67-5	3	21.00 ± 6.00	2.46 ± 0.52	4.05 ± 0.23	2.53 ± 0.06
67-6	2	18.00 ± 1.41	2.49 ± 0.04	4.72 ± 0.04	2.75 ± 0.07
71-7[1]	3	26.00 ± 1.00	2.86 ± 0.17	4.52 ± 0.08	2.92 ± 0.03
71-8[1]	3	17.00 ± 0.0	2.48 ± 0.08	4.25 ± 0.0	3.13 ± 0.06
Overall	25	22.72 ± 4.92	2.65 ± 0.21	4.22 ± 0.24	2.84 ± 0.21

[1] From the Island Lake population, 1971.

taken from individual 67-2 over the season. Out of a sample of 263 songs from this individual, 44 of which were spectrographed, the slight inflection in the opening notes of the song illustrated from 20 July 1967 was the only observed departure from the basic pattern of rising initial notes that graded into a final trill of dropping pitch.

Since individual variation was slight, a sample of songs, averaging 3 per bird, was used for measurements to summarize population characteristics in song morphology (Table 1). The average song duration in the population was 2.65 sec, with an average of 22.72 notes per song. Maximum frequency was 4.22 kHz and minimum frequency was 2.84 kHz.

Acceleration.—One of the most obvious characteristics of Field Sparrow song is the progressive shortening, or "acceleration," of the notes in the song. To examine this aspect of the song, note and interval durations in the songs of the individuals in Table 1 were plotted as a function of successive order in

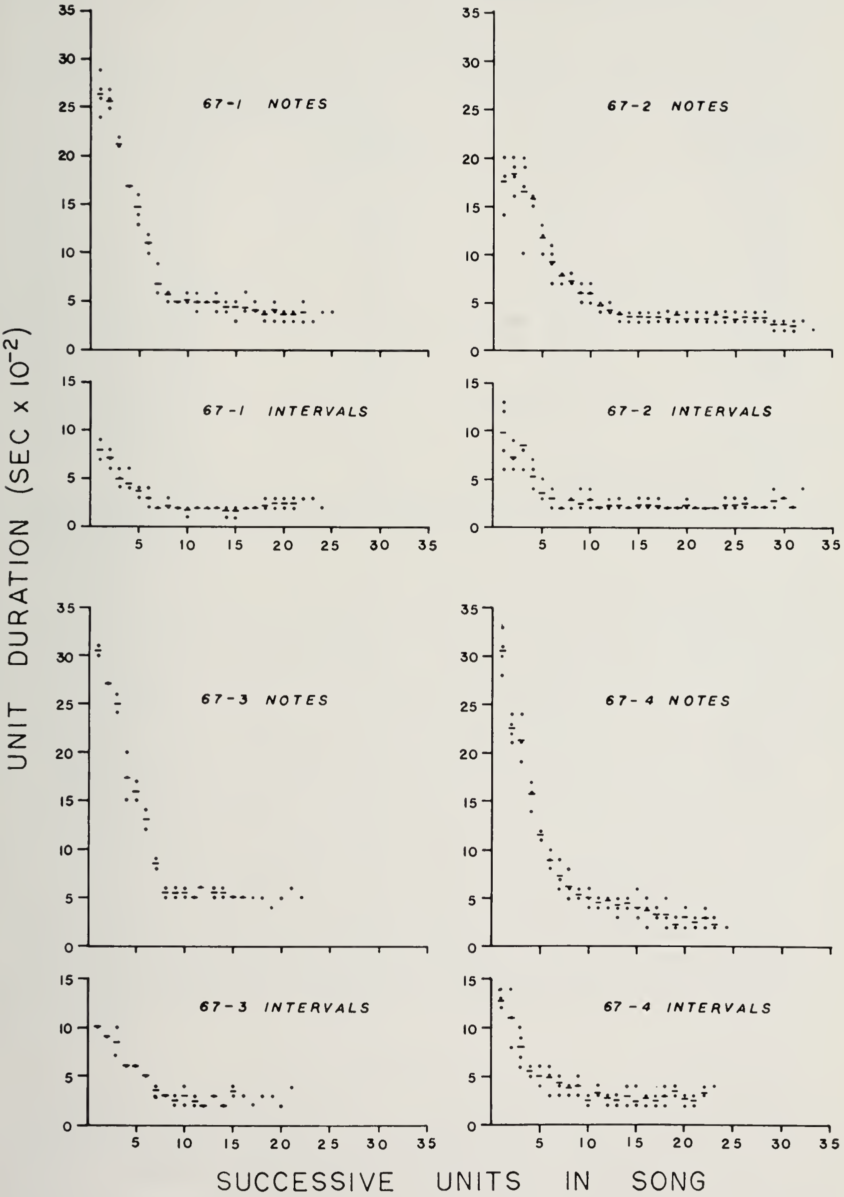

Fig. 4. Duration of song units as a function of order of occurrence in the song. Dots represent individual data points; horizontal lines show the mean for each unit. Designation of songs the same as in Fig. 1.

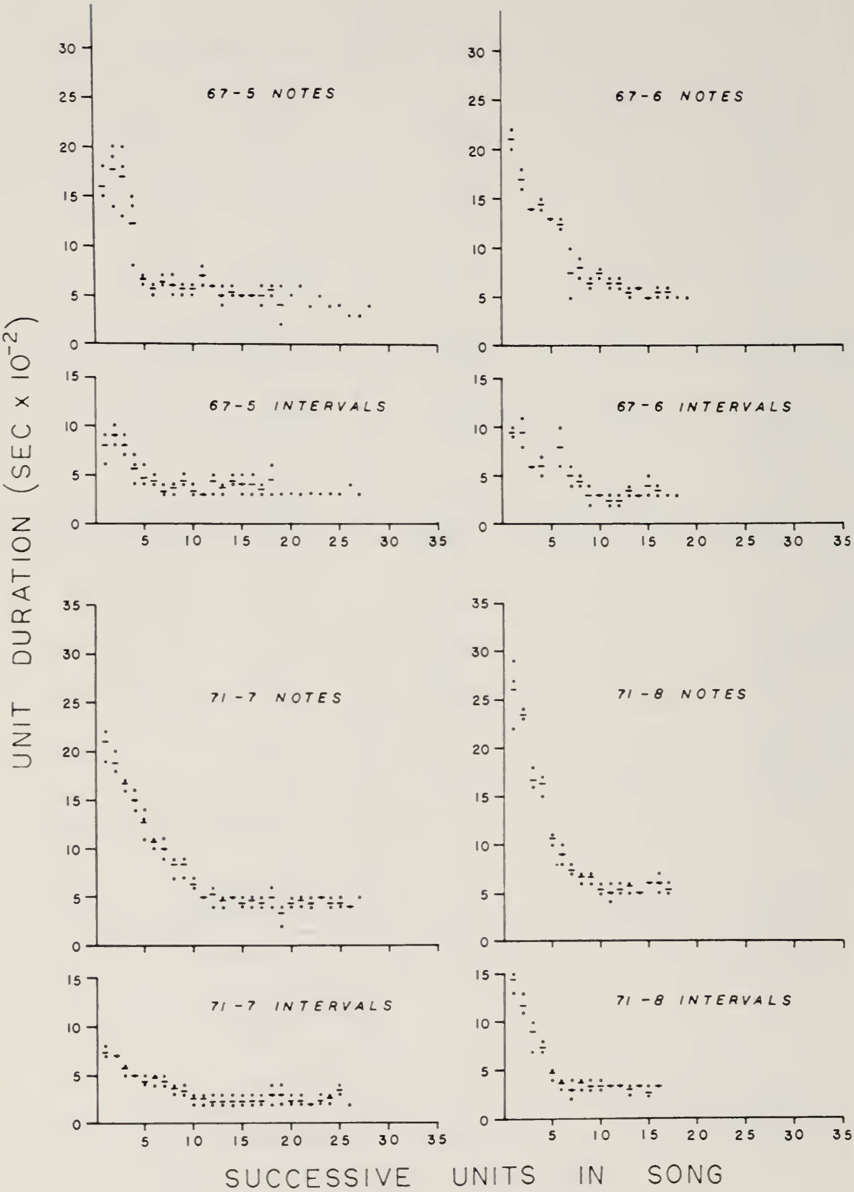

Fig. 5. Duration of song units as a function of order of occurrence in the song. Symbols the same as in Fig. 4 and designation of songs the same as in Fig. 2.

TABLE 2

ACCELERATION PATTERN IN THE NOTES AND INTERVALS OF FIELD SPARROW SONGS[1]

Birds	Initial Shortening Rate		Transition Point (%)	Final Shortening Rate of Notes[2] (sec/note)
	Notes[2] (sec/note)	Intervals[2] (sec/int.)		
67-1	–2.69	–0.83	40.9	–0.04
67-2	–1.40	–0.60	46.7	–0.13
67-3	–3.71	–0.94	42.1	–0.04
67-4	–3.88	–1.95	39.1	–0.21
67-5	–3.00	–1.13	23.8	–0.08
67-6	–1.81	–0.72	50.0	–0.15
71-7	–1.60	–0.52	42.3	–0.05
71-8	–3.40	–2.13	52.9	–0.15
Overall: ($N = 8$)				
$\bar{x}$	–2.69	–1.10	42.2	–0.11
s	0.98	0.61	8.8	0.06

[1] Rates estimated graphically from Figs. 4 and 5.
[2] Values x 10^{-2}.

the song (Fig. 4 and 5). Several curvilinear transformations were attempted to fit regression lines to the observed patterns. It was found that the simplest, and perhaps most straight-forward, fit was obtained by plotting separate linear regression lines by eye through early and late portions of the curves.

All of the songs examined showed the same pattern of acceleration (Table 2). There was a rapid initial rate of shortening of the notes, averaging –2.69 ± 0.98 × 10^{-2} sec/note, to an inflection point midway in the song. At the inflection the rate of shortening decreased to an average of –0.11 ± 0.06 × 10^{-2} sec/note. The average inflection point for the transition in rate of shortening came after 42.2 ± 8.8% of the song was completed. The intervals between notes showed the same trends, with an initial shortening rate of –1.10 ± 0.61 × 10^{-2} sec/interval. Interval duration became virtually constant after the inflection point, which tended to be slightly earlier in the intervals than in the notes.

CADENCES

Individual variation.—Table 3 summarizes the observed variations in cadence in the 1967 population at the Botanical Gardens. Analysis of variance indicated that there were significant differences in cadence among individuals in the population ($F = 6.32$, $P < .05$). The Student-Newman-Keuls test of Least Significant Range (Snedecor 1956) was used to test differences between individuals. Differences ($P < .05$) were found between the cadences of individuals 67-4 and 67-6, 67-3 and 67-6, and 67-5 and all others.

TABLE 3

INDIVIDUAL VARIATION IN CADENCES OF FIELD SPARROW SONGS

Bird	Sample Size[1] (*N*)	Mean (sec)	SD
67-1	5	12.47	2.41
67-2	16	11.86	1.87
67-3	10	13.80	1.39
67-4	7	13.42	1.55
67-5	3	17.63	7.62
67-6	9	9.99	0.88

[1] Number of bouts per individual.

Seasonal changes and circumstances.—Cadences from 1967 through 1970 were categorized in several ways to attempt to isolate the sources of the observed variation in the population. One possible source was the circumstance in which the bird was singing, i.e., if he was singing alone or if a neighboring bird was singing at the same time. Playback of recordings of an individual's own song was included as a third possible circumstance affecting singing rate, since differential response of an individual to his own song is one possible criterion for demonstrating individual recognition by song (e.g., Falls 1963, Hinde 1958).

Another source of variation might be the time in the breeding season. In fact, it would be reasonable to expect an increased singing rate assuming that most of the singers were unmated individuals and that one of the functions of singing is to advertise mating availability.

A 2-way comparison of seasonality and singing circumstances (Table 4) showed significant trends in cadences ($F = 3.39$, $P < .01$). Cadences were generally faster later in the season than earlier ($P < .01$). Comparing singing circumstances in this regard, cadences were significantly faster late in the season only when individuals were singing at the same time as a neighbor ($P < .02$); similar trends were seen when an individual was singing alone or after playback, but neither was significantly different between early and late in the season ($P > .20$ and $P > .60$, respectively). Differences were negligible between cadences of individuals singing alone and those that were singing at the same time as a neighbor ($t = 0.58$, $P > .50$). Birds singing in response to tape playback sang significantly faster than those singing alone ($t = 2.89$, $P < .01$) or at the same time as a neighbor ($t = 2.42$, $P < .05$).

Response to neighbors.—During field work, neighboring birds frequently were observed to sing at the same time. Often, one bird would start singing and nearby males would commence to sing shortly thereafter, so that onset of singing appeared to move as a sporadic wave across the study area. This

TABLE 4
CADENCES AS A FUNCTION OF TIME IN THE BREEDING SEASON AND CIRCUMSTANCES OF SINGING

Circumstances of Singing	Early in Season (April–May) $\bar{x} \pm s$ sec (N)[1]	Late in Season (June–July) $\bar{x} \pm s$ sec (N)
Singing alone	15.51 ± 2.51 (15)	13.80 ± 4.20 (13)
Singing when neighbors are	15.60 ± 3.70 (17)	13.86 ± 2.44 (16)
Singing after tape playback	12.29 ± 2.95 (5)	11.79 ± 1.78 (10)

[1] N = Number of bouts in each category.

phenomenon suggested another possible source of cadence variation, that neighboring birds were singing in response to each other. Without definite knowledge of response latencies or memory capacities of Field Sparrows, it would be most parsimonious to expect response to neighbors to be on a song-for-song basis, rather than on a basis of bout-for-bout. If males were responding to neighbors in this way, one observable effect should be that at any given encounter, neighbors should have more similar cadences than non-neighbors. Data were not collected with this question in mind, but it was possible to approach the problem by comparing cadences of birds singing alone and at the same time as neighbors (Table 5). Responsiveness to a neighbor's singing appeared to be sensitive to the distance between individuals. Birds 67-5 and 67-6 had adjacent territories with a common boundary, and 67-5 showed a strong shift in cadences, from 21.9 sec when singing alone to 9.0 sec when singing at the same time as 67-6. There were also subtler shifts in the cadences of the adjacent individuals 67-1 and 67-3, so that cadences were more similar when singing at the same time. Individual 67-2 was also a neighbor of 67-1, but there was an area of about 100 m between their territories that was unoccupied by either bird. The changes in cadence did not appear to indicate that these neighboring, but non-adjacent, birds were singing in response to each other.

Another test of whether neighboring birds were answering each other was to assume that they were singing simultaneously but independently. On that assumption, one would expect that a song of one bird could occur anywhere in the time interval between successive songs of a neighbor who was singing at the same time. This model was tested by examining 11 instances from

TABLE 5

CADENCES WHEN SINGING ALONE AND AT THE SAME TIME AS A NEIGHBOR

	Bird #1			Bird #2			Differences
	Mean[1]	SD	N[2]	Mean	SD	N	(Mean #1–Mean #2)
Bird #1 = 67-5 Bird #2 = 67-6							
Alone	21.9	13.1	18	9.8	1.7	42	12.11
Together	9.0	2.9	8	9.4	4.0	8	0.38
Bird #1 = 67-1 Bird #2 = 67-3							
Alone	13.5	2.3	30	15.3	2.3	10	1.83
Together	14.5	5.0	13	13.2	3.7	14	1.33
Bird #1 = 67-1 Bird #2 = 67-2							
Alone	13.5	2.3	30	11.1	1.6	36	2.39
Together	15.6	4.9	7	11.7	4.4	7	3.89

[1] Time in seconds.
[2] N = Number of cadences in bout.

1967 and 1970 in which cadences were recorded for an individual and his singing neighbor for at least 6 songs each; most commonly 7 to 9 cadences were measured for each. In each encounter, every time interval between successive songs of an individual was divided into 3 equal intervals, and the "answering" song of the neighbor was added as a count in one of the 3 intervals. This procedure was followed for every cadence interval in the song bout and for both birds in each encounter. In all instances, one bird seemed to be the initiator of the exchange and was observed at least to be the first singer in the encounter; the other seemed to be responding, or "following," so that separate tallies of songs were kept for initiating and following birds. This represents some *a priori* selection of data, but it does not seem directly related to the underlying assumption of the test, that a neighboring bird's songs should occur with equal probability in any of the 3 equal time intervals between songs if the birds are singing independently.

The tally over all such encounters resulted in strongly disproportionate distributions among the 3 time intervals. Among followers' songs, 39 were in the first, 30 in the second, and 9 in the third interval between initiators' songs ($\chi^2 = 18.24$, $P < .001$). For initiators' songs, 10 were in the first, 33 in the second, and 37 in the third interval between followers' songs ($\chi^2 = 16.96$, $P < .001$). Thus, the hypothesis for the model, that neighboring birds were singing independently, was rejected.

TABLE 6

CADENCE AS A FUNCTION OF TIME OF DAY

Time	Sample Size (N)[1]	Mean (sec)	SD	V[2]
Before 08:00	10	14.42	1.14	8.0
08:00–09:00	19	14.69	2.84	19.3
09:00–10:00	22	12.38	3.04	24.6
10:00–11:00	12	14.32	3.88	27.1

[1] N = Number of bouts.
[2] V = Coefficient of variation, (SD/Mean) × 100.

Time of day.—A comparison of cadences according to time of day that they were observed (Table 6) showed no particular trends in average cadence, although the variability in the samples increased as the day progressed. Observations before 08:00 were significantly less variable ($F = 6.13$, $P < .01$) than observations later in the day.

Matedness.—Walkinshaw (1968) stated that mated Field Sparrows markedly reduce their singing. From early season records where matedness was specifically noted, I found unmated males to have a cadence of 16.09 ± 2.33 sec ($N = 10$) and mated birds a cadence of 16.17 ± 4.87 sec ($N = 7$). The rate of singing as measured by cadences, then, was about the same ($t = 0.04$, $P > .50$). However, the cadences of mated birds were much more variable ($F = 4.39$, $P < .05$), indicating, perhaps, less attentiveness to singing during a bout by mated males.

DISCUSSION

Information about the manner in which messages are coded in communication signals has been obtained from experimental playback studies with altered song. Two studies have been outstanding in this regard, Emlen's (1972) work with Indigo Buntings (*Passerina cyanea*) and Falls's (1969) studies of White-throated Sparrows (*Zonotrichia albicollis*). They have generally confirmed earlier hypotheses of Marler (1959, 1960) that individual and species identification messages are coded in different parameters of the song.

Descriptive summaries of population characteristics of song, such as presented here, are a necessary prerequisite to experimental studies of message encoding. As such, they represent a first approximation to species specific characters of the song, providing an initial estimate of the limits of variation still recognized by the members of the population as a species specific signal. For instance, on the basis of the summary characteristics (Table 1), normal

Field Sparrow song is given between 2.8 kHz and 4.2 kHz with a duration between 2 and 3 sec. Progressive shortening of song units, or an "accelerating" tempo, appears to be a species specific characteristic. The rate of shortening does not appear to be critical, however, since it varied 3-fold (-1.4 to -3.9×10^{-2} sec/note) within the population. Similarly, the number of notes varied 2-fold, between 16 and 33 notes, suggesting that this is not a critical factor in species identification.

The structure of Field Sparrow song is relatively simple, suggesting that experimental playback studies could profitably use electronically produced synthetic songs, after the manner of Falls (1963, 1969) with White-throated Sparrows. Goldman (1973) played synthetic songs to territorial male Field Sparrows, comparing songs with accelerating tempo to songs with notes of equal duration and tempo. Synthetic accelerating songs produced a weaker response than actual recorded songs: non-accelerating synthetic songs produced no measurable responses. Beyond confirming the general importance of accelerating tempo, the significance of Goldman's observations cannot be assessed without more information about the criteria used to construct the synthetic song.

Other questions about specific *vs.* individual identification messages must await experimental analysis. Particular questions include: (1) Is the shortening pattern, with an initially rapid rate and a later, slower rate, a necessary specific character? (2) How long does the song have to be—either in number of notes or in duration? (3) How much variation in frequency is permissible? (4) How does the tonal quality of the notes affect species recognition? The amount of redundancy, and how it might be coded, also remains to be found.

Singing cadences were remarkably stereotypic in Field Sparrows, remaining essentially unchanged under a variety of circumstances. Aside from a slight increase in rate as the season progressed, experimental manipulations were required to produce significant changes in cadence. Even mated males appear to conform to a species specific singing rate while singing, albeit more variably than unmated individuals.

Walkinshaw's (1968) observations on the reduction in singing by mated males appear to refer to changes in the overall daily rates of singing, due to fewer bouts of singing by mated birds. I have unpublished data on captive Field Sparrows that confirm Walkinshaw's observations; in captivity male Field Sparrows stop singing almost entirely upon pair formation. This raises the interesting possibility that the faster cadences observed late in the season were primarily from unmated males, although I have no confirming evidence.

Several criteria have been used to demonstrate individual recognition of songs. One criterion has been to show differential responses of territorial males to the songs of neighbors and non-neighbors (Weeden and Falls 1959, Falls 1969, Emlen 1971). Goldman (1973) has shown that territorial male Field Sparrows respond more strongly to songs of non-neighbors than to those of neighbors.

Another criterion of individual recognition is based on differential response by a bird to his own song. Hinde (1958) found that Chaffinches (*Fringilla coelebs*) respond more strongly to songs resembling their own; and Falls (1963, 1969) has shown that Ovenbirds (*Seiurus aurocapillus*) and White-throated Sparrows tend to treat their own songs as unfamiliar, i.e., responses were intermediate between those given familiar songs and songs of a stranger. Data on cadences in the present study show differential responses to playback of a bird's own songs, confirming individual recognition by song in Field Sparrows.

SUMMARY

Descriptions are given for variations in song morphology in a population of Field Sparrows and for variations in singing cadences in a variety of circumstances. Each male Field Sparrow had a single song-type that was distinctive within the study population. Intra-individual variation consisted of adding or omitting notes, without alteration of the basic song-type morphology. Accelerating tempo within the song, due to progressive shortening of the notes, was characteristic of all songs.

Cadences, i.e., the time interval between successive songs in a bout, varied 2-fold within the population. Cadences were shorter later in the season, but cadence rates were unaltered by time of day or matedness of the singer. Neighboring birds appear to sing in response to each other. Differential responses of individuals to taped playback of their own songs confirm individual recognition by song in Field Sparrows.

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LITERATURE CITED

Brand, A. R. 1938. Vibration frequencies of passerine bird song. Auk 55:263–268.

Emlen, S. T. 1971. The role of song in individual recognition in the Indigo Bunting. Z. Tierpsychol. 28:241–246.

———. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41:130–171.

Falls, J. B. 1963. Properties of bird song eliciting responses from territorial males. Proc. 13th Int. Ornithol. Congr.:259–271.

———. 1969. Functions of territorial song in the White-throated Sparrow. Pp. 207–232, *in* Bird Vocalizations (R. A. Hinde, ed.), Cambridge Univ. Press, London.

GOLDMAN, P. 1973. Song recognition by Field Sparrows. Auk 90:106–113.

HINDE, R. A. 1958. Alternative motor patterns in Chaffinch song. Br. J. Anim. Behav. 6:211–218.

MARLER, P. 1959. Developments in the study of animal communication. Pp. 150–206, *in* Darwin's biological work, some aspects reconsidered (P. R. Bell, ed.), J. Wiley and Sons, New York.

———. 1960. Bird songs and mate selection. Pp. 348–367, *in* Animal sounds and communication (W. E. Lanyon and W. N. Tavolga, eds.), A.I.B.S. Publ. 7.

REYNARD, G. B. 1963. The cadence of bird song. Living Bird 2:139–148.

SAUNDERS, A. A. 1922. The song of the Field Sparrow. Auk 39:386–399.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace, and Co., New York.

SNEDECOR, G. W. 1956. Statistical methods, 5th ed. Iowa State Univ. Press, Ames.

WALKINSHAW, L. H. 1968. Eastern Field Sparrow. *In* A. C. Bent. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies (O. L. Austin, ed.), U. S. Natl. Mus. Bull. 237:1217–1235.

WEEDEN, J. S. AND J. B. FALLS. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76:343–351.

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FALL AND WINTER ROOSTING HABITS OF CAROLINA CHICKADEES

T. David Pitts

Although fall and winter roosting sites for some members of the genus *Parus* have been described, roosting habits of many species have not been thoroughly studied. During the months October 1972, through March 1973, I observed the types of roosts used by Carolina Chickadees (*P. carolinensis*), the frequency of use for each roost, the number of individuals using each roost, the relation of roost sites to flock ranges, the times of entry and departure, and the behavior of individuals prior to roosting and immediately after departure from roosts. A description of the fall and winter roosting habits of these chickadees is presented here.

METHODS AND STUDY AREA

Two adjoining farms in south Knox Co., Tennessee, served as the study area. The area was approximately 90 ha, about ½ of which was wooded. The non-wooded area either was used for cattle pasture or was idle ground undergoing secondary succession. Wooded areas were mostly deciduous with several patches of conifers. Dominant deciduous trees included oak (*Quercus* sp.), hickory (*Carya* sp.), and tulip poplar (*Liriodendron tulipifera*); Virginia pine (*Pinus virginiana*) was the most abundant conifer. All wooded areas had been selectively logged during the past 20 years. Consequently, few trees greater than 35 cm in diameter were present. A dense understory was present in most of the deciduous woods. Margins of the wooded areas supported luxuriant growths of herbaceous plants. Elevation varied from 275 to 335 m above sea level.

To supplement natural roost and nest sites, I placed 50 dark green nest boxes on the study area in December 1972. Each box had a cavity 9.5 cm wide, 8.9 cm long, and 23 cm deep with a 3.2 cm diameter entrance 17 cm above the floor. Twenty-five of the boxes contained 5 cm of sawdust. The boxes were attached 1–2 m above the ground to living and dead trees of various sizes.

I scouted the area for potential roosting sites by listening for chickadee calls and observing movements in late afternoon as indicators of nearby roosts. Each site was observed for periods of 15 to 60 min either in late afternoon or early morning. Presumptive roosts were also checked by attempting to flush roosting chickadees. A site was defined as a roost if a chickadee entered and remained in late afternoon or departed in early morning or flushed during normal roosting time.

A cylindrical cloth net 15 cm in diameter and 35 cm long attached to a 4 m pole was used to capture chickadees as they flushed from roosts. McCamey (1961) style traps at feeders were also used. Each trapped chickadee received a USFWS band plus a unique combination of colored plastic leg bands. In this paper individual chickadees are referred to by the last 3 digits of their band number.

I estimated the winter population to be 40 chickadees; 27 chickadees were captured and banded. Most of the unbanded chickadees had ranges that extended considerably beyond my study area. I determined the extent of each flock range by plotting flock

TABLE 1

DESCRIPTION OF CHICKADEE ROOSTS

Roost number	Height of entrance (m)	Direction entrance facing	Size of entrance (cm)	Substrate
1	4.5	up	5.0	dead maple limb
2	2.5	E	3.0	rotting maple limb
3	4.5	NW	4.0	dead maple limb
4	3.0	W	5.0	hollow maple limb
5	1.0	up	6.0	hollow fence post
6	1.2	NW	5.0	fence post
7	1.2	NW	5.0	dead box elder snag
8	6.0	E	4.0	dead willow[a] limb
9	7.5	W	3.0	rotting willow limb
10	3.5	W	3.0	dead ash[b] limb
11	1.2	E	4.0	rotting box elder snag
12	2.1	S	5.0	loose bark on willow
13	3.0	SE	4.0	dead box elder snag
14	4.5	NW	2.5	hollow sycamore[c] trunk
15	2.5	S	5.0	dead box elder snag
16	3.5	W	4.0	dead box elder snag
17	6.0	S	4.0	dead box elder
18	5.0	N	4.0	dead box elder limb
19	2.5	E	2.5	dead sassafras[d] trunk
20	3.0	N	4.0	dead dogwood[e] snag
21	5.5	NE	4.0	dead box elder limb
22	7.5	S	6.0	loose bark on oak limb
23	9.0	W	4.0	rotting oak limb
24	2.5	S	5.0	split hickory trunk
25	2.5	N	4.0	rotting snag

[a] *Salix* sp., [b] *Fraxinus* sp., [c] *Platanus occidentalis*, [d] *Sassafras albidum*, [e] *Cornus florida*.

movements on maps; this information was supplemented with data from observations of marked birds at feeders.

Light intensity measurements were made with a Gossen Lunasix light meter. Sunrise and sunset times were taken from the World Almanac (Long 1972).

RESULTS

Twenty-five chickadee roosts were found; each is described in Table 1. Chickadees were not observed roosting in sites other than natural cavities or enclosures resembling cavities. Table 2 summarizes the number of times I checked each roost, the number of nights each roost was used, and the chickadees captured at each roost. Each occupied roost contained only one chickadee at a time, although several chickadees might use a roost over a period of time. For example, at least 4 chickadees used roost 5. Individual chick-

TABLE 2

FREQUENCY OF ROOST USE AND CHICKADEES CAPTURED AT EACH ROOST

Roost number	No. nights checked	No. nights occupied	Band no. of chickadee captured at roost
1	9	9	110
2	5	2	N. C.[a]
3	11	4[b]	N. C.
4	10	8	107, 108
5	32	16	104,[c] 107, 110, 112
6	14	1	N. C.
7	18	3	N. C.
8	4	0[d]	N. C.
9	8	6	N. C.
10	37	11	106[c]
11	4	2	N. C.
12	4	2	N. C.
13	4	3	107
14	7	3	N. C.
15	5	1	N. C.
16	7	6	N. C.
17	2	1	N. C.
18	13	9[e]	103
19	1	1	105
20	2	2	N. C.
21	4	2[b]	109
22	12	2	N. C.
23	17	10	N. C.
24	8	1	N. C.
25	2	2	N. C.

[a] No chickadee captured.
[b] Roost was also used by Tufted Titmouse.
[c] Chickadee captured twice at same roost.
[d] Woodpecker repelled chickadee; see results.
[e] Roost was also used by Brown Creeper.

adees are known to have used several roosts; chickadee 107 was captured at 3 roosts (Table 2). Although some roosts appeared to be favored over others, no roost was occupied every night. All chickadees captured at roosts were within their flock range.

Each chickadee flock range appeared to have an excess of suitable roosting sites. Many roost sites, such as loose bark and hollow limbs, were naturally occurring and had not been altered by chickadees. Other roosts had been excavated by chickadees or woodpeckers. Downy Woodpeckers (*Dendrocopos pubescens*), but not chickadees, were observed excavating roosts. However, during the spring months chickadees did excavate nest cavities. Additional unused natural cavities and previously excavated cavities were present. None

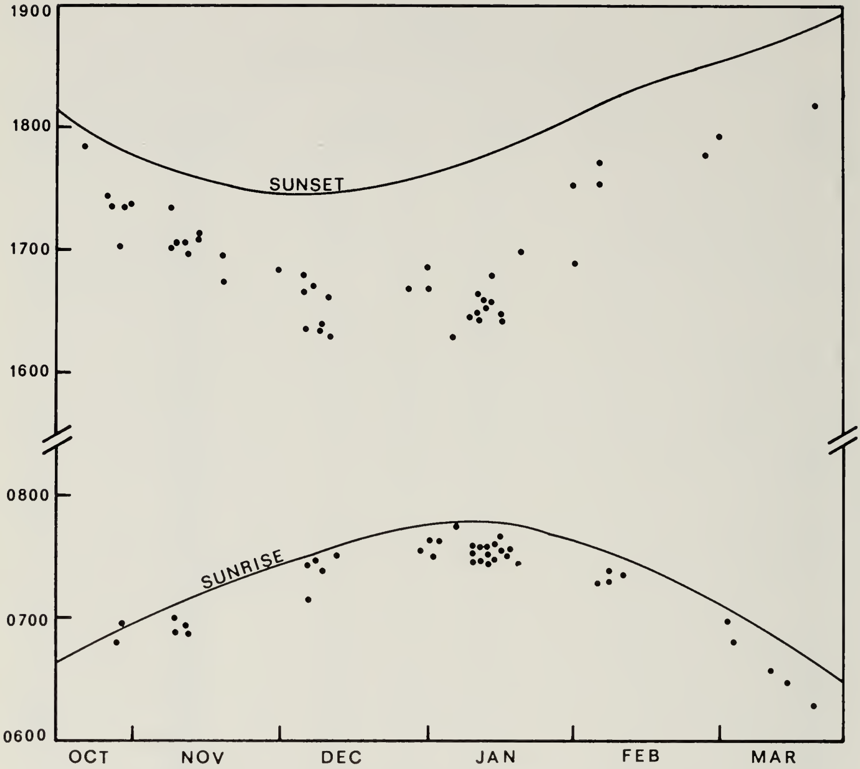

FIG. 1. Roost departures and entries in relation to sunrise and sunset.

of the nest boxes were used for roosts. None of the roosts I inspected contained any nesting materials, but most roosts did contain accumulations of feces. None of the roosts were used as nest sites the following spring.

Chickadees were observed departing from roosts 40 times and entering roosts 46 times (Fig. 1). Chickadees entered roosts before sunset and departed from roosts before sunrise. Light intensity was greater at entry than at departure. Chickadees varied entry and departure times in accordance with changes in daylength, but the precise times were variable. For example, entry times varied by as much as 32 min from 1 December through 11 December. Part of this variability was due to individual variation and part was due to weather. During inclement weather chickadees entered roosts earlier and departed later than on sunny days. Departure times were less variable than entries.

On several nights I observed a chickadee attempt to enter an occupied roost, but the occupant always repelled the invader. Chickadees repelled from one roost usually departed quickly and in direct flight, apparently to another roost. I observed a Downy Woodpecker successfully repel a chickadee at roost 8. As the chickadee attempted to enter the roost the woodpecker emerged and attacked the chickadee. In an encounter of less than 5 sec several chickadee feathers were dislodged. The woodpecker then returned to the cavity and the chickadee displayed in high intensity Head-Forward posture (Hinde 1952) before moving away. Several of the other roosts were used occasionally by Tufted Titmice (*P. bicolor*), and one roost was used by a Brown Creeper (*Certhia familiaris*) for at least 3 nights.

The behavior of foraging chickadees changed as roost entry time approached. Flocks which were noisy and slow moving suddenly became silent as the individuals sat quietly or flew rapidly toward roosts. Choice of roost sites was apparently not determined by the flock location at roost entry time, as chickadees frequently made long flights, sometimes the length of the flock range, just prior to roosting. Most chickadees were alert and wary as they approached roosts. Occasionally a chickadee would enter a cavity at the normal roosting time, only to depart a few minutes later. I observed several sites that were briefly occupied, some on several occasions, only to be vacated and never used as overnight roosts. Disturbances, such as loud noises, at roost entry time apparently caused some chickadees to move to other sites.

Members of some chickadee pairs remain together through the winter (Brewer 1961) and possibly roost in the same vicinity. On several occasions 2 chickadees were observed traveling together toward a roost. As one chickadee entered the roost the second chickadee would explore the immediate area and would frequently remain in a site that appeared to offer very little protection. Two large sugar maples (*Acer saccharum*) with overlapping limbs contained roosts 1, 2, 3, and 4. On one night these 4 roosts sheltered 3 chickadees and 1 Tufted Titmouse. On 6 nights at least 2 of these 4 roosts were occupied.

The roosting position of chickadees was observed at roosts 10 and 23. These roosts were in short, hollow horizontal limbs. Each chickadee normally entered at an opening other than the terminal opening and then moved to within 5 cm of the terminal opening. The roosting chickadee usually crouched and placed its bill in its scapulars. On several evenings, the chickadee in roost 10 was observed crouching with its bill pointing forward. I frequently observed chickadees with bent rectrices in the mornings.

Chickadees were neither the first diurnal birds to begin daily activities nor the last to retire. Many passerines, such as Mockingbirds (*Mimus polyglottos*), Song Sparrows (*Melospiza melodia*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), and Carolina Wrens (*Thryothorus ludovicianus*), were active earlier in the morning and later in the afternoon. Tufted Timice usually entered and departed roosts at about the same times as chickadees. Woodpeckers entered earlier and emerged later than the chickadees. During the shortest days of winter, chickadees frequently spent 15 hours per day in roosts.

Chickadees departed roosts quickly and silently, and they immediately began feeding and preening. Emerging chickadees did not carry feces in their bills. The first call notes were given 30 sec to 3 min after departing the roost, by which time a chickadee might have moved 100 m or more. Flock formation was initiated with the first call notes.

DISCUSSION

Chickadees on my study area apparently preferred natural cavities for roost sites; nest boxes and dense vegetation were abundant but were not used. Brewer (1963), in Illinois, found that Carolina Chickadees use sheltered branches and vines or cavities. Wallace (1964), whose study area was approximately 5 km from mine, observed chickadees roosting in cavities. Other members of the genus usually roost in dense foliage or small natural cavities (Odum 1942, Pielou 1957, Hinde 1952). Great Tits (*P. major*) in Holland roost in nest boxes (Kluyver 1950).

The number of available cavities may influence the choice of roost sites. Many box elder (*Acer negundo*) trees along Stock Creek, which flowed through the study area, rotting fence posts, and other dead trees provided an abundance of soft wood which could be easily excavated. Possibly in other areas the number of sites suitable for excavation was much smaller.

Failure of chickadees to use the nest boxes may have been partially due to the fact that nest boxes were erected in December by which time the chickadees had possibly selected their roost sites for the winter. Foraging flocks that I followed showed no interest in roost sites. Only once did I see a chickadee enter a roost cavity during midday; the cavity had, to my knowledge, not been previously used as a roost, but it was occupied that night. Chickadees probably explore new cavities, determine their potential as roost sites, and if suitable, return later. If such explorations occur primarily in late summer or early fall, newly appearing cavities would not likely be used unless a shortage of cavities existed.

The nest box cavities may also have been too large to serve as suitable roost sites. Although I was never able to inspect the interiors of some roosts, all of the roost cavities were smaller than the nest boxes, and some of the roost cavities were barely large enough for chickadees to enter. Flying squirrels (*Glaucomys volans*) began using some nest boxes shortly after the boxes were erected. Screech Owls (*Otus asio*) roosted in some of the woodpecker holes. Encounters with these larger cavity dwellers may have forced chickadees to use small cavities.

Kendeigh (1961) showed that a solitary House Sparrow (*Passer domesticus*) was able to raise the temperature in its roost cavity on cold nights. Chickadees may also raise the roost cavity temperature. However, the degree of protection provided by chickadee roost cavities varied. Some roosts had solid walls with a side opening thus providing protection from both wind and precipitation. Other roosts had numerous openings and probably provided no better protection than dense foliage.

Each chickadee used different roosts during the winter. Roost site selection may be influenced by disturbances at roost entry time, proximity of the dominant mate's roost, and feces accumulations in roosts. If predators are attracted by the odor of feces in roosts, which seems likely, it would be advantageous for chickadees to change roosts frequently. Downy Woodpeckers and White-breasted Nuthatches (*Sitta carolinensis*), which keep their roost cavities clean, roost individually in the same sites each night (Kilham 1971).

SUMMARY

Carolina Chickadees (*Parus carolinensis*) were observed roosting only in cavities during the fall and winter months in Knox County, Tennessee. Twenty-five roosts are described. Each chickadee roosted alone and changed roosts frequently during the season. All captured roosting chickadees were located within their flock range. Chickadees entered roosts before sunset and departed before sunrise. Chickadees remained in roosts for as long as 15 hours during mid-winter. During inclement weather chickadees entered roosts earlier and departed later than on sunny days.

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LITERATURE CITED

Brewer, R. 1961. Comparative notes on the life history of the Carolina Chickadee. Wilson Bull. 73:348–371.

———. 1963. Ecological and reproductive relationships of Black-capped and Carolina Chickadees. Auk 80:9–47.

Hinde, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour Suppl., No. II.

Kendeigh, S. C. 1961. Energy of birds conserved by roosting in cavities. Wilson Bull. 73:140–147.

Kilham, L. 1971. Roosting habits of White-breasted Nuthatches. Condor 73:113–114.

Kluyver, H. N. 1950. Daily routines of the Great Tit, *Parus m. major* L. Ardea 38: 99–135.

Long, L. H. (ed.) 1972. World almanac. Newspaper Enterprise Association, N. Y.

McCamey, F. 1961. The chickadee trap. Bird-Banding 32:51–55.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. Part 3. Auk 59: 499–531.

PIELOU, W. P. 1957. Life-history study of the Tufted Titmouse, *Parus bicolor* Linnaeus. Ph.D. thesis, Mich. State Univ.

WALLACE, G. O. 1964. Winter behavior and ecology of the Carolina Chickadee (*Parus carolinensis* Audubon) with related data on the Tufted titmouse (*Parus bicolor* Linnaeus). Master's thesis, Univ. of Tennessee.

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COMPARATIVE NESTING BIOLOGY OF SOME HOLE-NESTING BIRDS IN THE CARIBOO PARKLANDS, BRITISH COLUMBIA

Anthony J. Erskine and William D. McLaren

The purpose of this paper is to present comparative data on the nesting of certain birds using tree holes in central British Columbia. The stability of the hole-nesting community there had been disrupted by the appearance and increase of the Starling (*Sturnus vulgaris*) which, introduced into the eastern United States in 1890, had spread across the continent to British Columbia by 1947 (Myres 1958). Our data were collected incidentally in the course of studies of other aspects of the biology of hole-nesting birds (Erskine 1960, McLaren 1963).

STUDY AREA AND METHODS

Field work began on 3 May 1958 and 25 April 1959, and continued into August in both years. Searching for new nests was sporadic after mid-June; consequently, nests started later were probably under-represented in our samples. A number of known sites were checked in May 1964 when, however, no follow-up to determine nesting success was possible. Nesting data reported here were collected by AJE, except for 47 nests (21 in 1958, 26 in 1959), of Mountain Bluebird (*Sialia currucoides*) by WDM, and 3 nests of Common (Red-shafted) Flicker (*Colaptes auratus cafer*), 11 of Tree Swallow (*Iridoprocne bicolor*), and one of Mountain Bluebird, by A. J. Wiggs, who accompanied AJE in 1958.

Our studies were carried out in the Cariboo Parklands (Munro 1945), part of the interior plateau of central British Columbia between the Coast Range and the Cariboo Mountains. Areas receiving intensive coverage were centered near 105 Mile (AJE), Springhouse (WDM), and Riske Creek (both), but we also visited most lakes accessible by road between the main areas. We also made a few observations in comparable habitats south of Kamloops, near Knutsford and Bestwick.

These areas are in the interior Douglas fir zone (Tisdale and Maclean 1957), at elevations between 850 and 1050 m. Most of the intensive study areas were in parkland of groves and clumps of trembling aspen (*Populus tremuloides*) with grassland between. Others were in open, mixed-aged stands of Douglas fir (*Pseudotsuga menziesii*). Lodgepole pine (*Pinus contorta*), the other common tree in both communities, was seldom used by hole-nesting birds. We found some nests in ponderosa pine (*P. ponderosa*) south of Kamloops. Munro (1945) described the Cariboo Parklands habitats in detail, but his account underemphasized the importance of Douglas fir.

We searched for nests mainly by examining the trunks of all trees 20 cm diameter breast height or larger. In aspen parkland, we examined all groves back to 400 m from the nearest lake, but where closed stands prevailed we searched mainly within 135 m of the edge of lakes. Access to holes was by ladder, climbing irons, or by logs placed against the tree trunk. The contents of cavities were examined by reflecting the beam from a flashlight into the hole with a strip of mirror glass inserted at an angle. When nestlings were to be banded, a hole was drilled into the cavity at the side or back (Erskine 1959), or a portion of the sill was cut out and later nailed back into place. We also inspected contents of nest boxes in the area, erected for ducks by Lawson G. Sugden, then of the British Columbia Game Branch. Details of all nests of which the contents were determined were entered on nest record cards and deposited in the British Columbia Nest Records Scheme (now housed in the Provincial Museum, Victoria).

In evaluating the data on clutch initiation, clutch size, and nesting success, we were guided by the criteria of Myres (1955) and Snow (1955 a,b). However, the small size of most samples necessitated including all the data available, excepting those believed to represent renests or incomplete clutches.

RESULTS

Data are presented here for 4 species: Common Flicker, Tree Swallow, Mountain Bluebird, and Starling, which with the Bufflehead (*Bucephala albeola*) are the main species occupying flicker holes in this region. As the data were collected while we were inspecting sites that might be used by Buffleheads, nearly all the natural sites of Tree Swallows examined were of flicker origin, although this swallow also uses both larger and smaller holes (McLaren 1963). Data for Buffleheads (Erskine 1972) and Yellow-bellied Sapsuckers (*Sphyrapicus varius*) (Erskine and McLaren 1972) have been published elsewhere. The records for other hole-nesting species are too sparse to warrant extensive treatment.

First we considered the comparability of the data from nest boxes. Nearly all available nest boxes were used by some species, boxes with large entrances (12.5 cm) by Barrow's Goldeneyes (*Bucephala islandica*) or Tree Swallows, and those with small entrances (6.3 cm) by Starlings or Tree Swallows, with a few of other species in both sizes. No flickers used nest boxes in 1958 or 1959, and only 3 bluebird clutches (none followed up) were in boxes, so comparisons with natural sites were possible only for Tree Swallows and Starlings (Table 1). In view of the small samples, none of the differences in clutch size is convincing and the differences in laying dates are very slight. We thus felt justified in combining our data from nest boxes with those from natural sites in all subsequent comparisons.

For each of the 4 main species, we have summarized the data on clutch initiation dates (Fig. 1, Table 2), clutch size (Table 3), and nesting success (Table 4).

DISCUSSION

Data from nest boxes.—Our admittedly meager data (Table 1) suggest no striking differences between data obtained from nest boxes and those from natural sites, for the 2 species examined. This by itself neither justifies nor argues against treating nest box data as representative for other species, in-

TABLE 1

COMPARISON OF MEDIAN LAYING DATE AND MEAN CLUTCH SIZE FOR NESTS IN NEST BOXES AND NATURAL SITES, CARIBOO PARKLANDS, BRITISH COLUMBIA

Species	Year	Nests in	Median laying date	Mean clutch size
Tree Swallow	1958	Boxes	22 May (9)*	6.33 (9)*
		Tree holes	21 May (19)	5.75 (16)
	1959	Boxes	24 May (12)	5.64 (11)
		Tree holes	26 May (36)	5.88 (17)
Starling	1958	Boxes	29 April (7)	5.71 (7)
		Tree holes	2 May (7)	6.00 (1)
	1959	Boxes	8 May (6)	5.40 (5)
		Tree holes	10 May (32)	4.62 (24)

* Sample size.

cluding Mountain Bluebirds. The situation found for Buffleheads (Erskine 1972:87–88) and Barrow's Goldeneye (M. F. Jackson, pers. comm.), where clutches in nest boxes averaged markedly smaller than those from natural sites, indicates that one should not accept nest box data as equivalent to those from natural sites without some attempt to compare them.

Chronology.—The species differed in their responses to the different climatic regimes in 1958 and 1959. Warming began much earlier in 1958, and in that year the earliest nesting species, the Starling, began much earlier than in 1959. The Mountain Bluebird, which like the Starling forages for terrestrial arthropods in grassy habitats, also started nesting much earlier in 1958 than in 1959. The other species showed much less difference between years. These species have very different foraging habits from Starlings and bluebirds, and the observed differences in nesting chronology may reflect availability of food rather than being directly in response to temperature.

Flickers in temperate latitudes seem never to attempt second broods, but the passerine species may do so. A complete nesting cycle requires at least 44 days (nest lining, 5; laying, 6; incubation, 14; fledging, 19) for Tree Swallows, about 39 days (3, 5, 14, 17) for Mountain Bluebirds, and about 41 days (3, 5, 13, 20) for Starlings (various sources, including our own data). There seems to be no conclusive evidence of second broods by Tree Swallows anywhere in Canada, though both time and flying insects seemed sufficient for them to do so. In contrast, Barn Swallows (*Hirundo rustica*), which arrive and start laying later than Tree Swallows, commonly

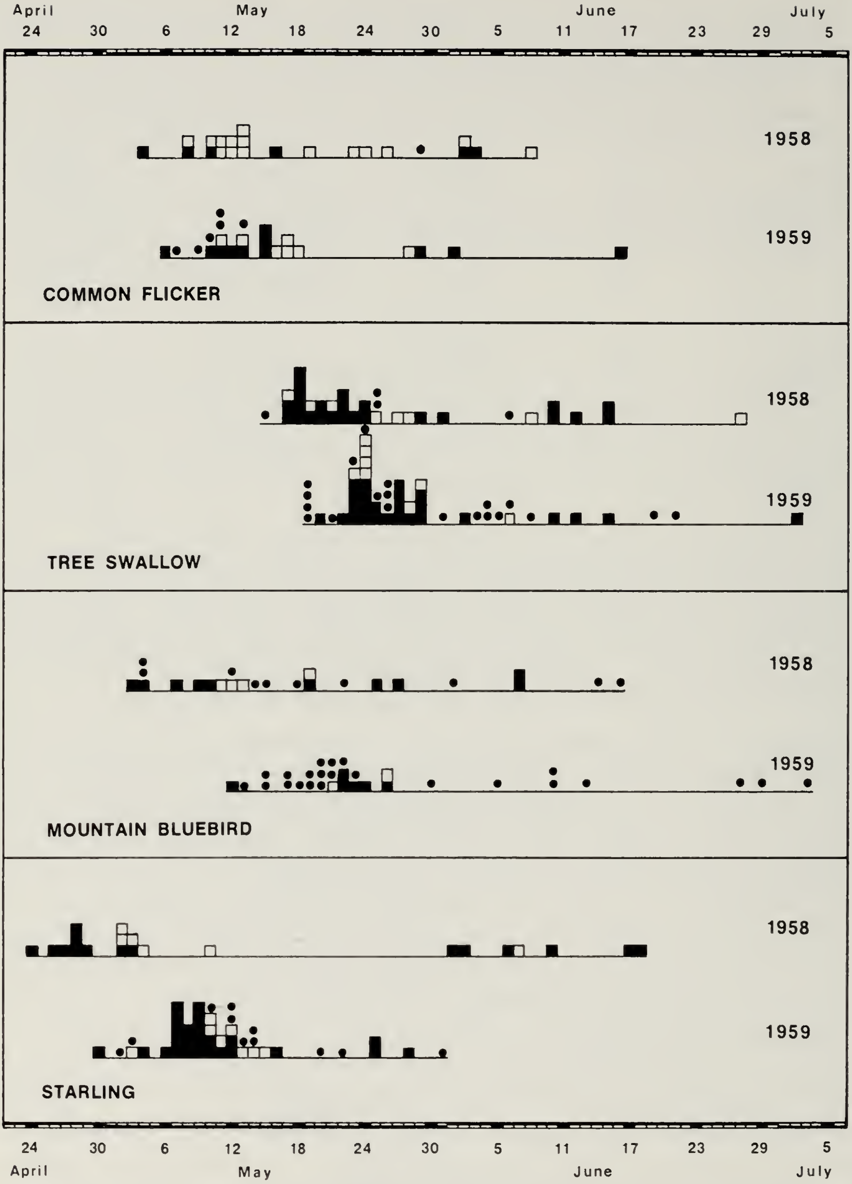

FIG. 1. Clutch initiation dates, Cariboo Parklands, British Columbia, 1958–59. Filled squares = dates known to ± 0–2 days; Open squares = dates known to ± 3–5 days; Filled circles = dates known to ± 6 or more days.

rear 2 broods through most of western Canada (unpublished data from Prairie and B.C. nest records). We did no marking of adults to check on the possibility of second broods, and the circumstantial evidence is good only for Starlings in 1958. A number of nest cavities were re-used after broods had fledged, with a period of 3 weeks separating the starts of the first and (assumed) second nestings (Fig. 1). We estimated that about 20% of Starlings attempted second broods in 1958; none had done so in 1955–57 when the population density was lower (M. T. Myres, pers. comm.), and we did not detect a single instance of second broods in 1959. Dunnet (1955) has shown that in western Europe the proportion of Starlings which attempted second broods varied among areas and among years, from about 70% to none. A few bluebird nests and 2 Tree Swallow nests were late enough that second broods seemed possible, since Mountain Bluebirds regularly raise 2 broods in Montana (Power 1966) and Alberta (J. L. Park, pers. comm.). Both these species suffered heavy nesting losses earlier in the season, and all of their late nests may have been renests rather than second attempts. Laying dates for first broods of bluebirds were similar to those found by Power (1966).

Starlings showed much less scatter in laying dates than did the other 3 species, all of which seem to have suffered to some extent in competition with the introduced species. The scatter was greatest in the bluebird, which is most directly in competition with the Starling, although the lack of precise laying dates for most bluebirds may have contributed to the scatter. Some flickers had to renest repeatedly; 3 nests, in which laying began on 17 May, 29 May, and 1 June, were all within 150 m of each other, and were believed to be of the same pair. Starlings destroyed the eggs in the first, and disturbed the flickers until they abandoned the second attempt. Starlings probably disturbed Tree Swallows less, since the latter started nesting when most Starlings were incubating (Fig. 1).

Clutch size.—The greater the spread in median dates of first laying between 1958 and 1959, the greater the spread in mean clutch sizes between years; all species showed a decrease in clutch size with later dates of nest initiation. The Starling data for 1964 and the second broods in 1959 also conform to this pattern. There seem to be few quantitative studies of any of these species in the northwest for comparisons, and eastern areas where such studies have been made differ so much in altitude, latitude, and climate that comparison with them seems futile. Tree Swallow data from Montana (Weydemeyer 1935) are roughly similar (mean 6.05 eggs), but Power (1966) reported a much higher mean clutch in Mountain Bluebirds (5.90 eggs for early first nests) in Montana, with no Starlings present.

TABLE 2

DATES OF CLUTCH INITIATION OF HOLE-NESTING BIRDS, CARIBOO PARKLANDS, BRITISH COLUMBIA

		Clutch initiation date	
Species	Sample size*	Median*	Interquartile range (no.)*
Common	14	11 May 1958	10–13 May (9)
Flicker	20	12 May 1959	11–15 May (11)
Tree	28	21 May 1958	18–24 May (17)
Swallow	47	25 May 1959	24–29 May (26)
Mountain	19	12 May 1958	9–19 May (11)
Bluebird	24	20 May 1959	18–22 May (12)
Starling	14	29 April 1958	28 April–2 May (7)
	38	10 May 1959	8–12 May (20)
	24	8 May 1964	8– 9 May (13)

* For first nestings only, not including re-nestings.

Nesting success.—Breeding success was highest in the Starling, and lowest in the bluebird, the species most directly in competition with the Starling. Flickers, unlike the other species, can make a new nest cavity when dispossessed by Starlings. Losses by flickers seem to have been relatively higher in the early stages, when Starlings were also establishing their nests (cf. Table 2). Overall, the success rates found for flickers are not far from the usual values for hole-nesters cited by Nice (1957).

A few swallow nests were lost in competition with Starlings or Buffleheads, and 1 or 2 to vandalism. Other nests were likely destroyed by squirrels, *Tamiasciurus hudsonicus* and/or *Glaucomys sabrinus*, which were common in all wooded areas. Since Starlings pre-empted most nest sites near open areas, Tree Swallows were more often found by lakes in woodland. In 1959 Tree Swallow nest losses were much higher than in 1958, and included many nests deserted with eggs intact. This probably reflected the cold, rainy weather of May and June 1959 (cf. Erskine 1972, Fig. 33, p. 190), when swallows may have had difficulty in securing food. The failure of Starlings to attempt second broods in 1959 may also have been a result of the adverse weather.

The nesting success data for bluebirds are not very complete, owing to lack of follow-up in many cases. Even by combining all records for each year, regardless of the stage at which the nests were found, not more than 3 nests out of 10 succeeded in 1958 and not more than 3 out of 6 in 1959,

TABLE 3

CLUTCH SIZES OF HOLE-NESTING BIRDS, CARIBOO PARKLANDS, BRITISH COLUMBIA

Species	Year	Mean clutch (sample size)	No. of clutches with 3	4	5	6	7	8	9	10	11 eggs
Common Flicker	1958	7.43 (7)			1	1	2	2			1
	1959	7.40 (15)				4	3	6	2		
Tree Swallow	1958	5.92 (25)	1		4	16	3	1			
	1959	5.79 (29)		3	10	8	7		1		
Mountain Bluebird	1958	5.29 (17)	1	2	5	9					
	1959	4.87 (23)	2	6	8	7					
Starling	1958	5.75 (8)*			4	3		1			
		4.17 (6)†		5	1						
	1959	4.63 (30)	4	8	11	7					
	1964	5.18 (17)	1	3	6	6	1				

* First nestings; † Second nestings.

with corresponding egg success of 13 young fledged from 44+ eggs and 10+ from 24+ (Table 4), which are very low success rates for a hole-nesting species (cf. Nice 1957). This low nesting success was probably not sufficient to maintain local breeding numbers, which were thought to have decreased greatly during the 1950's (M. F. Jackson, pers. comm.). This is well correlated with the dramatic increase in Starling numbers at that time (cf. Myres 1958), but we have only circumstantial evidence that Starlings were in fact responsible for the bluebirds' decline. Starlings too had less success in 1959 than 1958, but even then their success should have maintained the population without second broods, since they had increased rapidly prior to 1958 with only one brood a year. The breeding success rate compared favorably with those from studies elsewhere, but there are no comparative data from western Canada or the U.S.

Finally, we must emphasize that this account covers only one stage in the interaction between Starlings and other hole-nesting birds using flicker cavities in the Cariboo region. Starlings were first noted there in 1948, and increased rapidly up to 1958 (Myres 1958), when they had nearly saturated preferred nest sites in rural areas. By then, Mountain Bluebirds had markedly decreased from former numbers, but other hole-nesting species' populations had changed little. Unfortunately, no useful population data for any species are available from the pre-Starling period, and we have no density figures even from 1958–59. By comparison with flicker

TABLE 4

BREEDING SUCCESS OF HOLE-NESTING BIRDS, CARIBOO PARKLANDS, BRITISH COLUMBIA

Species	Year	Stage when found	No. of nests	No. (%) which fledged young	No. eggs – No. young fledged (%)
Common Flicker	1958	B or L*	5	2(40)	34+– 9+ (27)
		Eggs	6	5(83)	37+–26 (70–)
		Young	10	8(80)	66+–49 (74–)
	1959	B or L	16	11(69)	91 –47+ (52+)
		Eggs	5	— no follow-up —	
		Young	1	1(100)	4+– 4 (100–)
Tree Swallow	1958	B or L	25	12(48)	120 –43+ (36+)
		Eggs	3	3(100)	16 –13+ (81+)
		Young	1	1(100)	4+– 4 (100–)
	1959	B or L	20	7(35)	87+–21+ (24)
		Eggs	3	0(0)	13+– 0 (0)
		Young	3	— no follow-up —	
Mountain Bluebird	1958	B or L	5**	0(0)	18 – 0 (0)
			1†	1(100)	6 – 4 (67)
		Eggs	3	1(33)	15 – 4 (27)
		Young	1	1(100)	5+– 5 (100–)
	1959	B or L	3	1(33)	12 – 3+ (25+)
		Eggs	1**	1(100)	5 – 5 (100)
			1†	0(0)	4 – 0 (0)
		Young	1	1(100)	3+– 2 (67–)
Starling	1958	B or L	3**	3(100)	16 –15 (94)
			6†	5(83)	25 –14 (56)
		Eggs	6**	5(83)	30 –19+ (63+)
			1†	1(100)	2 – 1 (50)
		Young	3	3(100)	11+–11 (100)
	1959	B or L	19	13(68)	86+–39+ (45)
		Eggs	3	3(100)	10+– 5+ (50)
		Young	3	3(100)	8+– 8+ (100)

* B or L — Building or Laying; ** First nestings; † Second nestings.

densities in eastern Canada, where contact with Starlings had extended over 30 years or more, we anticipated that flicker numbers would gradually decrease after 1958. The availability of flicker holes would also decrease, but more slowly. Most sites used by Starlings were in aspens, the common tree around the open areas, and the majority of nests in aspens would be unusable within 10 years (Erskine 1972, Table 9, p. 70), although new ones would have replaced some of these. A new equilibrium among numbers of flickers, flicker holes, and birds and other animals using these holes might require 15 to 20 years for attainment. If flicker holes became scarcer, we would expect that competition for them would be intensified, and the resulting disturbance to nesting would affect most of the parameters here studied. We suggest that further studies of the hole-nesting birds in the region might profitably be undertaken now that 15 years have elapsed since our work there. In particular, quantitative estimates of the relative abundance of the species involved would be most desirable.

SUMMARY

Comparative statistics on laying chronology, clutch size, and nesting success are presented for 4 species of hole-nesting birds in the Cariboo region of British Columbia in 1958–59, about 10 years after Starlings first appeared there. Data obtained from nest boxes were similar to those from natural sites (flicker holes) for Starlings and Tree Swallows. Circumstantial evidence suggests that competition for nest sites affected Mountain Bluebirds adversely, these birds having a wider scatter in laying dates and lower nesting success than the others. Common Flickers and Tree Swallows showed considerable scatter in laying dates, with most nest losses occurring during periods when Starlings were establishing nests, but their nesting success overall was near normal. Starlings had the most closely synchronized laying schedule and the greatest breeding success. As the most successful species, they must be viewed as influencing the breeding of all other species which use similar nest sites. All species nested later and less successfully in the wet, cold season of 1959 than in 1958.

LITERATURE CITED

Dunnet, G. M. 1955. The breeding of the Starling *Sturnus vulgaris* in relation to its food supply. Ibis 97:619–662.

Erskine, A. J. 1959. A method for opening nesting holes. Bird-Banding 30:181.

———. 1960. A discussion of the distributional ecology of the Bufflehead (*Bucephala albeola*; Anatidae; Aves) based upon breeding biology studies in British Columbia. M.A. thesis, Univ. British Columbia, Vancouver.

———. 1972. Buffleheads. Can. Wildl. Serv., Monogr. Ser. no. 4.

——— and W. D. McLaren. 1972. Sapsucker nest holes and their use by other species. Can. Field Nat. 86:357–361.

McLaren, W. D. 1963. A preliminary study of nest-site competition in a group of hole-nesting birds. M.Sc. thesis, Univ. British Columbia, Vancouver.

Munro, J. A. 1945. The birds of the Cariboo Parklands, British Columbia. Can. J. Res. 23D:17–103.

Myres, M. T. 1955. The breeding of Blackbird, Song Thrush and Mistle Thrush in Great Britain. Part 1. Breeding seasons. Bird Study 2:2–24.

———. 1958. The European Starling in British Columbia: 1947–1957. Occas. Papers Br. Columbia Prov. Mus., no. 11.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

Power, H. W., III. 1966. Biology of the Mountain Bluebird in Montana. Condor 68: 351–371.

Snow, D. W. 1955a. The breeding of the Blackbird, Song Thrush, and Mistle Thrush in Great Britain. Part II. Clutch-size. Bird Study 2:72–84.

———. 1955b. The breeding of the Blackbird, Song Thrush and Mistle Thrush in Great Britain. Part III. Nesting success. Bird Study 2:169–178.

Tisdale, E. W. and A. Maclean. 1957. The Douglas fir zone of southern interior British Columbia. Ecol. Monogr. 27:247–266.

Weydemeyer, W. 1935. Efficiency of nesting of the Tree Swallow. Condor 37:216–217.

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FOOD HABITS OF RING-BILLED GULLS BREEDING IN THE GREAT LAKES REGION

William L. Jarvis and William E. Southern

The number of Ring-billed Gulls (*Larus delawarensis*) breeding on the Great Lakes has increased significantly during the last 3 decades (Ludwig 1966, 1974). Changes in the availability of nesting sites, fish introductions, and restrictions on human predation are among those factors probably responsible for the population explosion. Additionally, breeding adults may have intensified or perfected their exploitation of food resources not consistently used by the sympatric Herring Gull (*L. argentatus*). Both species consume large quantities of fish, but Ring-bills also actively secure sizeable numbers of terrestrial, aquatic, and aerial invertebrates to supplement their diet, particularly when feeding young. Intensified use of this latter food resource by Ring-bills may have reduced the dietary overlap between Ring-billed and Herring gulls and contributed to population changes. The observations of Pettingill (1958) and Mueller (1965) suggest that the reliance of Ring-billed Gulls on insects as an energy source is a recent innovation. It is possible that gulls capturing aerial insects may have escaped earlier notice by ornithologists, but it is equally plausible that this feeding method was increasing in frequency during these years when the Ring-billed Gull population was enlarging rapidly (Ludwig 1974).

We conducted this study to determine the food habits of Great Lakes Ring-billed Gulls during the breeding season. We have attempted to identify any seasonal and distributional trends in food habits by grouping samples by collection dates and locality. We believe that the degree of resolution provided by our method will be useful in development of an understanding of the ecological involvement of Ring-billed Gulls.

In the only other Great Lakes study, Ludwig (1966) reported that an undisclosed number of samples collected between 1963 and 1965 contained 265 alewives (*Alosa pseudoharengus*), 69 smelt (*Osmerus mordax*), 5 yellow perch (*Perca flavescens*), 5 other fish species (36 individuals) and 15,000 to 20,000 insects. In a later paper Ludwig (1974) further discussed the relative amounts of fish species occurring in samples. Two studies have been conducted at inland lakes in western Canada. Munro's (1936) study, based on 1 collection in May 1933 and 1 in June 1934, indicated that Ring-bills feed on grain, ground squirrels, carrion, ground beetles, and mice, named in order of their importance. Vermeer's (1970) more comprehensive study covered May through July (1964–65) and showed rodents to be an important food item throughout the season, with grain also being important in

May, insects in June, and refuse in July. Significant differences apparently exist between the food habits of Ring-billed Gulls breeding in the eastern and western portions of North America.

METHODS

Food samples were obtained by forcing adults and chicks to regurgitate. Cannon-netted adults and confined chicks often expelled food from the upper digestive tract. Usually an individual regurgitated a single, well defined bolus that we collected and sealed in a plastic bag containing 10% formalin. Most samples obtained after cannon netting were from adults but as we could not discriminate between chick and adult regurgitations late in the nesting season, we referred to each sample from the ground as an "individual sample."

Groups of chicks were confined in a box and transported to a site for orientation experiments. They occasionally regurgitated under these conditions. Food collected from the boxes during one day was combined as a "composite chick sample" because some mixing occurred. These samples each contained food from 15 to 50 chicks.

From May through July 1964, Southern collected samples at a mainland colony near Rogers City, Presque Isle Co., Michigan. All 76 samples were obtained when chicks were several weeks old; 65 (86%) were taken between 29 June and 1 July. Because no attempt was made to collect all available samples and preference was given to samples containing insects, this material is discussed separately.

A more comprehensive study was made from May through July 1971 at 3 Michigan colonies: Rogers City, where 141 individual samples were collected between 7 May (egg-laying stage) and 21 July (hatching peak, 1 June); Ile aux Galets (in Lake Michigan, 11.3 km offshore from Cross Village, Emmet Co.), 80 samples between 9 June and 20 July; and Bird Island (in Lake Huron, about 1 km offshore near Ossineke, Alpena Co.), 11 samples on 17 June. Ten composite chick samples were collected at Rogers City between 2 and 22 June (total = 242 samples). To assist in assessing for seasonal variation in diet, we grouped the individual sampling dates (see Table 1). Data for the 3 colonies have been kept separate as distance from the mainland probably influences foraging patterns.

For analysis each sample was placed on a 40-gauge wire screen, washed with water to remove mucus and to separate food items and drained. Total volume of each taxon per sample was measured to the nearest 0.5 cm^3 by water displacement in a 100 cm^3 graduated cylinder. For each sample we recorded the total number of individuals, volume of each taxon, and collection site and date. Most insects were keyed to family; fish were identified to species. Debris and plant material in samples was negligible except on 7–9 May (Table 1).

RESULTS

Composition of 1964 samples.—An incredible number and diversity of insects were contained in 76 samples; 17,581 individuals representing 12 orders and 80 families (68% of total sample volume). Fish, earthworms, and spiders also were recorded. The percent of total volume and frequency of occurrence, respectively, for the 4 major insect taxa found in over 50% of the samples are as follow: Homoptera—31%, 76% (Cicadidae 19%, 33%;

Cicadellidae 12%, 62%); Ephemeroptera—15%, 55% (mostly Ephemeridae); Hymenoptera—8%, 58% (Formicidae 4%, 50%; Tenthredinidae 3%, 32%); and Coleoptera—4%, 59% (Carabidae 2%, 41%; Elateridae 1%, 38%; Scarabaeidae 1%, 25%).

Fish represented 32% of the total volume. By percent volume and frequency of occurrence, respectively, the most important were yellow perch (11%, 4%), nine-spined stickleback (*Pungitius pungitius*) (4%, 20%), and alewives (4%, 3%). As collecting procedures in 1964 may have emphasized the insect composition of samples, these figures cannot be interpreted as representing the relative importance of fish and insects during the nesting period.

Composition of the 1971 samples.—The content of adult and chick samples from the 3 colonies is divided into taxonomic categories. Numbers following each category indicate the total individuals for that taxon, volume of taxon, percent of total volume and percent of the 232 individual samples in which the taxon occurred. "NA" indicates that the total number of individuals was not determined. The following provide a general overview of the diet of Ring-billed Gulls nesting in the Great Lakes Region:

Annelida (NA, 40.5 cc, 1.1%, 5.2%): Earthworms (Lumbricidae) constituted a major food source for Rogers City Ring-bills in May and early June (Table 1). During this time we also received reports from local farmers of large numbers of gulls feeding in their freshly-tilled fields. After mid-June worms did not appear in food samples. However, once, after a rain in late July, Jarvis observed young (7–8 week-old) Ring-bills picking earthworms from the grass at a Rogers City park. At Ile aux Galets worms were present in only 1 sample (9 June).

Decapoda (NA, 13.0 cc, 0.3%, 1.2%): Occasional crayfish exoskeleton fragments were found.

Ephemeroptera (2834, 90.5 cc, 2.3%, 9.9%): Mayflies represented a comparatively small portion of the total gull diet at Rogers City (1% vol., 5% freq.) but on several occasions they were quite abundant (Table 1). At Ile aux Galets, Ephemeroptera appeared to be a more important food item (4% vol., 20% freq.). Of 31 individual samples collected on 2 July, 14 contained 1500 mayflies (50% of total food items, 48% volume). Most of the recovered mayflies were Ephemeridae (some identified as *Hexagenia* spp.). They were in various stages of metamorphosis (including adults) but most appeared near the emergent stage, suggesting heavy water surface feeding by gulls.

Odonata (19, 4.5 cc, 0.1%, 3.0%): Occasional damselflies and dragonflies (adults, naiads) were recovered. Ten naiads (near emergent stage) were identified as *Ophiogomphus* sp.

TABLE 1

PERCENT FREQUENCY (f) AND VOLUME (v) OF MOST COMMON FOOD ITEMS IN RING-BILLED GULL REGURGITATIONS COLLECTED AT ROGERS CITY, BIRD ISLAND, AND ILE AUX GALETS (1971)

	May		June												July											
Sample dates No. individuals	7–9 22		2–3 [1]		8–12 [1]		9* 39		15–19 60		17** 11		23–24 12		1 7		2* 31		7 5		12–15 21		18–21 14		20* 10	
	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v	f	v
Lumbricidae	45	26	—	17	—	1	3	t	2	t																
Ephemeroptera			—	14	—	t									29	t	45	15			24	3			20	t
Hemiptera			—	t	—	t	33	1	2	t					29	t	35	t			10	t				
Homoptera					—	1	15	t	84	64	91	75	25	12	86	39	19	t	80	68	33	10				
Neuroptera			—	t	—	t	31	t									3	t			10	t				
Coleoptera	27	2	—	9	—	2	44	2	20	2			8	t	29	t	48	1			19	t				
Trichoptera			—	4	—	t	15	t					8	t	14	t	19	t			14	1				
Lepidoptera			—	7	—	1	33	t	2	t			17	1	57	3	55	3			24	2				
Diptera			—	10	—	2	44	3	7	t			17	t	43	1	48	3			14	t				
Hymenoptera			—	t	—	t	13	t	11	1					29	t	29	t			5	t				
Pisces	36	55	—	36	—	91	97	93	27	33	27	25	75	82	43	55	81	74	40	32	67	79	100	100	100	99
TOTAL	—	83[2]	—	97	—	98	—	99	—	100	—	100	—	99	—	98	—	96	—	100	—	95	—	100	—	99

t Designates trace volumes and numbers less than 0.5.

[1] Dates of composite chick samples; these samples are excluded from frequency of occurrence calculations.

[2] Low total volume due to presence of bird bones and egg fragments (8%), Decapoda exoskeleton fragments (3%), and debris (7%).

* Dates of Ile aux Galets samples.

** Date of Bird Island samples.

Orthoptera (1, 0.5 cc, trace, 0.4%): One grasshopper was recovered at Rogers City, but in 1975 Southern noted many in the diet.

Hemiptera (203, 9.5 cc, 0.2%, 12.5%): True bugs regularly included Pentatomidae, Nabidae, and Miridae.

Homoptera (1056, 645.0 cc, 16.7%, 29.9%): At Rogers City, 47% of the individual samples and 50% of the composite chick samples contained cicadas (Cicadidae: *Okanagana rimosa*). They appeared in the diet from 12 June to 12 July but were absent from Ile aux Galets samples. Ten of the 11 Bird Island samples contained 65 cicadas, accounting for 75% of the total volume. According to Moore (1966), this cicada is common to the pine barrens and pine-aspen woodlands on the Lake Huron side of northern Michigan but is unknown from the Lake Michigan shore. The Rogers City area cicada population is fairly regular in appearance with some emerging every year between mid-June and early July, although the life cycle between adult generations requires 9 or 10 years. We often observed large numbers of cicadas (alive and dead) floating in the lake or washed up on the beaches in the Rogers City area. T. E. Moore (pers. comm.) observed gulls taking *O. rimosa* from the ground and the water surface as well as "hawking" them in the air. Cicadas accounted for 25% of the diet volume at Rogers City. Leafhoppers (Cicadellidae) were occasionally present at Rogers City and Ile aux Galets.

Neuroptera (394, 2.0 cc, 0.1%, 5.5%): Virtually all lacewings (Hemerobiidae, Chrysopidae).

Coleoptera (886, 45.5 cc, 1.2%, 24.5%): The Carabidae was the most abundant family at both sites with ground beetles accounting for about 50% of the beetles at Rogers City, and 75% at Ile aux Galets. Next most abundant were Elateridae and Scarabaeidae. Although present in the diet of gulls throughout the sampling period, beetles (adults, larvae) were most abundant in May and early June (Table 1) and probably were acquired by gulls feeding in tilled fields.

Trichoptera (337, 8.0 cc, 0.2%, 8.7%): Most caddisflies were identified as Limnephilidae.

Lepidoptera (886, 38.5 cc, 1.0%, 18.0%): Moths were the only Lepidoptera recovered and most were members of the Noctuidae.

Diptera (4258, 57.5 cc, 1.5%, 19.3%): Chironomid midges, primarily *Chironomus* sp. in the pupal stage, were the most abundant dipteran at both colonies but particularly so at Ile aux Galets. Frequently mayflies and midges occurred in the same sample. Next most abundant were Anthomyiidae, Syrphidae, and various cycloraphan muscoids. Young Ring-billed Gulls, 5 weeks old and older, commonly turned over dead gull chicks in the colony and consumed fly larvae.

TABLE 2

MEAN PERCENTAGE VOLUME OF INSECTS AND FISH IN INDIVIDUAL RING-BILLED GULL REGURGITATIONS AT ROGERS CITY AND ILE AUX GALETS (1971)

ROGERS CITY

Sample dates No. individuals	7–9 May 22	15–19 June 60	23–24 June 12	1 July 7	7 July 5	12–15 July 21	18–21 July 14
Insects	trace[1]	89[2]	18	77	74	34	0
Fish	27[3]	11	80[3]	23	27	65	100[3]

ILE AUX GALETS

Sample dates No. individuals	9 June 39	2 July 31	20 July 10
Insects	4	20	trace
Fish	95[3]	76[3]	100[3]

[1] Balance of contents composed of earthworms (32 mean % volume—significantly greater than for insects for sampling period), egg fragments, bones and debris.

[2] Sample volume significantly greater than for fish for indicated sampling period.

[3] Sample volume significantly greater than for insects for indicated sampling period. Statistical significance ($P < 0.05$) determined by one-way analysis of variance on arcsine transformation equivalents.

Hymenoptera (185, 6.5 cc, 0.2%, 11.2%): Ants (Formicidae), largely winged, were most abundant with tenthredinid sawflies and ichneumonid wasps also being present.

Fish (689, 2915.5 cc, 75.5%, 62.2%): At Rogers City, 41 of the 141 individual samples contained smelt (77, 542.4 cc), 31 had alewives (62, 502.5 cc) and 20 included sticklebacks (172, 191.5 cc). Of the 80 individual samples from Ile aux Galets, 36 contained smelt (87, 672.5 cc), 30 included alewives (52, 397.0 cc) and 24 had sticklebacks (162, 161.0 cc). In the combined Rogers City samples, there were 4 yellow perch and 6 cyprinids; at Ile aux Galets there were 5 minnows.

Alewives and smelt consistently occurred in samples throughout the study, although smelt appeared to be the more abundant in May and June, and alewives predominated in July. Sticklebacks were most numerous in mid-July and ranked close to smelt in volume for the entire month of July.

Birds and bird eggs (NA, 9.0 cc, 0.2%, 0.8%): On 9 May at Rogers City, 1 sample contained gull egg shell and membrane fragments and another sample contained some bird bones of uncertain origin.

On numerous occasions, Southern has observed adult Ring-billed Gulls eating unattended eggs. Egg contents, because of soft consistency, would not show up during our sampling procedure and so the amount consumed cannot be determined. It is possible that adults observed consuming eggs were not breeding birds.

While banding chicks on Ile aux Galets in 1973, Southern noticed a 10-day-old chick that was apparently choking. Shortly after being picked up, it regurgitated a Ring-billed Gull chick that was about 1-day-old. On this same day, another Ring-billed Gull chick regurgitated 2 altricial nestlings, probably Red-winged Blackbirds (*Agelaius phoeniceus*). A few blackbirds nest on the island.

Mammals: In mid-May 1974, a vole (*Microtus*) was regurgitated by an adult Ring-billed Gull at the Rogers City colony. This is the only time in 12 years of cannon netting that Southern obtained evidence of this species feeding on rodents. Apparently this food source is exploited less in the Great Lakes Region than by Ring-billed Gulls in prairie regions of western Canada (see Vermeer 1970).

DISCUSSION

The mean percentage volume (Table 2) of earthworms, insects, and fish in Rogers City individual samples differed as the season progressed. Earthworms were the major food item in the May samples with fish ranking second and insects last. During 3 periods in June and July, insects were the major food item. The volume of insects increased from a trace in May to 89% on 15–19 June and ranged from 18 to 77% through 12–15 July (Table 2). Insect groups accounting for substantial percentages of total food volume were cicadas, mayflies, beetles, and dipterans (Table 1). Insects were present in 64% of the samples from all 3 colonies and represented 22% of the total volume of chick and adult samples. Smaller quantities of earthworms and insects were found in the Ile aux Galets samples suggesting that gulls at offshore colonies have less opportunity to exploit these food sources.

Fish were recorded during all 7 sampling periods although there were but 3 periods when fish composed the greatest sample volume. Smelt, alewives, sticklebacks, and unidentified fish flesh provided 76% of the total food volume and were present in 61% of the samples. Smelt decreased in frequency as the season progressed: May, 39% of volume; June, 45%; and July, 23%. This reduction may be associated with seasonal patterns of smelt movement between deep and shallow water (Lackey 1970). In contrast, alewife consumption increased as the season progressed: May, 4% of volume; June, 15%; and July, 37%. This could also be associated with spawning and seasonal movement patterns (Galligan 1962, Norden 1967). The proportion of alewives recorded during our study was less than reported for the mid-1960's (see Ludwig 1966), presumably because of a reduction in alewife abundance.

The quantity of sticklebacks in samples increased in late June, and during July represented 20% of the total volume and 71% of the total number of fish. McKenzie and Keenleyside (1970) reported that sticklebacks breed in shallow rocky water of northern Lake Huron at this time. Breeding activity in water 25–80 cm deep would make the fish available to gull predation.

At Ile aux Galets the dependence on fish appeared greater (88% of total volume compared to 11% insects). In fact, 71% of the total number of food items were aquatic and constituted 96% of the total volume while at Rogers City, 61% of the organisms were aquatic and represented 83% of the total volume. The greater dependence on aquatic food may be associated with the island colony being located 11.3 km from the mainland. Ile aux Galets birds appear to have a more diverse diet. Thirteen of the 20 major food categories were found in 10% or more of the individual samples while at Rogers City only 5 of the food categories were present in 10% or more of the samples.

In addition to seasonal variation, there is evidence of considerable daily variation. Time of day appeared to be correlated with the presence or absence of particular items. Although an accurate record was not maintained as to time of sample collection, general observations suggested a predominance of fish in early morning collections. Lower early morning temperatures probably made insects less available and increased the rate of fish capture. Therefore collection time could bias conclusions regarding food habits.

Weather conditions apparently influenced the availability of particular food items. For example, at Rogers City, mayflies were present in samples on 44% of the clear to partly cloudy days (< 50% cloud cover) and on only 14% of the overcast days (> 50% cloud cover). Neuropterans were present on 56% of the clear days and on only 14% of the overcast days. Lower temperatures and/or rain often accompanied overcast conditions and probably reduced the amount of insect activity. Under such conditions, Ring-bills showed increased use of fish. Alewives were present in samples on 78% of the overcast days but only 44% of the clear days.

In Ring-billed Gull food samples collected from 1963–67 at breeding colonies in lakes Michigan and Huron, Ludwig (1974) found 71% of the fish to be alewives, 20% smelt, and 9% various other fishes. He (1966) estimated that alewives provided 50–60% (wet weight) of the Ring-billed Gull's diet. Our 1971 data show that alewives constituted only 20% of all fishes eaten (24% of the total food volume); smelt, 27% (36% total volume); and sticklebacks, 50% (9% total volume). Although wet weight and volume are not comparable, our findings are substantially different from Ludwig's.

A possible factor underlying the differences between Ludwig's findings and ours could be the size of the various fish populations in the lakes. Smith (1970) reported a sharp decline in smelt and yellow perch in Lake Michigan as alewives became abundant in the late 1950's and mid-1960's. The smelt decline was at least partially a result of alewife predation on smelt fry. After the alewife population peaked, in about 1964 (Berst and Spangler 1973), smelt began to increase and presumably continued to do so after termination of Smith's study in 1968. If so, this could account for the larger proportion of smelt recorded during our study.

Smelt were originally established in the upper Great Lakes around 1923 as a result of introductions in Crystal Lake, Michigan from where they subsequently entered Lake Michigan. They were first noticed in Lake Huron at a point off Rogers City in 1925 and by 1941 they were known to visit every stream along the entire Georgian Bay during the spawning runs (Dymond 1944). After a massive dieoff in the early 1940's, prior to the alewife explosion in Lake Michigan, the smelt population was on the increase, although not nearly as rapidly as that shown by alewives in the 1950's and 1960's (Smith 1970). Perhaps the smelt introduction played a role in the pre-1940 reestablishment of the Ring-billed Gull as a successful breeding species on the Great Lakes (Southern 1974). The later abundance of alewives probably contributed to the more recent population increase as proposed by Ludwig (1974). As the Ring-billed Gull population has enlarged faster than that of the sympatric Herring Gull (Ludwig 1966), it is plausible that factors in addition to the availability of fish have contributed to the differential rate in population growth. From our findings on food habits, it appears that one of these factors may be the Ring-bill's supplemental dietary use of earthworms and insects during the nesting season. This additional energy source also may be of importance in maintenance of the present population.

Further changes in gull populations may occur as alewife and smelt populations respond to introductions of various predatory fishes, including coho salmon (*Onchorynchus kisutch*), chinook salmon (*O. tshawytscha*) and the resurgence of lake trout (*Salvelinus namaycush*).

SUMMARY

Regurgitated food samples were collected from Ring-billed Gulls at 2 breeding colonies on Lake Huron and 1 on Lake Michigan during May through July of 1964 and 1971.

Fish comprised 76% of the total diet volume, insects 22%, and earthworms 1%. By frequency of occurrence, fish appeared in 61% of the individual samples, insects in 64%, and earthworms in 5%. Frequency and volumetric data are provided for each major taxon.

Changes in diet were noted as the breeding season progressed. In May, June, and July, fish constituted 56%, 72%, and 84%, respectively, while for the same 3 months insects accounted for 2%, 28%, and 16% of the volume. Earthworms contributed 26% of the total May volume but declined to 1% in June and nothing in July. Food types in samples were indicative of aquatic, aerial, and terrestrial foraging. Food habits are discussed in relation to gull population dynamics on the Great Lakes.

Dietary differences were noted between gulls nesting at mainland and offshore sites. Fish accounted for 69% of the volume at Rogers City and 88% at Ile aux Galets; insects contributed 30% of the total volume at Rogers City and 11% at Ile aux Galets. There was a greater diversity of food items in the Ile aux Galets samples as well as a larger percentage of food of aquatic origin. The periods of peak abundance of the 3 fish species in the samples roughly coincided with the respective spawning seasons.

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LITERATURE CITED

Berst, A. H. and G. R. Spangler. 1973. Lake Huron: The ecology of the fish community and man's effect on it. Great Lakes Fish. Comm. Tech. Rep. No. 21. Ann Arbor, MI.

Dymond, J. R. 1944. Spread of the smelt (*Osmerus mordax*) in the Canadian waters of the Great Lakes. Can. Field Nat. 58:12–14.

Galligan, J. P. 1962. Depth distribution of lake trout and associated species in Cayuga Lake, New York. N.Y. Fish Game J. 9:44–68.

Lackey, R. T. 1970. Seasonal depth distributions of landlocked Atlantic salmon, brook trout, landlocked alewives, and American smelt in a small lake. J. Fish. Res. Board Can. 27:1656–1661.

Ludwig, J. P. 1966. Herring and Ring-billed Gull populations of the Great Lakes 1960–1965. Great Lakes Research Division, University of Michigan. Publication 15:80–89.

———. 1974. Recent changes in the Ring-billed Gull population and biology in the Laurentian Great Lakes. Auk 91:575–594.

McKenzie, J. A. and M. H. A. Keenleyside. 1970. Reproductive behavior of nine-spined sticklebacks in South Bay, Manitoulin Island. Can. J. Zool. 48:55–61.

Moore, T. T. 1966. The cicadas of Michigan (Homoptera: Cicadidae). Pap. Mich. Acad. Sci. Arts Lett. 51:75–96.

Mueller, H. C. 1965. Ring-billed Gulls feed on flying ants. Auk 82:504.

Munro, J. A. 1936. A study of the Ring-billed Gull in Alberta. Wilson Bull. 48: 169–180.

Norden, C. R. 1967. Age, growth and fecundity of the alewife, *Alosa pseudoharensus* (Wilson), in Lake Michigan. Trans. Am. Fish. Soc. 96:387–393.

Pettingill, O. S., Jr. 1958. Ring-billed Gulls hawking mayflies. Jack-Pine Warbler 36:154.

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99:754–765.

Southern, W. E. 1974. The annual range of Ring-billed Gulls in the eastern United States: with comments on potential bird/aircraft collision problems. Pp. 149–190, *in* Proc. Conf. Biol. Aspects of the Bird/Aircraft Collision Problem, Clemson Univ., (S. A. Gauthreaux, Jr., ed.). Air Force Office of Sponsored Research.

Vermeer, K. 1970. Breeding biology of California and Ring-billed Gulls: A study of ecological adaptation to the inland habitat. Can. Wildl. Serv. Rep. Ser. 12:1–52.

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OBSERVATIONS ON THE BREEDING BIOLOGY OF BLACK-BELLIED PLOVERS ON DEVON ISLAND, N.W.T., CANADA

David J. T. Hussell and Gary W. Page

Details of reproduction in many arctic shorebirds are poorly known, although excellent studies of some species have been published recently (e.g. Holmes 1966, Parmelee et al. 1968, Parmelee 1970, Jehl 1973). Particularly notable is the lack of data on growth of the young. Ricklefs' (1968, 1973) extensive compilations of growth rates in birds include only 5 species in the families Charadriidae and Scolopacidae. This dearth of information is undoubtedly related to the inaccessibility of many shorebird breeding ranges and to difficulties in studying breeding shorebirds under natural conditions.

In this paper we report on the breeding biology of the Black-bellied Plover (*Pluvialis squatarola*) at the northern limit of its known breeding range, on Devon Island. In North America this species breeds mainly in the high arctic region of Canada between 63°N and 76°N (Godfrey 1966), and on the north and west coasts of Alaska south to about 61°N (Gabrielson and Lincoln 1959). Some aspects of the breeding biology of the species have been described and earlier literature reviewed by Drury (1961), Parmelee et al. (1967), and Mayfield (1973). Our account is most complete for the later stages of breeding, including growth and development of the young, and tends to complement the work of other authors whose reports concentrate on the earlier events of the breeding cycle.

STUDY AREA AND METHODS

The study was conducted primarily between 7 June and 26 August 1968 on the Truelove Lowland (75°40′N, 84°35′W) about 24 km southwest of Cape Sparbo on the north coast of Devon Island. Additional data were collected there by Hussell and his assistants from 11 June to 14 August 1966, 9 June to 29 August 1967, and 8 June to 13 August 1969.

The Truelove Lowland is a coastal lowland situated between Jones Sound and the interior plateau of Devon Island (Fig. 1). It is traversed by a series of raised beaches, separated by numerous lakes, ponds, and poorly-drained meadows. Granitic and calcareous rock outcrops occur in several places. Plant life is sparse on the exposed beach ridges and outcrops, but is rich in the low-lying wet meadows. More detail on the topography and vegetation may be found in Bliss and Teeri (1971) and Barrett and Teeri (1973). At this latitude the sun remains above the horizon continuously from 27 April until 17 August. Summer temperatures rarely exceed 15°C and July temperatures average about 4°C. The breeding season of most birds on the Truelove Lowland is remarkably late, corresponding with a late melt (Hussell and Holroyd 1974).

In 1966 and 1967 most observations were made in the "census area" of about 308 ha shown in Fig. 1. General observations were recorded on Black-bellied Plovers and records

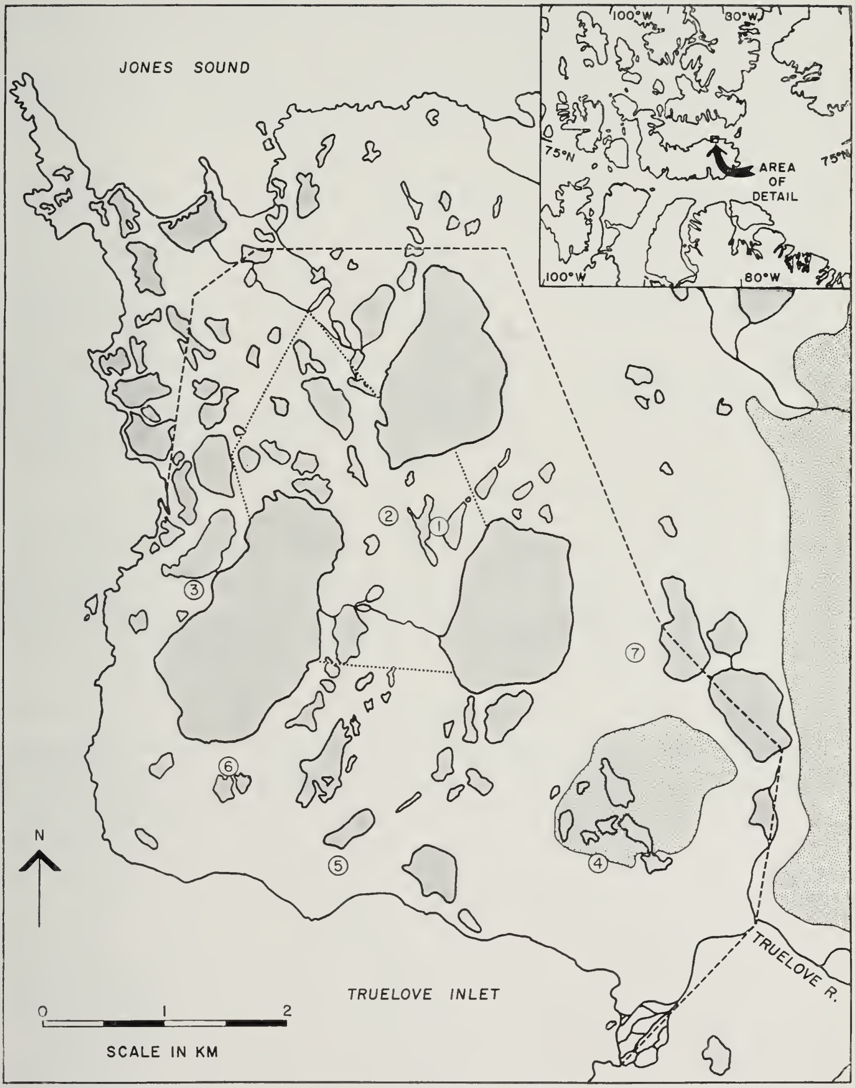

FIG. 1. Map of the Truelove Lowland, Devon Island. Numbered circles show locations of Black-bellied Plover nests found in 1968. Dotted and broken lines indicate limits of the "census area" and "study area," respectively (see text). Shaded areas are lakes or ponds. Land over 60 m elevation is stippled.

were kept of all nests. In 1968 a wider "study area" of 1940 ha was covered regularly (Fig. 1) and an effort was made to locate all plover nests in this area. From late July until our departure that year, Page spent most of his time working on plovers. In 1969 the census area and the eastern and central ⅔ of the study area were covered regularly, but although special attention was paid to the plovers, considerably less time was devoted to them than in the previous year.

Seventeen nests and 1 additional brood were located in the 4 years. On 31 July and 1 and 2 August 1968 we watched a nest from a blind during hatching, including 21 hours of continuous observation. At other times to observe plover behavior we concealed ourselves as best we could in the open habitat favored by the birds. Eggs found during the laying period were individually marked with ink, and laying and hatching times determined by repeated observations of the nests. During incubation we often avoided approaching nests closely as we thought that our visits might attract predators to the nests. Young plovers were banded when they were first found, usually within 24 h of hatching. Development was studied by measuring and weighing the young whenever they were found, and by collecting a series of known-age young. Eggs and young were weighed to the nearest 0.1 g with Pesola spring balances or an Ohaus triple-beam balance. Specimens are in the Museum of Zoology, University of Michigan, and nest records are in the Prairie Nest Records Scheme, Manitoba Museum of Man and Nature, Winnipeg.

In this paper "clutch size" refers to completed clutches determined by observations of the same number of eggs in a nest at 2 visits at least 48 h apart, or by a single observation of the number of eggs less than 25 days before the young hatched. "Incubation period" is the time from laying to hatching for the last egg in a clutch. "Fledging period" is the time from hatching to first flight for an individual bird. Times are in Mean Solar Time for the locality concerned.

RESULTS

Arrival and pre-nesting activities.—In the 4 years 1966–69, Black-bellied Plovers were first observed on the Truelove Lowland on 11, 12, 11, and 14 June, respectively. Most early arrivals were males, distinguished from females by their more boldly marked plumage (Van Tyne and Drury 1959). The majority of females arrived a few days after the males and by about 20 June each year pairs were scattered over the lowlands.

On Devon Island arrival dates are later than for most other parts of the breeding range (Table 1). At the southern limit of the range in western Alaska, Black-bellied Plovers arrive by the second week of May. They appear in the first week of June at many places in the Canadian arctic, and on Bylot Island (73°N), near the northern limit of the range, first arrivals are as late as on Devon Island.

Flight displays were observed infrequently each year, from as early as 12 June until late June. We have nothing to add to the descriptions of Drury (1961) and Parmelee et al. (1967) on the form of the display.

Copulation was observed by Hussell on 21 and 22 June 1969. In the first case the male, with head stretched out horizontally and wings drooped, ran quickly towards the female and straight onto her back, remained for about

TABLE 1

ARRIVAL DATES OF BLACK-BELLIED PLOVERS AT VARIOUS NORTH AMERICAN LOCALITIES

Locality	Latitude (°N)	No. of years	First arrival (range)	Sources
Devon Island	76	4	11–14 June	This study
Bylot Island	73	2	15–17 June	Tuck and Lemieux (1959) Drury (1961)
S. Banks Island	72	2	end of May–1 June	Manning et al. (1956)
Cambridge Bay, Victoria Island	69	3	28 May–4 June	Parmelee et al. (1967)
Jenny Lind Is.	69	1	4 June	Parmelee et al. (1967)
Southampton Is.	64	1	9 June	Sutton (1932)
Hooper Bay, Alaska	62	1	9 May	Brandt (1943)

20 sec while copulation occurred and then flew off to a distance of about 40 m. The male behaved similarly in the second case, except that during the run towards the female his head appeared more withdrawn. The tail was held slightly below the horizontal. This time the male remained on the female for about 30 sec, then flew about 10 m away. No special postures by the female were noted. The male's behavior was similar to the "rushing" which sometimes preceded copulation and often followed flight displays of Black-bellied Plovers on Victoria Island (Parmelee et al. 1967). The preliminary behavior of the adults prior to the copulations observed on Devon Island was not seen.

The pair observed copulating on 21 June was believed to be from Nest 3/69, which we found on 1 July. From hatching dates we estimate that the first egg was laid in it on 25 June. The pair seen copulating on 22 June was near the site of Nest 1/69, which contained 2 eggs when found on 26 June. The first egg in this nest was probably laid on 24 June.

Nest sites and breeding density.—Nests were depressions in the ground in relatively dry sites on or near raised beach ridges, and often on a prominent part of a ridge. Nest sites were usually on gravelly ground, sometimes with large boulders nearby, and typically sparsely vegetated with lichens, tufts of *Dryas integrifolia*, *Saxifraga oppositifolia*, *Salix arctica*, sedges (Cyperaceae) and grasses (Gramineae). Although many of these sites were among the first places free of snow in the spring, egg-laying did not usually start until the snow had disappeared from considerably wider areas (see Fig. 7).

We probably located all of the nests in the study area in 1968. Seven nests were found, but there were probably only 6 pairs of plovers, since the eggs

TABLE 2

BREEDING DENSITIES OF BLACK-BELLIED PLOVERS ON DEVON ISLAND

Year	Area[1]	No. of territories[2]	Density pairs/km^2
1968	S	6.5	0.34
1966	C	2.0	0.65
1967	C	3.0	0.97
1968	C	1.0	0.32
1969	C	1.5	0.49
mean	C	1.9	0.61

[1] "C" is the census area of 308 ha and "S" is the study area of 1940 ha (see Fig. 1 and text).
[2] No. of territories estimated from nests and broods found. Nests near the border of the area are counted as 0.5 territory. Numbers of nests involved for the census area are as follows: 3 in 1966; 4 in 1967; 1 in 1968; and 2 in 1969. For the study area in 1968, see text.

in Nest 1 disappeared before laying began in nearby Nest 2. One pair probably bred just outside the study area, as we found 2 large unbanded young from a previously undetected brood in the northwestern portion of the area on 23 August. Thus we count 6.5 pairs in the study area, giving a density of 0.34 pairs per km^2.

Estimated densities of breeding pairs in the census area each year are shown in Table 2. Densities were higher in 1966 and 1967 than in the following 2 years, a situation which was similar in Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*), and may have been related to the early melt in the first 2 years (Hussell and Holroyd 1974). We do not know whether breeding densities were higher for the entire lowland in 1966 and 1967, but the data in Table 2 support the idea that the density of 0.34 pairs per km^2 for the study area in 1968 may be lower than average for the Truelove Lowland. In 1969, only 3 nests were found in the study area. The wide distribution of these nests and absence of other territorial birds indicated that overall densities were at least as low as in 1968. In summary, the evidence suggests that densities of 0.3–1.0 pairs per km^2 are normal on the Truelove Lowland.

Breeding densities on Devon Island were similar to those on Victoria Island, but on Jenny Lind Island estimated densities were 1.2–2.3 pairs per km^2 (Parmelee et al. 1967). Drury (1961) found 4 nests in an area of less than 0.5 km^2 on Bylot Island.

Laying, incubation and hatching.—Black-bellied Plovers laid 4 eggs at approximately 36 h intervals on Devon Island (Fig. 2). Thus about 4½ days elapsed between the laying of the first and last eggs in a clutch. Our observations are consistent with the hypothesis that the 4th egg was always

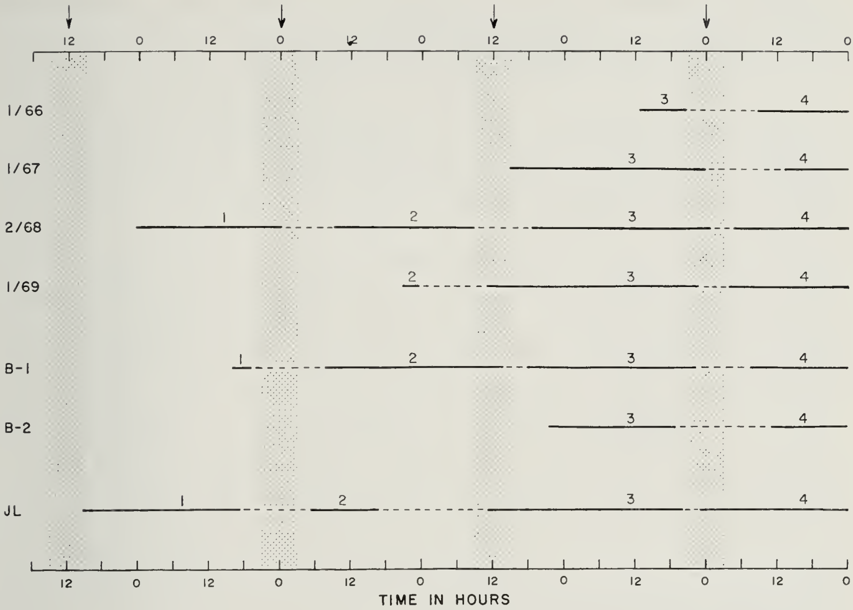

Fig. 2. Timing of egg-laying in 4 Black-bellied Plover nests on Devon Island, 2 on Bathurst Island (B-1 and B-2) (H. F. Mayfield, pers. comm.), and one on Jenny Lind Island (JL) (D. F. Parmelee, pers. comm.). Solid lines represent periods when indicated number of eggs were known to be present; dotted lines show periods during which egg-laying occurred. Arrows and stippled areas show hypothesized times of egg-laying. Nest histories are placed so that the night of clutch completion is below the right-hand arrow.

laid within about 3 h of midnight, and the 3rd, 2nd, and 1st eggs were laid within 3 h of noon, midnight, and noon, respectively. Records for 1 nest on Jenny Lind Island (Parmelee et al. 1967, and D. F. Parmelee pers. comm.), and 2 nests on Bathurst Island (H. F. Mayfield pers. comm.) also conform to this pattern.

We agree with other authors that completed clutches are almost invariably of 4 eggs. During our study 12 nests had completed clutches of 4 eggs, and 3 other nests containing 4 eggs were destroyed before we could determine if the clutch was complete.

During the laying period we found only the adult male in attendance at the nest, but after the clutch was complete both sexes shared incubation duties. On 5 occasions during the laying period the male was observed sitting on an incomplete clutch and on 7 occasions standing near the nest, but often no adult of either sex was found in the vicinity.

Table 3

Air Temperatures During Egg-laying

Nest(s) and year	Egg-laying dates	Daily temperatures °C[1] Minimum Mean and Range	Daily temperatures °C[1] Maximum Mean and Range
All 1966	20–28 June[2]	+0.7 (−2 to +1)	+6.0 (+5 to +8)
All 1967	19 June–3 July	+1.7 (−1 to +4)	+5.0 (+2 to +8)
All 1968	26 June–6 July	−0.7 (−4 to +1)	+2.1 (0 to +6)
All 1969	22 June–30 June	−0.8 (−3 to +1)	+3.1 (+1 to +6)
No. 2 1966	23–28 June	+1.3 (+1 to +2)	+6.1 (+5 to +8)
No. 2 1968	1–6 July	−1.6 (−3 to 0)	+2.6 (0 to +6)

[1] For methods see Hussell and Holroyd (1974).
[2] Temperatures for 22–28 June 1966, only.

That the incomplete clutch is partially incubated by the male and is often left unattended, raises the question of whether the eggs are in danger of chilling during the egg-laying period. Air temperatures during the known egg-laying season each year, and for Nests 2/66 and 2/68 (each of which had hatching periods of over 30 h—see below) are shown in Table 3. Daily minimum temperatures averaged close to 0°C but never fell below −4°C during the laying period.

Males were observed incubating completed clutches on 12 occasions compared to 5 for females. In 8 of the 12 instances when the male was incubating, however, he went to the nest after we visited it and may not have been incubating when we first approached. Males were observed alone near the nest on 13 occasions during the incubation period compared to 4 for females. Höhn (1957) found only the more brightly-colored adult (presumably the male) on the nest during incubation and Drury (1961) found that the male did most of the incubating on Bylot Island. In contrast, Mayfield (1973) reported that the female at one nest on Bathurst Island incubated 60% of the time during 23 hours of observation near the middle of the incubation period. Bent (1929) and Sutton (1932) state that both sexes incubate after the clutch is complete; Parmelee et al. (1967) agree, but note that the female is more reluctant than the male to incubate when a person is near the nest, an observation with which we concur. Considering the difficulty of seeing the drab females at a distance and their reluctance to go to the nest when an intruder is nearby, we think that incubation may be shared more equally by the sexes than our observations indicate.

The incubation period was determined to be about 27 and 26.5 days at 2 nests on Devon Island. At Nest 2/68 the incubation period was between 26 days, 22 h, 41 min and 27 days, 2 h, 36 min; and at Nest 1/69 it was between 26 days, 6 h, 25 min and 26 days, 22 h. At 2 other nests the last young hatched about 26 days after the completed clutch was found. Mayfield (pers. comm.) determined 2 incubation periods of 26 days, 17 h (± 8 h) and 27 days, 8 h (± 4 h) on Bathurst Island, N.W.T., in 1973. These data, together with two 27-day periods reported by Holmes and Black (1973), add weight to Mayfield's (1973) conclusion that the incubation period is usually 26–27 days and reports of shorter periods are probably erroneous.

The 4 eggs in a clutch usually hatched over a period of 1 or 2 days, indicating that there may have been effective incubation before the clutch was complete, as suggested by Parmelee et al. (1967). In Nests 2/66 and 2/68 the hatching periods were at least 30 h and about 36 h, respectively. In Nest 2/68 the eggs hatched in the order in which they were laid. The first young hatched was about 1 h old when we first saw it, and its down was still wet. The second egg hatched 6 h and 35 min later, the third 12 h and 49 min after the second, and the fourth 15 h and 35 min after the third (based on times of shell removal). At 2 other nests the last eggs hatched at least 24 and 11 h after the others. Drury (1961) reports that the eggs of the Black-bellied Plover hatch over a 2-day period, and Parmelee et al. (1967) generally agree, stating that the hatching period is usually between 24 and 48 h and only occasionally less than 16 h. Mayfield (1973) reported a hatching period of about 12 h in 1 nest.

At least 41 young hatched from 17 nests on Devon Island during our study. Five nests were destroyed during the incubation period, young hatched in 11 nests, and the fate of 1 nest was unknown. Four young were hatched in each of 9 nests not destroyed by predators, 3 eggs hatched in another and the 4th was infertile, and at least 2 hatched in the remaining nest. Based on the 15 nests for which full data are available, the plovers hatched an average of 2.6 young per nest.

Nesting success can be calculated more precisely on the basis of exposure (Mayfield 1961). The rate of loss of nests was 0.022 per nest-day after clutch completion, which represents a survival rate of 54.7% over the 27-day incubation period. Hatching success of individual eggs which survived the incubation period was 97.5% (39 out of 40), which gives an overall hatching success of 53.3% or 2.1 young hatched per completed clutch.

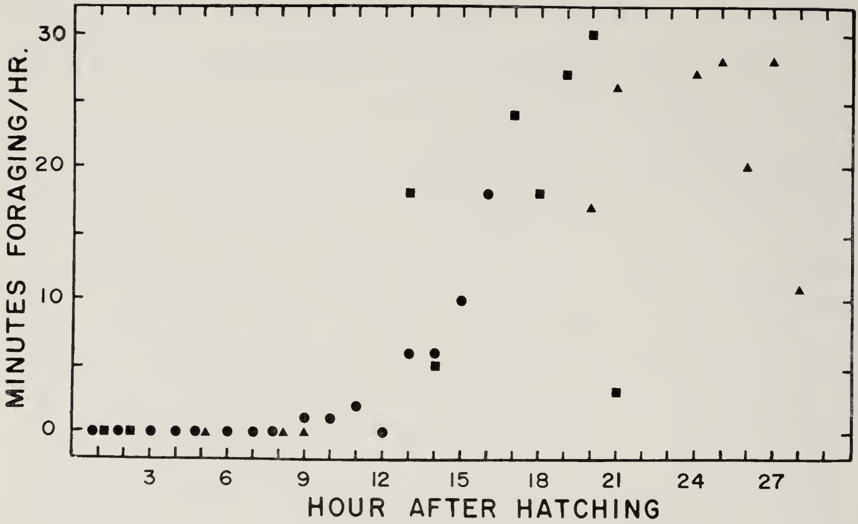

FIG. 3. Development of foraging behavior in young at Nest 2/68. Symbols show time spent away from brooding adult in relation to age: triangles, first hatched young; squares, second hatched young; circles, third hatched young.

Behavior during the hatching period.—At Nest 2/68 we saw eggshell removal by the adult female and the adult male after hatching of the 3rd and 4th eggs, respectively. In each case the bird picked up the shell and flew away with it. We did not determine the exact interval between hatching and shell removal in any case, but in only 3 other instances did we see shells in the nest with newly-hatched young, indicating that shells are removed quickly. Mayfield (1973) reported that shells were removed "within minutes after the young bird broke free."

The chicks remained in the nest for several hours after hatching while their down dried. Intensive observations at Nest 2/68 showed the progressive development of effective locomotory abilities and feeding behavior in the young (Fig. 3). The third chick hatched in this brood first left the nest 8 h and 25 min after hatching but returned under the brooding adult less than 1 min later. It appeared weak and stumbled frequently. During the next hour it made another short trip and pecked at something. In successive trips, this chick remained away from the brooding adult longer and strayed farther from the nest; by the time it was 13 h old it was definitely feeding.

On their trips from the nest, individual chicks foraged alone and were not assisted by adults in obtaining food. One young plover was observed pecking at a large midge (Chironomidae), but it hesitated and the midge escaped.

On another occasion a chick eyed a caterpillar near our blind. It turned away and moved off only to return seconds later and eye the caterpillar again. In this instance the bird did not attempt to eat it, but later one young plover, perhaps the same one, picked up a caterpillar and swallowed it after dropping it several times. On these feeding trips, the movements of the young were very like those of foraging adults—run, stop, peck. By the time the young were 24 h old they were venturing as far as 40 m away from the brooding adult.

During the observation period at Nest 2/68 the male spent 12 h and 13 min on the nest brooding the young compared to 7 h and 34 min spent by the female. The differing dispositions of the sexes to return to the nest after a disturbance may partially account for the greater amount of time we observed the male at the nest. The male returned to the nest 11 times after our activities had driven the brooding adult away, compared to only once for the female under similar circumstances.

The adults usually brooded quietly on the nest during the foraging trips of the young, but both sexes often used a quiet quivering trill when a chick was about to enter or leave the nest. At other times this note appeared to stimulate the chicks to come to the parent, particularly when a chick began peeping at some distance from the brooding adult. On the 3 occasions when this happened the adult responded with the trill note and the young plover returned to the parent brooding on the nest. When the adults had been disturbed by our activities and the young plovers were scattered nearby, one parent often brooded away from the nest while the other brooded on the nest. This occurred on 4 occasions when our activities caused all but the most recently hatched young to be away from the nest for an unusually long time.

When a person approached the nest either the brooding or the off-nest parent called in alarm when the intruder was as much as 250 m away. As the intruder came closer, one adult (usually the off-nest bird) flew to meet him and continued to call in alarm. Before he had approached to within 50 m of the nest, the brooding adult left and joined its mate, and the oldest chicks fled and crouched motionless nearby until the disturbance had passed. Close approach often elicited distraction behavior from the adults, as described by Drury (1961).

There was no noticeable difference in the reactions of adult male and female Black-bellied Plovers to predators near the nest at hatching, but their reactions were related to the species of predator and its behavior. In 2 instances when Glaucous Gulls (*Larus hyperboreus*) flew over the nest one of the parents called in alarm but made no attempt to chase the gulls. Long-tailed Jaegers (*Stercorarius longicaudus*) flew over on 4 occasions but did

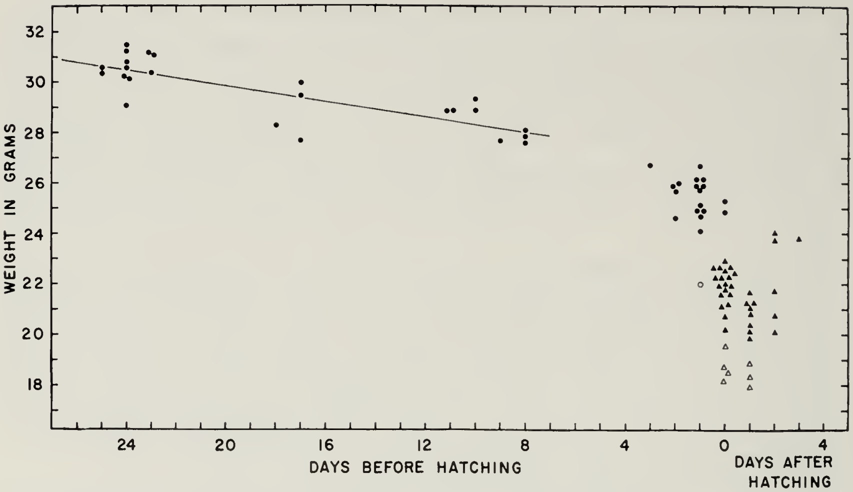

FIG. 4. Weights of eggs and newly-hatched young in relation to hatching date. Circles show weights of eggs; triangles, weights of young. Open symbols indicate weights of young and an egg in Nest 7/68. The line is a linear regression fitted to the data for eggs more than 7 days from hatching (see text).

not elicit any reaction from the plovers, other than causing the brooding female to flatten on the nest on one occasion. When a Long-tailed Jaeger landed near the brooding male, however, the female appeared quickly and chased the jaeger off. In contrast to the mild response to airborn Long-tailed Jaegers, on the only occasion when Parasitic Jaegers (*Stercorarius parasiticus*) flew over the nest, the male called several times in alarm, left the nest, and chased the jaegers until they left the vicinity.

After the last-hatched young had been brooded for several hours the plovers deserted the nest. At Nest 2/68 this occurred sometime between 8 and 15 h after the 4th egg hatched.

The behavior of Black-bellied Plovers at the time of hatching is poorly documented in the literature. Parmelee et al. (1967) found that both sexes were equally solicitous of the newly-hatched young at nests on Victoria Island and that after the young deserted the nest there was no evidence that they ever returned. Their findings are supplemented by Drury's (1961) observation that the young spent 1 night in the scrape after all had hatched in the 1 nest he examined. Mayfield (1973) mentions that while other young were hatching, the earlier hatchlings ventured only as far as 20 cm out of the nest and alternated sleep with vigorous activity within and outside the nest. His observations of the behavior of the young appear to correspond

TABLE 4

GROWTH OF YOUNG BLACK-BELLIED PLOVERS FROM HATCHING TO FLEDGING

UMMZ No.	Nest No./Yr.	Age Minimum days–hr	 Maximum days–hr	 Est. days	Sex	Weight g	Tarsus mm	Culmen mm	Wing chord mm	Outer primary mm	Outer rectrix mm
212791	2/66	0–02	0–23	0.5	–	–	33.4	12.6	–	–	–
215889	4/67	0–01	1–02	0.5	M	19.8	32.3	12.5	–	–	–
215906	4/68	3–00	4–02	3.1	F	23.6	34.1	13.1	–	–	–
215907	7/68	6–04	7–02	6.5	F	35.1	36.2	15.4	–	1	–
215908	6/68	6–02	7–03	6.7	F	48.0	37.1	16.9	–	6	–
215909	7/68	12–02	–	12.5	F	84.9	42.0	20.0	66	27	8
215944	1/69	17–23	–	18.4	M	154.0	45.0	25.3	116	64	28
215911	2/68	20–09	20–09	20.4	M	158.2	46.4	24.1	123	71	34
215910	7/68	20–22	–	21.4	M	152.8	43.3	23.5	117	61	27
215912	2/68	23–08	23–08	23.3	M	186.9	45.7	25.1	137	81	37
	–	–	–	5.0[1]	M	32.2	37.0	15.5	–	–	–
Full-grown birds (means)					M	185.0[2]	45.5[3]	27.8	183	126	70
					F	168.4[4]	43.8[5]	26.8	177	125	67

[1] Data for specimen from Jenny Lind Island (Parmelee et al. 1967:221).

[2] Mean weight of 1 young male in the Royal Ontario Museum (R.O.M.) from N.W.T. in September and 2 fledged males from N.W.T. in August from Parmelee et al. (1967).

[3] Mean measurements of 7 young males in R.O.M. from N.W.T. and Ontario in September.

[4] Mean weight of 1 young female in R.O.M. from N.W.T. in September and 3 fledged females from N.W.T. in August from Parmelee et al. (1967).

[5] Mean measurements of 7 young females in R.O.M. from N.W.T. and Ontario in September.

with ours for chicks less than 12 h old; that he did not see greater activity by the young is probably related to the shorter hatching period (about 12 h) and time spent at the nest (less than 15½ h) for the brood he observed.

Development and fledging of the young.—During the chick's embryonic development, the weight of the egg decreased by nearly 20% (Fig. 4). Twelve eggs weighed within 5 days of clutch completion averaged 30.6 g (S.D. = 0.6 g) in contrast to 12 pipped eggs which averaged only 25.2 g (S.D. = 1.3 g) on the day prior to hatching. The mean weight of fresh eggs is estimated at 31.0 g (S.D. = 0.26 g) and the average rate of weight loss is about 0.15 g/day during the first 20 days of incubation.

Twenty-three newly-hatched young (less than 1 day old) weighed considerably less than the pipped eggs, averaging 21.4 g (S.D. = 1.4 g). After hatching the young decrease in weight for several hours. The first chick hatched in Nest 2/68 weighed 20.7 g when about 3 h old, was down to 20.1 g at 18 h and had increased again to 20.7 g at 39 h. Likewise, the 3rd chick in Nest 1/69 weighed 21.9 g about an hour after hatching, was 0.7 g lighter 11 h later, but had regained 0.5 g after an additional 10 h. This trend of weight loss followed by recovery during the first 48 h after hatching can also be detected in Fig. 4.

The yolk sac was large in newly-hatched young and it had not entirely disappeared in 1 chick which was between 3 and 4 days of age. The contents of the yolk sac provide nourishment for the chick for the first day or 2 after it hatches and is learning to forage.

Eggs and newly-hatched young in Nest 7/68 were substantially lighter in weight than those in any other nest we observed (Fig. 4). On the day of hatching the 4 young averaged 18.8 g, about 12% below the mean for all newly-hatched young. This difference apparently persisted throughout the development of the young from this brood (see below).

Weight increased rapidly throughout the fledging period (Table 4, Fig. 5) and the value of *K* for a fitted logistic curve (Ricklefs 1967) is 0.194 with an asymptote of 205 g. The primaries and rectrices grew rapidly after about the 6th and 10th days, respectively, but the bill and tarsus, which were already well developed at hatching, grew more slowly. There was no trace of the juvenal plumage on the freshly-hatched downy young (Fig. 6). By the

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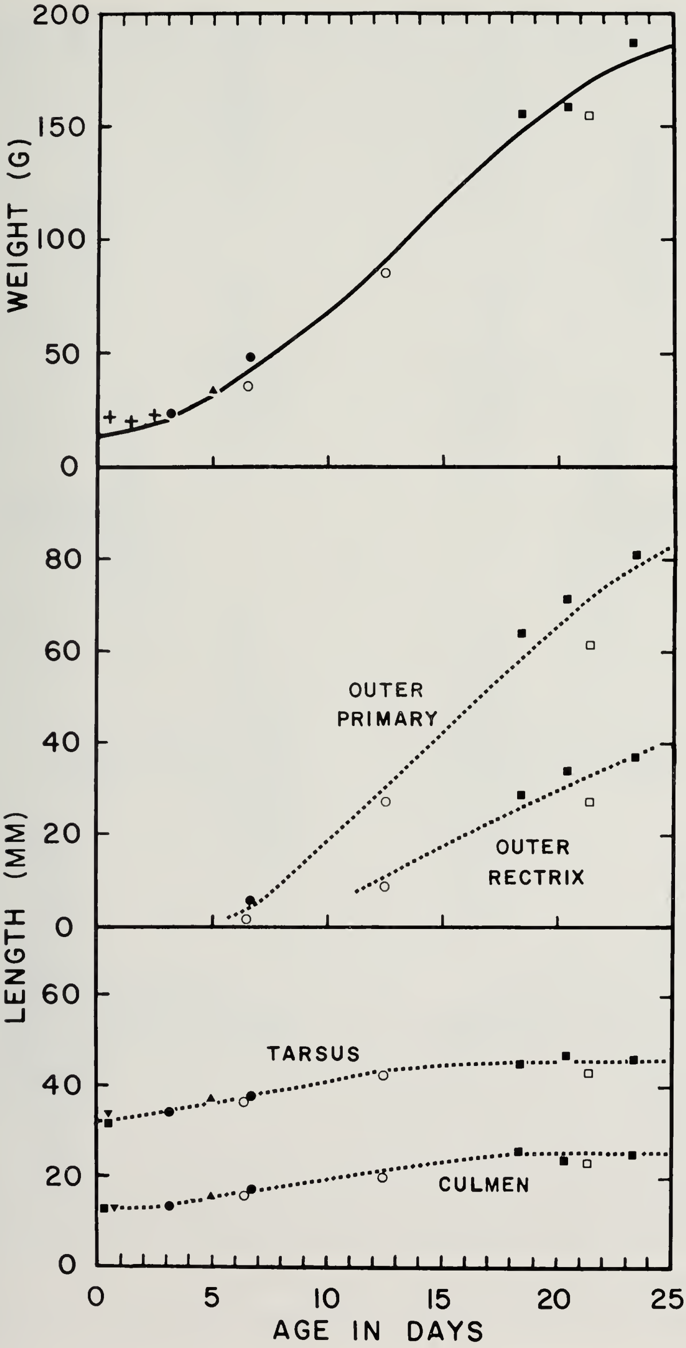
FIG. 5. Growth of young Black-bellied Plovers: squares—males; circles—females (open symbols are for young from Nest 7/68), triangle—data for one male on Jenny Lind Island (from Parmelee et al. 1967:221). Crosses indicate mean weights of 23, 11, and 5 young which were known or estimated to be 0–24, 24–48, and 48–72 hours old, respectively. The curve for growth in weight is a logistic fitted to the mean and individual weights of young more than one day old. All other curves were fitted by eye.


WEIGHT (G)
0
50
100
150
200
LENGTH (MM)
0
20
40
60
80
OUTER PRIMARY
OUTER RECTRIX
0
20
40
60
TARSUS
CULMEN
0
5
10
15
20
25
AGE IN DAYS

3rd day after hatching, however, the sheaths of the dorsal and ventral body feathers were visible beneath the skin and the primary feather sheaths were beginning to protrude through the skin. In a 6–7-day-old young (UMMZ No. 215,908), feather sheaths were protruding from the breast, abdomen, upper back and wings, and the 10th primary was 6 mm long. Juvenal feathering was noticeable over the entire body of a bird 12–13 days old (UMMZ No. 215,909), but the overall appearance was still that of a large downy young. The juvenal plumage is prominent in young 18–23 days old, with progressively less down adhering mainly to the nape, rump and underparts. There was considerable individual variation in growth rate and it was particularly noticeable that young from Nest 7/68 were retarded both in weight increase and feather development compared to birds from other broods.

The fledging period was determined as 23 days for 1 young plover in 1968. Although this bird's flight feathers were still growing, it made uninterrupted flights of about 150 m when it was 23.3 days old (UMMZ No. 215,912). Other chicks about 18.4, 20.4, and 21.4 days of age made no attempt to fly and were captured by hand.

Both parents were observed brooding young for up to 2 days after the chicks left the nest. The adults probably brooded older young but we did not see it. During the fledging period the adults acted as sentinels, using alarm calls to warn their foraging offspring of approaching danger. In response to the alarm calls, the young usually crouched motionless and consequently were difficult to find. They evidently fed in moist, grassy areas judging from the locations where specimens were collected, and the broods usually remained within about 1.5 km of the nest site. One young from Nest 7/68, however, was found about 3 km away when it was 21 days old.

The female parent deserted the brood before the male. In 1968 a female was last seen with a brood when the chicks were about 12 days old. In contrast, a male was still with young which were 23 days old. That year the last adult female was seen on 17 August, but males were still present on 25 August when we left. Parmelee et al. (1967) found that adult males sometimes attended fully fledged juveniles on Victoria Island; but adults of both sexes abandoned the nesting grounds soon after the young fledged, before the latter departed. We left Devon Island too early to determine when adult males deserted their broods and the Truelove Lowland, or when the young left the area.

Timing and length of breeding season.—Assuming that laying, incubation, and fledging periods are 4.5, 27, and 23 days, respectively, we can estimate the dates of the main events in the breeding cycle for the majority of the Black-bellied Plover nests on Devon Island (Fig. 7). The entire cycle, from laying of the first egg to fledging of the last young occupies about 55 days

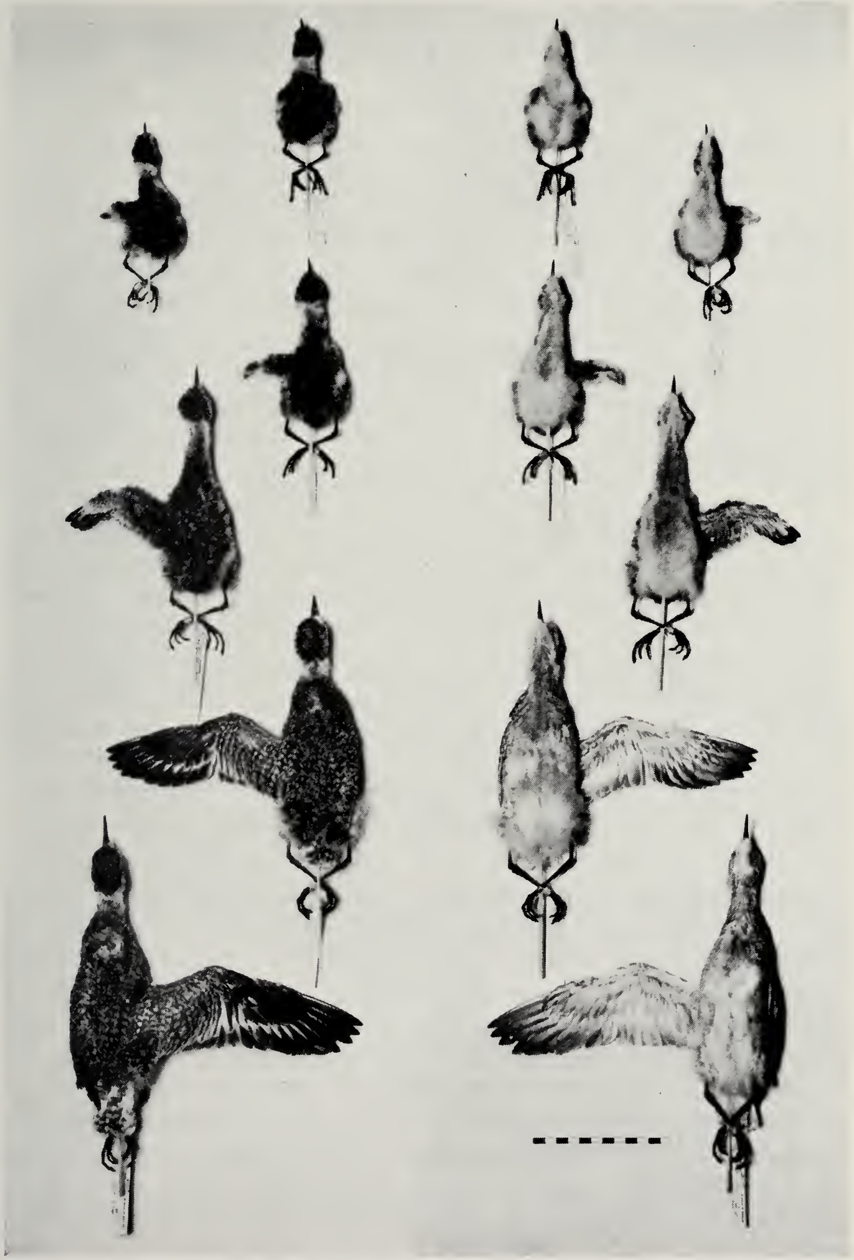


FIG. 6. Specimens of young Black-bellied Plovers collected on Devon Island. Known or estimated ages (from top to bottom) are 0.5, 3.1, 6.7, 12.5, 18.4, and 23.3 days (UMMZ Nos. 212791; 215906; 215908; 215909; 215944; and 215912). Each division on the scale at lower right is 1 cm.

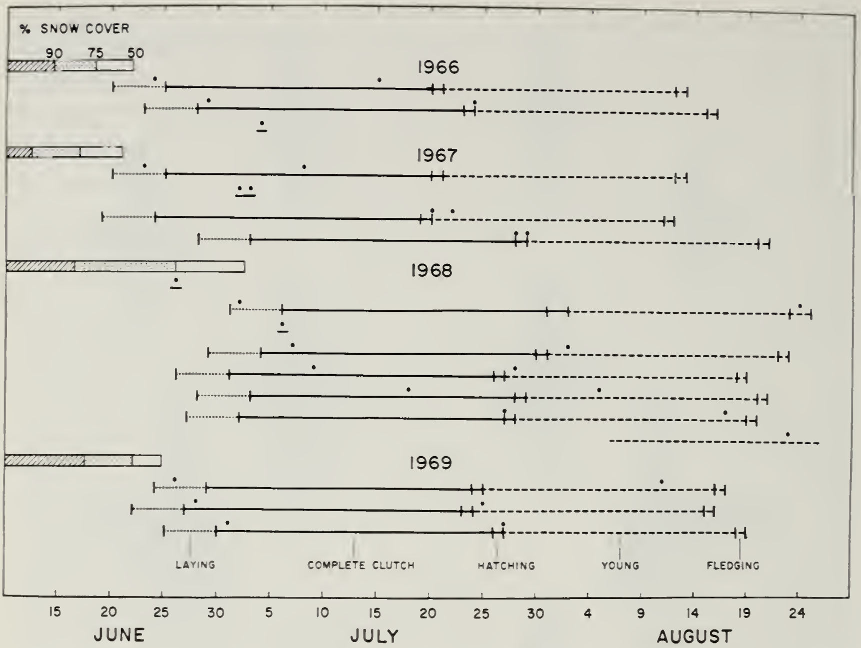


FIG. 7. Breeding phenology for 18 Black-bellied Plover nestings on Devon Island. Projected dates of laying, hatching, and fledging are shown for all nests for which sufficient information is available, including those known to have been lost to predators. See text for methods of calculation. Dates of first and last observations of a clutch or brood are indicated by a dot above the record for that nesting. Percent snow cover is based on estimates for the land surface within the "census area."

for a single nesting and about 68 days for the population as a whole. Median dates (and ranges) for starting laying, last egg hatching, and last young fledging were 25 June (19 June–1 July), 27 July (20 July–2 August), and 19 August (12–25 August), respectively. Although the sample is small, it appears that breeding was generally delayed in the cold, late season of 1968, and was more closely synchronized in any one year than indicated by the overall range of 13–14 days for all years.

At Cambridge Bay and at Jenny Lind Island, N.W.T., breeding apparently starts 7 to 10 days earlier than on Devon Island (Parmelee et al. 1967). Eggs from a "late nesting" on Jenny Lind Island hatched 26–28 July, which approximates the median date for Devon Island nests. Bylot Island hatching dates at 3 nests were 26–29 July and at another 22–24 July (Drury 1961), indicating that breeding is as late as on Devon Island. At these high arctic localities many young are not fledged until after the 3rd week of August and they may face severe problems in completing their growth and mobilizing energy for migration prior to the onset of adverse weather conditions.

DISCUSSION

Among the shorebirds, sandpipers exhibit a wide range of breeding systems (Pitelka et al. 1974) but plovers, and apparently other Charadriidae, are relatively uniform: they are usually monogamous and parental duties are shared almost equally by the sexes. This appears to be true for the Eurasian Golden Plover (*Pluvialis apricaria*) and the American Golden Plover (*P. dominica*), as well as for the Black-bellied Plover (*P. squatarola*), and perhaps for the majority of species in the genus *Charadrius* (Palmer 1967). The Dotterel (*Eudromias morinellus*) is polyandrous, however, and males take the major share of incubation and parental care (Pulliainen 1970, Nethersole-Thompson 1972); while Mountain Plovers (*Charadrius montanus*) often lay 2 clutches in quick succession, the first incubated by the male and the second by the female (Graul 1974).

Pitelka et al. (1974) have explored the ecological determinants of social systems and sexual dimorphism in sandpipers, and Norton (1972) has studied relationships between the mating system and incubation behavior, but relatively little attention has been given to the interaction between energetic factors, such as egg size and growth of the young, and the social system in birds with precocial young. Parmelee and Payne (1973) point out that laying of multiple clutches in both Temminck's Stint (*Calidris temminckii*) and Sanderling (*C. alba*) is associated with unusually small eggs relative to body size, and the same is true of the Dotterel and Mountain Plover (Graul 1974). Unfortunately growth rates of most shorebirds are so poorly known that it is difficult to assess the significance of the developmental patterns of the few species which have been studied.

The *Pluvialis* plovers have exceptionally large eggs (16–20% of body weight) for their size (Lack 1968:206, 210). Within a period of 4½ days the female Black-bellied Plover lays a clutch of eggs which weighs approximately 70% of her body weight. To produce these eggs she probably must spend a large proportion of her time feeding, so it is not surprising that only the male incubates during the egg-laying period.

Hatching is usually thought to be highly synchronous in shorebirds, but this was not true of Black-bellied Plovers; asynchrony extended to as much as 36 h in some nests. That the hatching period is not longer is no doubt due to incubation being incomplete (by the male alone) during the laying period. It is often assumed that there is strong selection for synchronous hatching in birds with precocial young, because it would tend to facilitate parental care (Lack 1968). In the Black-bellied Plover there was no evidence that late hatching eggs were abandoned, as Jehl (1973) reported for the Stilt Sandpiper (*Micropalama himantopus*). Although precise documentation is sparse, asynchrony in hatching of as much as 24 to 36 h may not be unusual in the Charadriidae, but there appears to be a greater degree of synchrony in the Scolopacidae (e.g. Davis 1943, Williamson 1948, Sutton and Parmelee 1955, Wilcox 1959, Parmelee et al. 1967, Parmelee et al. 1968, Parmelee 1970, Jehl 1973).

The hypothesis that asynchrony is a side-effect of selection to protect the egg from chilling during the egg-laying period is attractive, but is unsupported by evidence. First, minimum air temperatures during egg-laying are not extreme (Table 3). Second, other species can successfully hatch eggs which have been unattended for several days in similar high arctic conditions (Parmelee 1970). And third. there is evidence that some passerines can prevent chilling of eggs without raising the nest temperature enough for effective incubation (Haftorn 1966). Thus if there is strong selection for synchrony, there are ample reasons for supposing it could be achieved without danger to the eggs.

The incubation period of about 27 days is remarkably long for a bird breeding in the short arctic summer, but is similar to that in the Eurasian and American Golden plovers (Witherby 1940, Parmelee et al. 1967). Plovers generally have longer incubation periods than scolopacids: 23–26 days in the smaller *Charadrius* (but 27–28 days in the Piping Plover, *C. melodus*) (Palmer 1967) compared to 18–22 days for most small sandpipers (Godfrey 1966, Palmer 1967, Parmelee et al. 1967) and no more than 24 days for some of the larger species such as the Hudsonian Godwit (*Limosa haemastica*) and Whimbrel (*Numenius phaeopus*) (Jehl and Hussell 1966). The Charadriidae and Scolopacidae as a whole do not differ greatly in relative egg weight (egg weight as % of body weight), although there is much variation within each group (Lack 1968). Whether the long incubation period of plovers and the large eggs of *Pluvialis* are associated with characteristic embryonic developmental patterns remains to be determined.

Growth rates of shorebirds are poorly known and data for only 1 other plover, the Ringed Plover (*Charadrius hiaticula*). are given by Ricklefs (1973). This species has a growth rate (K) of about 0.13 (converted from Ricklef's data), slower than the 0.19 of the Black-bellied Plover. The significance of this difference is difficult to assess until information is available for more species, but it indicates that the range of variation in growth rates in the plovers may be as great as in the sandpipers. In view of the usual inverse relationship between growth rate and size it might be expected that the small plovers in the genus *Charadrius* would have a faster growth rate than *Pluvialis*, but the present evidence indicates otherwise. The few data given by Wilcox (1959) show a remarkably slow growth rate in the Piping Plover (*C. melodus*) and the feather development of a 17-day-old Semipalmated Plover (*C. semipalmatus*) photographed by Sutton and Parmelee (1955) appears little further advanced than that of a 12-day-old Black-bellied Plover specimen.

Fledging ages of shorebirds are also inadequately documented. In the sandpipers there is evidence of a fledging period of less than 14 days in the Semipalmated Sandpiper (*Calidris pusillus*) (Parmelee et al. 1967), 16–17 days in the White-rumped Sandpiper (*C. fuscicollis*) (Parmelee et al. 1968) and about 17 days in the Sanderling (*C. alba*) (Parmelee 1970). Among the plovers, fledging ages of 24 days and 21–23 days have been reported for the Ringed Plover (Palmer 1967, Ricklefs 1973), between 22 and 31 days in the Semipalmated Plover (Sutton and Parmelee 1955), 21–24 days in the Little Ringed Plover (*Charadrius dubius*) (Witherby et al. 1940), 30–35 days in the Piping Plover (Wilcox 1959), 33 days in the Eurasian Golden Plover, 33–34 days in the Mountain Plover (Graul 1975), and 39 days in the Lapwing (*Vanellus vanellus*) (Witherby et al. 1940). Thus the 23-day period for the Black-bellied Plover appears to be unusually short among the larger plovers.

SUMMARY

Black-bellied Plovers arrived on the north coast of Devon Island in the second week of June and occupied the coastal lowland at a density of 0.3–1.0 pairs per km^2. Most clutches were initiated in the last 10 days of June.

Four eggs were laid at about 36 h intervals. Fresh eggs averaged 31.0 g and lost 0.15 g per day during incubation. The incubation period is about 27 days. The interval between hatching of the first and last eggs in a clutch was sometimes as much as 36 h. Chicks remained inactive in the nest for 10–12 h after hatching. Older young foraged alone up to 40 m from the nest and brooding adult until the last-hatched young became active and the nest was deserted. The weight of newly hatched young declined for the first few hours then increased rapidly. Growth and development from hatching to fledging were described from a series of known-age specimens. The fledging period was about 23 days. Male and female adults both incubated and cared for the young, but the females deserted the broods earlier than the males, before the young had fledged.

The breeding cycle from first egg to last fledging took about 55 days for a single pair and about 68 days for the Devon Island population. Most young are fledged no sooner than the 3rd week of August.

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LITERATURE CITED

Barrett, P. E. and J. A. Teeri. 1973. Vascular plants of the Truelove Inlet region, Devon Island. Arctic 26:58–67.

Bent, A. C. 1929. Life histories of North American shorebirds. Part II. U.S. Natl. Mus. Bull. 146:1–412.

Bliss, L. C. and J. A. Teeri. 1971. Devon Island programs 1970. Arctic 24:65–67.

Brandt, H. 1943. Alaska bird trails. Bird Research Foundation, Cleveland, Ohio.

Davis, E. 1943. A study of wild and hand reared Killdeers. Wilson Bull. 55:223–233.

Drury, W. H., Jr. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk 78:176–219.

Gabrielson, I. N. and F. C. Lincoln. 1959. The birds of Alaska. The Stackpole Company, Harrisburg, Pa.; and The Wildlife Management Institute, Washington, D.C.

Godfrey, W. E. 1966. The birds of Canada. Natl. Mus. Canada Bull. 203:1–428.

Graul, W. D. 1974. Adaptive aspects of the Mountain Plover social system. Living Bird 12:69–94.

———. 1975. Breeding biology of the Mountain Plover. Wilson Bull. 87:6–31.

Haftorn, S. 1966. Egg-laying and incubation in tits based on temperature recordings and direct observations [in Norwegian, English summary]. Sterna 7:50–102.

Höhn, E. O. 1957. Observations on display and other forms of behavior of certain arctic birds. Auk 74:203–214.

Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in Northern Alaska. Condor 68:3–46.

——— and C. P. Black. 1973. Ecological distribution of birds in the Kolomak River-Askinuk Mountain region, Yukon-Kuskokwim delta, Alaska. Condor 75:150–163.

Hussell, D. J. T. and G. L. Holroyd. 1974. Birds of the Truelove Lowland and adjacent areas of northeastern Devon Island, N.W.T. Can. Field-Nat. 88:197–212.

Jehl, J. R., Jr. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. Wilson Bull. 85:115–147.

——— and D. J. T. Hussell. 1966. Incubation periods of some subarctic birds. Can. Field-Nat. 80:179–180.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., Ltd., London.

Manning, T. H., E. O. Höhn, and A. H. MacPherson. 1956. The birds of Banks Island. Natl. Mus. Can. Bull. 143:1–144.

Mayfield, H. F. 1961. Nesting success calculated from exposure. Wilson Bull. 73: 255–261.

———. 1973. Black-bellied Plover incubation and hatching. Wilson Bull. 85:82–85.

Nethersole-Thompson, D. 1972. The Dotterel. Collins, London.

Norton, D. W. 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. Condor 74:164–176.

Palmer, R. S. 1967. Appendix, p. 139–267. *In* The shorebirds of North America. (G. D. Stout, ed.) Viking Press, New York.

Parmelee, D. F. 1970. Breeding behavior of the Sanderling in the Canadian high arctic. Living Bird 9:97–146.

——— and R. B. Payne. 1973. On multiple broods and the breeding strategy of arctic Sanderlings. Ibis 115:218–226.

———, H. A. Stephens, and R. H. Schmidt. 1967. The birds of southeastern Victoria Island and adjacent small islands. Natl. Mus. Can. Bull. 169:1–229.

———, D. W. Greiner, and W. D. Graul. 1968. Summer schedule and breeding biology of the White-rumped Sandpiper in the central Canadian arctic. Wilson Bull. 80:5–29.

Pitelka, F. A., R. T. Holmes, and S. F. MacLean, Jr. 1974. Ecology and evolution of social organization in arctic sandpipers. Am. Zool. 14:185–204.

Pulliainen, E. 1970. On the breeding biology of the Dotterel (*Charadrius morinellus*). Ornis Fenn. 47:69–73.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978–983.

———. 1968. Patterns of growth in birds. Ibis 110:419–451.

———. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177–201.

Sutton, G. M. 1932. The birds of Southampton Island. Mem. Carnegie Mus. 12 (Part II, Sect. 2):1–275.

——— and D. F. Parmelee. 1955. Breeding of the Semipalmated Plover on Baffin Island. Bird-Banding 26:137–147.

Tuck, L. M. and L. Lemieux. 1959. The avifauna of Bylot Island. Dan. Ornithol. Foren. Tidsskr. 53:137–154.

Van Tyne, J. and W. H. Drury, Jr. 1959. The birds of southern Bylot Island, 1954. Occas. Pap. Mus. Zool., Univ. Mich. 615:1–37.

Wilcox, L. 1959. A twenty year banding study of the Piping Plover. Auk 76:129–152.

Williamson, K. 1948. Field notes on nidification and distraction-display in the Golden Plover. Ibis 90:90–98.

Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst, and B. W. Tucker. 1940. The handbook of British birds. Vol. 4. Witherby, London.

LONG POINT BIRD OBSERVATORY, P.O. BOX 160, PORT ROWAN, ONTARIO N0E 1M0; AND POINT REYES BIRD OBSERVATORY, BOX 321, BOLINAS, CA 94924. ACCEPTED 9 SEPT. 1975.

GENERAL NOTES

Effects of a severe thunderstorm on airborne ducks.—This note reports the groundings and deaths of over 100 airborne ducks during a severe storm which struck Stuttgart, Arkansas at 15:50 CST on 23 November 1973. Irregularly shaped hail up to 5 cm diameter fell for about 10 min; a brief calm followed before heavy rains and strong winds began. Lightning apparently occurred throughout the storm, the bulk of which had passed by 16:30. During the storm 1 or 2 small funnel clouds passed within 1 km of the southern and eastern edges of Stuttgart. I report the incident here because its daylight occurrence in a populated area yielded numerous immediate observations—circumstances not existent in other such cases reported.

I obtained details from accounts and photographs in a Stuttgart newspaper, *The Daily Leader*, and from a survey form printed in that newspaper on 29 January 1974. On the form I asked persons who picked up ducks or were witnesses to groundings to provide the following information: (1) location and time of observations; (2) number, species, and sex which were (a) dead, (b) crippled and helpless, or (c) grounded but escaped or were released; (3) physical condition of the birds, e.g., broken bones, bruises, wounds, ice-coated; (4) weather conditions before or coinciding with the groundings; and (5) observations of duck flights prior to the groundings. I received 28 forms; newspaper accounts, 4 photographs, and 1 personal contact completed the sources of information. While additional ducks undoubtedly were killed (Ray Roth, pers. comm.), I consider this sample representative. I requested clarifications or verifications of some responses. When this involved species identification, I sent unlabeled pictures clipped from Robbins et al. (Birds of North America, Golden Press, New York, 1966) of both sexes of the species likely to be involved to the respondent with a request to choose the one most resembling the duck reported.

Reports came from a 14.5 × 3.2 km area roughly paralleling the southwest–northeast path of the storm but most were from a 3.2 × 2.1 km area of residential and business sections in the town. There was evidence that additional ducks probably went unobserved in adjacent agricultural land.

Most of the ducks were picked up during or shortly after the storm. Of the 106 ducks tabulated (Table 1), 76 were dead when found; 9 were crippled and helpless; and 9 were grounded but escaped or were released. Twelve were of undetermined condition. Some crippled birds probably died before they were found. The rapid recovery and escape of several dazed birds suggests that the grounded–escaped category may have been larger than reported.

Some ducks had several injuries and 8 had no detected injury. Eighteen of 19 ducks with fractures were dead. The breaks were mostly in wings but also included legs and necks. Two persons who found 18 ducks specifically noted no breaks; of course, subtle fractures could have been undetected. The second most common condition, a frozen or ice-encrusted body, occurred in 18 ducks of which 15 were dead. A photograph in *The Daily Leader* of 26 November 1973 shows a Mallard (*Anas platyrhynchos*) female with chunks of ice 2 cm diameter frozen on the tips of the feathers of the neck, breast and sides. Ice-covered ducks were found up to 1 hr after the hail, during which time most of the ducks were picked up. Three persons expressly said there was no ice on 24 ducks picked up shortly after the storm. Wounds (13 ducks) and bruises (14 ducks) often were associated with broken bones. Eleven of the wounded and 14 bruised ducks were dead. Wounds were described as "torn gashes," large cut on head" and "wounds on back." Bruises were specified as on the back in one case. A unique report described the head

TABLE 1

SPECIES AND SEX OF DUCKS FOUND AFTER STORM, STUTTGART, ARKANSAS, 23 NOVEMBER 1973

Species	Male	Female	Unknown	Total
Mallard	4	9	19	32
Pintail	9	5	15	29
American Wigeon	4	2	5	11
Gadwall	1	0	4	5
Redhead	2	0	0	2
Wood Duck	0	0	2	2
Blue-winged Teal	0	1	0	1
Unknown	0	2	22	24
TOTAL	20	19	67	106

feathers of 4 dead ducks as "kinky, as if burned." In 3 cases where no injury was observed the ducks nevertheless were flightless.

Respondents related 11 ducks to a specific stage of the storm. Six fell during the hail and were dead when retrieved shortly thereafter; 4 were ice-coated and one also had wounds and bruises; 2 were not checked. Most of the grounded ducks probably came down during the hail. The same updrafts, freezing temperatures at high altitudes, and precipitation which formed the hail probably caused the ducks to freeze or become ice-encrusted. Hochbaum (Travels and Traditions of Waterfowl, U. Minn. Press, Minneapolis, 1957) described flightless Starlings (*Sturnus vulgaris*) with iced feathers. The cuts, back bruises, and the broken bones, especially wings, suggest that some birds also were hit by hail while in flight. Broken wings were rare among ducks killed in a hailstorm in Alberta in which the birds apparently remained on the ground (Smith, Aud. Mag. 62: 170, 171, 186, 1960). This was not so in the present case; there were 3 reports of frenzied, confused, low-level flights of 10–100 ducks at the start of the hail and after the storm peak. Massive bruises and neck and skull fractures also have characterized victims of hailstorms (e.g. Smith, op. cit.; Johnston, Kans. Ornithol. Soc. Bull. 18:9–10, 1967). Skull injuries may have gone undetected in the Arkansas case because the heads were not picked during cleaning. Some injuries, of course, may have occurred on impact with the ground. Lightning, heavy rains, and downdrafts may have caused a few groundings including those with no apparent injuries. The person who saw the 4 ducks with possibly burned feathers fall noted that the hail was over and the rain had not started when a "large lightning flash" occurred. The same person caught a dazed duck which he saw land in a street during the ensuing heavy wind and rain. After 30 min it became active, was released and flew away. Torrential rains and heavy winds have caused other groundings (e.g. Hicks and McCullers, Bird-Banding 37:54, 1966).

I received no mention of any birds other than 7 species of ducks being affected by the storm. Mallard, Pintail (*Anas acuta*), and American Wigeon (*Anas americana*) predominated (Table 1). The Redheads (*Aythya americana*), uncommon in that area, were identified by an experienced duck hunter. The Blue-winged Teal (*Anas discors*) was unusual since most should have migrated from Arkansas by that time (Dave Donaldson, pers. comm.). The identification was verified from pictures of Blue- and Green-winged Teal (*Anas crecca*). Pictures of Gadwalls (*Anas strepera*) and American Wigeon were sent to persons reporting "Wigeon" to clarify those identifications. Failure to include a female Pintail in this choice may have produced some error. No attempt was made to verify the identity of the Wood Ducks (*Aix sponsa*) or to identify any of the unknowns. Sex identification of 39 ducks gave a 1:1 sex ratio overall.

The species involved often are found together in the flooded rice and soybean fields of eastern Arkansas in winter. Dave Donaldson (pers. comm.) noted that there was much surface water in the fields at that time and suggested that the mixture of species probably reflects the composition of ducks which were feeding in the fields. Thus, the mixed flock may have been caught up in the rapidly moving storm as they tried to move ahead of it out of the fields. The other possibility is that a locally migrating flock happened to move into the storm path. There was no major migration occurring on that day (Dave Donaldson, pers. comm.).

Garner Allen of *The Daily Leader* expedited the printing of the survey form and encouraged responses through the paper's columns. I thank the 28 persons who took time to respond, including some who kindly answered requests for clarification. Dave Donaldson, Waterfowl Biologist, Arkansas Game and Fish Commission, also provided useful information. E. G. Bolen, D. F. Bray, J. R. Karr, J. K. Rosenberger, and Aileen and R. W. Rust made suggestions on the manuscript. Mr. and Mrs. Ray Roth, my parents, called my attention to the event, provided a first-hand report, and aided me in other ways. This is Miscellaneous Paper No. 709 of the Delaware Agricultural Experiment Station and Publication No. 434 of the Department of Entomology and Applied Ecology, University of Delaware.—ROLAND R. ROTH, *Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark 19711. Accepted 25 July 1975.*

Feeding rhythm in nestling White Ibis.—Daily rhythms are important homeostatic mechanisms in most animal species (Kleitman, Physiol. Rev. 29:1–30, 1949; Bunning, The Physiological Clock, Springer-Verlag, N. Y., 1973). Diel feeding rhythms exist in most species. Hunting techniques, food availability, and exposure to predation interact to produce an adaptive complex of feeding and hunting patterns. Young, cared for by adults, must have a daily feeding pattern adjusted to the adult's foraging regime. It is not so obvious whether the diurnal feeding patterns of nestlings are merely the result of the pattern of adult attentiveness or are instinctive on the part of the young and can continue without the mediating influence of parental care. Here I present the results of an experiment which shows the existence of an inherent feeding rhythm in nestling White Ibis (*Eudocimus albus*) removed from parental care at hatching.

Nestlings were removed from nests in Broward and Highland counties, Florida as pipped eggs and maintained at 30°C. Each hour they were fed as much as they would eat of a ground mixture of shrimp, sardines, water, and vitamin supplement. The feeding rhythm of 30 captive nestlings was measured over a total of 150 bird-days as the percentage of the daily ration consumed each hour. Data on wild birds were collected during 5 min periods at hourly intervals. The feeding rhythm of 50 wild nestlings was measured as the percentage of the total number of feedings observed. Nest attentiveness by male and female White Ibis was measured as the percent of the total number of adults on nests. All data were collected for chicks less than 3 weeks old. Data were combined into 3-hour blocks starting at 0300.

In the wild, adult White Ibis, the sexes of which are distinguishable in the field, differed in their patterns of nest attentiveness. Males were present most of the day and females most of the night (Fig. 1a). There were 2 exchanges of nest duties, one in the morning and one in the evening. Wild nestlings showed a bimodal pattern of feeding

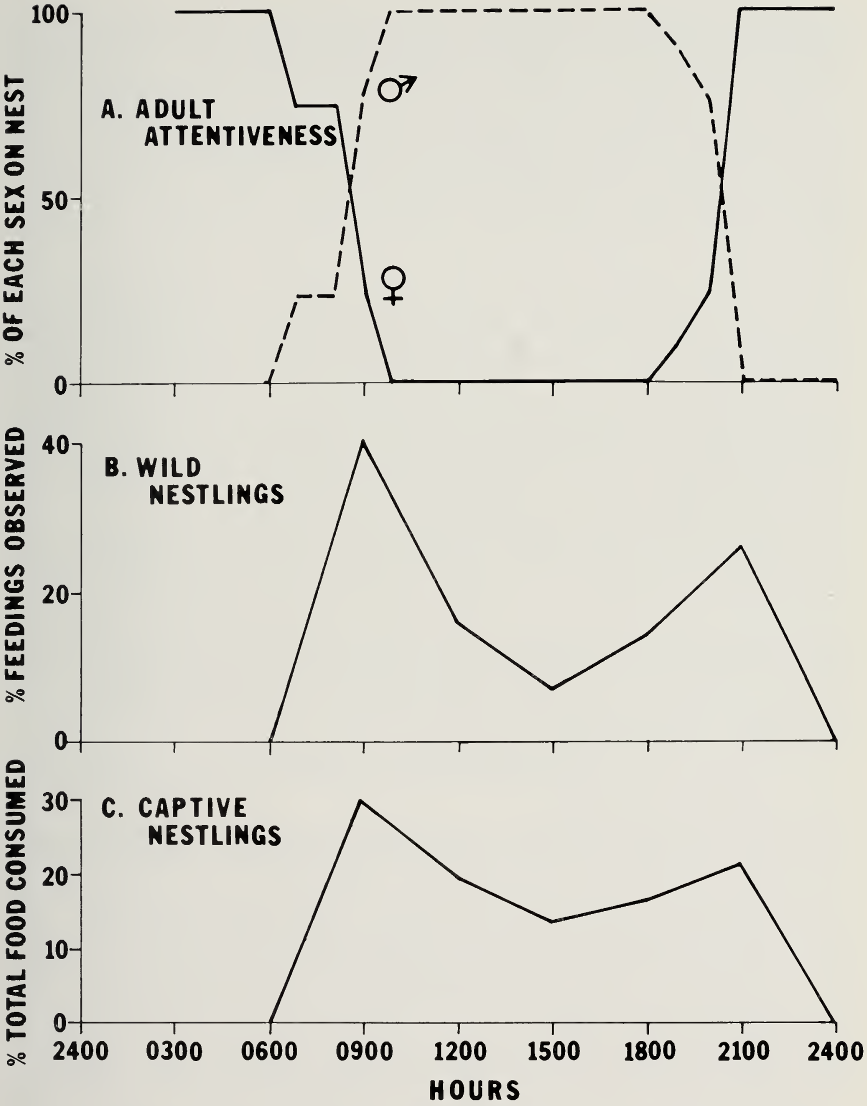

FIG. 1. Diurnal pattern of White Ibis feeding activity: (a) nest attentiveness by male and female White Ibis, (b) feeding pattern of wild nestlings, (c) feeding pattern of captive nestlings.

activity corresponding to the periods after nest exchange when one parent had just returned from the feeding ground (Fig. 1b). Little feeding of young nestlings occurred in the middle of the afternoon; no feeding occurred between 2400 and 0600. Nestlings in captivity showed a bimodal daily feeding rhythm with peaks at 0900 and 2100 hours corresponding to the peaks of feeding activity by wild nestlings (Fig. 1c). Thus the pattern seen in wild nestlings depends not only on adult foraging, but also on an independent nestling rhythm that persists after their removal from the proximal stimulus of adult attentiveness. The feeding pattern of nestlings is therefore governed by the coadaptation of nestling physiology and adult behavior relative to the ecological pressures that determine foraging patterns of the adult. I thank O. T. Owre for support, M. S. Kushlan for assistance, and J. L. Dusi and D. F. Werschkul for comments.—JAMES A. KUSHLAN, *Dept. of Biology, Univ. of Miami, Coral Gables, FL 33124 (*Present address: *U.S. National Park Service, Everglades National Park, Homestead, FL 33030). Accepted 24 Sept. 1975.*

Observations of Swainson's Hawk nesting in northeastern Illinois.—We checked 18 large nests in northern Kane County, Illinois, for incubating raptors during early May 1973. Of the 11 active nests, 6 were of Red-tailed Hawk (*Buteo jamaicensis*), a common nester here. The other 5 were of Swainson's Hawk (*Buteo swainsoni*). These 5 nests were within 85 km of downtown Chicago between latitudes 41°58'N and 42°08'N and longitudes 88°21'E and 88°30'E. Several Swainson's Hawks had been sighted prior to these nesting discoveries, and it is our opinion that additional nests were likely present and could have been located, time permitting. The small sample size available suggests the density of nesting Swainson's approached that of the Red-tail.

Two of the 5 nests did not produce young. Desertion is known to occur frequently with the Swainson's Hawk (Bent, U.S. Natl. Mus. Bull. 167:224, 1937). One nest was deserted prior to egg laying—probably due to nearby farming operations which began after nest site selection. At the approximate time of desertion of the second nest, a dead adult female was found at the base of the nest tree. The cause of death was unknown (fluoroscopy indicated it had not been shot). The bird had a large brood patch, but the exact stage of incubation could not be determined. A deer mouse (*Peromyscus leucopus*) was in the mouth of the dead hawk.

The remaining 3 nests fledged 5 young. Two were hatched in each nest, but one nestling disappeared at approximately 2½ weeks of age. The estimated dates of hatching were from 12 June to 26 June.

Behavior of the adult pair was markedly different from that of Red-tails and made detection of the nesting pair difficult without close observation. The incubating bird remained motionless and nearly unnoticeable on the nest. Only once was a bird flushed from the incubating position—that occurred when one investigator had climbed ½ the distance up the nest tree. Incubating Red-tails, in comparison, readily left their nests when we approached. The non-incubating member of the pair was seen near the nest site only twice during incubation. On both occasions our approach resulted in the immediate departure of the bird.

After hatching occurred, the female became defensive of the nest site and would soar overhead and scream at our approach. Once, a bird folded its wings and stooped toward us at a 45° angle with legs extended downward. The bird pulled out of the dive when approximately 15 m from us. Red-tails also stooped, but never with wings folded tight to the body or legs extended.

To determine if the birds had returned the following year, we checked the 5 nest sites during the 1974 nesting season. One nest was missing, 1 contained 2 young Great-horned Owls (*Bubo virginianus*), 1 was being defended by a pair of adult Red-tails, and the remaining 2 nests were occupied by incubating Swainson's Hawks. Great-horned Owls and Red-tailed Hawks are earlier nesters than the Swainson's (Bent, U.S. Natl. Mus. Bull. 167:

151, 224–225, 1937; and 170:298, 1938) and, therefore, have first selection of existing nests. The other 3 pairs of Swainson's may have returned and been forced to use different nest sites. We did not search for these pairs.

The normal breeding range for the Swainson's Hawk extends from Alaska to Manitoba, western Minnesota, and, uncommonly, Illinois to California, south-central Texas, and, rarely, Missouri (A.O.U. Check-list, 108, 1957). Atypical weather conditions may have resulted in a temporary eastward extension of the breeding range of this western raptor. The winter of 1972–73 was unusually mild throughout most of the U.S., and there was an "impressive number of western species in the east" during the spring of 1973 (Am. Birds 27:745, 1973). However, we believe this species now occurs more commonly in Illinois than the literature would indicate. There have been 3 previous reports of nesting Swainson's Hawk in Illinois—one nest in 1900 (Hess, Auk 27:22–23, 1910), one nest in 1947 (Prentice, Audubon Field Notes 1:177, 1947), and 3 nests in 1958 (Johnson, et al., Audubon Field Notes 12:416, 1958). Johnson (pers. comm.) indicated a breeding population was well established in eastern Winnebago and Boone counties until the mid 1960's. Late April 1960 and early May 1971 sightings (Southern, pers. comm.) in Dekalb and Ogle counties and 2 adult female specimens (Northern Illinois Univ. collection) taken in late April 1965 and early September 1973 from Kane and DuPage counties suggest the presence of breeding birds in the northern part of the state. Combined with the above information, the high nesting densities we observed and the use of those same nest sites, where available, in 1974 indicate the possibility that a permanent breeding population of Swainson's Hawk may be established in this section of northeastern Illinois.

Photographs of the dead adult female and one of the 5 nestlings (approximately 30 days old) have been deposited in the National Photoduplicate File (accession numbers 342-2C and 342-3C, respectively). A study skin of the adult is in the Zoological Museum of the University of Wisconsin (catalogue number UWZA 20273).—JAMES R. KEIR, *Wisconsin Dept. of Natural Resources, Ranger Station, Friendship, WI 53934 and* DEANN DE LA RONDE WILDE, *Belleville, WI 53508. Accepted 30 May 1975.*

Foods of 6 Fulvous Whistling Ducks in coastal South Carolina.—The Fulvous Whistling (Tree) Duck (*Dendrocygna bicolor*), which historically wintered only in South America, has rapidly expanded its winter range during the past 2 decades. Baird (Audubon Field Notes 17:4–8, 1963) and Jones (Chat 30:4–7, 1966) marked the winter of 1955–56 as the start of this range expansion. Now this species is sighted all along the Atlantic coast (Bellrose, Ducks, Geese and Swans of North America, Stackpole Co., Harrisburg, Pa., 1976). It was first reported in South Carolina in 1955 when 4 were seen in the Pon-Pon area along the Edisto River in Colleton County (Jones, op. cit.). Since then, it has become common in estuaries of South Carolina, especially in diked impoundments managed for waterfowl.

During a study of waterfowl management in this region of South Carolina (Morgan et al., Proc. Southeastern Assoc. Game and Fish Commissioners 29, in press, 1976), we analyzed the diet of 684 ducks taken by hunters (Landers et al., J. Wildl. Manage. 40, in press, 1976). Gullets and gizzards of 6 Fulvous Whistling Ducks collected during January 1974 were included in a sample of ducks from the Pon-Pon area. Since little is known of its feeding ecology, especially in this recently established range, food habits of this species were analyzed for separate presentation.

Foods identified in Fulvous Whistling Ducks differed markedly from those in the other

TABLE 1

FOODS OF 6 FULVOUS WHISTLING DUCKS FROM COLLETON COUNTY, SOUTH CAROLINA

Item[a]	Occurrence (No. Stomachs)	Percent Volume		
		Gullet	Gizzard	Total
Panicum dichotomiflorum	6	67.9	40.9	62.8
Cuphea carthagensis[b]	5	22.5	4.3	19.0
Panicum agrostoides	6	4.3	30.4	9.3
Fimbristylis autumnalis[b]	1	3.6	15.9	5.9
Paspalum boscianum[b]	5	1.0	2.4	1.3
Eleocharis sp.	3	—	4.9	0.9
Echinochloa walteri	6	0.6	0.6	0.6
Paspalum dissectum[b]	5	0.1	—	0.1

[a] Items which contributed only a trace amount ($<0.1\%$) in either the gullet or gizzard are *Cladium jamaicense, Cyperus polystachyos, Digitaria sanguinalis, Hydrocotyle* sp., *Panicum verrucosum, Paspalum floridanum,*[b] *P. laeve,*[b] *P. setaceum,*[b] *Polygonum hydropiperoides, P. lapathifolium, P. punctatum, Rhynchospora macrostachya,*[b] *Scirpus olneyi, Setaria glauca,* bivalves (Mollusca), and insects (Insecta).

[b] These occurred in no other duck species in the peat marsh area.

14 duck species in the samples. We identified 24 food items, but only 7 contributed more than trace amounts to the diet (Table 1). Grasses made up 74.1% of the total food volume, and fall panic grass (*Panicum dichotomiflorum*) composed about 63%. Redroot (*Lachnanthes caroliniana*), which was the principal item in other ducks (mostly *Anas* spp. and *Aythya* spp.) from the peat marsh, did not occur in the Fulvous Whistling Ducks. Fall panic grass and redroot were managed species of food plants in impoundments in the peat area. Seeds of 8 species that did not occur in other ducks from this marsh composed over 26% of the volume. Of these, marsh waxweed (*Cuphea carthagensis*) and fringed sedge (*Fimbristylis autumnalis*) were particularly important.

These foods are similar to those used by the species in Louisiana, as revealed by analysis of digestive tracts and droppings from areas under rice cultivation (Meanley and Meanley, Wilson Bull. 71:33–45, 1959). Meanley and Meanley (op. cit.) described areas where most food plants grew as grassy places in rice fields that were just high enough above water for convenient feeding. The 8 major food plants and most lesser food plants in our analysis grew most abundantly along dikes and impoundment margins, except for fall panic grass that was abundant inside impoundments as well. Rylander and Bolen (Auk 91:86–94, 1974) depict this duck as an aquatic siever with skeletal structures adapted for this feeding niche.

Further studies are needed to gather information on the natural history and behavior of this little-known species. Its successful range expansion may be reflected partially in the adaptation to similar feeding habitats between old and new range sites.—J. LARRY LANDERS AND A. SYDNEY JOHNSON, *School of Forest Resources and Institute of Natural Resources, Univ. of Georgia, Athens 30602. Accepted 6 Aug. 1976.*

Some effects of human activities on the Great Blue Heron in Oregon.—During the breeding season of 1974 we took part in a survey to determine the locations and number of nests in heronries of the Great Blue Heron (*Ardea herodias*) on the Oregon coast. We collected data on nesting activity, physical size of the heronries, and, indirectly, on

TABLE 1

SUCCESS OF GREAT BLUE HERONS AT HERONRIES IN WESTERN OREGON

Location (Co.)	Number of Nests		Area (ha)	Fledging Rate*	Notes
	Active	Inactive			
Columbia R., Clatsop Co.	161	14	0.36	2.70 (n = 43)	undisturbed
Wheeler, Tillamook Co.	33	21	0.24	2.20 (n = 21)	logging road
Ball Mt., Lincoln Co.	15	0	0.12	—	newly formed
Mill Creek, Lincoln Co.	18	—	1.21	—	undisturbed
Yaquina Bay, Lincoln Co.	35	—	—	—	newly formed
Beaver Creek, Lincoln Co.	32	18	0.41	—	clearcut near
Reynolds Ck., Lincoln Co.	44	14	0.65	—	clearcut near
Siuslaw R., Lane Co.	88	4	0.36	2.53 (n = 16)	undisturbed
North Spit, Coos Co.	97	7	0.36	—	undisturbed
South Slough, Coos Co.	86	3	0.24	2.58 (n = 30)	undisturbed
Bandon, Coos Co.	97	12	0.53	2.18 (n = 22)	undisturbed
Rogue R., Curry Co.	38	—	0.08	—	undisturbed

* This is an average number of young per successful nest at 7–8 weeks.

the influence of man in the heronry. In those heronries we examined, Great Blue Herons typically built their nests from 7 to 25 m in red alder (*Alnus rubra*), western hemlock (*Tsuga heterophylla*), and sitka spruce (*Picea sitchensis*). Great Blue Herons were the only ardeids present in those heronries examined.

Five of 12 heronries (42%) had been affected by logging operations. Three of the heronries had recent clearcutting or road construction within 0.5 km, and 2 had newly formed in 1974 after destruction of nearby 1973 heronries by logging or logging related activities. Seven heronries were undisturbed in terms of current land management or other obvious influences of man. Mean colony size for the areas with logging operations was 36.3 active nests ($n = 3$), while for undisturbed areas it was 107.2 active nests ($n = 5$). We have no information on colony size in previous years. Colony size for the 2 newly formed heronries was 15 and 35 active nests (Table 1). Nest density was measured for the area enclosed by the peripheral nest trees. There was an average of 94.4 active nests/ha for the 3 disturbed heronries and 259.2 active nests/ha for the 5 undisturbed heronries ($t = 3.98$, $p < 0.01$). Nest density for 1 newly formed heronry was 35.8 active nests/ha. Data on fledging success per successful nest were collected from blinds when the young were approximately 7–8 weeks old at 4 undisturbed heronries and 1 disturbed heronry. Though we realize fledging rate should have been measured at more disturbed sites, it is worth mentioning that the fledging rate at the Wheeler heronry (disturbed) was 2.2 young per nest ($n = 21$), one of the lowest figures obtained at any of the heronries.

Nest occupancy, defined as active nests in relation to total number of nests, was significantly higher in undisturbed areas. In the disturbed areas 67% ($n = 162$) were active; 93% ($n = 573$) were active in undisturbed areas ($\chi^2 = 79.8$, $p < 0.005$). Within a disturbed heronry the probable effect of human disturbance on nest occupancy could be quantified. For example, the average distance from the nearest point of disturbance to active and nonactive nests in the Wheeler heronry (Table 1) was 148 m ($n = 21$) for inactive nests and 219 m ($n = 33$) for active nests ($t = 5.62$, $p < 0.001$). This phenomenon of nesting activity shifting away from the point of disturbance was observed in those heronries with logging operations nearby and such a movement in any direction was unnoticed in undisturbed heronries.

This study was in part financed by a grant from the Portland Audubon Society and a NSF Grant (GY-11420).—David F. Werschkul, *Dept. of Zoology, Miss. State Univ., Mississippi State 39762;* Ellen McMahon, *Oregon Inst. of Marine Biology, Charleston 97420;* and Mary Leitschuh, *Dept. of Biology, Univ. of Oregon, Eugene 97421.* *Accepted 13 October 1975.*

Swimming by Bobwhite chicks.—On 8 June 1975 when driving over an unpaved rural road in Granville County, North Carolina, I saw a female Bobwhite (*Colinus virginianus*) cross the road close in front of me with her brood of 8 recently hatched chicks. On coming to the water-filled ditch at the side of the road the mother bird flew across the ditch, and the chicks followed her by swimming. The ditch was about 0.5 m wide and the water in it a maximum of 8 cm deep.

To further test the swimming ability of Bobwhite chicks, I later placed 2 three-day-old incubator-hatched chicks on the water of a farm pond about 1 m from its shore. The chicks quickly swam to shore, swimming with the head and about ½ of the body above the surface of the water.

I know of no published report of swimming by Bobwhite chicks. However, Stoddard (The Bobwhite Quail its Habits. Preservation and Increase, Charles Scribner's Sons, New York, N. Y., 1931) noted that older Bobwhites swam when placed on a water surface after removal of their flight feathers. Also, Schorger (The Wild Turkey its History and Domestication, Univ. Okla. Press, Norman, 1966) reported Turkey (*Meleagris gallopavo*) poults being able to swim surprisingly well.—Paul A. Stewart, *203 Mooreland Drive, Oxford, NC 27565.* *Accepted 13 July 1976.*

Seasonal variation in foraging territory of Red-cockaded Woodpeckers.—The habitat requirements of the endangered Red-cockaded Woodpecker (*Dendrocopos borealis*) must be known in order to implement effective forest management practices for the preservation of this species. The few published estimates of territory size for this woodpecker are of 2 types. Estimates derived by dividing the size of a discrete area by the number of clans occupying that area can provide information on their minimum requirements if it is assumed that (a) all of the habitat is suitable, and (b) the birds are present at maximum density. This technique has produced estimates of 26.7 and 67.7 ha per clan in 2 Texas forests (Lay and Russell, Auk 87:781–786, 1970) and 86.2 ha per clan in South Carolina (Beckett, EBBA News 37:3–7, 1974).

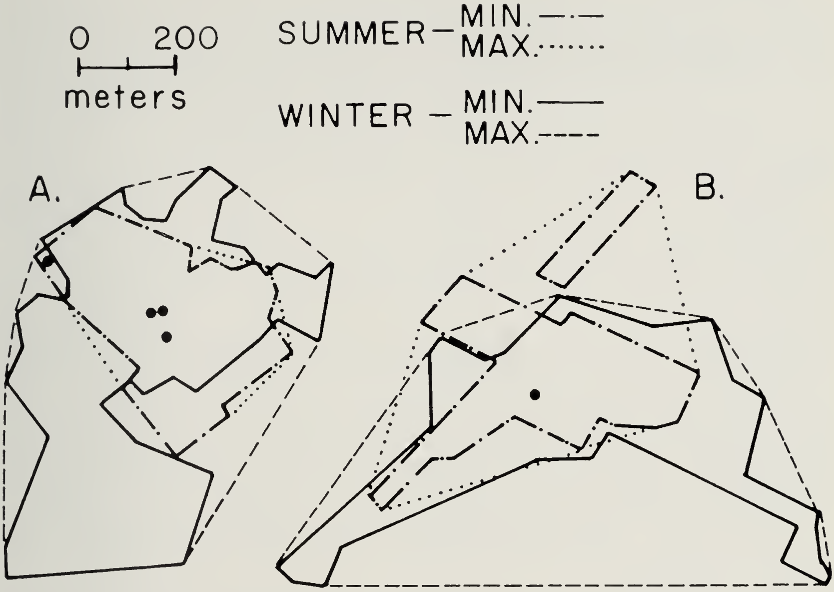

Fig. 1. Seasonal variation in foraging territories of Red-cockaded Woodpeckers.

The second technique is based upon direct observations of foraging by birds of a particular clan (a mated pair, their offspring, and/or associated helpers) and subsequent mapping to determine the area foraged. The obvious variables in this technique are the number of birds in the clan, the type of habitat foraged, and the season of the year when the birds are observed. This technique has produced estimates of 14.4 and 20.0 ha for adult pairs in spring in Florida (Crosby, p. 60–73 *in* R. L. Thompson, ed., The Ecology and Management of the Red-cockaded Woodpecker, Bur. Sport Fish. Wildl. and Tall Timbers Research Sta., Tallahassee, 1971) and 65.6 ha for a clan of 5 adults and 3 juveniles during summer in Florida (Baker, p. 44–59 *in* R. L. Thompson 1971).

We have determined the summer and winter foraging territories for 2 clans of Red-cockaded Woodpeckers on the Savannah River Plant, a 78,000 ha National Environmental Research Park of the U. S. Energy Research and Development Administration near Aiken, South Carolina. The birds were followed for periods of 2–7 h per day and each tree in which they were positively observed to forage was marked. The perimeter of the marked trees was subsequently mapped (Fig. 1) and the enclosed area calculated (Table 1). The maximum area foraged was determined by the polygon connecting the outermost foraging points. The minimum area foraged was determined by the irregular polygon connecting as many perimeter foraging points as practical.

Clan A consisted solely of a mated pair, without helpers, which hatched one chick. This nestling survived at least 19 days but failed to fledge, possibly because nearby logging operations disrupted feeding visits to the nest cavity by the adults. The birds were observed foraging for 36 h in June–July and 32 h in January. The minimum area of 15.8 ha of longleaf pine (*Pinus palustris*) habitat foraged by these birds in summer increased 112.7% to 33.6 ha in winter. The extreme distance across the territory was

TABLE 1
ESTIMATED FORAGING TERRITORIES OF RED-COCKADED WOODPECKERS

	Clan A	Clan B	A–B Δ %
SUMMER			
minimum	15.8 ha	18.3	15.8%
maximum	17.6	35.9	104.0
min–max Δ %	11.4%	96.2	
WINTER			
minimum	33.6 ha	31.4	–7.0%
maximum	48.3	65.8	36.2
min–max Δ %	43.8%	109.8	
TOTAL AREA			
minimum	37.3 ha	36.6	–1.9%
maximum	48.3	80.4	66.5
min–max Δ %	29.5%	119.7	
WINTER EXPANSION			
minimum	112.7%	71.6	
maximum	174.4	83.3	

1.0 km and the furthest point from the occupied cavity trees was 0.7 km. The large winter expansion may have been affected by logging operations which clearcut 8 ha and selectively removed a large number of other mature pines from the territory. The total territory was principally longleaf pine of which 51% was 66 yrs or older, 10% 33 yrs, 22% 23 yrs, and 17% was clearcut between the summer and winter measurements.

Clan B also consisted of a mated pair, without helpers, who successfully fledged 2 nestlings. These birds were observed foraging for 45 h in June–July and 23 h in January. The adults foraged over 16.0 ha while feeding the chicks in the cavity. After fledging, foraging activity shifted somewhat to incorporate more distant pine stands (the disjunct summer minimum unit of Fig. 1B) but the total area foraged increased only 2.3 ha. The 2 juveniles were present in late August but the clan had decreased to 2 birds in January. The habitat occupied by these birds was a seemingly less optimal mixture of small hardwoods and longleaf and loblolly pine (*Pinus taeda*) with 36% loblolly 33 years or older, 60% longleaf 13 yrs, and 4% longleaf saplings. The minimum 18.3 ha foraged in summer increased 71.6% to 31.4 ha in winter. The 2 areas only partially overlapped and the combined annual territory was 36.6 ha. The extreme distance across the territory was 1.3 km and the furthest point from the single cavity tree was 0.8 km.

This study has provided an interesting evaluation of this technique for estimating territory size. A casual glance at the maps tends to substantiate equally casual field appraisal that Clan B required a larger foraging area in the "less optimal" habitat it occupies. Yet scrutiny of the minimum territory data reveals that while Clan B foraged a 15.8% greater area than Clan A in summer, they foraged 7.0% less in winter and 1.9% less total area. When the 16.0 ha foraged by Clan B adults before their nestlings fledged is compared with the 15.8 ha foraged by Clan A adults, the 1.3% difference here, and the 1.9% difference in total area foraged, must be considered insignificant due to the crudeness of the technique. This tends to substantiate the opinions of other researchers that this species can be found in habitat judged unsuitable, by human standards, while often absent from areas similarly judged as ideal.

It is also of interest to note that neither pair of birds foraged in hardwood trees during peak food abundance in summer. However, 10% of all trees foraged in winter were hardwoods, indicating that the available prey on pine trees during this season may be a limiting factor.

These data clearly indicate that the increased winter foraging requirements of this species must be considered by forest managers attempting to reconcile the dictates of timber production with the conservation measures necessary to insure the future survival of these birds.

This study was supported by contracts AT(38-1)-819 and AT(38-1)-708 between the Energy Research and Development Administration and the University of Georgia. The senior author was also supported by a National Science Foundation Undergraduate Research Participation Program, an Oak Ridge Associated Universities travel grant, and the Frank M. Chapman Fund of the American Museum of Natural History. The cooperation and assistance of U. S. Forest Service personnel and S. E. Williams are gratefully acknowledged.—J. P. SKORUPA AND R. W. MCFARLANE, *Savannah River Ecology Laboratory, P. O. Drawer E, Aiken, S. C. 29801.* *Accepted 17 May 1976.*

Choice of nest boxes by Starlings.—In 1973 a series of experiments was started to determine the preferences of cavity nesting ducks for nest boxes with various features. The boxes were located in Ontario on Elk Lake (44°44′N 80°20′W) and Long Lake (47°52′N 79°00′W), Timiskaming District, on the Nonquon River (44°06′N 79°00′W), Ontario County and on the Lindsay sewage lagoons (44°20′N 78°46′W), Victoria County. Starlings (*Sturnus vulgaris*) made substantial use of these boxes and their preferences for certain features are clear.

The boxes used were made from 1.27 cm sheeting grade plywood with a rough surface. They were of standard design but there was some variation in the dimensions (generally less than 2%). Internally the boxes were approximately 45 cm high at the back with a sloping roof to a height of 42.5 cm at the front. They were 24 cm from back to front and 21 cm wide. The majority were mounted on trees close to the shore, facing the water, and about 3 m above ground. Branches and shrubs were trimmed so that the boxes were clearly visible from the water.

The first test was a comparison of interior colors. Two boxes were mounted about 60 cm apart on horizontal supports. One of each pair was painted black inside, the other was left unstained. All exteriors were stained light brown. All boxes had oval entrances 10.5 cm wide by 8 cm high, with the lower edge located 31 cm from the bottom of the box.

The second test provided a choice of 3 entrance hole sizes, large (13 × 10 cm), medium (10.5 × 8 cm) and small (7.5 × 6 cm). These boxes were mounted about 45 cm apart on horizontal supports nailed to trees. All boxes were stained gray externally and painted black inside. They were arranged in sets of 3 in a latin square design, with the sets spaced roughly 0.6 to 1.2 km apart.

Jackson and Tate (1974 Wilson Bull. 86:435–449) in a survey of nest box use by Purple Martins (*Progne subis*), House Sparrows (*Passer domesticus*) and Starlings

(*Sturnus vulgaris*) reported that the latter showed no statistically significant preference for white or dark interiors in their nest structures. However, they found that 1% of the white interior structures were occupied by Starlings compared to 1.6% of those with brown or natural wood interiors.

In 132 sets of the interior color test in the present Ontario study, 34 pairs of Starlings laid eggs in boxes with black interiors and only 3 nested in the unstained boxes, a highly significant difference ($\chi^2 = 21.3620$, $P < 0.001$).

Forty-two pairs of Starlings laid in the 102 sets presenting a choice in the size of entrance hole. Thirty-five chose the small entrance hole, 7 the medium, and none the large. This also is a choice pattern that is highly significant ($\chi^2 = 40.7879$ 2 d.f. $P < 0.001$). Starlings might be expected to choose the center box which was in line with the tree trunk. Seventeen chose the left, 13 the center and 12 the right side box, indicating no such selection ($P > 0.10$).

The boxes used are of a suitable design for cavity nesting ducks. Their dimensions are probably much too large to be optimum for Starlings.

Nevertheless, Starlings showed a clear preference for boxes of this size with a black interior and with the smallest of the 3 sizes of entrance holes offered. I have seen Starlings trying unsuccessfully to squeeze into a bluebird type box through an entrance hole 3.5 cm in diameter. The optimum size of hole is probably much smaller than the 7.5 × 6.0 cm chosen in this duck nesting study.

I wish to acknowledge the help of G. Bain, J. Knowles, F. Close, R. Stitt, D. Rivett and A. O'Donnell who helped to check the boxes. This is Fish and Wildlife Research Br. Contribution No. 76-3.—HARRY G. LUMSDEN, *Fish and Wildlife Research Branch, Ministry of Natural Resources, Maple, Ontario.* *Accepted 13 July 1976.*

Wing-flashing and other behavior of a Mockingbird toward its dead young.—On 7 June 1975 my dog caught a fledgling Mockingbird (*Mimus polyglottos*) that was still being fed by the parents. The fledgling was the only young of the unmarked pair. At the time of capture, both adults gave the usual distress calls and diving flights. When the dog released the still living fledgling, one of the adults immediately flew to the young. A few minutes after I picked up the young it died. I then placed the fledgling in a crotch formed by a branch and the trunk of a nearby tree. One of the adults saw me make this placement. Throughout the remainder of the day an adult Mockingbird flew to the dead young. Sometimes the adult produced a soft squeak-like sound as it cautiously approached the dead fledgling. Each time the adult flew to the dead bird, it gave a series of quick wing-flashes—in most cases while facing the young. The wing-flashes appeared to conform to the "low-intensity" type as described by Horwich (Wilson Bull. 77:264–281, 1965). In addition the adult frequently pecked and nudged the dead bird with its bill. I never detected food in the adult's bill. Until noon of the following day the same events previously observed occurred. They culminated when the adult pulled the young from the tree. At first the adult returned to the young lying on the ground; these trips soon ceased. Though the subject of wing-flashing in the Mockingbird and closely related species has received considerable attention in recent years (e.g. Horwich op. cit.; Michael, Wilson Bull. 82:330–331, 1970) no author has mentioned wing-flashing involving a situation as described above.

I thank Jack P. Hailman and Robert Ricklefs for their constructive comments regarding this note.—WALTER KINGSLEY TAYLOR, *Dept. of Biological Sciences, Florida Tech. Univ., Orlando 32816.* *Accepted 18 Sept. 1975.*

Feeding of nestlings by the Caracara in Costa Rica.—A Caracara (*Caracara cheriway*) nest was located on the edge of a fresh water marsh near Las Canas in Guanacaste Province, Costa Rica. The large bushy nest was approximately 30 m up in a 40 m *Pseudobombax septinatum* tree, and contained 2 nestlings that were close to fledging. I used spotting scope and binoculars to identify prey items brought to the young and the frequency with which the young were fed. The nest was observed during the dry season from 26 January through 30 January 1975. I spent 23 hours watching the nest from 06:00 to 11:30 and from 16:00 to 18:00 daily. The adult pair foraged over the marsh and in the surrounding areas of savannah and second growth arid scrub habitat.

During the 23 hours of observation, 47 visits were made to the nest by the adults, averaging about 2 trips to the nest per hour. The adults brought food to the young on 25 of these visits to the nest, or slightly more than once an hour. On only 5 occasions did more than an hour elapse between feedings. The food was torn apart in the nest by the adults and presented bite by bite to the nestlings—a feeding process typical of many raptors (Brown and Amadon, Eagles, Hawks, and Falcons of the World, Vol. I, McGraw-Hill, 1968). It took the adults an average time of 12 min to aid the young in consuming the prey.

Bent (U.S. Natl. Mus. Bull. 170, 1938) reports that some species of caracara feed their young fresh meat as opposed to carrion. Much of the food I observed brought to the nest (though difficult to ascertain) appeared to be freshly killed. The following food items were observed: Birds—3 *Jacana spinosa* (1 adult, 1 juvenile, 1 juvenile leg), 1 unidentified small bird; Mammals—1 peccary (lower jaw of *Tayassu pecari*), 1 cotton rat (*Sigmodon hispidus*); Reptiles—2 tails of *Ctenosaura similis*, 2 tails of *Iguana iguana*, 4 *Ameiva* lizards (probably *festiva*); Amphibians—1 large frog; Fish—2 fish of the family Eleotridae; Arthropods—1 tarantula or large insect; Miscellaneous—3 unidentified pieces of carrion. In addition to these, 4 items brought to the nest could not be identified at all before they had been fed to the young. The freshwater fish of the family Eleotridae were probably found in nearby ponds and waterways that were quite shallow as a result of the dry season. The cotton rat (*Sigmodon hispidus*) appeared to have been freshly decapitated and was one of the few instances in which the adult Caracara carried the food in its feet instead of with the bill. The peccary jaw was identified after an adult, flustered by an attack by a Tropical Kingbird (*Tyrannus melancholicus*) dropped the jaw and I retrieved it.

The Caracara is usually described as a carrion feeder (Glazener, Condor 66:162, 1964), and is sometimes seen in association with vultures (Monroe, Ornithol. Monogr. No. 7, 1968). It is of interest that only in 4 cases (including the peccary jaw) did the adults bring what appeared to be carrion to the nest. Since occasionally both adults joined the young in the nest after one of the mates brought food, it is possible that the adults were feeding along with the nestlings on the food brought to the nest. Thus during the nesting season the adult *Caracara cheriway* may feed on more fresh prey than hitherto reported.

I am indebted to Norman Scott for his help in identifying the prey, to Indiana University for supplying the funds for my participation in the Tropical Biology course sponsored by the Organization for Tropical Studies, and to Rollin Richmond for reading the manuscript.—ANN RELLER RICHMOND, *Zoology Dept., Indiana Univ., Bloomington 47401.* *Accepted 22 Sept. 1975.*

Unusually large vulture roost in Virginia.—On 29 December 1975, in the Radford Army Ammunition Plant (RAAP), 14 km west of Blacksburg, Va., we saw a large roost of Black (*Coragyps atratus*) and Turkey vultures (*Cathartes aura*). We counted 813

Black and 320 Turkey vultures. A review of the literature indicates this to be a large roost. Most reported Turkey Vulture roosts contain no more than 300–400 birds and average about 50 (Leach, Condor 31:21–23, 1929; Tyrrell, Auk 55:468–470, 1938; Eifig, Auk 16:299, 1944; Nauman, M.S. Thesis, Ohio State Univ., 1963). The 2 species are reported roosting together by Robbins (Wilson Bull. 62:36, 1950), who recorded 1 Black Vulture in a roost of more than 50 Turkey Vultures; and Grube (Wilson Bull. 65:199, 1953), who saw 12 Black Vultures among "a large flock of Turkey Vultures."

The roost near Blacksburg was counted in December of 1973, 1974, and 1975. It contained 401, 1047, and 1133 birds (both Black and Turkey vultures) respectively. Weekly counts were made throughout January and February 1975 and totals ranged between 320 and 708 for both species. Counts were made by 2 observers who visited the roost 1 h before dusk. A position was selected directly across the river, approximately 200 m from the roost. Birds already roosting were counted using binoculars. The surrounding horizon was then divided into areas of responsibility and incoming birds were tallied as they crossed an imaginary line located sufficiently distant from the roost to avoid counting any birds twice.

Our data indicate the roost near Blacksburg to be one of the largest vulture roosts ever reported for North America. Bussjaeger (Condor 69:425–426, 1967) saw a flock of Turkey Vultures migrating over Vera Cruz, Mexico, which he estimated to contain several thousand individuals. Stevenson (Am. Birds 28:629, 1974) reported a Turkey Vulture roost at Lake Okeechobee, Fla., which he estimated to contain 4000 birds. This estimate was made on 28 February 1974, and the vultures represent overwintering migrants (Paul Sykes, pers. comm., 1974). The majority of the RAAP birds are nonmigratory Black Vultures and the season of the counts seems to preclude transient migrants.

There are about 20 other vulture roosts reported in or near the State of Virginia. Most of these are located on the eastern shore of Virginia or bordering the Chesapeake Bay on either the Virginia or Maryland side. Only 3 other roosts are reported in mountainous sections of Virginia near Lexington, Staunton, and Charlottesville; all are located beside rivers (Robert Downing, pers. comm. 1975). The bulk of all 20 roosts are composed of Turkey Vultures, none exceeds 300 birds, and most number below 50.

The RAAP roost site is composed of large (32 m) sycamores (*Platanus occidentalis*) at the base of a 30 m bank along the New River. In this respect the physical aspects of the roost site do not differ from many others. There are no obvious concentrated food sources (e.g. slaughter houses) to attract the birds. However, the general public is denied admission to the plant, firearms are not permitted, and vehicular traffic in the roost area is minimal. This protection may account, in part, for the size of the roost.

This concentration of birds raises several questions. The most obvious is: what quantity of food is required to support such a population? We found a maintenance diet for caged Turkey Vultures approximates 140 g of meat per bird per day. A population of 1000 birds could require in excess of 140 kg of carrion per day. How large an area is needed to supply such a quantity? How far can these birds range in search of food? Continued observations at the roost near Blacksburg may provide some insight into these questions.

These observations were made possible through the cooperation of the Radford Army Ammunition Plant.—IRVINE D. PRATHER, RICHARD N. CONNER, AND CURTIS S. ADKISSON, *Dept. of Biology, Virginia Polytechnic Institute and State Univ., Blacksburg 24061. Accepted 21 Apr. 1976.*

Prey items of Goshawks in southwestern New York.—In evaluating food habits of North American accipiters, Storer (Auk 83:423–436, 1966) noted the paucity of data for breeding Goshawks (*Accipiter gentilis*). European work is available (Hoglund, Viltrevy 2:271–328, 1964; Vanbeusekom, Ardea 60:72–96, 1972), but information from North American populations comes mainly from Meng (Wilson Bull. 71:169–174, 1959) and Schnell (Condor 60:377–403, 1958).

We studied Goshawk food habits by identifying bits of food items near nests and feeding perches of nesting pairs at 10 nest sites in southwestern New York between 1964 and 1973. Table 1 summarizes the results.

Prey items can be organized into 3 main size categories. First, the grouse–crow type, comprise 23.4% of the food items, and include 18.2% Ruffed Grouse and 5.2% Common Crow. Small sciurids, including eastern chipmunk, gray squirrel and red squirrel, form the second type and comprise 33.8% of the total food items. Medium-sized birds (American Woodcock, Common Snipe, Common Flicker, Blue Jay, Robin, Starling, Eastern Meadowlark and blackbird) are the third type and made up 31.2% of the total.

Meng (1959) concluded from his data that Ruffed Grouse are not an important prey item of Goshawks. Our data are in accord with Eng and Gullion (Wilson Bull. 74:227–

TABLE 1

PREY OF GOSHAWKS BREEDING IN CHAUTAUQUA, CATTARAUGUS, AND ALLEGANY COUNTIES, NEW YORK: 1964–73

Species	M[1]	A	M	J	J	A	Total	Percent Total
BIRDS								
Ruffed Grouse (*Bonasa umbellus*)	1	4	3	3	2	1	14	18.2
American Woodcock (*Philohela minor*)	–	1	–	2	–	–	3	3.9
Common Flicker (*Colaptes auratus*)	–	–	1	–	3	–	4	5.2
Blue Jay (*Cyanocitta cristata*)	–	–	1	4	2	2	9	11.7
Common Crow (*Corvus brachyrhynchos*)	–	1	–	3	–	–	4	5.2
American Robin (*Turdus migratorius*)	–	1	–	1	–	–	2	2.6
Thrush sp. (*Catharus* sp.)	–	–	–	–	1	1	2	2.6
Eastern Meadowlark (*Sturnella magna*)	–	1	–	2	–	–	3	3.9
Other birds[2]	–	–	3	2	1	–	6	7.8
MAMMALS								
Eastern Chipmunk (*Tamias striatus*)	1	3	4	3	1	–	12	15.6
Gray Squirrel (*Sciurus carolinensis*)	–	–	1	4	–	–	5	6.5
Red Squirrel (*Tamiasciurus hudsonicus*)	–	1	4	4	–	–	9	11.7
Other mammals[3]	–	1	3	–	–	–	4	5.2
							77	100.1

[1] Months in chronological order beginning with March.

[2] Other birds included 1 each of the following: Common Snipe (*Capella gallinago*), Starling (*Sturnus vulgaris*), Scarlet Tanager (*Piranga olivacea*), blackbird sp. (Icteridae), warbler sp. (Parulidae), unidentified bird.

[3] Other mammals included: 1 deermouse (*Peromyscus* sp.), 1 eastern cottontail (*Sylvilagus floridanus*), and 2 unidentified.

242, 1962) indicating that a good portion of the diet of Goshawks includes Ruffed Grouse. Meng noted crows (in the same size class as grouse) to make up 44.9% of his total. Medium-sized birds included 31.2% of our total, but only 13.5% of Meng's. Sciurids compared nicely—33.8% in our study to 37.3% in Meng's. Goshawks may be looking for a particular prey size, and differences may represent variation of abundance and availability of species of a particular prey size.

Schnell (op. cit.) recorded food items from one nesting pair in California. Sciurids comprised 21.6% and medium-sized birds 59.1% of the total food items taken. His study, however, began in June with young in the nest, and differences may reflect seasonal variation. Our data from June through August show 50% of the food items to be medium-sized birds, which would agree with Schnell.—JOSEPH A. GRZYBOWSKI AND STEPHEN W. EATON, *Dept. of Biology, St. Bonaventure Univ., St. Bonaventure, N.Y. 14778. (Present address JAG, Dept. of Zoology, Univ. of Oklahoma, Norman 73069).* *Accepted 22 Sept. 1975.*

Extra-parental assistance by male American Kestrel.—On 5 June 1975, in the township of Minetto, New York, I first observed 2 adult male American Kestrels (*Falco sparverius*) alternately carry mice (probably *Microtus*) to the same female kestrel at the nest. The 2 male kestrels preyed on mice from utility wires extending across an open field approximately 1 km from the nest. Within a 10 min period the female kestrel received a partially denuded mouse from each of the males during flight. The female carried the mice to the decayed roof molding of a farmhouse. Investigation of the cavity revealed the female brooding 5 downy young.

I observed the birds daily until 29 June 1975, at which time the 5 kestrels were fledged. During this period I witnessed 47 instances of prey transfer from the male kestrels to the female. On a daily basis it appeared that one male carried a greater number of prey items to the female, but I was unable to determine whether this was the same individual from day to day. The female was not seen foraging during the 24-day period.

I have made occasional observations on the nesting kestrels at the farmhouse during the past 2 years. Kestrels have used the same nest site for at least 3 breeding seasons. Prior to the spring of 1975, I never witnessed a third kestrel assisting the breeding pair, or hunting in the established territory of the pair. Skutch (Condor 63:198–226, 1961) reviewed documented instances of extra-parental assistance in bird species and the American Kestrel was not among 134 species listed. More recently, Vries (An eco-geographical study with special reference to its systematic position, Vrije Universiteit te Amsterdam, Netherlands, 1973) documented polyandric trios of the Galapagos Hawk (*Buteo galapagoensis*). He established that pair bonds persisted from year to year in this species, and that polyandry varied in frequency with population density, occurring more often among denser populations.—WILLIAM A. WEGNER, *324 Shuart Ave., Syracuse, NY 13203.* *Accepted 4 Nov. 1975.*

Yellow-crowned Night Herons defecate, disgorge pellets on shore.—Watching Yellow-crowned Night Herons (*Nyctanassa violacea*) fish in a small piedmont stream at Woodlawn, Baltimore Co., Maryland, in 1973 and 1974, I found that they quite regularly went ashore to defecate, and then reentered the water. I saw this sequence 16 times; another time a bird flew out of sight instead of reentering the stream. In contrast, I saw one bird defecate while standing in the water, and twice saw one defecate into the stream while flying above it.

This behavior has been reported (this note; Brackbill, Wilson Bull. 78:316, 1966; Recher and Recher, Auk 89:896, 1972) for every North American ardeid except *Bubulcus ibis, Egretta garzetta, Nycticorax nycticorax* and the 2 bitterns. Reynolds (Br. Birds 58: 384, 1965) and the Rechers have discussed the possibility that the behavior prevents the spread of endoparasites.

Another habit which might have that value was shown by the Yellow-crowns. They went ashore to disgorge undigestible material and then promptly reentered the stream. I saw this sequence 3 times, including once by an immature bird. A fourth time, a heron that had caught a small crayfish carried it a few meters to a sand bar, biting it to death on the way, placed it on the ground, disgorged, ate the crayfish and reentered the stream. Only once did I see a Yellow-crown regurgitate into the water. I find no mention of this behavior in the literature, and have no data on disgorging by other herons.—HERVEY BRACKBILL, *2620 Poplar Drive, Baltimore, MD 21207. Accepted 6 Oct. 1975.*

Mourning Dove, Common Grackle cleaning bills.—Reviewing avian bill-wiping, Clark (Wilson Bull. 82:284, 1970) comments that he has not seen this done by Mourning Doves (*Zenaida macroura*). These doves visit my window feeding shelf in numbers, and in the frequent fights that occur tufts of small feathers are sometimes torn out. Usually these at once fall or blow away, but occasionally one sticks to the attacker's bill. Since 1962 I have noted that 1 bird dislodged such a tuft by shakes of the head, and 6 birds wiped it off by a stroke of the foot; I have never seen the bill wiped on the feeder rim or floor. I have also 5 times seen Common Grackles (*Quiscalus quiscula*) brush things off the bill with a foot; this species is on Clark's list of wipers.—HERVEY BRACKBILL, *2620 Poplar Drive, Baltimore, MD 21207. Accepted 6 Oct. 1975.*

Cliff Swallow breeding in south-central Florida.—The breeding range of the Cliff Swallow (*Petrochelidon pyrrhonota*) in the southeastern United States has been expanding in recent years and the first breeding records for Georgia and South Carolina were reported from Hartwell Dam on the Savannah River in 1965 (Tedards, Chat 29:95–97, 1965). On June 1975, I discovered 9 Cliff Swallow nests beneath U. S. Highway 441 bridge (Lat. 26°59′N, Long. 80°37′W) across the St. Lucie Canal, Port Mayaca, Martin Co., Florida. The bridge is located about 200 m east of Lake Okeechobee. This locality is approximately 840 km south of the nearest known nesting site at Hartwell Dam, Georgia–South Carolina line. How long Cliff Swallows may have been nesting in Martin County is unknown. No additional colonies were found during a search within a radius of 32 km from Port Mayaca.

Four visits during June to the Florida colony revealed that 2 nests were used by swallows, 3 by House Sparrows (*Passer domesticus*), and 4 were empty. I watched as 2 young fledged from one nest on 10 June; the other nest contained much smaller nestlings. An adult male in breeding condition (right testis, 9.5 × 7.5 mm, left, 11.5 × 7.5 mm) was collected on 17 June from the nest where young had fledged. I knocked the nest down to retrieve the specimen and found that it contained 2 fresh eggs. This specimen (NMNH 567576) of the nominate race and eggshell fragments are at the U. S. National Museum. Adults were still feeding young in the remaining nest on my last visit to the site on 19 June.

The nests were located at the top of 2 sets of concrete pillars supporting the bridge spans. Each set of pillars is connected at the top by a concrete cap and by a large transverse beam just below the cap. Such structures create artificial "cliff" faces protecting the mud nests from wind and rain. The 2 active nests were 3.3 m above the water (bottom of nests to water). The "neck" of the nest at which fledging was observed had broken off prior to 10 June or it was never completed before being used. The other active swallow nest was the gourd-shaped mud structure typical of the species. Three of the other 7 nests were intact and 4 had the "neck" partly broken or missing. Variation in the "neck" is well known (Gross, *In* U. S. Natl. Mus. Bull. 179, 1942).

I wish to thank Roxie C. Laybourne, U. S. National Museum, for confirming the subspecies of the specimen.—PAUL W. SYKES, JR., *U. S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Field Station, P. O. Box 2077, Delray Beach, FL 33444. Accepted 28 Oct. 1975.*

Minimum temperature for feeding by Purple Martins.—Allen and Nice (Am. Midl. Nat. 47:606–665, 1952) stated that Purple Martins (*Progne subis*) "seem able to withstand several days of cold weather and to be able to feed at surprisingly low temperatures...." Sprunt (Bent, U.S. Natl. Mus. Bull. 179:489–509, 1942) on the other hand (and many authors since) wrote that severe cold so eliminated insects that martins died from starvation. However, I have been unable to find any published information on the exact minimum temperatures at which martins are able to successfully forage.

In 1974 and 1975 I investigated the minimum temperature at which martins successfully fed and studied the behavior of Purple Martins in temperatures below that minimum in north central Texas (Sherman, Grayson Co.). While martin deaths due to starvation may be infrequent in north central Texas, there are many days on which cool weather restricts activity and feeding.

On days of cold weather I closely watched a backyard martin colony containing 7 martin houses and noted temperatures periodically. I also noted temperatures whenever martins left their houses and were seen flying nearby, erratically wheeling and presumably hawking for insects. The numbers of martins present at the colony varied from 5 at the time of their arrival to at least 30 near the end of March. Temperature measurements were obtained with a thermometer attached to the outside of a window screen. Possible temperature differences between the level of the window and the level of the martin houses I believe were negligible.

The major difficulty I had was in determining if martins were actually feeding. Purple Martins are far-ranging feeders and rarely feed near their colonies. However, when I observed the birds twisting and hawking, I assumed they were foraging successfully. I also assumed that the birds were foraging successfully when all the martins present at the colony disappeared in the afternoon and did not return until nightfall. It is unlikely that the birds would consume energy needed for flight unless they were finding food, especially at cooler than average temperatures.

On days of temperatures 13°C or above, martins presumably located ample food. Days of cold weather varied from the time of the martins' arrival in Sherman on or about 14 February throughout March. Only on 2 occasions did temperatures below 13°C extend for longer than a 2-day period.

On 14 days during February and March, 1974 and 1975, I recorded temperatures of 6°C or lower. Martins spent most of each of these days inside the martin houses. On 4 days with temperatures of 9°C during the afternoon, the martins remained away from the houses the entire afternoon.

On one occasion during 1974 I recorded temperatures of 6°C or lower for a 3-day period. On the first 2 days of this period, the martins' territorial defense and pair bonds were maintained. Although singing and flight were reduced, trespassing martins and

House Sparrows (*Passer domesticus*) were not tolerated. But on the third day territorial defense was abandoned; several birds of the same sex entered and remained in the same room of the martin house. A group of martins gathered on the south side of one of the martin houses, and birds of the same sex huddled together with no display of hostility.

All of the martins present at the colony spent most of the day and night of the third day in the largest of the 7 martin houses—this house was at least twice the size of the others. I counted as many as 10 martins using the same room for roosting on that night. Under normal circumstances only a pair at a time roosts in one room, and other martins are not allowed to perch on the porch in front of that pair's room.

In 1975 one martin at this colony and 3 at nearby colonies died following a 4-day period in mid-March when temperatures were 6°C or lower. These were the first martin deaths I could attribute to cold weather in the Sherman area since I began studying martins in 1969. During this cold period in 1975, the martins displayed behavior similar to that I observed in 1974.

Thus it appears, based on observations during 1974 and 1975, that Purple Martins in north central Texas cannot successfully forage at temperatures of or below 6°C, but that they can forage to some extent at 9°C, and at temperatures of 13°C they seem to be able to locate ample food to sustain their existence.

I am grateful to Warren M. Pulich, Sr., for suggestions on the preparation of the manuscript.—Charles R. Brown, *2601 Turtle Creek Drive, Sherman, TX 75090.* *Accepted 13 Nov. 1975.*

How do cowbirds find and select nests to parasitize?—The widely accepted conclusion that female Brown-headed Cowbirds (*Molothrus ater*) usually, if not always, find and select nests to parasitize by watching the host's building activities (Hann, Wilson Bull. 49:145–237, 1937; Hann, Wilson Bull. 53:211–221, 1941) is based primarily on 2 frequent observations: (1) female cowbirds spend long periods surveying their surroundings and watching the building of nests (Norris, Wilson Bull. 59:83–103, 1947; Mayfield, The Kirtland's Warbler, Cranbrook Inst. Sci., Bloomfield Hills, Michigan, 1960; Mayfield, Wilson Bull. 78:162–166, 1961; Norman and Robertson, Auk 92:610–611, 1975); and (2) cowbirds usually synchronize their laying with the brief egg-laying period of the host (Hann, Wilson Bull. 53:211–221, 1941; Walkinshaw, Wilson Bull. 61:82–85, 1949).

Despite this evidence, it can be objected that occasional observations of female cowbirds attentively watching nest-building do not justify the conclusion that most host nests are found in this way. Also, synchronization of the parasite's laying with that of the host is not perfect, for cowbirds are known to lay during inappropriate stages of the host's nesting cycle (Hann, op. cit., 1941; Mayfield, op. cit., 1960; Norman and Robertson, op. cit.) as well as in abandoned, empty nests (Nolan, pers. comm.). It could be argued that cowbirds find many nests simply by searching and parasitize them whatever their stage of development (see, e.g., Norman and Robertson, op. cit.). But if hosts usually accept only cowbird eggs laid during their own egg-laying period, ejecting those laid at other times, cowbird eggs laid after the host's laying has ended would rarely be found. Rothstein (Am. Nat. 105:71–74, 1971) points out that ejected eggs will go unobserved and absence of parasite eggs is insufficient evidence to conclude that none was laid. However, the likelihood that stage-dependent differences in host acceptance actually occur is reduced by Rothstein's observations (Condor 77:250–271, 1975; Auk 93:675–691, 1976) that the stage of the host's nesting cycle (egg-laying vs. incubation) is not a strong factor affecting acceptance or rejection of cowbird eggs in all but one of the 30 species that he tested; the exception is the Cedar Waxwing (*Bombycilla cedrorum*), which tends to accept during incubation and to reject during egg-laying.

In light of these plausible objections, we think the conclusion that cowbirds usually find nests by watching the host's building activities ought to be tested experimentally. Such an experiment might consist of exposing suitable nests supplied with eggs to potential cowbird parasitism, thereby eliminating the host's building and other activity around the nest. An opportunity to observe any cowbird parasitism of experimentally furnished nests was provided to us as the by-product of an experiment in which we investigated factors that might affect the nest-predation rate in old-field habitats.

Our experimental design was as follows: Each week between 4 May 1975 and 26 July 1975, 20 nests (12 to 14 of Cardinals, *Cardinalis cardinalis*, and 6 to 8 of American Robins, *Turdus migratorius*) collected after their owners had stopped using them were placed in typical nest sites in old-field habitat (10 ha) on the Bachelor Estate of Miami University, Oxford, Ohio. Two Japanese Quail (*Coturnix coturnix*) eggs were placed in each. An even dispersion of the 20 experimental nests over the study area was achieved each week by dividing the tract into 40 plots and placing each nest near a site chosen at random within alternating plots. We made daily visits to 10 of the nests, none to the other 10. After 6 days all surviving nests and eggs were collected; the next day the experiment was repeated using some new nests and all new eggs and sites. Thus during 12 weeks we exposed nests for 6 days apiece in 240 locations. Controls were nests of Field Sparrows (*Spizella pusilla*), Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow-breasted Chats (*Icteria virens*), Indigo Buntings (*Passerina cyanea*), and Cardinals that bred on the study area and in adjacent fields; the number of cowbird eggs these nests received was recorded. These species were selected because they were the only ones that we know were parasitized on the study area and adjacent fields in 1975.

No experimental nest received a cowbird egg, although cowbirds were common on the study area. The intensity of cowbird parasitism on hosts' nests varied seasonally, so we compared the frequency of parasitism of experimental nests exposed and free of predation and weather interference for 6 days with that of the foregoing parasitized species during each month: May, none of 47 experimental nests and 11 of 29 hosts' nests ($\chi^2 = 17.9$, df = 1, $P < 0.001$); June, none of 51 experimental nests and 12 of 25 hosts' nests ($\chi^2 = 25.6$, df = 1, $P < 0.001$); and July, none of 61 experimental nests and 8 of 22 hosts' nests ($\chi^2 = 20.6$, df = 1, $P < 0.001$).

These results are consistent with the idea that activity of the host at its nest is important in determining which nests female cowbirds find and select to parasitize. The only other experimental approach to this question seems to have been made by Laskey (Wilson Bull. 62:157–174, 1950), who ". . . put up dummy nests of several sorts, placing in them Bluebird (*Sialia sialis*) eggs from deserted nests and marked House Sparrow eggs. These eggs disappeared, but no Cowbird eggs were laid in the nests."

One serious objection that can be raised about our experimental design is the use of Japanese Quail eggs. Although some hosts reported by Friedmann (U.S. Natl. Mus. Bull. 233, 1963), such as the Brown Thrasher (*Toxostoma rufum*) and the Wood Thrush (*Catharus mustelina*), lay large eggs (27.3 × 19.8 mm and 25.4 × 18.6 mm, respectively) (Bent, U.S. Natl. Mus. Bull. 195, 1948; 196, 1949), the quail eggs are considerably larger (31.7 × 24.5 mm) than the eggs of the observed hosts on the study area (Cardinal, 24.8 × 18.5 mm; redwing, 24.8 × 17.6 mm; chat, 21.9 × 16.9 mm; Indigo Bunting, 18.7 × 13.7 mm; Field Sparrow, 17.9 × 13.5) (Bent, U.S. Natl. Mus. Bull. 203, 1953; 211, 1958; 237, 1968). Although we regard egg-size to be a problem (cf.

King, Am. Zool. 13:1259) and think that future tests should use smaller eggs, as Laskey (Wilson Bull., op. cit., 1950) did, our results do provide a systematic experimental test of, and are consistent with, the widely held conclusion that the activity of the host is important in determining which nests female cowbirds select to parasitize.

We thank Miami University for permission to work on the Bachelor Estate and Val Nolan Jr., Michael W. Monahan, and David R. Obsorne, who also provided the quail eggs, for reading a draft of this note.—CHARLES F. THOMPSON AND BRADLEY M. GOTTFRIED, *Dept. of Zoology, Miami Univ., Oxford, OH 45056.* (Present address CFT: *Dept. of Biology, State Univ. College, Geneseo, NY 14454*). *Accepted 8 Dec. 1975.*

White-throated Swifts following farm machinery.—On 15 December 1973 between 1435 and 1445 in the Avra Valley, 25 km northwest of Tucson, Pima Co., Arizona we observed approximately 50 White-throated Swifts (*Aeronautes saxatalis*) following a harvester. The harvester was first observed traveling north to south in a quarter section field of sorghum. A large cloud of dust was carried 200 m from the machine by a westerly wind. The swifts, flying in a counterclockwise elliptical circuit on the leeward side of the machine, entered the dust cloud ca. 3 m from the harvester then turned downwind and flew 100–150 m before circling back upwind. This behavior continued until the harvester reached the southern edge of the field where it slowed to turn about. During this pause the dust cloud dissipated and the swifts ceased circling, quickly rose to an altitude of 150–200 m, and dispersed over a broad area. When the harvester began cutting again, the swifts rapidly congregated and resumed their counterclockwise circuit in the new dust cloud. Although we were not close enough to observe prey capture, we presume the swifts were taking insects disturbed by the harvester. Several species of birds are known to benefit from the disturbance created by agricultural machinery, however we could find no records for swifts.—STEPHEN M. ALDEN AND G. SCOTT MILLS, *Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, Arizona 85721.* *Accepted 17 Dec. 1975.*

Common Terns feed on mole crabs.—I camped on Ocracoke Island, Hyde Co., North Carolina on 21–23 July 1973. On my first visit to the ocean beach I noted Common Terns (*Sterna hirundo*) flying over the wave-washed sand, picking up and eating small prey. Observations from a distance of 10 m or less with a 10 × 40 binocular revealed that the birds were capturing and eating small mole crabs (*Emerita talpoida*). These crabs were frequently exposed momentarily by a wave breaking on the sand after which they rapidly burrowed back into the sand. An inspection of the wave-washed zone of the beach revealed that the mole crab population was several orders of magnitude greater than I have observed on any Carolina beach in my 7 years of regular visits to the coast. A handful of sand randomly taken from the appropriate zone of the beach usually yielded at least 1 crab, sometimes 3 or 4. The crabs were all quite small, ranging approximately 1.5–2.5 cm long. I scanned up and down the beach and estimated that about 70 terns were hunting for crabs in about 1 km of beach. No Common Tern was observed over the water and no other species of tern was observed hunting for crabs. Least Terns (*Sterna albifrons*) were observed catching fish 5–100 m offshore, Gull-billed Terns (*Gelochelidon nilotica*) were seen catching insects in the interior of the island, and Royal Terns (*Thalasseus maximus*) and one Sandwich Tern (*Thalasseus sandvicensis*) were seen flying over the area.

I visited the beach at least 10 times during 3 days and saw Common Terns catching crabs each time. On all visits I saw only 2 Common Terns over the water; neither was seen diving.

I spent 3 to 5 August 1973 on Bogue Bank, Carteret Co., North Carolina, and again observed Common Terns catching mole crabs on all of 7 visits to the beach. A few Common Terns were observed over the water, and one was seen plunging into the water, but most birds were hunting crabs. The crabs were almost as abundant as on Ocracoke Island.

I have visited the Carolina coast frequently in the past 7 years, and in the last 4 years 2 of my graduate students have been studying tern behavior. These observations of Common Terns capturing mole crabs are remarkable because we have not seen the behavior before, and because almost all Common Terns seen were catching crabs. Common Terns are known to feed on *Emerita* (Palmer, Proc. Bost. Soc. Nat. Hist. 42:1–119, 1941), but my observations appear to be unique because apparently most if not all Common Terns were feeding largely if not entirely on mole crabs over a wide area and for a period of at least 2 weeks.

Common Terns usually feed on fish, and heavy predation on crustaceans has been correlated with low availability of fish (Langham, Ph.D. thesis, Univ. Durham, 1968). I saw Least Terns feeding on fish while Common Terns were feeding exclusively on mole crabs. I suggest that the unusual abundance of relatively small mole crabs provided an easily obtained and sufficient diet for the terns. Mole crabs are relatively easy to capture but it seems unlikely that searching for crabs at normal population levels would result in sufficient captures to justify the effort. Fully grown mole crabs are probably too large for easy handling by Common Terns. My observations suggest that Common Terns can shift normal feeding behavior to exploit an unusual food source. The switch from a normal, essentially exclusive, fish diet to mole crabs is consonant with L. Tinbergen's specific searching image hypothesis (Arch. Neerl. Zool. 13:265–343, 1960).—HELMUT C. MUELLER, *Dept. of Zoology and Curriculum in Ecology, Univ. of North Carolina, Chapel Hill 27514.* *Accepted 6 Nov. 1974.*

REQUEST FOR ASSISTANCE

Owl bibliography.—"A working bibliography on the Order Strigiformes (Aves) from the world literature" is the title of a bibliography currently being compiled by R. J. Clark, D. G. Smith and L. H. Kelso. Particularly sought are articles appearing in local journals and sportsmen publications. Faunal lists, however, will not be included. The bibliography attempts to cover the world literature and distribution of it will also be worldwide. *All* reprints received prior to 1 July 1977 and dealing with owls *will* appear in the bibliography. No guarantee for reprints received after this date can be made. To insure inclusion of your work please send 2 reprints of each article to:

Owl Bibliography, c/o Richard J. Clark, Department of Biology, York College of Pennsylvania, York, Pennsylvania 17405.

ORNITHOLOGICAL LITERATURE

Waterfowl of North America, by Paul Johnsgard, Indiana University Press, 1975: 575 pp., many line drawings, maps, and color and black-and-white photos. $25.00.—During the winter of 1970–71 Paul Johnsgard made an ambitious commitment to a book dealing with the ecology and reproductive biology of all waterfowl breeding in North America. He planned to integrate recent field studies by wildlife biologists, ecologists, and ethologists while at the same time presenting the material in a book understandable to nonprofessionals. Coupled with this intent was the desire to present practical means of waterfowl identification under both field and in-hand situations. In this lengthy and handsome volume, Johnsgard has admirably met his goals.

The book has two major divisions. The first is a tripartite introduction containing chapters on the biology of waterfowl, waterfowl distributions and migrations, and waterfowl hunting and recreational values. The second part contains species accounts for the waterfowl breeding in North America, including marginal species such as the Falcated Duck, Baikal Teal, Tufted Duck, and the introduced Mute Swan.

In the introductory material Johnsgard provides a characterization of waterfowl biology; the diversity of the group often precludes really incisive commentary. For example, "In most species of North American waterfowl the actual clutch size is variable, although the 'normal' size of initial clutches may be fairly predictable, especially in species having smaller clutches" (p. 6). No author faced with the vicissitudes of such biological phenomena as clutch size, incubation periods, and food habits can adequately treat these subjects in a generalized account. The problem is, of course, addressed satisfactorily in the species accounts that follow.

Each of the species accounts contains material on other vernacular names for the species, a description of the bird's range, subspecies (if any), measurements of folded wing and of culmen for each sex (often taken from Delacour's 4-volume treatise and thus lacking such details as sample sizes) and weights. These data are followed by a description of the bird in the hand and in the field, and an outline of age and sex criteria. An account of distribution and habitat is separated into breeding and wintering locations. The account of "General Biology" includes the following: age at maturity; pair bond pattern; nest location; clutch size; incubation period; fledgling period; nest and egg losses; juvenile mortality; and adult mortality. The penultimate section is entitled "General Ecology" and includes comments on food and foraging; sociology, densities, territoriality; interspecific relationships; and general activity patterns and movements. The final heading in the species account is "Social and Sexual Behavior" and here Johnsgard's intimate knowledge of waterfowl comes to the fore. Subheadings include flocking behavior; pair-forming behavior; copulatory behavior; nesting and brooding behavior; and postbreeding behavior. Each species has its own range map showing the bird's distribution in North America (distributions elsewhere, if any, are not shown but are mentioned in the text). In all, the coverage given each species is certainly sufficient for a book of this sort and one must commend the author for the awesome task of compiling details necessary to address this broad range of topics.

The volume is liberally infused with color plates of many species and with many additional black-and-white photographs (often of the same species appearing in color elsewhere). The species accounts are introduced with a pen and ink sketch by the author, thus adding further attractiveness to the volume. Many of the color plates are exceptional as, for example, the delicate photograph of an adult Trumpeter Swan that was also selected for the dust jacket. Other color plates are of lesser quality, for example, the uncrisp photos of Buffleheads and Common Mergansers. The black-and-white photographs are necessarily less attractive and too often they are repetitive (for example, the Wood Ducks and Falcated Ducks).

In some cases Johnsgard deviates from the nomenclature recognized by the A.O.U. Among the systematic comments of note are the recognition of a complex, the "southern Mallards" consisting of *Anas platyrhynchos diazi* (Mexican Mallard), *A. p. fulvigula* (Florida Mallard) and *A. p. maculosa* (Mottled Mallard). He chides (p. 235) ". . . neither the technical nor the vernacular names used by the A.O.U. (1975) provide a clear indication of the relative relationships of these forms to one another or to *platyrhynchos*, and the A.O.U. decision not to recognize vernacular names for subspecies tends to maintain an unwarranted degree of taxonomic separation of these populations." This is a commendable position by a recognized authority on the problems of "mallard" taxonomy, and I applaud his forthright stance on the matter. The author likewise treats Brant as a single species with 2 races, *Branta bernicla hrota* (Atlantic Brant Goose) and *B. b. nigricans* (Pacific Brant Goose). The Hooded Merganser joins others of its group in the genus *Mergus*. Recognition of the North American dendrocygnids as "whistling ducks" brings this vernacular terminology into welcome agreement with ornithologists elsewhere in the world. There are other changes, but these serve to illustrate the nature of Johnsgard's systematic thrust in preparing this volume.

I did not routinely cross check all of the citations mentioned in the text with those cited in the extensive bibilography although I did check—perhaps immodestly—the accuracy of those attributable to me and my co-authors and found that one cited on p. 48 was omitted in the literature citations; the correct spelling for "Rolle" is Rollo on p. 217. Another includes Ferguson (1965) cited as Ferguson (1966) in the bibliography. There are additional slips, mostly in format, in the literature citations ("Sources") but none that impairs location of the original material. No citation is given for "A Utah Study . . ." on p. 296 or for the Bufflehead banding data noted on p. 459. There may be similar errors throughout the text but these are, after all, rather minor miscues that inevitably creep into a work of this scope.

Perhaps my most critical comments are reserved for the lengthy, and therefore confusing, sentences dotting the text. "Although among geese and swans the parental attachment for the young persists through the entire post-hatching period and the following migration, the brood bond of female ducks toward their offspring is much weaker and more variable, presumably being dependent on hormonal controls" (p. 7) is both lengthy and awkward. Some tight editorial work would have helped the text in several places. Johnsgard can be pithy, if long, however. The last paragraph on p. 22 is a fine example. He writes, in part ". . . the sight of a migrating goose flock represents far more than a simple measure of the passing seasons; it is an unwritten testimony to dogged persistence in spite of adversity, to an inherited trust in this species' long-term design for survival in the face of individual starvation and violent death. It is an example that should lift the human spirit; despite indivdual disasters, the geese endure. We can ask for no greater symbol of determination despite appalling hardships than is provided by waterfowl; we should be content with no less than a maximum commitment to their continued existence." Save for long sentences and the questionable inclusion of several photographs, there is little to fault in this *tour de force* of North American waterfowl.

The past year has witnessed the publication of several important books on waterfowl, perhaps justifying the designation, "Year of the Duck." In any case, a copy of Johnsgard's important contribution ought to grace the library of anyone—ornithologist and hunter alike—concerned with our continent's bountiful waterfowl resources.—ERIC G. BOLEN.

ORNITHOLOGICAL GAZETTEER OF BOLIVIA. By Raymond A. Paynter, Jr., Melvin A. Traylor, Jr., and Blair Winter. Privately printed, 1975: vi + 80 pp., 1 map, paperbound. $1.75. Order from Bird Dept., Museum of Comparative Zoology, Harvard Univ., Cambridge, Mass. 02138 *or* Bird Division, Field Museum of Natural History, Chicago, Ill. 60605.—Paynter and Traylor, as an adjunct to their respective research on the distribution of Neotropical birds, independently maintained card file gazetteers of "ornithologically significant localities," usually collecting localities but occasionally places where ornithological observations were made but no specimens taken. Winter is a volunteer, working with Traylor at the Field Museum, trying to complete the files for given countries. These authors have pooled their files and produced this modestly priced gazetteer for Bolivia, choosing that country for their first publication venture because it has relatively few places that have been visited by ornithologists.

The authors attempted to include the following items for each locality: "department (similar to a state), geographical coordinates, altitude, collector at that site with the time of his visit (often not inclusive dates), and an indication of the habitat. The last information, unfortunately, has been recorded infrequently by collectors. . . ." Documentation is extensive, and the 108-title bibliography includes most of the literature of Bolivian birds. The sources of information for the gazetteer include localities on specimen labels in the authors' own museums and those found in a literature search. No attempt was made to obtain localities at which birds now in other museums were collected, but which have not been mentioned in the literature. Although understandable, as this project has been necessarily a peripheral effort of the authors, this omission is nonetheless regrettable. There are less than half a dozen museums in the world with major holdings of Bolivian birds. Had a photocopy of the gazetteer typescript been circulated among these museums prior to publication, a closer approach to completeness could have been attained. The authors realize, of course, that their list is incomplete, and add ". . . surely there are specimens in museum drawers from Bolivian localities that we have yet to hear of." At least for some museums, adding to the authors' list of localities would not have entailed searching through trays of specimens, as museums other than the M.C.Z. and Field Museum have locality files or other helpful documents. Carnegie Museum of Natural History has something over 9000 Bolivian birds. By scanning our catalogues, I found that we have birds from 16 localities not listed by Paynter, Traylor and Winter. In addition, I found (on maps or written itineraries provided by the collector) four of the localities listed as "not located" by the authors, plus five unlisted variations in orthography (the authors have done a great service by indexing incorrect or variant spellings encountered in the literature). In response to the stated request of the authors, I have sent them this supplementary material, but I would have preferred to have done it for incorporation in their original manuscript, although a revised edition or a supplement may be published eventually.

Inclusive dates of a collector's visit to a locality are usually given for areas represented in the authors' own museums. Otherwise, unless a published paper includes an itinerary, the dates given are those that have been encountered in the literature in connection with certain specimens. For example, under San José, Cochabamba, only the date 19 May 1921 is given, with the name of the collector (J. Steinbach) who was there then. From the references supplied, one finds that 19 May 1921 is a miscopying of the date of collection (it should be 29 May) of the type specimen of *Pulsatrix melanota philoscia* Todd. Consulting our catalogue, however, I find that Steinbach was at San José for more than two months (5 May through 10 July 1921). The full dates of itineraries of collectors are often not this easy to determine, but when available they are potentially quite useful to workers interested in records of seasonal phenomena: occurrence of migrants, molt, breeding, etc.

The points raised above are shortcomings that could be rectified in a second edition of the Bolivian gazetteer, and that should certainly be kept in mind for future publications of this kind. I hope the reception given to the Bolivian volume will be sufficiently enthusiastic to encourage the authors to continue this highly worthwhile project. I urge all curators of collections of Neotropical birds to offer their full cooperation—I don't envy the authors the job of compiling ornithological localities for Brazil!—KENNETH C. PARKES.

BREEDING BIRDS OF NORTH DAKOTA. By Robert E. Stewart. Foreword by Chandler S. Robbins. Tri-College Center for Environmental Studies, North Dakota State University, Fargo, ND 58102, 1975: 295 pp., 18 color paintings, 81 photographs (16 in color), 185 maps. $18.50.—North Dakota, with more federal wildlife refuges than any other state (63), but with no state ornithological society and relatively neglected by ornithologists, has long needed a state bird book. The author of this volume, associated with the Northern Prairie Wildlife Research Center, U. S. Fish and Wildlife Service, Jamestown, ND, has attempted to document available information concerning the past and present status of breeding birds in North Dakota. He has succeeded admirably.

Initial chapters describe the climate, physiography, and geological history of the state. The author then delineates the biogeographical relationships of the state avifauna, listing species typical of the north-central plains region, and then listing additional species that are more typical of major biotic areas to the east, west, and north of the state.

Four major biotic areas are recognized in the state, correlating with four physiographic regions, with characteristic species listed for each. Three large state maps delineate physiography, biotic areas, and political subdivisions. Particularly impressive is a large section describing ecological associations of breeding birds, divided into six major associations: agricultural, prairie, wetland, forest, badlands, and towns and cities. Each of these is subdivided by habitat, e.g. the prairie association into tall-grass, eastern and western mixed-grass, short-grass, black sage, and prairie thicket communities. Each habitat type is described with primary, secondary, and extraneous avian species listed, along with characteristic plant species. Sixteen excellent color photographs illustrate most habitats.

Central to the book are the species accounts, describing only those species known to breed in the state, past or present, and arranged phylogenetically by family; orders are not given. Taxonomy follows the AOU checklist (1957), amended by the thirty-second supplement (1973), and incorporates changes proposed by Mayr and Short (1970, Species taxa of North American birds. Publ. Nuttall Ornithol. Club, No. 9). Subspecies generally are not described except for three groups where distinct subspecies can be recognized in the field: the flickers, orioles, and towhees.

Of the 196 breeding species listed (including 190 native), large individual breeding range maps are included for 182 species. Several species are not given maps presumably because breeding in the state is hypothetical, or they are exceedingly common, e.g. House Sparrow and Starling. The maps are well done and include symbols indicating whether nests and/or dependent young, or territorial males and/or pairs were observed, and whether recently (since 1950) or in the past. Thus, the reader can, at a glance, evaluate the records. The description of each species includes breeding range and abundance, habitat with plant species composition, nesting and hatching dates, nest descriptions, and clutch sizes. Relevant references are cited, especially for rare species. Morphological descriptions, behavior, etc., are not included, and are probably superfluous to the intent of the book. Keys to field identification are not given either; thus birders will also want a good field guide.

The volume is well illustrated with eighteen paintings of nineteen typical prairie species by Walter A. Weber (13), and Roger Tory Peterson (5). Sixty-five excellent black-and-white photographs of birds, appropriately placed throughout the book, were all taken in the state and include date and location. Most of these were taken by Ed Bry, editor of *North Dakota Outdoors*, and well known for his wildlife photography.

Appendices include literature cited with over 350 references, common and scientific names of plants, a large synopsis of publications concerning state birds excellently organized by topic and year, and a bird species index.

Although one can nitpick here and there (Upland Sandpiper is still called a Plover; the table of contents does not give page numbers for families; some references in literature cited are not cited in the body), the volume represents an excellent, lavish, and consistent treatment. It is a definite contribution to the avian literature of North America, and will be of great value to researchers and bird watchers in North Dakota.—L. HENRY KERMOTT.

BEHAVIOR AND ECOLOGY OF THE AMERICAN KESTREL (*Falco sparverius* L.) IN THE SIERRA NEVADA OF CALIFORNIA. By Thomas G. Balgooyen. Univ. of Calif. Publ. Zool. Volume 103. Berkeley, Calif., 1976. 83 pp., 2 plates, 27 figures.—This is a report of field observations of Kestrels in the eastern Sierra Nevada of east-central California in 1970 and 1971. The field data are mainly concerned with nesting chronology, nest-site characteristics, egg measurements, body measurements, growth rates, interspecific aggressive encounters, hunting success, prey, and measurements of the composition and spatial qualities of the plant communities. Included also are accounts of hunting techniques, territoriality, weather effects, and fledging behavior. A major section discusses the significance of sexual dimorphism in Kestrels, and raptors in general.

Balgooyen has mingled extensive discussions with the presentation of his data. This, coupled with frequent, but not always thorough, reference to the literature, tends to create uncertainty in the reader as to what the findings actually were. An incomplete methods section is so brief that interpretation of the data is occasionally difficult and the hope of close comparison with other studies small. For example, it is unclear how individual Kestrels were distinguished in the field, a question central to discussions of home range and behavioral interaction. The population densities of various small animals ranging from flying insects to lizards and birds were estimated from line transects, but the author does not discuss how the densities of these animals were computed from the transect counts.

The paper deals with many familiar aspects of raptor biology. Sexual size dimorphism in raptors remains an intriguing problem. The author argues that males are smaller because the energy costs to the male, in supplying food to the female, are less because males have lower total energy requirements than females. No data are given to support this view and the idea is not easy to rationalize, especially since size dimorphism in Kestrels is small. The hypothesis will no doubt prove difficult to substantiate because it is generally recognized that larger birds transport a unit of body weight over a distance with less energy cost than small birds, and because of variables such as changes in wing loading and other aerodynamic factors while burdened with prey. In any case, a satisfying explanation of the adaptive value of size dimorphism in raptors will need to explain why males are the smaller sex, why the degree of dimorphism varies so much among species, and why it seems most pronounced among species that take prey that is especially evasive or large in relation to the raptor. Bird-eating raptors and other swift and aggressive species, including Bonelli's Eagle (*Hieraaetus fasciatus*) and Booted Eagle (*H. pennatus*) are strongly dimorphic. Kestrels and other rodent and insect feeders tend to be less dimorphic.

The interpretation of field data is not always careful. "Selection" of east-facing nesting holes cannot be demonstrated unless it can be shown that holes facing other directions are less favored and remain unused. It could well be that the tendency of Kestrels to use east-facing holes is most influenced by the choice Common Flickers (*Colaptes cafer*) make in excavating them in the first place.

The author discusses somewhat minor topics at length. The toothed maxillary tomium in falcons is supposed to make possible a finer and stronger point by providing support at its base. If so, the presence of a notch in the mandible opposing the tooth, remains, unfortunately, a separate problem. The illustration of the beaks of accipiters and falcons does not suggest strongly that accipiter beaks are any less sharp than in falcons. The result that Kestrel hunting success increases markedly as easily-taken insects become more available probably does not merit the considerable space allocated to the topic.

Some statements are not clearly argued. Hovering ability is attributed to small size and low wing-loading of Kestrels, that being small, gain "needed lift." Actually, many larger species, e.g., Rough-legged Hawks (*Buteo lagopus*), hover quite well. That Peregrines (*Falco peregrinus*) do not hover while hunting is attributed to their high wing loading *per se*, and no mention is made of the specialized high speed hunting strategy evolved by Peregrines.

Ethologists will not always find terminology used in the accepted way. The term "search image" is used to describe the momentary appearance of a single prey individual, and not the development of habituation for preying on a type of prey.

The author states that the feet of male and female Kestrels are of similar size because their prey is of similar size. It might just as logically be stated that foot-size is similar because there is no advantage in the sexes taking dissimilar prey. But even this seems a useless approach because the author elsewhere asserts that sexual size dimorphism in raptors is not related to differential prey selection.

Balgooyen has new and interesting information on Kestrel nesting success (87% of eggs laid result in fledged young), and he found a slower attack rate in areas with better cover for prey. Kestrels hunt from perches 97% of the time and hovering and hawking are uncommon.

This publication touches on many aspects of raptor ecology and should prove provocative to its readers who must, nevertheless, remain open on some of the positions taken. Data such as these are gained only by great effort in the field and will provide opportunity for further analysis.—JAMES H. ENDERSON.

FLAMINGOS. Janet Kear and Nicole Duplaix-Hall (eds.). T. and A. D. Poyser Ltd., Berkhamsted, Great Britain, 1975:246 pp., drawings, paintings, charts, black and white and color photographs. £8.00.—This book is the proceedings of the 1973 International Flamingo Symposium held at the Wildfowl Trust, Slimbridge, England. With an introduction by Peter Scott, chapters by 29 authors, and illustrations of all species and races of flamingos in most of their plumage variations, it is a must for anyone interested in flamingos. One important result of this symposium is the standardization of common

English names (Caribbean, Greater, Chilean, Lesser, Andean, James') of the 6 flamingos. There was also unanimous agreement that the Chilean Flamingo should revert to specific status. The introduction gives a brief summary of our knowledge of the taxonomic relationships of flamingos, some interesting influences flamingos have had on human culture, and comments on conservation problems relating to flamingos.

The first section of the book, "Populations, ecology and the conservation of flamingos," comprises 14 chapters dealing with specific populations and a summary chapter by M. P. Kahl on the distribution and numbers of flamingos. Low-flying aircraft are a serious disturbance to several populations. Environmental change due to industrial development, urbanization, or drainage threatens the very specific habitat of flamingos in many areas. A. R. Johnson reports that the breeding success of Greater Flamingos at the Camargue has slightly surpassed the average for the last 60 years. R. W. McFarlane reports that populations of the three South American flamingos seem to be increasing in recent years, but new roads, increased agricultural developments, and mining may reverse this trend. Other populations have declined. Populations have decreased recently in Sardinia (A. Toschi, Ch. 2), and there was a 42% decline in Iranian populations from the 1971–72 to the 1972–73 census, though an estimated 80–85% of the population occurs on protected lands (D. A. Scott, Ch. 3).

Chapters by A. Sprunt and A. Crego-Bourne, J. E. Cooper, H. H. Berry, H. Poulsen, A. Studer-Thiersch, N. Duplaix-Hall and J. Kear discuss techniques and problems associated with capture, transport, and keeping flamingos in captivity. The chapter "Ritualised Displays" summarizes our knowledge of ritualized behavior of flamingos and attempts to standardize descriptions from previous studies. Most of these displays are illustrated by outstanding black and white photographs. In another chapter A. Studer-Thiersch discusses group display in the genus *Phoenicopterus.* There is considerable overlap in these two chapters on behavior.

T. Clay discusses the taxonomic relationships as suggested by feather lice. The Greater, Caribbean, Chilean, and Lesser flamingos all have the same species of wing louse though each has a separate species of head louse. The James' Flamingo apparently has different wing and head lice species than other *Phoenicopterus.* No taxonomic conclusions are given.

D. L. Fox presents a thorough discussion of carotenoids in pigmentation, including some discussion of birds other than flamingos. His study includes the origin of carotenoids, results of experimental feeding of carotenoids to flamingos, and analysis of carotenoid content of flamingo eggs, crop milk, chicks, and feathers. His chapter ends with a brief evaluation of finely cut grass as a carotene-rich foodstuff for flamingos. Chapters by H. Thommen, J. A. Griswold, and H. Wackernagel contribute additional information on the metabolism of carotenoids and dietary requirements of flamingos.

The final 3 brief chapters by P. N. Humphreys, J. V. Beer and J. Kear, and N. A. Wood describe diseases and injuries of flamingos, but there are few suggestions given for treatment. Appendices provide weights and measurements of flamingos, a longevity table, instructions for pinioning flamingos, and a description of leg bands for flamingos. The bibliography of 303 references will be of great use to researchers.

The editors are to be congratulated for a well-organized and error-free volume. The quality of the photographs, line drawings, and paintings is such that this book could compete well with most "coffee table" bird books as well as being a good review of our knowledge of flamingos. This volume should certainly be ordered by university or zoo libraries.—Jerome A. Jackson.

THE PLEASURE OF BIRDS: AN AUDUBON TREASURY. Edited by Les Line. J. B. Lippincott Co., Philadelphia and New York, 1975. 191 pp., 28 drawings and 18 color photographs. $14.95.—For this anthology Les Line has assembled a well balanced and carefully edited selection of 25 recent articles, by as many contributors, from *Audubon* magazine. Subject matter varies from a bit of philosophy in Brooks Atkinson's lead article "The Bird Habit," through some well presented lessons in avian biology and conservation by such well known naturalist-writers as Louise de Kiriline Lawrence, Roger Tory Peterson, John K. Terres, and George Laycock. George Plimpton's amusing recounting of his initiation into the world of the Christmas Bird Counts, "*Tsi-lick*! Goes the Henslow's," lends a lighter touch. A lot of good *Audubon* reading is reprinted here, and the book should have a wide appeal even among those who have been longtime subscribers to the magazine. Each selection is headed by a few introductory sentences by Line, along with a painting (or "drawing") by Chuck Ripper. Unfortunately these illustrations appear to have been hastily prepared, and certainly do not represent the artist at his best. Many of the drawings fail somehow to capture the "feeling" of the species, and errors of anatomy, balance, and proportion are all too frequent. Having all of the lead illustrations prepared by a single artist is of course an advantage in bringing the widely varied selections together in a common format, and in providing a sense of unity. In this, Ripper's paintings succeed well enough. To the reviewer, however, any article by George Miksch Sutton (in this case "The Footprint Thieves") not illustrated by Sutton himself is somehow incomplete; and there will be those who will miss Peter Parnell's illustrations in the Angus Cameron selection, "The Power of the Owl." Also included in the book are two portfolios totaling 18 beautifully reproduced full page photographs (by 14 different photographers), including two by G. Ronald Austing and four by Frederick Kent Truslow. As with the articles, these photos have previously appeared in the pages of *Audubon*. The subject matter is decidedly unbalanced in favor of water birds and birds of prey, passerines being represented only by a particularly handsome portrait by Eliot Porter of a Winter Wren at its Maine nest site. Although the photographs are completely unrelated to the text, they do add to the attractiveness and sales appeal of the volume, and presumably to the price. But in final analysis it is the quality and variety of the literary selections themselves, not the illustrations, that are the real measure of a good anthology. For pleasant reading *The Pleasure of Birds* lives up to its name. It is indeed a pleasure.—ROBERT C. LEBERMAN.

Erratum.—Catherine H. Ream's current address should be inserted at the end of her article in the September Wilson Bulletin (88:427–432, 1976). Her address is: 4217 Timberlane, Missoula, MT 59801.

ORNITHOLOGICAL NEWS

ANNUAL MEETING

Plan now to attend the 58th Annual Meeting of the Wilson Ornithological Society. The meeting will be held at Mississippi State University near Starkville, Mississippi from 18–21 May 1977. A special feature of the meeting will be a symposium on woodpeckers which will be chaired by Lester L. Short. Persons interested in presenting papers at the general sessions should submit a one page abstract to George A. Hall, Program Chairman, Department of Chemistry, West Virginia University, Morgantown, WV 26506, before 1 April 1977. Indicate how much time and what audio-visual equipment will be needed for the presentation.

In addition to the scientific program, there will be several field trips and other activities. Trips to Noxubee National Wildlife Refuge will include visits to nests of Red-cockaded Woodpeckers, Black Vultures, and other southern species. A trip to a local heronry will allow observation and photography of Little Blue Herons, Cattle Egrets, Great Egrets, and others. One field trip will be by canoe down the Tombigbee River. Trips will also be scheduled to ante-bellum homes and to local industries.

FRANK M. CHAPMAN FUND

The Frank M. Chapman Memorial Fund gives grants in aid for ornithological research and also post-doctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. Applications are due on 15 September and 15 February. Information on form and content of applications may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024.

FIFTY-YEAR INDEX TO THE JACK-PINE WARBLER

A 50-year index (1923–1972) to The Jack-Pine Warbler, the quarterly journal of the Michigan Audubon Society, has been prepared. The 4″ × 6″, 242-page subject and author index is available for $5.00 including mailing, from the Michigan Audubon Society Bookshop, 7000 North Westnedge, Kalamazoo, Michigan 49007.

COLONIAL WATERBIRD GROUP

A Colonial Waterbird Group (CWG) was formed at the North American Wading Bird Conference on 16 October 1976. The group combines the North American Wading Bird Group, and the Atlantic-Gulf Coast, and Interior Colonial Waterbird Group. Objectives of the CWG are (1) to encourage and coordinate standardized wader surveys, (2) to publish a newsletter, (3) to assist efforts by conservationists related to protection and management of wetland ecosystems, and (4) to act as a clearinghouse of information for on-going research and research opportunities. The group has established a newsletter as a channel of communication among the CWG members and plans a meeting next year.

Chairperson of the pro tempore Steering Committee for CWG is John C. Ogden, editor of the Newsletter is Mitchell A. Byrd, and Secretary-Treasurer is Joanna Burger. All those interested in joining are urged to contact Joanna Burger, Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903. Dues for 1977 are $5.00.

NOMINATING COMMITTEE

President Berger has appointed the following Nominating Committee for 1976–1977: Dr. Olin Sewall Pettingill, Jr., Chairman, Wayne, Maine 04284; Dr. H. Lewis Batts, Jr., 2315 Angling Road, Kalamazoo, Michigan 49008; Mr. Phillips B. Street, Route #1, Chester Springs, Pennsylvania 19425.

Candidates for Second Vice-President and Elected Member of Council are needed for the 1977 Annual Meeting at Mississippi State University. Members of the Society may send names to any member of the committee not later than 15 March 1977.

REQUESTS FOR ASSISTANCE

Purple Martin color-marking.—A Purple Martin color-marking project was initiated in 1975 for Prince George's and Montgomery Counties, Maryland and in 1976 for Saxis, Virginia. Observers are asked to look for and report any color-marked (wing tags and/or plastic leg bands) Purple Martins. Please record the color of the band, which leg it is on, age and/or sex (if either is known), where and when observed, and whether the bird was in a roost, staging flock, migratory flock, or established at a nest site. All reports should be sent to Ms. Kathleen Klimkiewicz, 13117 Larchdale Rd. #2, Laurel, Maryland 20811.

Color-banded Long-billed Curlews.—Adult and juvenile Long-billed Curlews have been banded with red, yellow, green, or light blue plastic bands and with U.S. Fish and Wildlife Service metal leg bands in the Columbia Basin of southeastern Washington. The color bands are the same size as the U.S. Fish and Wildlife Service bands and are placed on the opposite leg. They each have a black number (from 1 to 100) printed on them, and are visible on standing or perching birds.

Status, behavior, migration, and territory selection are several of the most important points I am studying. Should you see any of these birds, please write: Bird Banding Laboratory, Office of Migratory Bird Management, Laurel, Maryland 20811. Include date, time of day, and location of the observation: plus name of observer(s), color of band, and if possible, the number printed on the band. Also include the activity of the bird at the time of sighting, the type of habitat it was sighted in (e.g., grassland, mudflats along a lake, etc.), and the number of other curlews associated with the marked individual(s). —Julia N. Fitzner, Battelle-Northwest Laboratories, P.O. Box 999, Richland, Washington 99352.

EASTERN BIRD BANDING ASSOCIATION RESEARCH AWARD

The Eastern Bird Banding Association is again sponsoring a $250 grant for an undergraduate or graduate student in a recognized college or university in the Western Hemisphere for research in ornithology involving bird banding. Applicants should submit a resume of their planned project to Dr. Bertram G. Murray, Jr., 249 Berger St., Somerset, NJ 08873. The deadline for receipt of completed applications is 15 March 1977.

WILSON BULLETIN REFEREES

The following 167 individuals have assisted in the publication of the Wilson Bulletin during the past year by acting as referees for submitted manuscripts: K. P. Able, C. S. Adkisson, D. Ainley, P. Alden, D. Amadon, K. A. Arnold, W. W. Baker, R. P. Balda, R. Banks, L. Baptista, D. P. Barash, J. Barlow, C. Black, E. R. Blake, C. Blem, C. E. Bock,

W. J. Bock, E. G. Bolen, C. Braun, R. D. Brewer, P. Brodkorb, C. H. Buckner, J. Burger, E. H. Burtt, D. F. Caccamise, T. J. Cade, W. A. Calder, Jr., K. Campbell, D. E. Capen, J. Chambers, C. Cink, M. H. Clench, C. Collins, S. Conant, G. D. Cormons, A. Cruz, R. W. Dickerman, J. J. Dinsmore, W. H. Drury, J. DuPont, J. L. Dusi, T. J. Dwyer, C. A. Ely, J. T. Emlen, S. T. Emlen, A. Erskine, J. A. Feduccia, M. S. Ficken, C. D. Fisher, G. A. Fox, L. H. Fredrickson, S. Fretwell, A. S. Gaunt, S. Gauthreaux, F. B. Gill, W. D. Graul, O. Hackney, H. Hadow, J. P. Hailman, G. A. Hall, P. Hamel, J. W. Hardy, R. F. Harlow, D. S. Heintzelman, S. L. Hilty, E. E. Hoover, M. A. Howe, J. P. Hubbard, P. Humphreys, G. Hurst, D. A. James, F. James, F. L. Johns, N. K. Johnson, D. W. Johnston, R. F. Johnston, H. W. Kale, J. R. Karr, S. C. Kendeigh, D. Keppie, B. Kessel, L. Kilham, J. R. King, E. E. Klaas, K. M. Klimkiewicz, G. Krapu, J. C. Kroll, R. L. Kroodsma, J. S. Kushlan, W. E. Lanyon, C. F. Leck, F. E. Lohrer, G. H. Lowery, L. Martin, H. F. Mayfield, R. McFarlane, D. F. McKinney, R. P. J. McNeil, H. Meng, R. M. Mengel, D. W. Mock, D. Morse, E. Morton, H. C. Mueller, B. G. Murray, D. M. Niles, R. E. Noble, V. Nolan, J. Ogden, H. M. Ohlendorf, S. L. Olson, J. O'Neill, G. H. Orians, O. T. Owre, J. W. Parker, K. C. Parkes, D. F. Parmelee, O. S. Pettingill, S. Postupalsky, I. Prather, D. G. Raveling, R. E. Ricklefs, J. D. Rising, C. S. Robbins, W. B. Robertson, Jr., J. Robins, S. A. Rohwer, S. I. Rothstein, J. P. Ryder, R. A. Ryder, D. E. Samuel, G. D. Schnell, R. W. Schreiber, S. G. Sealy, J. M. Sheppard, L. L. Short, N. Sloan, D. G. Smith, W. E. Southern, P. L. Stallcup, H. M. Stevenson, F. G. Stiles, R. W. Storer, G. M. Sutton, J. L. Tate, Jr., D. J. Tate, M. Thompson, R. E. Tomlinson, H. B. Tordoff, M. D. Udvardy, E. K. Urban, K. Vermeer, G. E. Watson, III, W. Weber, M. W. Weller, D. Werschkul, G. West, J. O. Whitaker, C. M. White, R. C. Whitmore, M. Wible, M. Willson, J. L. Wolfe, G. E. Woolfenden, J. D. Yarbrough, J. H. Zar, R. L. Zusi.

PAST SECRETARIES OF THE WILSON ORNITHOLOGICAL SOCIETY

Lynds Jones, 1888–89
J. Warren Jacobs, 1890–91, 1893
Willard N. Clute, 1892
William B. Caulk, 1894
J. E. Dickinson, 1895–97
W. L. Dawson, 1898–1901
John W. Daniel, Jr., 1902–1905
Frank L. Burns, 1906
Benj. T. Gault, 1907–11
C. W. G. Eifrig, 1912–13
Orpheus M. Schantz, 1914
Thos. L. Hankinson, 1915–16
G. A. Abbott, 1917
Albert F. Ganier, 1918–22
Gordon Wilson, 1923–25
Howard K. Gloyd, 1926–28
Jesse M. Shaver, 1929–31
Lawrence E. Hicks, 1932–36
Olin Sewall Pettingill, Jr., 1937–41
Maurice Brooks, 1942–46
James B. Young, 1947–48
Harold F. Mayfield, 1948–51
Phillips B. Street, 1952–55
Fred T. Hall, 1956–57
Aaron M. Bagg, 1958–61
Pershing B. Hofslund, 1962–66
Jeff Swinebroad, 1967–70

PROCEEDINGS OF THE FIFTY-SEVENTH ANNUAL MEETING

JAMES TATE, JR., SECRETARY

At the invitation of the Cornell Laboratory of Ornithology, Cornell University and the Cayuga Bird Club, the 57th annual meeting of The Wilson Ornithological Society was held at Ithaca, New York, from 3 to 6 June 1976. The Society met in the Statler Auditorium on the main campus of Cornell University. The Executive Council of the Society held one meeting in a conference room at the North Campus Union. Business meetings of The Wilson Society were held in the meeting room at the Statler Auditorium.

An open house was held at the Laboratory of Ornithology on Thursday evening while the Executive Council of the Society was holding its meeting on campus. Short field trips were held on Friday and Saturday mornings to local birding areas. On Sunday 2 field trips took delegates and visitors to the Montezuma National Wildlife Refuge at the north end of Cayuga Lake and to the Southern Highlands, a prime birding area southeast of Syracuse.

On Friday morning, the General Sessions of the meeting were started with a first business meeting of the Society. A full day of scientific papers followed. Friday evening found most delegates and visitors at the Laboratory of Ornithology for a reception sponsored by the Cayuga Bird Club. Special exhibits at the Laboratory of Ornithology during the meetings included 30 paintings of birds of prey by Louis Agassiz Fuertes which were on loan from the Church and Dwight Company. A photographic exhibit of the wildlife of East Africa by Barrett Gallagher occupied the main hallways of the laboratory. During the entire meetings, an exhibit of sound analysis and recording equipment was set up at the Statler Hotel. Prior to Friday's reception, a film "The Arctic Islands—A Matter of Time" was shown at Uris Auditorium. Saturday morning found a full schedule of scientific papers, including concurrent sessions both morning and afternoon. A second business meeting of the Society was held in the Statler Auditorium on Saturday afternoon. Delegates and guests attended a barbecue at the Little Red Barn on the campus, followed by awards and a film on the Peregrine that was shown in the auditorium of Uris Hall.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Berger at 0912 in the Statler Auditorium. The proceedings of the meeting held at Bozeman, Montana were approved by the membership as published in the *Wilson Bulletin* (87:572–588, 1975). The president appointed the Alexander Wilson prize committee with Tony Erskine as chairman. The nominating committee was announced as Kenneth C. Parkes, chairman, Jerome A. Jackson, Harold Mayfield. The auditing committee was announced as James F. Ponshain, George M. Wickstrom. The standing resolutions committee was announced as: Bob Burns, chairman, Sally Hoyt Spofford, Sidney Gauthreaux.

Reports of officers and committees follow:

REPORT OF THE TREASURER—1975

GENERAL FUNDS

Balance as of Last Report, 31 December 1974	$27,790.70

RECEIPTS

Membership Dues			
Active for 1975	$ 3,583.00		
Active for 1976	9,346.00		
Total Active		$12,819.00	
Sustaining for 1975	255.00		
Sustaining for 1976	600.00		
Total Sustaining		855.00	
Subscriptions to *The Wilson Bulletin*			
For 1975	1,717.00		
For 1976	3,502.00		
Total Subscriptions		5,219.00	
Advance Renewals		180.00	
Sales of back issues of *The Wilson Bulletin*		587.91	
Interest and Dividends on Savings & Investments			
Income from General Endowment Fund	3,866.82		
Income from G. M. Sutton Colorplate Fund	1,339.98		
Interest on Endowment Savings Account	1,132.72		
Interest on Regular Savings Account	629.45		
Total Interest and Dividends		6,968.97	
Royalties from microfilming back issues of *The Wilson Bulletin*		402.47	
Receipts from Annual Meeting		370.92	
Total Receipts		$27,403.27	

DISBURSEMENTS

The Wilson Bulletin (Printing & Engraving)	24,231.26		
Less contributions from authors & others	342.75	23,888.51	
The Wilson Bulletin (Mailing & Maintenance)		1,833.72	
Colorplate Processing Expense		2,369.82	
Editor's Expense		1,769.21	
Review Editor's Expense		0.00	
President's Expense		113.13	
Secretary's Expense		102.15	
Treasurer's Expense		1,068.67	
Committee Expense		2,200.29	
Annual Meeting Expense		164.92	
Transfers to Research and Grants-in-aid		28.00	
International Council for Bird Preservation		30.00	
Miscellaneous Expense		15.40	
Total Disbursements		$33,583.82	
Excess of Disbursements over receipts			$ 6,180.55

GENERAL CASH FUND

Checking Account			11,624.15
Savings Account			9,464.80
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1975			$21,088.95

JOSSELYN VAN TYNE MEMORIAL LIBRARY FUND

Balance as of Last Report, 31 December 1974	$ 385.27
RECEIPTS	
Sale of Duplicates and Gifts	$ 1,017.64
DISBURSEMENTS	
Purchase of Books	598.64
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1975	804.27

LOUIS AGASSIZ FUERTES RESEARCH FUND
MARGARET MORSE NICE FUND
EDWARDS AND W.O.S. PAPER FUNDS

Balance as of Last Report, 31 December 1974			$ 1.472.00
RECEIPTS			
Contributions			613.00
Transfer from General Funds			128.00
Total			$ 741.00
DISBURSEMENTS			
Grants-in-Aid			
To William E. Southern	$200.00		
To Rodman and Dorcas Ward	100.00		
To Margaret E. McVey	200.00		
To Roger L. Boyd	200.00		
To Jerome J. Barry	100.00		
To Douglas W. Mock	100.00		
Total			$ 900.00
Transfer to Endowment Fund		$ 1,000.00	
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1975			$ 313.00

AARON MOORE BAGG STUDENT MEMBERSHIP AWARD FUND

Balance as of Last Report, 31 December 1974	$ 200.00
RECEIPTS	
Contributions	$ 200.00
Balance in Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1975	$ 400.00

ENDOWMENT FUNDS

GENERAL ENDOWMENT FUND

Balance in Endowment Savings Account as of Last Report of 31 December 1974	$ 22.315.00

RECEIPTS

Life Membership Payments		$ 3,675.00

DISBURSEMENTS

Transfer to Investment Funds	$19,000.00	
Balance in Endowment Savings Account, Old Kent Bank and Trust Company, Grand Rapids, Michigan, 31 December 1975		$ 6,990.00

Investments held as of 31 December 1975		
United States Government Bonds	$ 5,000.00	
International Bank Bonds	9,270.00	
Canadian Provincial Bonds	3,700.00	
Corporate Bonds	18,862.50	
Convertible Corporate Bonds	2,300.00	
Convertible Preferred Stocks	10,943.75	
Common Stocks	39,548.12	
Investment Trusts	6,876.08	
Uninvested Principal	–0–	
Total Investments		$ 96,700.45
Total General Endowment Fund, 31 December 1975		$103,490.45

George Miksch Sutton Colorplate Fund

Investments Held as of 31 December 1975		
International Bank Bonds	$ 1,030.00	
Canadian Provincial Bonds	4,350.00	
Corporate Bonds	14,275.00	
Common Stocks	2,950.00	
Total Investments		$ 22,605.00
Total Combined Wilson Ornithological Society Endowment Funds, 31 December 1975		$126,095.45

Ernest E. Hoover, *Treasurer*

REPORT OF THE EDITOR—1975

From 1 January through 31 December 1975 I received 192 manuscripts not counting book reviews, news items, and the President's Page. I received 95 manuscripts during 1976 through 25 May. Rejection rate for manuscripts received during 1975 and processed to some definite outcome was 34.2%. For manuscripts received thus far in 1976, the rate has been 34.0%. While this rejection rate is up from the June 1974–June 1975 rate of 26.3% and the June 1973–June 1974 rate of 19.9%, at our present rate of receiving and publishing manuscripts, our backlog will continue to increase.

We have a new contract which calls for at least a 12.7% increase in publication costs. The likelihood of further increases in postage and paper costs suggests to me that we have to act now on a dues increase. I would like to be conservative and raise dues to $10, but increase subscriptions to $15. I feel that such action might be more than adequate and I also feel that it is to our advantage to keep our dues less than the other 2 major societies.

Processing time (time of receipt to acceptance of papers published in Volume 87) was slightly less than for the previous year: an average of 107.4 days for major papers and 74.3 days for notes. Time for receipt to rejection averaged 44 days. For comparison, the respective means for the period June 1974–June 1975 were: 120.6, 76.3, and 47.8 days.

Three other matters were discussed relating to publication costs: (1) The Council agreed that we should continue using the same grade of paper in the Wilson Bulletin, though a lighter weight paper would reduce some costs. (2) Lengthy manuscripts are now sent to referees by 4th class mail. (3) We have had to relent to using plastic envelopes for mailing the Wilson Bulletin. These offer some advantages and are less expensive.

Jerome A. Jackson, *Editor*

REPORT OF THE MEMBERSHIP COMMITTEE—1975–76

A major innovation of the 1975–76 membership campaign was the inclusion in the annual dues notice of a space in which members of the Society could recommend friends or acquaintances for membership. As we have never tried this technique before, we have no basis upon which to judge the response, but our opinion is that it was enthusiastic. For the past several years approximately 50–60 members of the Society have sponsored new recruits. This year 93 members of the Society sponsored new members, and many more suggested possible recruits. Many members also took advantage of the tear-out pages in 3 issues of The Wilson Bulletin to provide the Membership Committee with the names of prospective members. This cooperation on the part of the membership is reflected in a markedly increased enrollment to 241 new members. By way of contrast, last year, which was the best recruiting year in recent history, we enrolled only 186 new members. We also lost fewer members this year than in the recent past; 7 members were reported deceased, and 89 were suspended. Hence, we have a net increase of 145 in the membership. The new members are from 44 states, Washington, D.C., 5 Canadian provinces, and 6 other foreign countries.

We are not certain whether the tear-out page in the Bulletin or the recommendations space on the dues notice is more effective in producing new recruits. It appears, however, that the dues notice technique elicits a wider range of response, and it is certainly cheaper. A review of Membership Committee reports for the last several years indicates that the activities of individual members is one of the most effective techniques for obtaining new members. In fact, such activity has traditionally accounted for more new members than the Membership Committee. We therefore suggest that the Society continue to provide the membership at large with the encouragement and mechanisms to suggest new members.

Abbot S. Gaunt, *Chairman*

REPORT OF THE STUDENT MEMBERSHIP COMMITTEE—1975

Letters requesting membership nominations of students interested in ornithology and inviting applications from exceptional students to be considered for Aaron M. Bagg Student Membership Awards were sent to all members affiliated with educational institutions. This resulted in 88 student nominations of which 22 received Aaron M. Bagg Awards. The award recipients were announced in the March 1976 issue of *The Wilson Bulletin.* There were 17 additional student nominations submitted on nomination forms printed in the June, September and December 1975 issues of *The Wilson Bulletin.* Another 9 student nominations were received from other sources. Thus a total of 114 student nominations was processed. Evaluation of the number of these that actually joined was not pursued.

Douglas James, *Chairman*
James R. Karr
Douglass H. Morse
Stephen M. Russell
Glen E. Woolfenden

REPORT OF THE CONSERVATION COMMITTEE—1975

Four specialists James H. Enderson, Charles J. Henny, Heinz Meng and Alva G. Nye, Jr. were asked to consider the committee's chosen topic. The report, Falconry: The Effects on Raptor Populations and Management in North America was prepared and submitted to the Council of the Wilson Ornithological Society. It can be expected to be published in the *Wilson Bulletin* in a forthcoming issue. The Conservation Committee asked the Council for guidance on future topics for consideration.

Clait E. Braun, *Chairman*

REPORT OF THE LIBRARY COMMITTEE—1975

The calendar year 1975 saw the business of the Josselyn Van Tyne Memorial Library moving smoothly with very substantial progress in bringing records up to date, correcting long-standing errors, and whittling away at the huge backlog of clerical work.

The Library Committee, as reconstituted, includes Janet Hinshaw and Ernest Hoover as members, the former still carrying on the major part of our actual operation.

During the year, a number of purchases were made from the New Book Fund, which was also substantially augmented through sale of duplicates. Thirty-six loans were made to 31 members, involving 67 books, reprints and xerox copies. The 100 exchanges received for The Wilson Bulletin involved 123 journals and newsletters, plus reprints.

Generous donations continued, with 1703 items (16 books, 658 journals [including back issues of WB], 1017 reprints, 2 theses, 5 pamphlets and 5 translations) given by 18 members. Donors were Karl Bailey, Barbara G. Beddall, A. J. Berger (to whom we owe special thanks for about half the items), R. S. Butsch, George A. Clark, Jr., Allen J. Duvall, A. Dzubin, F. C. Evans, H. F. Howe, Leon H. Kelso, H. C. Mueller, R. B. Payne, R. W. Storer, J. G. Strauch, D. Walker, Warren F. Walker, Jr., L. H. Walkinshaw and the Western Bird Banding Association (by C. T. Collins). Our appreciation to each.

We can only urge increased use of the growing collection by the membership, and continued support by gifts, especially of books and major items which can, directly, or indirectly through sale, be used to fill important gaps.

William A. Lunk, *Chairman*
Library Committee

Lists of new members were posted in the meeting hall by the Secretary. Announcements were made that the 58th Wilson Ornithological Society meeting is planned for Mississippi State University from 18 through 21 May 1977. The 59th annual meeting is currently planned for Jackson's Mill, West Virginia 4 through 7 May 1978. It was moved and seconded to approve the minutes of the 1975 meeting. Motion was passed. The first business meeting of the Society adjourned at 09:30.

SECOND BUSINESS MEETING

President Berger called the meeting to order at 14:40 on Friday. A motion was made by President Berger to accept the proposed amendments to the constitution of the Wilson Ornithological Society as published in the *Wilson Bulletin.* Motion was seconded and passed unanimously. The report of the auditing committee was accepted.

AUDITOR'S REPORT

We have examined the treasurer's records, bank statements, cancelled checks, account books and other financial records of the Society covering transactions occurring during the past fiscal year. The financial status of the Society is substantially as set forth in the treasurer's report dated 31 December 1975.

Our examination has ascertained that all income has been applied to the proper funds and no expenditures have been made except as authorized.

James F. Ponshair, *Member*
George M. Wickstrom, *Member*

Audit completed 18 May 1976.

The secretary called for a vote to accept the list of proposed members of the Society as posted. Motion was made to accept the persons named on said list: seconded and passed by voice vote. President Berger read the proposal of the nominations committee, chaired by Kenneth C. Parkes. The nominations committee proposed the following slate of officers: President, Andrew J. Berger; First Vice-President, Douglas A. James; Second Vice-President, George A. Hall; Secretary, James Tate, Jr.; Treasurer, Ernest E. Hoover. Elected Council member term to expire in 1979, James R. Karr. There being no further nominations from the floor, nominations were closed. The membership directed the secretary to cast a unanimous ballot for the proposed slate.

The following resolutions were read and passed at the second business meeting:

WHEREAS, the Wilson Ornithological Society has held its 57th annual meeting at Cornell University in Ithaca, New York, 3 through 6 June 1976 and

WHEREAS, the members have benefited greatly from the efforts of the Committee on Arrangements, chaired by Douglas A. Lancaster, and the gracious facilities and service provided by Cornell University, therefore

BE IT RESOLVED that the Wilson Ornithological Society extends its sincere appreciation to the Cayuga Bird Club, the Cornell Laboratory of Ornithology, Cornell University, and to the local committee on arrangements for their contributions toward providing this memorable meeting.

WHEREAS, Alexander Wetmore, you are about to celebrate your 90th birthday and you have been and are a long and honored member of the Wilson Ornithological Society, and

WHEREAS, your many contributions both in the field of ornithology and to other ornithologists are too many and too varied to mention here,

BE IT RESOLVED, Alexander Wetmore, that we the members and friends of the Wilson Ornithological Society send our warmest birthday greetings and heartfelt thanks to you on this very special occasion.

The president closed the second business meeting at 14:50.

At the awards ceremony Saturday evening the following awards and prizes were announced:

Margaret Morse Nice Award

Charles R. Brown, "Breeding biology of the Purple Martin (*Progne subis*) in North Texas"

Louis Agassiz Fuertes Grant

Richard O. Bierregaard, Jr., "A study of the structure of grassland raptor communities"

Louis Agassiz Fuertes Grant—Second Award

Ms. Susan Hannon, "The relationship of behavior and reproductive physiology of female Blue Grouse to their distribution on the summer range"

Edwards Prize

S. T. Emlen, J. D. Rising and W. L. Thompson, "A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains"

Edwards Prize—Second Award

A. J. Wiseman, "Changes in body weight of American Goldfinches"

PAPERS SESSION

Stanley A. Temple and Barbara L. Temple, Cornell Laboratory of Ornithology, Ithaca, New York, *Avian population changes in central New York State, 1935–1972.*

Joseph B. Platt, Cornell Laboratory of Ornithology, Ithaca, New York, *Gyrfalcon breeding behavior in wild and captive populations.*

Donald A. McCrimmon, Cornell Laboratory of Ornithology, Ithaca, New York, *Data record programs at the Laboratory of Ornithology.*

James R. Karr, University of Illinois, Champaign, *On the relative abundances of migrants from the north temperate zone in tropical habitats.*

Roland R. Roth and Peter S. Martin, University of Delaware, Newark, *Habitat heterogeneity and bird species diversity.*

Ronald K. Paulick and John L. George, Pennsylvania State University, University Park, *Avian habitat utilization of a planned community.*

David L. Pearson, Pennsylvania State University, University Park, *A comparison of Old World and New World tropical lowland forest bird community structure.*

W. W. H. Gunn, LGL Ltd., Edmonton, Alberta, *Recording bird sounds for scientific use.*

John William Hardy, University of Florida, Gainesville, *Establishing and curating a sound archive in a modern museum.*

James L. Gulledge, Cornell Laboratory of Ornithology, Ithaca, New York, *Sound analysis and avian vocalizations.*

Wesley E. Lanyon, American Museum of Natural History, New York, *Vocal characters—an early warning system for detecting cryptic species of birds.*

Luis F. Baptista, Occidental College, Los Angeles, California, *Geographical variation and "dialects" in the Chaffinch rain-call.*

Eugene S. Morton, Smithsonian Institution, Washington, D.C., *Carolina Wren communication: the relation of sound structure to the communicative function(s) of the sounds.*

W. John Smith, University of Pennsylvania, Philadelphia, *The displays of* Todirostrum cinereum, *a quiet flycatcher.*

Abbot S. Gaunt, Ohio State University, Columbus, *New problems for the interpretation of syringeal action.*

Stephen T. Emlen, Cornell University, Ithaca, New York, *Bioacoustics: an overview assessment of accomplishments, and speculations for the future.*

Robert C. Whitmore, West Virginia University, Morgantown, Herbert H. Frost, Brigham Young University, Provo, Utah, and James A. Mosher, Naval Arctic Research Laboratory, Barrow, Alaska, *Spring migrant mortality in response to unseasonable weather.*

Kenneth P. Able, State University of New York, Albany, *The flight behavior of individual passerine nocturnal migrants: a tracking radar study.*

Donald A. McCrimmon, Cornell Laboratory of Ornithology, Ithaca, New York, *Nest-site characteristics of five species of herons and egrets nesting on the North Carolina coast.*

Emil K. Urban, University of Arkansas, Fayetteville, *Movements of juvenile Great White Pelicans from Lake Shala, Ethiopia.*

Charles M. Weise and John R. Meyer, University of Wisconsin at Milwaukee, *Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee.*

Paul W. Woodward, University of Maryland, College Park, *Sunflower seed selection by the Carolina Chickadee and Tufted Titmouse; preliminary investigations.*

Ben Pinkowski, 15738 Millar, Fraser, Michigan, *Feeding ecology of the Eastern Bluebird.*

Tim Manolis, D. Dwight Clark, and Annette Adams, Purdue University, West Lafayette, Indiana, *Foraging habits and sociality of migrating wood warblers.*

Ralph W. Dexter, Kent State University, Kent, Ohio, *Nesting success of Chimney Swifts related to age and helpers at the nest.*

Peter G. Merritt, Western Michigan University, Kalamazoo, *Gap formation: a reproductive isolating mechanism for Black-capped and Carolina Chickadees in northern Indiana.*

Ronald I. Orenstein, University of Michigan, Ann Arbor, *The affinities of* Prosopeia *and the distribution of parrots in the South Pacific.*

Robert J. Raikow, University of Pittsburgh, Pittsburgh, Pennsylvania, *The evolution of the Hawaiian Honeycreepers (Drepanididae).*

Stephen R. Borecky, University of Pittsburgh, Pittsburgh, Pennsylvania, *The appendicular myology and phylogenetic affinities of the birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae).*

Gregory D. Bentz, University of Pittsburgh, Pittsburgh, Pennsylvania, *The appendicular myology and phylogenetic relationships of the Old World finches.*

Robert F. Andrle, Buffalo Museum of Science, Buffalo, New York, *The Whistling Warbler of St. Vincent, West Indies.*

Robert W. Storer, University of Michigan, Ann Arbor, *A look at the Hooded Grebe.*

Stephen M. Russell, University of Arizona, Tucson, *Maintenance of peripheral populations of the Rufous-winged Sparrow.*

William Post, Department of Mental Health, Raleigh, North Carolina and James W. Wiley, Institute of Tropical Forestry, Rio Piedras, Puerto Rico, *Impact of an expanding population of the Shiny Cowbird.*

Richard N. Connor, Virginia Polytechnic Institute and State University, Blacksburg, *Selected aspects of the vocal behavior of the Common Raven in Virginia.*

Jake Rice, Memorial University of Newfoundland, St. John's, *Song characteristics of a social mimic.*

Kenneth A. Shiovitz, University of Michigan. Dearborn, *Attraction and display eliciting properties of Indigo Bunting song.*

Ann Shreve, Route 2, Box 486-K, Charleston, West Virginia, Constance Katholi, 930 Woodland Avenue, South Charleston, West Virginia, and James L. Gulledge, Cornell Laboratory of Ornithology, Ithaca, New York, *An unusual warbler from West Virginia.*

James W. Parker, Wilmington College, Wilmington, Ohio, *The reproductive biology of the Mississippi Kite.*

Neil D. Woffinden, University of Pittsburgh, Pittsburgh, Pennsylvania, *Ferruginous Hawk (*Buteo regalis*) nesting habitat vacancy during a jackrabbit (*Lepus californicus*) decline.*

Douglas M. Campbell, Western Michigan University, Kalamazoo, *Some aspects of injuries occurring among seabirds in West Central Florida.*

Norman Woldow, Maryville College, St. Louis, Missouri, *A newly reported aerodynamic function of a bird's tail.*

Irvine D. Prather, Richard N. Conner, and Jerry W. Via, Virginia Polytechnic Institute and State University, Blacksburg, *The social structure of caged Turkey Vultures (*Cathartes aura*).*

Robert A. Lewis, Corvallis Environmental Research Laboratory, Corvallis, Oregon, *Nutritional and bioenergetic aspects of the postbreeding period in the Mourning Dove.*

Frederick E. Wasserman, University of Maryland, College Park, *Mate attraction as a function of song in the White-throated Sparrow.*

Carter T. Atkinson, Dickinson College, Carlisle, Pennsylvania, and Doris J. Watt, University of Maryland, College Park, *Polymorphism in the White-throated Sparrow: a study of plumage variables.*

Doris J. Watt, University of Maryland, College Park, and Carter T. Atkinson, Dickinson College, Carlisle, Pennsylvania, *The role of polymorphism in dominance relationships of the White-throated Sparrow.*

ATTENDANCE

ALASKA: *Barrow*, James Mosher.

ARIZONA: *Tucson*, Stephen Russell.

ARKANSAS: *Fayetteville*, Emil K. Urban.

CALIFORNIA: *Los Angeles*, Louis Baptista.

COLORADO: *Ft. Collins*, Clait Braun, Gustav Swanson; *Denver*, James Tate, Jr.

CONNECTICUT: *Old Lyme*, Roger Tory Peterson; *West Hartford*, Theodore Ryder.

D.C.: *Washington*, Eugene Morton.

DELAWARE: *Newark*, Roland Roth.

FLORIDA: *Gainesville*, J. W. Hardy; *Winter Haven*, Peggy MacQueen.

HAWAII: *Honolulu*, Andrew J. Berger.

ILLINOIS: *Champaign*, James R. Karr; *Colchester*, Edwin Franks; *Northbrook*, Carl Becker.

INDIANA: *West Lafayette*, Annette Adams, Tim Manolis; *Martinsville*, Thomas Potter; *Hanover*, Dan Webster.

IOWA: *Davenport*, Herbert Hodges.

MAINE: *Orono*, Charles Nicholson; *Wayne*, Olin Sewall Pettingill, Jr.

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By D. Jean Tate

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THE WILSON BULLETIN

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