nj - 6)

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY
WEST VIRGINIA U. • MORGANTOWN, W. VA.

VOL. 81 NO. 1 MARCH 1969 PAGES 1–120

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—H. Lewis Batts, Jr., Dept. of Biology, Kalamazoo College, Kalamazoo, Michigan 49001.

First Vice-President—William W. H. Gunn, Apt. 1605, 155 Balliol Street, Toronto, Ontario.

Second Vice-President—Pershing B. Hofslund, Dept. of Biology, University of Minnesota Duluth, Duluth, Minnesota 55812.

Secretary—Jeff Swinebroad, 8728 Oxwell Lane, Laurel, Maryland 20810.

Treasurer—William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107.

Elected Council Members—Kenneth C. Parkes (term expires 1969); Andrew J. Berger (term expires 1970); C. Chandler Ross (term expires 1971).

Membership dues per calendar year are: Sustaining, $10.00; Active, $5.00.
Life memberships, $150 (payable in four installments).
THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 104 periodicals as gifts and in exchange for *The Wilson Bulletin.* With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to "The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan." Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically.

THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December, at Morgantown, West Virginia. The subscription price, both in the United States and elsewhere, is $6.00 per year. Single copies, $1.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $1.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan.

Second class postage at Lawrence, Kansas, U.S.A. 66044

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

THE
WILSON BULLETIN

A Quarterly Magazine
of
Ornithology

GEORGE A. HALL
EDITOR

ORNITHOLOGICAL LITERATURE EDITOR
OLIN SEWALL PETTINGILL, JR.

Volume 81
1969

Published
by
THE WILSON ORNITHOLOGICAL SOCIETY

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by The Wilson Ornithological Society

VOL. 81, NO. 1 MARCH 1969 PAGES 1–120

CONTENTS

A STUDY OF THE RUFOUS-FRONTED THORNBIRD AND ASSOCIATED BIRDS. PART 1. LIFE HISTORY OF THE RUFOUS-FRONTED THORNBIRD .... *Alexander F. Skutch* 5

SUMMER BIOLOGY OF THE GADWALL AT DELTA, MANITOBA .... *Lewis W. Oring* 44

THE RADIUS AND RELATIONSHIP OF OWLS .... *Walter J. Bock and Allan McEvey* 55

RESPONSES OF BLUE-WINGED WARBLERS AND GOLDEN-WINGED WARBLERS TO THEIR OWN AND THE OTHER SPECIES' SONG .... *Millicent S. Ficken and Robert W. Ficken* 69

TERRITORIAL STABILITY IN SHARP-TAILED GROUSE .... *Roger M. Evans* 75

HATCHING BEHAVIOR OF THE BOBWHITE .... *Robert A. Johnson* 79

BEHAVIORAL ONTOGENY OF THE MOCKINGBIRD .... *Robert H. Horwich* 87

GENERAL NOTES

A CASE OF TURKEY VULTURE PIRACY ON GREAT BLUE HERONS .... *Stanley A. Temple* 94

UNUSUAL CASES OF RE-NESTING MALLARDS .... *Anders Bjärvall* 94

BUILD-UP OF GRIT IN THREE POCHARD SPECIES IN MANITOBA .... *James C. Bartonek* 96

TIME FREQUENCY BETWEEN SUCCESSIVE DRUMMING PERFORMANCES OF RUFFED GROUSE .... *Walter L. Palmer* 97

INCREASE IN HERRING GULL COLONY IN CAPE MAY, NEW JERSEY *Salvatore F. Bongiorno and Jeff Swinebroad* 99

BARRED OWL FEEDS ON CROW .... *Charles R. Sindelar* 100

BEHAVIOR OF A RUBY-THROATED HUMMINGBIRD IN A ROOM .... *Edwin C. Franks* 101

EGG MEASUREMENTS OF CALIFORNIA AND RING-BILLED GULL EGGS AT MIQUELON LAKE, ALBERTA, IN 1965 .... *Kees Vermeer* 102

HOUSE SPARROW OCCUPANCY OF CLIFF SWALLOW NESTS .... *David E. Samuel* 103

FACTORS INFLUENCING BREEDING RANGE EXPANSION OF THE AZURE BLUEBIRD
J. David Ligon 104

PLASTIC DEVICE CAUSES GULL MORTALITY .... *Scott C. Rea* 105

DISTRACTION DISPLAY OF A PAIR OF BLACK-THROATED GREEN WARBLERS
Douglass H. Morse 106

MEADOWLARKS FEEDING ON ROAD-KILLS
John P. Hubbard and Claudia L. Hubbard 107

ORNITHOLOGICAL NEWS 109

ORNITHOLOGICAL LITERATURE 110

Alexander F. Skutch, *Life Histories of Central American Highland Birds*, reviewed by Hugh C. Land; Oliver H. Hewitt (Ed.), *The Wild Turkey and its Management*, reviewed by Robert A. McCabe; George E. Watson, *Seabirds of the Tropical Atlantic Ocean*, reviewed by K. E. L. Simmons; Philip Wildash, *Birds of South Vietnam*, reviewed by James C. Greenway, Jr.; John Sparks and Tony Soper, *Penguins*, reviewed by R. L. Penney; C. J. Skead, *The Sunbirds of Southern Africa: Also the Sugarbirds, the White-eyes, and the Spotted Creeper*, reviewed by Austin L. Rand.

LETTERS TO THE EDITOR 119

A STUDY OF THE RUFOUS-FRONTED THORNBIRD AND ASSOCIATED BIRDS

Alexander F. Skutch

Hanging from isolated trees in northern Venezuela are compact masses of interlaced twigs so large and conspicuous that they can hardly escape the attention even of the traveler speeding along the excellent highways of that country. From a Venezuelan companion he may learn that the oblong masses of sticks are nests of the *guaití*; but without patient watching he is not likely to see the retiring, wren-like builder of these incongruously large structures. The *guaití* bears the English book-name of Rufous-fronted Thornbird (*Phacellodomus rufifrons*) and is a member of a large Neotropical family, the Furnariidae or ovenbirds, second to no other avian family in the world in the diversity of its nidification. The brief accounts that I had read of this remarkable bird, suggesting unusual social habits, whetted my desire to learn more about it.

A grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History provided financial support for an extended visit to Venezuela. Correspondence with Paul Schwartz gave hope that we could find a suitable place to live while studying thornbirds. He met us at Maiquetía Airport soon after midnight on 12 March 1966 and, after showing us over the Parque Nacional "Henri Pittier" (Rancho Grande), took us to "La Araguata." This large cattle farm, belonging to the bird artist Walter Arp and his wife Elena, is situated, at an elevation around 1,400 feet, in a basin among low mountains near Pirapira, about 20 miles south of Valencia in the state of Carabobo. For over four months the Arps, then living in Valencia, gave us the use of their comfortable farmhouse and with unforgettable kindness forwarded our endeavor in innumerable ways. My wife Pamela kept house and helped with the observations on thornbirds. To all those who in these various ways contributed to the success of our visit to Venezuela, I am most grateful.

Part 1. Life History of The Rufous-fronted Thornbird

THE BIRD AND ITS HABITAT

The Venezuelan race of the Rufous-fronted Thornbird (*Phacellodomus rufifrons inornatus*) is a rather long-tailed bird about six inches in length, with no noticeable differences between the sexes. Its dorsal plumage is brownish olive, slightly rufescent on the rump, upper tail coverts, and the exposed bases of the remiges. The stiff, lanceolate feathers of the forehead and fore part of the crown give these regions a streaked aspect. The rufous on the forehead is not conspicuous and may escape casual observation. There is an indistinct light superciliary line set off by a faint dark postocular streak. The chin and throat are whitish, becoming grayer hindward and merging into pale cinnamon-buff on the lower abdomen, flanks, and under tail coverts. The upper mandible of the slender bill is dusky, the lower is gray, and the interior of the mouth is black or nearly so. The legs and toes are grayish. The iris of a breeding thornbird will at one angle appear yellowish brown or gray, at another, as the bird turns it head, pale blue.

The species *P. rufifrons* is widely distributed over the more arid and open parts of South America, east of the Andes, from the Caribbean coast to northern Argentina. The race *inornatus* is widespread in Venezuela north and west of the Orinoco, not only in the mountainous northern part of the country but in the flat *llanos* to the south. It is primarily a bird of the warm lowlands; the highest point at which I noticed it was in the botanic garden at Caracas, at about 3,000 feet above sea level, where its nests were conspicuous. It appears to be permanently resident wherever it is found; established pairs probably never wander more than a few hundred yards from the nest which is their center of interest and their dormitory at all seasons. These nests often hang prominently near human dwellings; for the thornbirds, lacking bright plumage and elaborate song, escape the persecution which afflicts their more brilliant avian neighbors and accordingly are more trustful of man. I never found it necessary to conceal myself while studying them.

Thornbirds are ground-foragers that prefer low, dense thickets and weedy fields, with here and there a large or small isolated tree to support their nests. They avoid heavy forest and even light woodland with a closed canopy. At Pirapira, where the dry season is long and severe, I failed to find them in the second-growth woods with crowded slender saplings but sparse ground cover that occupied large areas of abandoned farmlands on the lower slopes of the hills. They were likewise absent from the stony upper slopes of these hills, where low, thick-barked, gnarled trees and a few fire-resistant shrubs grew scattered amid bunch grass that was often swept by fire in the dry season. During a day spent on the *llanos* in the state of Cojedes, we did not notice any thornbirds' nests on trees that stood in the midst of extensive areas of grassland; but these structures were abundant in or near open stands of trees with bushy undergrowth. The tree chosen for the nest may, indeed, grow 100 feet or more from the nearest thicket, in the midst of a bare cultivated field or a pasture of tall or short grass, across which the birds fly rapidly when approaching or leaving their abode. In intensively cultivated districts, thornbirds are found chiefly along bushy roadsides and fence rows, and about farmhouses surrounded by shade trees and shrubbery. (Fig. 1).

Wherever they occur, thornbirds travel through the dense, concealing vegetation in family groups which probably rarely exceed seven or eight

Fig. 1. View at "La Araguata." Rufous-fronted Thornbirds foraged in the thickets bordering the extensive pastures and nested in trees amid these pastures. In the line of trees to the left of the roadway was a nest in which six thornbirds slept. July 1966.

individuals; but they are so secretive that to count them accurately one must watch as they retire into their nests at nightfall or emerge at dawn. They are sociable birds who do not hold their companions aloof. Although I did not see one preen another, I watched one come close to another that was arranging its feathers and lightly touch the other bird's plumage with its bill. To scratch their heads, thornbirds raise a foot over and within the relaxed wing on the same side of the body, which is the usual method in passerine birds.

FOOD AND FORAGING

To learn what thornbirds eat, I watched them forage and noticed what they brought to their nestlings. Since it was difficult to keep them in view for long as they hunted through thickets hardly penetrable by man, the second method yielded more information. As with the other members of the ovenbird family with which I am familiar, thornbirds take little or no vegetable food. They subsist chiefly upon small or middle-sized insects in the larval, pupal, and mature stages. Spiders are sometimes captured. Rarely I saw a parent carrying a small round object which may have been a berry but was more probably some kind of egg case.

Thornbirds forage chiefly on the ground, beneath bushes and weeds. In the dry season, when fallen leaves cover the soil, they spend much time searching beneath the litter, often pushing their foreparts beneath it, sometimes even disappearing under a loose accumulation of dry leaves, to emerge on the other side. I never saw them throw or push fallen leaves aside, as many other ground-foragers do; their habit of creeping beneath the litter makes this effort superfluous. Sometimes the thornbirds ascend higher to investigate masses of dead leaves that have lodged in bushes and vine-tangles, occasionally pulling out a leaf and dropping it. Although not averse to rising to the crowns of small or even large trees, where they often build their nests, thornbirds rarely forage far above the ground. While searching for food they utter low, slight, sharp notes and from time to time burst into loud song. At "La Araguata" they sometimes hunted with Pale-breasted Spinetails (*Synallaxis albescens*) and Buff-breasted Wrens (*Thryothorus leucotis*), whose foraging habits are rather similar.

A pair of thornbirds feeding nestlings close by the house at "La Araguata" often hunted in a pile of rotting leaves that had been raked up from the garden, and in heaps of brush, into which they vanished. They hopped over a small patch of ground where the weeds had been chopped close, leaving the area bare and brown, and they searched the exposed bases of some banana plants growing there. One of the thornbirds climbed up through a skein of drying vines that draped a tree trunk, disappearing into the tangle. Sometimes they hunted on the bank of the neighboring brook. Their methods of foraging differed little from those of a Southern House Wren (*Troglodytes musculus*) also hunting food for nestlings in the same area at the same time, except that the wren often walked over the ground with alternately advancing feet, while the thornbirds always hopped with their feet together.

VOICE

Thornbirds are seldom long silent, and their frequent outbursts of loud, ringing song, no less than their spells of quieter twittering, suggest a cheerful, contented nature. Their varied utterances fall into three main classes, which may be briefly characterized as: (1) singing or calling, (2) twittering, and (3) chipping.

The song is a series of rapidly repeated, similar notes that always sounds bright and joyous and at its best is beautiful. This is especially true when the loud, rather sharp notes with which the series begins are followed by somewhat lower, mellower notes. It then reminds me of the song of the Scaly-throated Leaftosser (*Sclerurus guatemalensis*), one of the best songsters among the ovenbirds, but it is not quite so lovely. Loudest of the thornbird's utterances, the song also serves as a call, to communicate with a distant mate. When singing at fullest intensity, the thornbird stretches its body upward until it is almost vertical, with the head tilted skyward until, at times, the bill points straight up, while the downwardly directed tail beats time to the notes. At lower intensity, the song is delivered from a more normal posture. Variations in the song are chiefly in loudness and length, as, in common with other tracheophones, the thornbirds lack a diversified repertoire.

Mated thornbirds often duet, especially while building or attending their nests. Perching side by side or facing each other on their hanging mass of sticks, they lift up their heads and pour out their bright notes in unison. There is little difference between the songs of the two sexes; but in some pairs it has seemed to me that one, doubtless the male, had the stronger voice. Yet variations in the loudness of the songs of each individual tend to mask sexual differences, if indeed they occur. The thornbirds often sing not only on their nests but also within them, especially in the dim light of dawn before they emerge in the morning, or after they retire in the evening, or even while incubating or brooding. The song of one family often stimulates the members of a neighboring family to raise their voices. Loud singing accompanies territorial disputes.

Twittering consists of a rapid, continuous flow of low weak notes, which are sometimes squeaky. Occasionally the twitter is punctuated by little *peep*'s It is often heard issuing from a nest into which several birds have just retired for the night, and again while they rest inside, doubtless huddled together, before sallying forth at dawn. At such times it may continue, with brief intermissions, for minutes together. Thornbirds also twitter much while building and attending their eggs or young. A duet by a mated pair may be followed by twittering. Thornbirds twitter while close to each other rather than alone, seeming thereby to express contentment or mild, pleasant excitement.

The third class of the thornbirds' utterances consists of monosyllables which, according to circumstances, vary from slight *tick*'s to loud, sharp *chip*'s. These notes are strongest and most penetrating when an actual or potential enemy, such as a snake, a cat, or a man, approaches a nest containing eggs or young or parents foraging with fledglings. In such situations they undoubtedly express alarm or anxiety. As one watches a nest in the evening, slight *tick*'s issuing from the neighboring thicket often announce that a thornbird is about to fly up to its dormitory. Here, too, the bird may feel some degree of anxiety as it prepares to leave the dense protecting vegetation for a flight through the open air, exposed to the attack of raptorial birds, on its way to its high nest. Sounds of much the same character are commonly heard from thornbirds foraging over the ground, and in this case they appear to be primarily location notes that serve to keep the flock together.

In each of these three classes of utterances—song, twittering, and chipping—there are endless variations in intensity, tone, and tempo; but they are too difficult to describe, and their meaning too obscure, for profitable discussion.

TERRITORY

Despite their sociability, thornbirds are territorial and resist the intrusion of members of other families. I made no attempt to trace the limits of territories, which at "La Araguata" traversed impenetrable thickets, chiefly on the more steeply sloping land between the extensive pastures; but on several occasions my attention was drawn by what appeared to be territorial disputes. On the morning of 22 May, attracted by loud singing, I found half a dozen or more thornbirds in the undergrowth of a patch of light woods, about midway between two nests each occupied by six grown birds. They were flitting about excitedly, and sometimes one bird mildly chased another. Once two confronted each other momentarily, but they did not clinch together. Soon the birds drifted apart.

Twice, while I watched the thornbirds attend their eggs at nest 8, in which only the mated pair slept, the incubating bird suddenly left the nest to drive away a third thornbird who had appeared in the vicinity. On the first occasion there was much singing and some chasing; and after the trespasser had vanished, the resident pair were most vociferous, singing and twittering together. On the second occasion, the intruder came so silently that I was unaware of its approach until the incubating bird emerged from the nest to drive it away. How did the bird inside the nest sense the arrival of the other, whom it could hardly see? After chasing away the intruder, the resident bird perched in the top of a small tree near its nest and rapidly repeated sharp *chip*'s before it returned to its eggs.

This pair of thornbirds ignored the presence of a pair of Vermilion-crowned Flycatchers (*Myiozetetes similis*) busily feeding nestlings in a domed nest close by their own. Another incubating pair of thornbirds did not chase a Red-crowned Woodpecker (*Centurus rubricapillus*) who foraged only two or three feet from their nest. Indeed, as far as I have seen, thornbirds make little effort to drive away birds of other species, not even those intent upon appropriating their nests, a matter which will be treated in detail in Part II of this paper.

The territoriality of thornbirds is also manifested by their attempts, often

FIG. 2. A large nest of the Rufous-fronted Thornbird on the Venezuelan *llanos* at hato "El Milagro" in the state of Cojedes. 22 July 1966.

unsuccessful, to prevent strangers of their own species from lodging in their nests (see p. 27–28).

NEST BUILDING

Site of the nest.—I found no thornbirds' nest in the midst of the thickets where they forage. For their nest site they prefer a tree standing alone, in a pasture or cultivated field or beside a road (Fig. 2). Such a tree may be as much as 50 yards from the dense, low vegetation that affords them food and concealment by day. If no completely isolated tree is available, they select one growing with only a few others, or even one at the edge of a thicket or patch of woodland, beside an open field, a roadway, or a pond. In such cases the birds place their nest on the more exposed side of the tree. Their goal seems to be a nest hanging in an open space, untouched by surrounding branches. Occasionally a dangling vine is chosen to support the structure.

The nests that I saw in northern Venezuela ranged in height from seven to about 75 feet above the ground. Both of these extremes were found in the same locality on the *llanos* of the state of Cojedes. The lowest nest was

FIG. 3. A nest of the Rufous-fronted Thornbird built on a horizonal bough of an *Erythrina* tree, photographed in the dry season when the tree had shed its foliage. Pirapira, Carabobo, Venezuela, April 1966.

completed but contained neither eggs nor young. The highest was in a large, spreading tree with an open crown in which a flock of Wood Ibises (*Mycteria americana*) were resting. At Pirapira the vertical range of nests was somewhat less. The lowest that I noticed, only eight feet up, was never finished. The highest was at about 50 feet.

The thornbirds build their nest at or near the end of a slender leafy branch at the outside of the tree's crown, often at the bottom of the crown. At times the nest is placed upon a horizontal or even an ascending branch, but usually a drooping branch is chosen, sometimes one which hangs vertically (Fig. 3). The thornbirds' nests which most often catch the attention of the hurried traveler are large structures dangling from vertically descending, often leafless, branches (Fig. 4). Such nests tend to create a false impression of the kinds of sites which thornbirds choose. Many of these nests were begun on slightly descending, or even horizontal, leafy branches, which gradually sank beneath the weight of the growing mass of sticks, lost their foliage, and finally died. All the nests that I noticed in early stages of construction were on leafy branches, with lateral twigs to prevent the nest from slipping off.

FIG. 4. A nest of the Rufous-fronted Thornbird attached to a hanging woody vine. About seven feet long, this nest was the tallest seen. Hato "El Milagro," Cojedes, Venezuela, 22 July 1966.

In Central America, I have seen the bulky globular nests of the Red-faced Spinetail (*Cranioleuca erythrops*) and the Rose-throated Becard (*Platypsaris aglaiae*) hanging from slender branches in just such sites as thornbirds might have chosen.

Thornbirds sometimes build amid colonies of oropendolas and caciques. At "La Araguata" a nest was placed high in a Spanish plum tree (*Spondias* sp.) that held seven nests of the Crested Oropendola (*Psarocolius decumanus*), and on the *llanos* I found two large thornbirds' nests in the midst of a colony of 13 active nests of the Yellow-rumped Cacique (*Cacicus cela*) (Fig. 5). The nests of the thornbirds and those of their icterid neighbors were built at the same height and in quite similar situations, at the ends of slender drooping branches, with the difference that the woven pouches of the icterids hung free below the tips of the twigs, while the thornbirds' castle of sticks was built up around the supporting branch.

Exceptionally a nest is built around the upright main trunk of a slender tree. One such nest that I noticed was a large structure that surrounded, for a distance of several feet, the trunk of a young cecropia tree; but this nest had been abandoned. Along the

FIG. 5. Two nests of the Rufous-fronted Thornbird (the largest masses, left and right center) in a colony of 13 active nests of the Yellow-rumped Cacique. Hato "El Milagro," Cojedes, Venezuela, 22 July 1966.

highway between Caracas and Valencia, I saw several nests on service poles, supported by the cross-arm or the struts which strengthened it. At "La Araguata" I discovered a pair of thornbirds building on the stub of a petiole of a dead frond of a yagua palm growing in a pasture. The nest site, about 30 feet up, was behind hanging dead fronds, old dry spathes, and richly branched spadices from which the flowers or fruits had long since fallen. The birds had difficulty passing their material through all this drapery, which somtimes knocked a stick from their bill. This most atypical nest was never finished.

Gathering and placing the sticks.—Aside from the lining, the thornbirds' nest is composed wholly of sticks, which are often two or three times as long as the six-inch bird who raises them high into the trees. The longest stick that I found in a nest measured 21 inches. Sticks over a foot in length are frequent, but many are only a few inches long. The thicker ones are about a quarter-inch in diameter—the thickness of a lead pencil. Many of the sticks are fairly straight and branchless; some are crooked or branched. At Pirapira, where there was abundant rainfall during the wet season and most of the woody plants were thornless, the majority of the sticks brought to the nest were not thorny. Probably in more arid districts, where the vegetation bristles with spines, our bird uses enough thorny twigs to justify its name.

Occasionally, building thornbirds attempt to break sticks from trees, and they may even deliver a few woodpecker-like pecks to recalcitrant twigs; but unless the piece is far advanced in decay, it will not yield to the tugs of their slender bills. If not transferred from an earlier nest of the same pair, most of the sticks used in building are loose ones gathered on or near the ground. The bird grasps a single twig in its bill, at or near the point of balance, and may hop and flit upward through the nearest shrubs and trees to a point near or even above the level of the nest, which it may then reach by a horizontal or slightly inclined flight across the intervening open space. The heavier the piece, the more the bird seeks the aid of convenient branches to raise it gradually to the nest, resting here and there on the way. Often, however, the stick is borne upward on a fairly long and strongly ascending flight. Sometimes the bird's rapidly beating wings barely suffice to raise it aloft, and occasionally it is borne downward by the weight of its burden. Although they live so much amid thickets where there is little need for long flights, thornbirds are strong and swift flyers.

After it has chosen a stick, the thornbird shows an indomitable will to carry it to its destination. It displays considerable skill in maneuvering the clumsy piece through obstructing twigs, but now and then the stick is knocked from the bird's bill. On one occasion a builder bringing a long, branched twig to its nest lost its balance when the piece struck an obstruction; but the bird's grip on the stick was so tenacious that bird and burden fell four yards to the ground together. Losing no time, the bird carried the piece to the base of the rough, leaning trunk of the nest tree, up which it crept and hopped with it heavy load to the supporting branch, then flitted along this bough to the nest. Unlike the Firewood-gatherers (*Anumbius acuticaudatus*), of whose stupid neglect of fallen sticks Hudson (1920, I:225) wrote, thornbirds frequently retrieve pieces that they drop from the nest. I have repeatedly seen them dive straight downward 25 feet or more to the ground in pursuit of a falling stick, then return it to the nest by a circuitous course. Although twigs which slip unperceived from the bottom or sides of the nest may be allowed to remain on the ground, I have not seen a large accumulation of dropped material beneath a recently built thornbirds' nest.

My best opportunity to watch the very beginning of a thornbirds' nest was lost by the necessity to make a trip to Caracas to obtain official permission to prolong my sojourn in Venezuela. During the two days of my absence. this pair of birds started their nest by lodging sticks near the end of a slender, descending, leafy branch of an algarrobo tree (*Hymenaea courbaril*), at a point where a curvature of the branch and lateral twigs provided support. This initial stage was doubtless the most difficult part of the whole building operation. When I returned, the builders had a small platform of sticks on which they could stand while they added more to their structure. From this stage onward, I have watched building at a number of nests.

Nearly always one finds two birds working in closest cooperation, although occasionally, as will be told in due course, they have a helper or two. Building proceeds with much singing, by means of which the partners keep in touch and encourage each other while separated by their search for sticks, with duetting and twittering when they come together on the nest. Despite the strenuousness of their task, the birds seem to enjoy it! Often, after alighting on the nest with a long stick laboriously raised to it, the builder continues to stand for a short while holding the piece in its somewhat raised bill, sometimes waving it around, in what appears a foolish, abstracted attitude. I surmised that the bird felt about its burden much as I did about the heavy stepladder that I carried for long distances across the fields to examine thornbirds' nests: although eager to be relieved of the load, setting it down was so awkward an operation that I sometimes stood holding it for some seconds after I had reached my destination.

Its moment of abstraction over, the bird proceeds to fit the new piece into the nest. The placing of the stick seems not to be preceded by a survey of the structure leading to a decision as to just where the latest contribution is needed and will be deposited. On the contrary, the thornbird holds the stick near the middle, with one end lower than the other, and makes sideward movements with its head while it continues to step about over the nest. Often it must repeat these apparently random movements a number of times before the lower end of the stick—more or less by accident, it seems—slips in between those already present. Although sometimes the new piece is promptly accommodated in the fabric, at other times minutes are spent with a recalcitrant stick that does not seem to fit anywhere. Such a stick may finally be laid loosely on top of the others. The attempt to push the new twig into the nest is accompanied by a vibratory or jerking movement of the head, which keeps the end of the stick in slight agitation until it encounters an interspace which it can enter, then facilitates its passage through the maze of interlaced sticks. If the new twig fits too loosely, the bird may pull it out and continue to poke it sideways as before. After finally placing a new piece, the builder often seizes in turn the projecting ends of a number of sticks, testing their stability and pushing them deeper into the fabric if they are loose. Instead of bringing more sticks, the birds may devote five or ten minutes to arranging materials already present, sometimes removing loose sticks from the bottom of the nest and working them in at the top. This continual testing and rearranging makes the fabric strong.

One day I watched a thornbird trying to pull up a very long stick that had slipped through the bottom of a newly started nest but was prevented from falling by a fork at its upper end. With its bill, the bird drew up the stick as far as it could; but as soon as it released its hold for another lower on the stick, the piece slipped down until stopped by the fork. The bird tried this a dozen times, sometimes pulling the stick almost halfway out; but always the stubborn object fell back after the bird had lifted it as far upward as it could stretch and needed a lower hold to complete the operation. In the end, the thornbird flew off leaving the stick dangling below the nest. By using a foot to retain the stick while it secured a new grip with its bill, the bird might easily have solved its problem. Likewise, it might have drawn out the stick with its mate's cooperation. But thornbirds seem never to use their feet for holding things, and the manipulation of each stick is always the task of a single bird.

Helpers.—As a rule I found only two birds working at a nest, and this was invariably true at nests in which only a mated pair slept. But when more than two grown birds lodged together, more than two might join in building. At nest 3, a large structure that was occupied nightly by three thornbirds who kept close company and two more who appeared to be intruders (see p. 27–28), three built actively for a while, adding a new chamber, on the morning of 30 April. At other times, however, I found only two birds working at this nest and its successor. When three were at the nest together, they uttered many, low, squeaky notes; when only two were present, such notes were far less frequent than song.

Nest 11 was occupied by six grown birds who seemed to form a united family; and when a new structure was started close by it, three individuals built actively, as I saw during prolonged watches on two mornings. All three brought many sticks and arranged them in the nest. At times five or six birds were present, but I was not convinced that all were contributing to the new construction. Once, indeed, I saw four individuals carrying sticks simultaneously, but one of the birds deposited its burden on the neighboring old nest, from which the more active builders were transferring materials to the new edifice. After visiting the nests briefly, the second trio would drift away, leaving the other three at work.

At nest 16, in which four grown birds slept, at least three either adjusted sticks already present or brought new ones, at a time when active building had ceased. Four birds were sometimes at the nest in the daytime, but without being able to distinguish them individually, I failed to prove to my satisfaction that all contributed to the maintenance of this structure. At still another nest, a third thornbird occasionally brought a stick.

Gilliard (1959*a*:19) "observed four birds building a nest at one time. Once two of them were side by side on the top vigorously arranging sticks, when a third, which was carrying a stick, arrived and landed beside them." The additional birds that engage in building are apparently grown offspring of the mated pair (see p. 40).

Rates of working.—When building a new nest or actively enlarging an old one, thornbirds begin work soon after leaving their dormitory at daybreak, after an interval in which doubtless they find their breakfast. In the cool early morning they start off with great energy, but they seem soon to tire of their strenuous task; their trips to the nest with sticks become more widely spaced, and by the middle of the forenoon they as a rule rest from their toil. On 30 March, two birds working at a recently begun nest brought 31 contributions from 06:35 to 07:35, 12 from 08:30 to 09:00, but only one from 09:00 to 09:30. On 15 May, three birds brought material 38 times between 07:20 and 08:05, 12 times from 08:05 to 08:25, and three times from 08:25 to 08:45. Some of these sticks were taken from an older nest hanging a few yards away, greatly reducing the task of gathering material. At another nest, three birds brought 36 contributions in the hour between 07:00 and 08:00 on 3 April. On 31 May, from 08:40 to 09:40, two of these birds brought 25 sticks to a replacement nest, taking some from the older structure. After their concentrated building in the early morning, thornbirds may work sporadically at their nest at almost any hour of the day; and in the evening, shortly before they retire for the night, there may be a brief spurt of active building.

Removing foliage.—While building, thornbirds are often bothered by the leaves which cluster around their growing structure, impeding the arrangement of their long sticks. Sometimes the birds push the disturbing leaves outward, only to have them return to their original position after they are released. More often I have seen the builders try to tear away the offending foliage, usually with little success, for their bills are ill-fitted for such work. Sometimes the thornbirds reach far up to seize a leaf with a foot while they tug at it with their bill. One thornbird clung to a large mango leaf with both feet while pulling it with its bill. Occasionally the bird pecks the recalcitrant leaf. Although such leathery leaves as those of the mango are obdurate to the thornbirds' efforts, by dint of great persistence they do succeed in detaching small leaflets from compound leaves, or in tearing pieces from the edges of leaves. In removing some of the leaves which cluster around their nest, thornbirds differ from most other arboreal birds, which seek concealing foliage. The removal of leaves to increase exposure is known to occur in a few species of birds of which the males display for an extended period in one particular spot, such as the Blue-backed Manakin (*Chiroxiphia pareola*) (Gilliard, 1959*b*), the Magnificent Bird of Paradise (*Diphyllodes magnificus*) (Rand, 1940), and occasionally in the Orange-collared Manakin (*Manacus aurantiacus*) (Skutch, 1969).

Lining the nest.—If, while searching for sticks, a thornbird finds some soft or flexible material—a feather, a fragment of reptile skin, a shred of fibrous bark, a scrap of paper or cellophane, or the like—it may bring the piece for the lining, even to a nest that is still hardly more than an open platform. I never saw thornbirds concentrate on lining their nest, as many other birds do; but they bring appropriate material as they find it, not only while building but also with frequency while incubating their eggs, and even occasionally while feeding nestlings. One family of thornbirds tore apart an old covered nest of a Great Kiskadee (*Pitangus sulphuratus*) to augment the lining of their own bulky nest, which had long been finished.

Completion of the nest.—As building proceeds, the sides of the platform of sticks with which the nest begins are built up faster than the center, converting it into a shallow bowl and then a deeper cup. Then the walls contract inward, until finally the hollow is roofed over, becoming a nearly spherical chamber. Instead of proceeding to thatch this chamber with broad pieces of material, as castlebuilders (*Synallaxis* spp.) do, the thornbirds continue to bring more sticks and build a second, similar, chamber above the first. The first surge of building activity rarely dies away until this upper chamber is covered with at least a few sticks, and sometimes it persists until a third chamber is begun atop the second.

Since thornbirds are indeterminate builders, adding to their structure at all seasons, while they incubate and even occasionally while feeding nestlings, it seems incorrect to say that a nest is ever completed. However, after the upper chamber is at least loosely covered, some pairs relax their efforts, and the nest may be considered as temporarily finished.

In April, one pair took only 10 or 12 days to build a two-chambered nest, with the upper compartment scantily roofed; and after this they rested for five weeks before they began to lay. Later in the season, in July, another pair started to lay about 18 days after they began their nest, at which time their upper chamber, although well lined, was still an open cup without a vestige of a roof. Yet this second pair, which built more slowly, transferred much of their material from their older nest only two yards away; whereas the first pair had no such convenient quarry and perforce sought their sticks at a greater distance.

Two-chambered nests, which are the smallest ones in which, as a rule, one finds thornbirds sleeping or breeding, may be about 15 or 16 inches high and from 9 to 14 inches in diameter, not counting the ends of sticks which on all sides project far beyond the main mass, giving the nests a bristly, unkempt aspect. The globular chambers that they contain are about 4.5 to 5 inches in diameter. The entrances to these chambers take various forms. That of the lowest chamber, in which the brood is usually raised, may be an upwardly directed passageway through the sticks, which here bulge out farther than on the other sides of the nest. This passageway may be five or six inches long by about two inches in diameter. Sometimes it is shaped like the spout of a teakettle, and it may dilate inward so as to form a sort of vestibule or antechamber in front of the main chamber. Very often the entranceway bends in one direction or another, so that one cannot look straight down it and see what is inside the nest; but sometimes it has a simpler form that makes inspection easier. Although typically the external opening of the lowest chamber is near the top of a two-chambered nest, if the supporting branch has sunk far downward under the structure's weight, rotating its long axis through nearly 90 degrees, the doorway may be at the side, near what has now become the bottom of the structure. In an old nest with a number of compartments, the entranceways may take various directions, some leading downward to the chamber, others upward, and yet others horizontally; but as a rule all open on the same side of the nest. Each compartment has its own opening to the outside and there is no internal communication between them; they are separated by partitions formed of interlaced sticks.

The chambers are lined on the bottom with almost any soft or flexible material that the thornbirds find. The lining of one nest was composed largely of strips of fibrous bark; that of another, in the midst of a pasture, of fibrous pieces of decaying stems and leaf-sheaths from the tall grass. Thin and curving pieces of material are preferred to wide ones; but in one nest I found broad flakes of inner bark, apparently from a neighboring woodpile, and a piece of decaying wood 5 inches long by ⅞ inch broad, as well as some small shrivelled leaflets. Nests near human habitations have more varied contents, including scraps of cellophane, pieces of plastic bags (in one case six inches square), brightly colored candy wrappers, tinfoil, paper, feathers, etc., as well as vegetable fibers, scraps of wood, and strips of bark. I was told by a Venezuelan that the place to look for a lost love-letter is in a *guaití's* nest! The presence of lining in a compartment cannot, as I once supposed, be taken as an indication that it has been, or will be, used for breeding. An unfinished upper chamber may be as well, or better, lined as that which contains the eggs. While incubating, the birds may deposit at least as much new lining in an upper chamber as in the one where their eggs rest.

From time to time, the thornbirds add a new chamber to the top of their nest, or to the higher side if it is on an inclined rather than a vertical branch, until it becomes an enormous mass, all out of proportion to its diminutive builders. They are so strongly attached to their nests that they might continue all their lives to enlarge them, but a limit is often set by what the supporting branch will bear. It may break under the growing weight, or, as seems more frequently to happen, an angle or curvature of the branch makes further upward building impracticable. It was doubtless no accident that the tallest nest that I saw was built around a long, slender, vertically hanging liana, which seemed to invite the thornbirds to build up and up indefinitely (Fig. 4). This inaccessible nest, on the *llanos* of Cojedes, was estimated to be seven feet high, and it appeared to contain eight or nine chambers. Nests three or four feet high, with four or five chambers, are not uncommon. Usually the chambers are in a single series, one above another; but an exceptionally broad nest, measuring about 20 inches in height by 18 inches in diameter, contained one chamber in the bottom and two, side by side, at the top. I was told of thornbirds' nests that weighed hundreds of pounds, but I could procure no definite record of such heavy structures.

Despite their considerable weight, thornbirds' nests seem rarely to fall unless the branch that supports them breaks from the tree. They do not become detached from the branch because they are built around it; it is firmly embedded in the wall, usually at the rear. Despite the simple technique used in their construction and the lack of any cement or other binding material, the wall surrounding each chamber is surprisingly strong. To make an aperture large enough to insert a small mirror and electric bulb for viewing the eggs, I forced a stout pointed stick into the fabric, which I could hardly open with my fingers. After each inspection, I worked twigs into the gap to close it; and the birds seemed not to notice what I had done.

Significance of the multichambered nest.—A thornbirds' nest is notable for its magnitude rather than its comfort or elegance. Made of a single kind of material, lined with almost anything soft or flexible that the birds can find, it is a crude construction compared to the smaller, single-chambered nests of certain species of *Synallaxis*, notably *S. erythrothorax*. These more secretive, less sociable birds may use sticks of different sizes for different parts of their structure; their lining is of a single, carefully selected material, often of soft downy leaves, which may be shredded and felted together; nearly always the chamber that shelters the eggs and nestlings is thickly roofed with broader pieces which shed the rain. Thornbirds make no provision to keep the interior of their nest dry; the top is covered with sticks no thicker than those in the walls and floor. Probably little rain seeps into the lower chambers of very large nests; but in a nest with only two compartments, the loosely covered upper one must serve as a basin to catch the rain water, which pours through the thin floor into the lower chamber where the birds sleep or attend their eggs and young. I have many observations that thornbirds, although they inhabit semi-arid country, care little for dryness. I repeatedly failed to find them taking shelter in their nest from a daytime shower; and a rain in the evening hardly advances their time for retiring. They may begin to sleep in a new nest while it is still a roofless cup. A family whose nest tree was cut down retired at nightfall into the hollow end of a rotting stub that afforded some concealment but no protection from the downpours frequent at this season. Although thornbirds inhabit some of the drier parts of the tropics rather than rain forest, the wet season, when they breed, may be a period of heavy rainfall.

The large nests of thornbirds remind one of the many-chambered structures of the Social Weaver (*Philetairus socius*) of southern Africa, the Gray-breasted Parakeet (*Myiopsitta monachus*) of southern South America, and the Palm-Chat (*Dulus dominicus*) of Hispaniola. These birds, as is well known, build compound nests in which a number of pairs breed, each in its own compartment. The suggestion has been made (Gilliard, 1958:262–263) that the thornbirds' nest is similarly an avian apartment house; but none of the score of nests that I investigated was occupied by more than one breeding pair, in some cases with additional, self-supporting but nonbreeding individuals, who were evidently their offspring of the preceding year. The strong territoriality of the Rufous-fronted Thornbird would prevent social nesting.

Why, then, do thornbirds start with two-chambered nests, to which additional compartments are from time to time added? One possibility is that the complexity of the nests might make it more difficult for predators to find the eggs or nestlings. A snake or small mammal, advancing along the supporting branch, would first reach the upper chamber, in which breeding rarely occurs—only, in my experience, when the lower part of the nest is occupied by intruders of another species. Finding nothing edible here, the predator might abandon the search; and even if it did not, the delay caused by the upper chamber might give feathered nestlings time to escape. In case of a night attack, the delay might save the lives of the grown birds sleeping in the lower compartment. That the complexity of the nest does make it difficult to find the eggs I can attest from personal experience. I was watching for laying to begin in a recently completed nest, which I periodically examined while balancing myself on a high, self-supported ladder that restricted my movements. On my earlier visits of inspection, I had looked only into the upper chamber and the antechamber of the lower one, which I mistook for the lower compartment itself. Then one day, after I had been examining the nest for several minutes, a thornbird flew out past my face, evidently having come from some part of the bulky nest that escaped my scrutiny. Thereupon I made a hole in the side and, inserting my light and mirror, saw two eggs which the bird had been incubating—the first thornbird's eggs that I ever saw.

While attending eggs or nestlings, parent thornbirds enter the unoccupied chamber(s) of their nest with confusing frequency, and one may have to watch a long while to learn just where their progeny lie. An approach to the two-chambered nest of the thornbird is found in the nest of the Barred Waxbill (*Estrilda astrild*) of Africa, which builds a domed structure entered through a tubular lateral tunnel from 5 to 14 inches long. Surmounting the dome is an open cup, resembling the nest of many a small bird, to which the function of diverting attention from the brood chamber below has been ascribed (van Someren, 1956:492). A similar function was long ago attributed to the always eggless "dummy" nests of various species of wrens. It is now known that these nests serve as dormitories, or they are built by the male to give the female a choice of sites; although neither of these functions precludes the one earlier attributed to them, that of confusing predators. Like the nests of certain wrens, those of thornbirds are used as dormitories, and the upper chamber may serve as a bedroom for the nonbreeding members of the family while the parents incubate eggs or brood nestlings in the lower one.

Against the theory that the complex structure of the thornbirds' nests serves to confuse predatory animals weighs the fact that, despite their strength and relative inaccessibility, they are frequently pillaged. Of their use as dormitories there is no doubt; but a smaller nest with a less permeable covering would, it seems, make a drier and more comfortable bedroom. Whatever we may finally conclude as to the selective advantages which have favored the evolution of these ponderous nests, it is evident that they represent one of the fullest expressions of a propensity widespread in the family to which the thornbirds belong, as in certain other tropical families, such as the wrens: that of building for its own sake, of constructing or bringing additional material to nests as an outlet for excess energy or a pastime. This tendency, evident in the castlebuilders (*Synallaxis*), is carried to far greater lengths in the massive structures of the Rufous-fronted Thornbird and certain other South American members of the ovenbird family of which Hudson (1920) has given us fascinating glimpses, but of which adequate modern studies are still lacking.

Attachment to the nest site.—The sedentary thornbirds cling stubbornly to their chosen homesite. As long as they can, they add new chambers to their old nest rather than start a new nest. If their nest falls, they build another as close to the old site as they can. The same occurs when the old nest is taken from them by some stronger bird, such as the Troupial (*Icterus icterus*), or after they have built upward to the limit of the supporting branch. When they have been robbed of eggs or nestlings, they either lay again in the pillaged structure, often in the same chamber as before, or build a new nest nearby. These masses of coarse sticks last a long while, even after they have been abandoned; and one often finds two, and sometimes even three, hanging conspicuously from the same tree. In one case, a family of thornbirds, finding it no longer practicable to add a chamber to the top of their nest in the usual manner, built a new nest below the old one, at the end of the same branch, which had grown longer since the earlier structure was started. When the new nest was finished, the projecting ends of its sticks overlapped those of the old nest above it. I surmised that with time the two nests would be fused indistinguishably; but before this could occur, the overladen bough snapped off and all the birds' work was lost.

Although the growing weight of thornbirds' nests usually makes them sink lower, occasionally the reverse occurs. A nest built in a mango tree in the midst of green fruits rose about two feet when the mangos ripened and fell, relieving the supporting branch of much of its load.

OCCUPANCY OF DORMITORIES BEFORE THE BREEDING SEASON

On the evening of 16 March, the day after our arrival at "La Araguata," I watched a three-chambered nest that hung conspicuously, 13 feet up, from a tree growing in a fence line between pastures, close by the farm buildings. Nearby the Diesel engine that drove the electric generator was chugging loudly. At 18:50, when the light was growing dim, I heard repeated sharp notes. Soon several thornbirds appeared low in the weedy fence line about 100 feet from the nest. Passing through the pungent fumes from the engine, seeming not to be troubled either by its noise or by my unconcealed presence, they advanced, staying among the herbage near the ground. When near the nest, they flew up to it, either directly or by way of a neighboring tree. Four entered through two separate doorways, and after a few minutes two more joined them. It was then nearly dark. Although in the four days that I had already spent in Venezuela I had noticed many thornbirds' nests along the highways, these were the first thornbirds that I saw, with the exception of two that flew from a roadside nest as we speeded by.

At 06:25 next morning, as it was growing light, I watched the six thornbirds fly from their nest. After leaving, they vanished down the fence line, uttering a few sharp notes. Soon they sang amid the dense vegetation on a bank beside a neighboring stream.

It was then the height of the long, severe dry season, which was to last well into May. As I became more familiar with the farm, I found enough thornbirds' nests to suggest that they were among the most abundant birds in the area; although the thornbirds themselves remained so well hidden that I rarely saw them except while I watched their nests. There was still no sign that they were breeding, and I decided to make a survey of the nests and learn how many thornbirds slept in each. The counts could be made only as the birds entered at nightfall or emerged at dawn, hence no more than two in a day. Since the birds darted in or out very quickly, sometimes it was necessary to count a second or third time for certainty. By 1 May, I had investigated 14 nests situated within about a mile and a half of my residence. Although rarely I counted seven birds at a nest, I could never repeat these counts; either I miscounted, or the seventh bird was an intruder who did not continue to sleep in the nest. No nest that I studied had more than six regular occupants; three nests had this number. One nest was occupied nightly by five thornbirds; at another, I sometimes found five and sometimes four. In each of three nests there were three sleepers. Six nests were occupied by pairs of birds. In May and June, when many thornbirds were breeding but there were still no independent young of the year, I investigated eight additional nests, finding in each no more than two birds past the nestling stage. Thus, before the number of grown birds was increased by young hatched in the present season, 14 out of 22 nests, or 64 per cent, were occupied by only a mated pair. These couples without grown companions were, I believe, in most cases either young birds who had not previously nested, or older ones who in the preceding year had tried vainly to rear young.

In general, the thornbirds retired late in the evening and arose early in the morning; but there was a good deal of variation between nests, and even between the several occupants of the same nest. The birds who slept near the noisy electric plant went to rest very late, when little daylight remained, possibly because of this and other disturbances. But even farther afield, where there were no sounds save those of the natural world, families differed in the hours they kept. The six birds who slept in nest 11 flew forth in the dim light of dawn, so early that after watching them leave I could reach nest 17, 100 yards away, some minutes before the six sleepers left this nest. Similarly, these birds retired earlier than their neighbors of nest 11. And even at a single nest with three or more occupants, the first might enter 10 or 15 minutes before the last. The latest arrivals, who might enter in the dusk when there was hardly enough light to see them, were, at least in some cases, intruders rather than members of the family. These interlopers will be considered in the following section.

When only two thornbirds occupied a nest, I always found them sleeping in the same chamber, whether or not they had eggs or nestlings. When three or more were present, it was often difficult to learn how they distributed themselves among the several available bedrooms. Often they would enter by different doorways, but then they might shift from chamber to chamber: and these restless movements would continue until the light had become so dim that I could hardly distinguish the dark birds as they crept rapidly over their dark nests from one entrance to another. In the growing obscurity, I could never be sure that I had witnessed the last of these changes. Similarly, in the dim light before the birds flew down at dawn, they would often shift from chamber to chamber; and I could not be sure that this activity had not started before there was enough light to reveal it to me. Another difficulty was that if I paid too much attention to how the birds distributed themselves among the available bedrooms, I was likely to miscount the number that entered or left the nest as a whole.

Despite these perplexities, repeated observations convinced me that the thornbirds were not consistent in their occupancy of the available chambers. At times one would force its way in with others who resisted its intrusion, when it might without opposition have entered another compartment of the same nest. Parents with eggs or nestlings sometimes tried to exclude their older offspring from the brood chamber, not always successfully. On the other hand, the several occupants of a nest might elect to sleep in different chambers when there was no evident antagonism among them. Thus, at nest 1 on the evening of 17 March, four birds entered the top compartment, two the bottom compartment, of this three-chambered structure. One of the latter soon emerged and went to the middle chamber, so that, apparently, four birds slept together and two singly, in different chambers. Two evenings later, two birds retired into the top compartment of this nest, three into the middle compartment, and one into the bottom compartment. At daybreak on 20 April, all six of the occupants of this nest emerged from the middle chamber, where apparently they had passed the night; but before flying down, two of them briefly entered the top chamber.

Since nest 1 was much closer to the house than any other that had more than two occupants, I was able to follow the vicissitudes of this family in most detail. During the second half of March, I consistently found six birds lodging in nest 1. On 10 April only three entered, but on 13 April four emerged at dawn. By 20 April all six were again in residence. On 4 May the number of occupants was reduced to four, and during the following night only two were present. This time I discovered where the others had gone. A new nest was being built about 350 feet away, in the direction that this family took to forage. On the night when only two slept in the old nest, four occupied the new one. For some unknown reason, the new nest was abandoned a day or two later, and then I again found six sleepers in nest 1.

On the evening of 20 May, I clearly saw seven birds enter this nest. One was an intruder who did not stay, and on the following nights only six were present. This was the last time that I found six birds at this nest. On 6 June there were four; on 12 June, five; and on 16 and 28 June again four. As far as I saw, nest 1 had during the last three months failed to receive the usual maintenance care, its occupants neither bringing new sticks nor tucking in loose ones (as happens at most nests), and it had become dilapidated. Indeed, it would have fallen if I had not tied up the supporting branch before it broke from the tree. By 5 July the mated pair at this nest, after several failures to establish a home at a distance, had started a new nest only six feet from the old one. By this time the number of occupants of nest 1 had been reduced to three—the building pair and one other—and all moved to the new nest a few days later. Possibly the noise and fumes from the electric plant, or the distance of nest 1 from the foraging area, had caused this pair to depart at first from the usual practice of building their new nest in the tree that holds, or held, the old one; but after two, or possibly three, nests that they had built at a distance had been abandoned for reasons unknown, they at last laid their eggs in the new structure in the old familiar tree.

At more distant nests, where I counted the occupants at longer intervals. I failed to notice such temporary fluctuations in their number as I recorded at nest 1 in April and May. It was evident, however. that during these months the composition of the families remained nearly constant. Twelve nests, at which I first counted the birds from mid-March to the end of April, had at this time a total of 44 occupants: and in late May these 12 nests or their replacements still had 44 occupants, not counting nestlings. In one nest the number of lodgers had fallen from three to two, but in another it had risen from three to four. In June and July, the larger families began to disperse, a process which was perhaps accelerated by the loss of nests from the breaking off of branches and the felling of a tree. Of the three largest families present in March and April, I have already recorded the dissolution of that which occupied nest 1. The six birds of family 11 remained together through May, moving successively to two newly constructed nests when their dormitories were invaded by Troupials, but by late June their number was reduced to four. The six grown birds who in late April occupied nest 17 were still present in early June, when their family had been increased by two fledglings; but by 21 July three of the eight had vanished. Apparently in June and July, when many pairs were incubating or feeding nestlings, yearlings were leaving the parental abode to seek mates and establish homes of their own. Observations reported in a later section of this paper suggest that their departure may have been hastened by the antagonism of the breeding pairs.

The Rufous-fronted Thornbird is by no means the only member of the ovenbird family that sleeps in a dormitory. According to Hudson (1920, I:224), the young of the Firewood-gatherer sometimes "remain with their parents for a period of three or four months, all the family going about and feeding in company, and roosting together in the old nest." Other members of the family roost singly. The Plain Xenops (*Xenops minutus*), which nests in a cavity excavated in a decaying stub by itself or by a piculet, sleeps alone in an old woodpecker's hole or some other cranny in a tree. The Red-faced Spinetail (*Cranioleuca erythrops*) sleeps singly in a bulky hanging nest of moss and other soft materials, such as it uses for breeding. In the coastal range of Venezuela, Paul Schwartz showed me mossy inverted pockets, attached to the rocky face of a highway cutting, in which Spotted Barbtails (*Premnoplex brunnescens*) slept, always alone. Much remains to be learned about the sleeping habits of ovenbirds.

BEHAVIOR OF BIRDS THAT LOST THEIR NESTS: INTRUDERS

As the sun set on 29 March, I stood beside an unpaved roadway, watching a large nest with several compartments that hung from a tree standing alone in the adjoining pasture. At 18:55, in the fading light, a thornbird flew up from the roadside bushes and entered the central compartment of this nest. It sang loudly and was answered by song from across the road. In a minute or so, it was joined by two more birds. Then, after an interval of about 10 minutes, when it was nearly dark, another bird entered the nest, causing an outburst of song within. A minute or two later, still another bird went into the nest. Although at first these late-comers entered different compartments, all the five finally settled down, I believe, in the central chamber. This was practically a repetition of what I had witnessed at this nest four evenings earlier.

Nearly two months passed before I again, on 25 May, watched this distant nest at nightfall. Two thornbirds arrived almost together, sang loudly while resting on the front of the nest, then entered the middle compartment. A minute or two later, a third bird joined them there. Then many minutes passed before another thornbird appeared. It perched in a roadside tree and uttered low, sharp notes, seeming to be nervous about approaching the nest. Finally, it flew up to the structure, only to dart away a moment later. Then, when the light had become dim, this bird and another flew up to the nest at the unusually late hour of 19:07. Now excited twittering came from the dark structure. I could distinguish the birds only when they were silhouetted against the sky, as happened from time to time as one or more of them flitted restlessly over the nest. Finally, the movement and voices ceased, and the birds seemed to have settled down for the night; but I could not tell whether they were all together or in different compartments.

At this nest I had earlier watched three birds building a new chamber on top of the old structure. From these observations, I concluded that the three who entered first in the evening were members of the same family—probably parents and an offspring of the preceding year—while the other two were interlopers who, even after two months, had not been accepted as companions. Fresh light on the subject of intruders was unexpectedly gathered three weeks later, when, to my intense annoyance, I found that the tree that supported this nest had been newly felled for posts. In the deepening twilight of the day on which the tree was cut, or perhaps the day after, I discovered one of the thornbirds flitting through the roadside trees, dismayed by the loss of its lodging. Finally it vanished amid the foliage, where doubtless it slept that stormy night.

When I returned late on the following afternoon, there was a handful of sticks far out on a slender, descending branch of a small tree that grew beside the stump of the recently felled tree. The thornbirds deprived of their old nest had already started a new one, only eight feet above the ground. At about sunset, three of them came and stood on the small accumulation of sticks. Then they flew back to the roadside bushes, but ten minutes later the three again alighted on the incipient nest. They did not remain here, but entered the hollow end of a lichen-covered stub in a neighboring tree. This cavity, only 12 feet above the ground, not only had a wide gap in the side but was completely open above; it offered no protection from the heavy rains of this season but afforded some concealment and doubtless gave the thornbirds the sensation of being in an enclosed space. After nervously going in and out a number of times, and peering forth intermittently as the light grew dim, the three thornbirds, evidently feeling insecure in their strange lodging, settled down to pass the night in the hollow stub. Yet in plain view of this stub, not 100 yards away, hung a very large, multichambered nest in which a pair of thornbirds and a pair of Piratic Flycatchers (*Legatus leucophaius*) were incubating. Here the three might have found a drier lodging.

What had happened to the other two thornbirds who had slept in the ruined nest? After the trio had retired into the stub, I heard a thornbird's *chip*'s in the roadside shrubbery near the felled tree. These low notes betrayed the bird's progress along the bushy roadside toward the high nest where the thornbirds and flycatchers incubated. It was now about 19:20, long past the thornbirds' bedtime and nearly dark; but the high nest was silhouetted against the sky, with a wide clear space in front of it. Soon the dark figure of a thornbird passed across the clear space to this nest, which it seemed to enter. Low notes came from the nest, then a bird flew out. Soon, however, it returned; and this time it stayed, apparently in the compartment with the incubating birds of its own kind rather than with the Piratic Flycatchers. The last dull glow of sunset was then fading from the dark clouds low in the west. I failed to find the fifth occupant of the ruined nest.

Although the three thornbirds who formed an integrated group had respected the territory of their neighbors when their neighbors' nest might have afforded welcome shelter, the unattached bird had no such inhibition. Taking advantage of the dim light, it had boldly forced itself into a nest where it was not wanted. This observation helped to explain some of the fluctuations in the number of occupants of a single nest that I sometimes noticed. A little later, another case of intrusion came to my attention. A nest in a roadside *Erythrina* tree had been extended upward along an inclined branch as far as possible, and then its occupants built a new nest below it on the growing end of the same bough. The four occupants of the old nest moved to the new one. Presently the overladen limb snapped under its load, whereupon the birds started another nest on a neighboring branch of the same tree. On an evening at the end of June, when the new structure was only a platform or at best a shallow bowl, I watched to learn where the thornbirds would sleep. After sunset I found two of them bringing sticks to the new nest. Soon they settled on the platform, as though to roost there amid the foliage that clustered above it; but after staying a few minutes, they suddenly flew off in the direction of a sandbox tree (*Hura* sp.), about 250 feet away, in which there was a small nest. In a short while, the two returned to their unfinished nest, only to depart again in the same direction. Then a single bird returned, rested on the platform in the failing light, but finally flew toward the sandbox tree. The other two thornbirds who had slept in the *Erythrina* tree before the branch fell failed to appear this evening.

All this while my wife was watching the nest in the sandbox tree, a new structure occupied by a single pair. She saw four birds arrive, one by one. Two entered, but the third met resistance at the doorway. One of the first two grappled with the third, and they fell into the bushy growth below the nest. The third bird persisted in trying to force its way in, giving rise to much singing and twittering, much going in and out of the nest. When I joined my wife at this nest, the intruder was resting in the doorway with its tail sticking out into the light of the rising moon. Finally it pushed inside, causing more twitters to issue from the hanging nest.

Meanwhile, we continued to hear the sharp *chip*'s of the fourth bird coming from the low, tangled vegetation below the nest. They did not cease until the moon and stars were shining brightly. We waited until 19:35 without seeing this bird fly up to the nest; we could hardly have missed it, because it would have been silhouetted against the moonlit sky. Evidently, too timid to face the opposition of the resident pair, it passed the night amid the foliage.

On the following evening, my wife watched the *Erythrina* tree while I watched the nest in the sandbox tree. She reported that two birds came to the unfinished nest, left, came again, but after a little while flew off toward the sandbox tree. Then a single bird returned, rested on the nest, departed, and finally came back to pass the night on the open platform.

Meanwhile, at 18:47, I saw the resident pair enter the nest in the sandbox tree, followed by the usual loud singing and contented twittering. Nearly a quarter of an hour later, another thornbird flew up to the nest, but instead of at once entering the lower chamber with the first two, it remained for some minutes on the top, or perhaps on the farther side—at least, I lost sight of it. Finally, it approached the doorway of the lower chamber; but it was apparently denied admittance by the unseen birds within, for it withdrew a sort distance. Again and again it tried to enter but was repulsed. Soon it adopted a maneuver to meet this situation. After each ineffectual attempt to enter, it turned around and stood with its tail in the doorway, reminding me of a Red-crowned Woodpecker entering tail-first a hole of which it is slightly suspicious. This about-face and presentation of its tail to, I supposed, the pecks of an unseen bird within happened many times, while the nearly full moon grew brighter and more stars shone out. Finally, at nearly 19:30, the intruder pushed in at least far enough to pass from view and stayed.

On the following evenings, the interloper entered the nest in the sandbox tree 15 or 20 minutes after the resident pair, who had evidently become more or less reconciled to its presence and seemed no longer to try strenuously to keep it out. A single bird roosted in the *Erythrina* tree, on the new nest which continued to grow slowly. By mid-July this nest had been covered over and two birds slept in it. To my surprise, the sandbox-tree nest was still occupied at night by three thornbirds, one of whom left at daybreak considerably earlier than the other two. Had the bird who all this while continued to roost in the unfinished nest in the *Erythrina* tree acquired a new partner? Or had the bird who forced its way into the nest in the sandbox tree rejoined its mate in the *Erythrina* tree, and another homeless thornbird found lodging in the sandbox tree?

By waiting until it is almost dark, when the rightful occupants have become drowsy and can hardly see the intruder or distinguish it from members of their family, homeless thornbirds become unwanted guests in their neighbors' nests. At times, apparently, they may continue for months to impose themselves upon their reluctant hosts.

THE BREEDING SEASON: THE EGGS

At Pirapira, in late March and April, when the long dry season was at its height, a number of common, wide-ranging American flycatchers (Tyrannidae), along with some other birds which subsist largely on insects caught in the air or gleaned from foliage, were incubating, attending nestlings, or even feeding fledglings, at the same time as such birds breed in the wetter climate of Costa Rica and Panamá at about the same latitude. Meanwhile, I found no indication of breeding by the many families of thornbirds that I had under observation. Like other ground-feeders, they waited until the returning rains had soaked the ground-litter and quickened the small creatures which inhabit it.

According to Schäfer and Phelps (1954:93), in north-central Venezuela the *guaití* breeds from April until September. For northeastern Venezuela, Friedmann and Smith (1955:521) indicate breeding in January and October; but it is not clear from their tabular presentation on what evidence this rather surprising statement is based. Apparently, Smith mistook building as an indication that breeding was about to follow (see Friedmann and Smith, 1950:498).

First to breed of all the thornbirds whose fortunes I followed at Pirapira was a pair that on 15 May was already feeding nestlings in an inaccessible nest in which six grown birds slept. Their eggs had evidently been laid at the end of April. This family was established on low ground near a stream, where doubtless the soil remained moister, and its insect life more abundant, than on areas that were better drained. In another inaccessible nest, also near a stream, incubation began early in May. Although in early May there were occasional light showers and increasing humidity, the wet season of 1966 was delayed and did not become well established until after the middle of the month. During the second half of May, when rain was frequent and hard, pastures and hillsides that had long been brown gradually recovered their verdure. Now the thornbirds began to lay more freely, and by late May and June many pairs were incubating. By late July, when I left Venezuela, the pair that nested earliest was incubating a second brood, and another pair, that had so far failed to rear fledglings, had newly laid eggs. The young of this last pair could not have fledged before September.

It was not easy to see what was inside tightly closed nests hanging in mid-air, far from a trunk or branch that could uphold a climber or support a ladder. To examine the nests, it was necessary to use a four-legged ladder, heavy to carry and troublesome to set up on uneven ground. I saw only three full sets, each consisting of three eggs. These eggs were immaculate pure white, as is usual in the ovenbird family. I have seen no published record of the eggs of this common bird.

The eggs were nearly always laid in the lowest compartment, even in large nests to which a chamber had recently been added at the top. The only exception that I noticed was at a nest in which a pair of Piratic Flycatchers were established in one of the lower chambers. Here the thornbirds incubated in a newly built compartment at the top.

INCUBATION

Both sexes of the thornbird incubate, as is usual, but not invariable, in the ovenbird family. I devoted most time to studying incubation at a nest attended by a pair of which one member was quite tailless at the beginning of April and remained in this condition during the next four months. I believe that this apparently permanently tailless bird was the female; but the two partners took such equal shares in attending the nest that the designation of their sexes is of little importance. Both had bare incubation patches on their abdomens, as I saw clearly when they preened while standing in their doorway with their breasts toward me. As at other nests, both parents slept every night in the chamber with the eggs.

I watched this nest throughout the morning of 26 May and the afternoon of the following day. On 26 May activity began at 06:11 when the tailless one flew out leaving its mate with the eggs; and on 27 May it ended when the normal bird joined its incubating mate in the nest at 18:52. Considering the two consecutive half days as the equivalent of one whole day, this gives an active period of 761 minutes. Omitting four minutes of a session that I did not time in full, the tailed partner took 20 sessions in the nest, ranging in length from 5 to 33 minutes, totalling 314 minutes, and averaging

15.7 minutes. The tailless parent took 16 sessions, ranging from 1 to 49 minutes, totalling 365 minutes, and averaging 22.8 minutes. The birds were absent from the brood chamber (although usually not from the nest) for 23 periods ranging from 1 to 12 minutes, totalling 78 minutes, and averaging 3.4 minutes. One partner or the other was out of sight in the brood chamber, presumably warming the eggs, for 683 out of 761 minutes, or 89.8 percent of the day, which in my experience is unusually high constancy for an ovenbird (Skutch, 1962, table 1).

Although frequently one partner stayed in the brood chamber until the other came to replace it, sometimes it left before relief arrived. It the mate did not promptly take over, the same bird would return to the brood chamber. Thus the interval during which each partner was in charge of the nest, or the interval between change-overs, might include several consecutive sessions of the same bird, with brief intermissions between them. The longest interval between change-overs occurred in the middle of the day, when the normal partner took charge of the nest for 79 minutes, sitting for periods of 20, 32, and 21 minutes, with intermissions of 2 and 4 minutes.

I watched this nest again through the morning of 3 June and the afternoon of the following day. The birds' active period began and ended in the same way as during my earlier observations and extended from 06:11 to 19:01, 770 minutes. In the forenoon the thornbirds incubated more steadfastly than they had done a week earlier, leaving their eggs unattended for only seven minutes, but in the afternoon they were restless, coming frequently to look through their doorway or to climb over the outside of the nest. I counted these interruptions of incubation only when they lasted a minute or more. Treating the two half days as one whole day, the tailed partner took 21 sessions in the brood chamber, ranging from 4 to 42 minutes, totaling 348 minutes, and averaging 16.6 minutes. The tailless mate incubated for 23 intervals, ranging from 3 to 54 minutes, totalling 335 minutes, and averaging 14.6 minutes. Omitting 8 minutes of a recess that I did not time in full, there were 27 intervals of neglect, ranging from 1 to 8 minutes, totaling 79 minutes, and averaging 2.9 minutes. The thornbirds were out of sight in the brood chamber for 683 out of 770 minutes, or 88.7 per cent of the day, which is very nearly the same as their constancy in the preceding week when they sat less restlessly in the afternoon.

Taking the four half days together, the tailed partner took 41 sessions totalling 662 minutes; the tailless partner, 39 sessions totaling 700 minutes. The sessions of the former ranged from 4 to 42 minutes and averaged 16.1 minutes; those of the latter varied from 1 to 54 minutes and averaged 17.9 minutes. The longest interval when neither was in the brood chamber was 12 minutes. The longest interval between change-overs was 79 minutes, when the tailed bird was in charge of the nest. During the next-to-longest interval, 54 minutes, the tailless one was in charge.

Although on the warm, sunny afternoon of 4 June each thornbird left the eggs once, twice, or even thrice during its period in charge of the nest, it rarely left the nest itself. During my whole watch on 3 and 4 June, the nest was unattended only two minutes, while the tailed bird chased a trespassing thornbird. When not inside the brood chamber, the bird in charge stood in the doorway, preening, singing, or simply gazing out. Or it would emerge and go over the nest, pulling up falling sticks and tucking in loose ones, sometimes shifting a piece of material from one place to another, as castle-builders often do.

When coming to take their turns at incubation, or on special trips, the thornbirds often brought additional material to their nest, sometimes a stick, more often fragments of snakeskin, slender petioles or rachises of compound leaves, fine fibers, feathers, fluffs of cotton from a wild cotton plant, strips of fibrous bark, or some other pliable material. Although I never saw a thornbird carry more than one stick at a time, when bringing finer materials, such as slender rachises, they sometimes carried several pieces together. The soft and flexible materials, and even an occasional stick, were deposited inside the nest, not only in the lowest compartment where the eggs rested, but very often in the middle compartment of this three-chambered nest. A piece of material was sometimes transferred from one chamber to another, and occasionally it was thrown out or carried away from the nest—as I have seen other species of ovenbirds, and also woodcreepers, do. The parents' frequent entry into the middle compartment might have led a casual watcher to conclude that they were breeding there.

Throughout the day, these thornbirds often sang, while standing in their doorway, resting on top of the nest or on a stick that projected from its side, on a neighboring branch, or even inside the nest. The mate might answer from the distance; or they might duet, especially as one replaced the other on the eggs. There was also much twittering. Sometimes the tailless bird twittered while the normal partner sang loudly, leading me to suspect that the former was the female.

Once, when both partners were in front of the nest, neighboring birds of other kinds sounded an alarm, probably because a hawk that I did not see was passing by. Both thornbirds instantly dived into their nest, where they stayed in silence for about two minutes. This was not the only time that I saw a thornbird retire precipitately into its nest when it heard alarm notes. Evidently thornbirds feel safe from aerial predators inside their castles of interlaced sticks.

I watched another nest throughout the forenoon of 17 May, a cool, mostly cloudy morning with intermittent fine drizzles. I did not learn to distinguish by their appearance the two partners who shared incubation, but one rather consistently sang in a deeper voice than the other. Their 13 sessions of incubation ranged from 1 to 59 minutes and averaged 28.9 minutes. The eggs were unattended for only three periods, totalling 10 minutes. The longest interval between change-overs was 66 minutes, during which a single bird sat for 5 minutes, spent 2 minutes on the outside of the nest singing and adjusting sticks, then attended the eggs for 59 minutes until its relief arrived. During 6.5 hours, this pair incubated with a constancy of 97.4 per cent, the highest that I have recorded in an ovenbird. Often the bird coming to take its turn in the nest brought something soft for the lining. Twice during the morning a flock of Groove-billed Anis (*Crotophaga sulcirostris*), coming to eat the arillate seeds of the annonaceous tree that supported the nest, jumped all around the structure, shaking it, and even alighted upon it; but on neither occasion did the incubating thornbird so much as look out.

Even while inside the nest, thornbirds sing back and forth with their mates in the distance. They are reluctant to leave their eggs unattended, and if the mate is tardy in coming to take its turn at incubation, they sing loudly to recall it to its duty. One morning I watched a thornbird, whose partner was evidently neglectful, stand in the doorway of its nest and sing over and over. After many minutes of this loud calling, it seemed to grow hoarse, for its notes became distinctly higher and weaker. Finally, failing to obtain a response, it flew down into the thicket and continued to sing in its altered voice.

All the foregoing observations on incubation were made at nests in which only the incubating pair slept, both of them in the brood chamber, as has been said. At a nest with six grown occupants in which incubation had just begun or was about to begin, some members of the family retired into the brood chamber at nightfall in a manner which suggested that a parent within was trying to keep them out. One evening a bird who had just entered this nest emerged slowly and apparently reluctantly, as though being driven from within. After clinging a while beside the doorway, it went in again; and again a bird, this one or another, was forced slowly outward. This happened over and over, but finally five or six thornbirds stayed to sleep in the compartment used for breeding. Unfortunately, Troupials broke up this nesting before I could make further observations. At another nest occupied by recently fledged young as well as by older, nonbreeding birds, the parents tried energetically to exclude the rest of the family from the chamber in which they were incubating a second brood, as told in more detail in the section on "The Second Brood."

At one nest the incubation period, measured from the laying of the last egg of a set of three to the hatching of the last nestling, was 16 or 17 days. This may be compared with the incubation periods of certain other ovenbirds: 15–17 days in *Xenops minutus*; about 16 days in *Cinclodes antarcticus*; 17 to 19 days in *Synallaxis* spp.; 20 to 22 days in *Automolus ochrolaemus*; at least 21 days in *Sclerurus guatemalensis* (Skutch, 1969).

THE NESTLINGS

Development.—Thornbirds hatch with pink skin that bears the sparse, gray down typical of passerine nestlings. The interior of the mouth is yellow, rather than black as in the adults. They are 10 days old before their feathers begin to emerge from the sheaths. At the age of 12 days their upper parts are fairly well covered with the juvenal plumage, but their remiges and rectrices are still largely ensheathed. They linger in the nest for another 10 days, not venturing forth until they have attained practically adult size and have fully developed plumage much like that of their parents.

Feeding.—Both parents continue to sleep in the same chamber with the nestlings, as they did with the eggs; and sometimes nonbreeding birds, doubtless their older brothers and sisters, also pass the night with them.

I devoted the morning of 1 July to watching a nest containing three nestlings 10 and 11 days old. At this nest there were no grown birds other than the parents. The first parent left in the dim light at 06:07, and the first meal was brought to the nestlings at 06:15. By 06:30 the young had been fed 11 times by both parents. The number of meals brought each hour, from 06:07 to 12:07, was as follows: 31, 20, 31, 11, 10, 18. In the six hours of the morning, the three nestlings were fed 121 times, or at the rate of 6.7 times per nestling per hour.

On the afternoon of 3 July, we watched this nest from 12:07 until the second parent retired for the night at 19:06. The last meal was brought in the fading light at 18:55. From 12:07 on, the number of meals brought each hour was as follows: 14, 22, 19, 19, 17, 22, 21. In nearly seven hours of the afternoon the nestlings were fed 134 times, or at the rate of 6.5 times per nestling per hour. Taking the records of 1 and 3 July together, the three nestlings received 255 meals in a day of nearly 13 hours.

On 11 July, when the three nestlings were 20 and 21 days old, both parents left the nest at 06:10, and the first meal was brought at 06:22. In successive hours from 06:10

onward, meals were brought as follows: 18, 10, 7, 16, 23, 25. The total of 99 meals in six hours of the forenoon is substantially less than the 121 meals that these nestlings had received in this interval 10 days earlier. Such a reduction in the rate of feeding is not unusual with nestlings which linger in the nest for days after they have passed their period of most rapid growth and become fully feathered.

Although the parents of this brood were difficult to distinguish, they seemed to be taking equal shares in attending their nestlings. As far as I could see, on each visit to the nest they brought only a single article of food, held conspicuously in the tip of the bill. Aside from an occasional round object which may have been a berry but was more probably an egg case of some sort, the nestlings were nourished wholly with insects and other invertebrates which, quite small at first, were rarely large even after the young were feathered. Small brown pupal cases were brought with great frequency. Other items that I recognized were green caterpillars, small grasshoppers, small or middle-sized moths, and rarely a spider. Occasionally the parents of nestlings bring a stick or some lining to the nest instead of food.

The unfinished upper chamber of this recently constructed nest had developed a hole in the rear wall in addition to the doorway in front. When coming with food, the parents nearly always passed through this chamber from back to front, then climbed down the front of the nest to the lower compartment where their nestlings rested. On leaving, they reversed this course, traversing the upper chamber from front to rear before they flew away. I doubt whether this indirect approach to, and departure from, the brood chamber could have deceived any attentive, would-be predator for long; it seemed to be primarily an expression of the thornbirds' predilection for creeping through closed spaces. When carrying away a dropping in their bill, the parents omitted this passage through the upper chamber, as likewise when, as they exceptionally did, they foraged west of the nest instead of to the east or south. The parents promptly removed the shells from which the nestlings hatched, and kept the nest clean at all times.

Brooding.—During the forenoon of 1 July, when the three nestlings were 10 and 11 days old and their plumage was beginning to expand, a parent stayed in the nest, presumably brooding, on 18 occasions, for intervals ranging from 1 to 13 minutes and totalling 70 minutes. The morning was clear except for about an hour when the sky was clouded, and from 11:00 to noon the sun shone hotly. Two days later, when the nestlings were faily well covered by their rapidly expanding feathers, they were, during seven hours of the afternoon, brooded for 11 periods ranging from 2 to 38 minutes and totalling 170 minutes. Sunshine alternated with showers that were mostly short and light. Even as late as 7 July, when the well-feathered nestlings were 16 and 17 days old, they were, during two hours of a sunny afternoon, brooded for intervals of 8, 11, and 4 minutes. Thereafter, I noticed no more diurnal brooding. By night the parents were probably in close contact with the nestlings as long as they remained in the nest, even if they did not always brood them.

Departure from the nest.—When these nestlings were 18 and 19 days old and no longer brooded by day, the parents, who had formerly gone quite inside to deliver food, sometimes fed with the end of their tail projecting from the doorway. The young birds greeted the arrival of a meal with fine, rapidly repeated, insect-like notes. On the following day, I first heard the nestlings give a weak version of the adult's song. When they were 21 days old, they sometimes advanced far enough into the antechamber to take a meal from a parent who remained outside, in front of the doorway. Occasionally a nestling revealed itself in the entrance while it was fed—hitherto the young had always remained out of sight. Once one of them came out, turned around, dropped its excreta over the side of the nest, and promptly reentered. Now the young birds often repeated their weak song, and sometimes they uttered an infantine version of the *chip*. I did not hear nestlings twitter.

At this nest, as at another, the nestlings left on the day after that on which I first saw them expose themselves briefly in front of their doorway. Evidently the parents were excited by their imminent departure, for early in the morning of this day I saw one of them give an old feather to a nestling as though it were food. This indigestible offering was apparently not swallowed. Soon after this occurred, a young bird, following a parent who had just delivered a meal, emerged from the chamber and crawled around the side of the nest, but it promptly reversed its course and reentered. I thought that the young would remain inside another day; but by 08:00 one was resting in the top of a neighboring rose-apple tree. A tuft of nestling down still adhering to its head, together with its brighter, fresher plumage, its shorter bill, and the yellow corners of its mouth, helped me to distinguish it from its parents, who were preening nearby. The young bird was about as large as the adults and its tail seemed as long as theirs. Its two nestmates came out later that same day. The two older nestlings had stayed in the nest 22 days, the younger one about 21 days.

Earlier, on 5 June, I watched the departure of another brood, raised in an inaccessible nest into which I had first seen the parents carry food on 15 May. Song floated down from the high nest as I arrived at 06:00. Six grown birds slept in this nest, and although the situation was confused by shifts from chamber to chamber in the morning twilight, it appeared that during the night just passed four or five had lodged in the brood chamber with the two nestlings, while one or two slept in the upper compartment. After leaving the nest, these thornbirds called much and were obviously excited. About the time the last grown bird emerged, two nestlings appeared in the doorway. One crept forth, climbed to the top of the nest, then reentered the brood chamber. Soon some of the adults returned, without food, and stood beside the young in the doorway. The latter came out in front and withdrew into the nest again. Then, at 06:23, with no parental prompting that was evident to me, one fledgling launched forth, and a minute later the other followed. The three-week-old thornbirds flew well and, on descending courses, went direct to trees 75 and 100 feet, respectively, from the nest. The adults sang much after their departure. The fledglings soon vanished amid low, dense vegetation, whence I heard their weak *tsip*'s, although I could no longer see them.

Helpers.—When I found three, and possibly four, thornbirds building together, I confidently expected that I would later see extra birds helping the parents to attend the nestlings. My first opportunity to look for this came at this nest which I found about the time the eggs were laid, when active building had ceased. Since six grown birds slept here, there were four potential helpers. At various times throughout the nestling period, I spent a total of about 12 hours watching this nest, which was high and unfavorably situated for observation. As I could not distinguish the birds individually, the only way that I could prove that three or more were attending the nestlings was to see them bring food together, or almost together, or to see two arrive with food while another was brooding. Although it was soon evident that two adults were feeding the nestlings, they showed no tendency to come together with food. The most rapid feeding that I recorded at this nest with only two nestlings was 16 times in an hour; after brooding ceased, visits to the nest were brief; and accordingly the likelihood of seeing three attendants at the nest together, even if so many were visiting it, was small. I gathered no evidence that extra birds were helping the parents. One morning, however, a thornbird alighted in a small tree near me with a particle in its bill. Here it delayed, repeating low *chip*'s, before it flew up to the top of the nest. Then, instead of giving what it held to a nestling, it flew down into a thicket still bearing the object. Evidently it was a young bird with budding parental instincts.

Unfortunately, in consequence of various reverses, none of the families in which I had seen more than two birds build succeeded in hatching out nestlings before I left "La Araguata" in late July. I have little doubt that, with more opportunities to watch nests with three or more grown occupants while they held nestlings, I should have found helpers attending the young.

THE FLEDGLINGS

Late in the afternoon of 5 June, I found the two newly emerged fledglings with some grown birds, amid dense bushy growth along a fence between two pastures, where they had gone after leaving the nest early in the morning. Here they remained until, at about 18:25, the parents led one of them up through the branches of a mango tree that grew beside the fence. When they had reached the top of the tree, one of the parents flew across to the nest, entered the brood chamber as though to inspect it, then promptly rejoined the others in the mango tree. Now the fledgling, accompanying its two parents, easily flew to the nest tree, a distance of about 100 feet on a nearly level course. The adults went directly to the nest, but the young bird continued past it and alighted in a fork of the nest tree. From here it immediately flew back to the nest and without perplexity found and entered the lower chamber, where it had been raised. It was then 18:30, and the summits of the western hills were still bathed in golden sunshine, although the valley where I watched lay in shadow.

After the entry of the fledgling, the parents continued to pass back and forth between the brood chamber and the upper chamber. Soon one flew down. A good while later the other parent, evidently hearing the weak calls of the second fledgling, left the nest. Now the second fledgling, who had stayed behind in the bushes, was led to the top of the mango tree, and from here it flew with its parents to the nest tree. It, too, continued past the nest to alight in a crotch, and with only a little more difficulty than the first had experienced, passed from here to the brood chamber, at 18:47. The parents, after a little more going in and out, stayed in the lower chamber with the young. These two adults alone led the fledglings back to the nest; the other four grown birds who lodged here were still absent. About a quarter of an hour elapsed before they arrived. The first three went directly into the upper chamber, while the last joined the parents and fledglings in the brood chamber, at 19:05. Including the two fledglings, this nest now sheltered eight thornbirds, the largest number that I found lodging in any nest.

Six days later, I again watched this family retire in the evening. As before, the parents and fledglings ascended to the top of the mango tree, whence, at 18:34, a parent and both young flew across to the nest. The young birds promptly entered the lower chamber. Another adult, doubtless the other parent, arrived at the nest a minute later, and both busied themselves arranging sticks before they went inside. At 18:57 two more grown birds arrived. There was so much passing from chamber to chamber that I could not learn in which of them the grown birds slept. The other two grown birds who formerly lodged in this nest failed to appear, and I never, to my knowledge, saw them again. Probably these two represented the parents' first brood of the preceding year, while the two nonbreeding adults who remained were from the second brood. Thus, soon after the latest brood was fledged, the number of occupants of this nest was again reduced to six.

I last saw one of these fledglings receive food from a parent on 17 June, when it had been out of the nest for 12 days and was about 34 days old.

The first days in the open of the fledglings of certain woodpeckers, wrens, and other birds that sleep in dormitories are considerably shorter than those of the adults. They leave the nest late in the morning, retire early in the evening, and are fed by their parents after their return to the nest. But I never saw a thornbird feed a fledgling in the nest after its first flight. From the beginning, the young thornbirds spend a long day in the open. On the day they first left the nest in the algarrobo tree, the three young remained abroad with their parents until 18:45, when the family of five gathered in a small, acacia-like tree close to the nest. A parent flew to the nest, as though to inspect it, and the others followed. All tried to enter together, jamming the passage. Then some came out while others still attempted to push in, causing more confusion. By 18:54, however, all had settled down inside, except one parent, who had gone off carrying a dropping. At 18:59 this adult returned and entered. Thereafter none left, although from time to time one peered through the doorway as daylight waned.

Next morning at 06:04 the parents flew from the nest. They sang much, and the young still inside joined in with their weaker voices. A parent reentered, then left, the brood chamber; but no food was brought. The three fledglings left the nest between 06:13 and 06:15. Much singing greeted their departure. Six days later, the parents and two surviving young left the nest together at 06:10. The third fledgling had fallen victim to a cat.

THE SECOND BROOD

Early in July, the pair of thornbirds whose nestlings I had watched leave on the morning of 5 June gave indications that they would breed again. Late in the forenoon of 5 July, I found two adults and a juvenile on the nest in which the latter had been hatched. The adults were arranging sticks. On the following day, toward noon, two adults and a juvenile were again at the nest, and one of the former brought a stick. One of them bit the young bird mildly, but the latter did not retreat. On the next morning, 7 July, I saw only the two adults at the nest. By 12 July it was evident that incubation had begun in this inaccessible structure, in the chamber where the first brood had been reared. The members of the pair were taking turns in this compartment, and also bringing new material, most of which was deposited, not here, but in the chamber above it. One of the parents, coming to the nest with a stick, was followed by the two juveniles of the first brood. Three times the adult flew mildly at the young birds; but it did not press the attack, and the youngsters retreated only a few inches. Then they climbed unmolested over the nest.

These parents became increasingly antagonistic to the other birds who continued to sleep in their nest. When I arrived at sunset on 20 July, a juvenile, recognized by its whiter throat and breast, was resting on top of the nest, preening and at times lightly adjusting a stick. A parent was in the lower chamber, incubating, and from time to time coming to the doorway to look out. The other parent brought a long stick. The juvenile, then the adult, flew down.

When, a little later, a thornbird came to the entrance of the brood chamber, as though to retire, the parent who was within darted out and chased it down into the bushes. Then one parent entered the brood chamber and another bird, probably the other parent, went into the upper chamber. As the light grew dim, three more thornbirds arrived and rested on some sticks projecting from the bottom of the nest. Whenever one of these late-comers ascended to the doorway of the brood chamber, the parent sallied forth and attacked it, making it retreat, then returned inside. This happened over and over. As the twilight deepened, the parent in the upper chamber joined its mate in the brood chamber. Then two of the birds who had been waiting at the bottom of the nest cautiously climbed up and entered the upper chamber; whereupon a parent emerged from the brood chamber, ascended to the upper chamber, and forced them out. But they stayed close to the doorway, and when the parent returned to the brood chamber, as it promptly did, they reentered the upper chamber. Then the third of the late arrivals climbed up and joined them. By 19:10, when it was nearly dark, all had settled down, three in the upper chamber and two, doubtless the parents, in the brood chamber.

At break of the following day, I watched this nest again, to check my count. The five sleepers left late, when there was much daylight. While waiting to fly down, one or more of them passed repeatedly from one chamber to the other. They also emerged only to turn around and reenter the same room. Now I detected no discord among the five.

The six thornbirds that in March and April I found sleeping in this and each of two other nests were evidently a mated pair with the young of two broods raised in the preceding nesting season. If the parents habitually show such antagonism to their offspring as I witnessed on the evening of 20 July, how, it may be asked, can a family of six be built up, if no more than three young are raised in a brood? No other thornbirds that I watched displayed such violent enmity to the birds who shared their nest, whether members of their own family or interlopers. Nevertheless, their attempt to exclude the other sleepers was, as we have seen, ineffectual; and the parents' bad temper apparently did not persist until the following morning. Thornbirds who lack nests of their own are amazingly pertinacious in entering the nests of other thornbirds, and this pertinacity is probably greatest when the nest is the familiar abode in which they grew up. Doubtless the antagonism of these parents was associated with the onset of incubation of the second brood and would wane after the eggs hatched, so that at the end of the breeding season they would again dwell peaceably with whatever offspring remained with them.

In Golden-naped Woodpeckers (*Tripsurus chrysauchen*) the young of the single brood that is normally raised continue to lodge in the same hole with their parents until the latter are about to lay again in the following year; and when, as rarely happens, two broods are raised in a season, both remain with their parents, making a family of seven or eight. In these woodpeckers whose family bonds are so strong, an exceptional bird, usually a male, will try to exclude other members of the family from their common dormitory; but his churlish pecks are not always effective in keeping them out (Skutch, 1969). I have even known Southern House Wrens, birds far less sociable than the thornbirds, to persist against strong parental opposition in sleeping in the nest where their mother is rearing a later brood; and if they overcome this opposition, they may minister like parents to their younger siblings. But family groups of House Wrens seem never to endure from one breeding season to the next, as in more sociable birds, such as Golden-naped Woodpeckers, Banded-backed Wrens (*Campylorhynchus zonatus*), and Rufous-fronted Thornbirds they commonly do, despite sporadic outbursts of unsocial behavior.

ENEMIES

One might suppose that the nests of thornbirds, hanging from slender branches, strongly enclosed, and of a complex structure that might confuse predators, would be safer than the nests of most birds. Yet when I left "La Araguata" in late July, only two pairs had succeeded in rearing fledglings, a total of five. Six pairs had certainly lost eggs or nestlings, and several other pairs, which I visited only infrequently, had probably also lost their broods. One of the six pairs had lost two sets of nestlings. After twice losing their broods from the same nest, this pair built a new nest on a neighboring branch of the same small tree, transferring to it many sticks from the ill-fated older structure. I also found another pair incubating again in the nest from which they lost eggs or nestlings. The pair that included the tailless bird laid again in a new nest in the same tree, after losing one brood of nestlings from the old nest.

One set of eggs and one brood of nestlings were destroyed by Troupials, as told in Part II of this paper. Otherwise, the despoilers of the nests escaped detection. Since, except the nests ruined by the Troupials, the pillaged structures had not been torn open, it seemed evident that the predator was either slender or had a long reach. Probably snakes were the culprits. Although I did not surprise a serpent in the act of pillaging a thornbirds' nest. I had an excellent opportunity to watch the behavior of parents when one threatened their nestlings.

At noon on 9 July, the repeated sharp *chip*'s of alarm of the pair of thornbirds nesting nearest the house drew my attention to a snake over six feet long, a *tigra* (apparently the same species as the Central American *mica*, *Spilotes pullatus*), resting on a low branch of a rose-apple tree whose boughs interlaced with those of the algarrobo tree that held the nest. Seizing a stick, I tried to knock the serpent to the ground; but interfering branches broke the force of the blow, and the reptile climbed beyond reach into the crown of the rose-apple tree. The parent thornbirds continued to hop close around the snake, repeating their alarm notes. When the snake stretched out, they pecked or bit the tail of this creature so much larger than themselves, as I saw clearly through my field glasses. When the serpent coiled up, they did not touch it, as far as I saw, but often they approached within a few inches of the thick part of its body.

For at least an hour an a half, the thornbirds continued to watch and worry the snake. During this interval, I saw them take no food to their nestlings, who remained silent. Finally becoming active, the snake moved toward the nest in the most direct line, which took it into some lower trees between the rose-apple and the nest tree. Here I knocked it to the ground, over which it raced away so swiftly that I could not catch it. The thornbirds continued to look for it in the trees near their nest. After a while, they resumed feeding their nestlings, who flew from the nest three days later.

SUMMARY

Rufous-fronted Thornbirds forage, in pairs or family groups of three to six or eight, through thickets and weedy fields, gathering from the ground most of the insects and other small invertebrates on which they subsist. They disappear beneath the ground litter, and ascend into bushes and vine-tangles to investigate accumulations of dead leaves.

Their vocalizations consist of singing or calling, twittering, and chipping. The loud, ringing song is often delivered as a duet by a mated pair. The birds twitter when close

together, chiefly inside the nest. According to its intensity, chipping expresses mild anxiety or acute alarm.

The territoriality of thornbirds is manifested by boundary disputes that consist chiefly of singing and chasing, and by their often ineffectual efforts to keep intruding thornbirds out of the nest, which at all seasons is used as a dormitory.

The bulky nests of interlaced sticks are built on exposed branches of more or less isolated trees, at heights ranging from about seven to 75 feet. The slender leafy bough chosen for the nest's attachment may be horizontal or even ascending, but more often it droops. Frequently it sinks beneath the structure's growing weight until it hangs vertically.

The nest is built by both members of a pair, sometimes assisted by one or two other thornbirds, evidently their grown offspring of the preceding nesting season. Sticks, up to 21 inches long, are gathered from the ground, attempts to break them from trees being mostly futile. Dropped sticks are often retrieved. The builders try, rather ineffectually, to tear away leaves that interfere with their work. The nest's lining, consisting of almost anything soft or flexible—feathers, snakeskin, vegetable fibers, paper, cellophane, tinfoil, etc.—is added as found, from an early stage in construction to the incubation period, and even later.

The first stage in building usually results in a nest with two enclosed chambers, one above the other. Later, more chambers are added, always at the top, until the nest may contain eight or nine, and become seven feet high. The compartments do not intercommunicate, but each has it own opening to the outside.

The multichambered nest is not an avian apartment house; none of the more than 20 that were investigated was occupied by more than one breeding pair, sometimes with full-grown, nonbreeding offspring. The additional chambers provide lodging for the non-breeding birds while the parents attend eggs or nestlings. Although the complexity of the nest evidently makes it more difficult for predators to locate the eggs or young, many nests are pillaged. The construction of these incongruously large nests evidently represents an exaggeration of the propensity, widespread in the Furnariidae, to build superfluously, as a pastime or outlet for excess energy.

Twenty-two nests were investigated before any young were fledged. In each of three, six grown birds slept; there were two nests with four or five occupants; three nests had three occupants; and 14 were occupied by single pairs. These family groups remained fairly constant from March through May; but in June and July, while breeding was in progress, many nonbreeding birds left the established nests.

Thornbirds who have lost their nests may forcibly intrude into neighbors' nests, in the late twilight many minutes after the resident family has retired. Even after months, the intruders may not become integrated with the family.

As is typical of ground-foragers, the majority of the thornbirds did not begin to breed until the long, severe dry season ended in mid-May. Only a few pairs established on low, moist ground started earlier. The three pure white eggs were laid in the lowest, oldest chamber, except in a nest whose lower portions had been invaded by Piratic Flycatchers. Both parents passed the night with the eggs. When nonbreeding birds were present, they might sleep in the brood chamber—sometimes despite parental opposition—or in an upper chamber.

By day, the parents alternated on the eggs, the two taking nearly equal shares in incubation and attending the eggs for from 89 to 97 per cent of the daytime. Continuous sessions of incubation were rarely as long as an hour and averaged, for different birds, from 16 to 29 minutes. During the incubation period, the parents devoted considerable time to tucking in loose sticks and keeping their nest in order. They brought much additional lining, some of which was deposited in the brood chamber and some in an unoccupied upper chamber. In one instance, the incubation period was 16 or 17 days.

The nestlings, hatched with sparse down, are fairly well feathered at 12 days but remain in the nest until 21 or 22 days old. Both parents bring them small larval, pupal, and mature insects, rarely a spider, always carrying a single item in the end of the bill. Three nestlings about 12 days old were fed 255 times in a day of nearly 13 hours. Brooding continued, in diminishing amounts, until they were 17 days old.

From the first, fledglings fly strongly and may cover 100 feet on their first attempt. In the evening, they are led back to sleep in the nest with their parents and sometimes also older siblings. They were not fed in the nest after their first flight.

A pair whose young left the nest on 5 June were incubating a second brood by 12 July. They now tried hard to exclude their grown offspring from the nest at nightfall, but the latter persisted in entering.

LITERATURE CITED

Friedmann, H. and F. D. Smith, Jr. 1950. A contribution to the ornithology of northeastern Venezuela. Proc. U.S. Natl. Mus., 100:411–538.

Friedmann, H. and F. D. Smith, Jr. 1955. A further contribution to the ornithology of northeastern Venezuela. Proc. U.S. Natl. Mus., 104:463–524.

Gilliard, E. T. 1958. Living birds of the world. Doubleday and Co., Garden City, New York.

Gilliard, E. T. 1959*a*. Notes on some birds of northern Venezuela. Amer. Mus. Novitates, 1927:1–33.

Gilliard, E. T. 1959*b*. Notes on the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). Amer. Mus. Novitates, 1942:1–19.

Hudson, W. H. 1920. Birds of La Plata. J. M. Dent and Sons, London and Toronto.

Rand, A. L. 1940. Results of the Archbold Expeditions. No. 26. Breeding habits of the birds of paradise: *Macgregoria and Diphyllodes.* Amer. Mus. Novitates, 1073:1–14.

Schäfer, E. and W. H. Phelps. 1954. Las aves del Parque Nacional "Henri Pittier" (Rancho Grande) y sus funciones ecológicas. Bol. Soc. Venezolana Cien. Nat., 16:3–167.

Skutch, A. F. 1962. The constancy of incubation. Wilson Bull., 74:115–152.

Skutch, A. F. 1969. Life histories of Central American birds. III. Pacific Coast Avif. No. 35, in press.

van Someren, V. G. L. 1956. Days with the birds: studies of habits of some East African species. Fieldiana: Zoology, 38:1–520.

EL QUIZARRÁ, SAN ISIDRO DEL GENERAL, COSTA RICA, 3 OCTOBER 1966.

SUMMER BIOLOGY OF THE GADWALL AT DELTA, MANITOBA

Lewis W. Oring

In conjunction with a study of Gadwall (*Anas strepera*) molts carried out at the Delta Waterfowl Research Station in southern Manitoba (1962–64), data on other aspects of summer biology were gathered. In the main, studies on the Gadwall have concentrated on breeding biology with special emphasis on productivity or related factors. The present paper attempts to demonstrate the relationship between breeding and postbreeding activities. Wherever possible, comparisons between wild and hand-reared captive populations have been made.

NESTING

First Gadwalls appeared in mid-April though the peak arrival of residents did not develop until early May of 1964. This peak was 23 days earlier than the average date of nest initiation. Considering that Sowls (1955) and Dane (1966) have shown the length of time between arrival and laying to be dependent upon local weather conditions, the period of 23 days here observed is not strikingly different from the 28 day period recorded by Gates (1962) at Ogden Bay, Utah.

Nest initiation.—The average initiation dates at Delta of nine wild nests in 1963 was 26 May (range 22 May to 1 June), of 21 wild nests in 1964 was 29 May (range 24 May to 6 June), and of nine captive nests in 1964 was 28 May (range 17 May to 11 June). These averages are just a few days later than those recorded at Ogden Bay in 1956–57 (Gates, 1962). At Lower Souris, North Dakota in 1959–60, the average initiation date was about a week later than at Delta (Duebbert, 1966) whereas, judging from hatching peaks, nest initiation at Pea and Bodie Islands, North Carolina was one or two weeks earlier than at Delta (Parnell and Quay, 1965).

Nest sites.—In the wild, nest sites did not differ in any significant way from descriptions already in the literature (Miller and Collins, 1954; Gates, 1962; and others). In general, nests at initiation were surrounded by dense green cover, were on dry ground, and were near water (especially on islands, peninsulas, and dikes). For a detailed description of vegetation, cover, and surrounding landmarks see Oring (1966). In captivity nests were tolerated as close as 2½ meters provided they were initiated 10–15 days apart. Chronological spacing of nests seemingly was brought about by a high intensity of aggression. When the aggression peak of one drake subsided, another pair was able to initiate a nest where previously it had been thwarted. Duebbert (1966) did not observe chronological spacing of nests in his study of a dense island population. In captivity, a few nests were built in abnormal places such as a plywood box and a reed basket but most sites were typical of those in the wild.

Clutch size and laying.—Eight first clutches in the wild averaged 11.75 in 1963 as compared to 10.05 for 18 initial clutches in 1964. This difference, significant at the five per cent level according to an unpaired *t*-test, is probably due to my having collected most of the hens in the study area in 1963. Most of the 1964 clutches were therefore laid by yearlings. Dane (1965) has shown that yearling Blue-winged Teal (*Anas discors*) lay smaller clutches than do older birds. The combined average of 26 wild nests was 10.57 (range 8–14) compared to 8.67 (range 5–11) for nine nests in captivity. This difference is significant at the one per cent level according to an unpaired *t*-test. The average clutch size of 92 Gadwall nests which Gates (1962) considered initial was 11.1—a figure not significantly different from the combined average of my 26 nests. His assumption that all nests with 10 or more eggs were initial and that all with nine or fewer eggs were re-nests may have raised his average a little. The average size of 686 clutches in northern California (Miller and Collins, 1954; Rienecker and Anderson, 1960) was 11.0 (excluding parasitic eggs). In a dense island population, however, Duebbert (1966) observed an average clutch size of only 9.6 for 130 nests. The smallness of clutches in captivity and in dense island populations may be a result of crowded conditions.

Of 43 nests found in the wild at Delta, four were re-nests and two others may have been. Duebbert (1966) observed a similar low incidence of re-nesting at Lower Souris but Gates (1962) found a significantly greater proportion of re-nests at Ogden Bay. Since success rates at Delta and Ogden Bay were nearly identical, this may best be explained by the fact that some birds at Ogden Bay began nesting as much as two weeks earlier than at Delta and that the summer season in Utah is longer. The birds therefore had more time in which to nest following predation or desertion. Sowls (1955) and Gates (1962) have shown that second Gadwall clutches are smaller than initial ones. At Delta, four re-nests averaged 8.25 (range 6–9). The differences I observed between initial (10.57 average) and re-nest clutch sizes were, according to an unpaired *t*-test, significant at the one per cent level.

In captivity, all eggs were laid before noon. Hens sat on nests four to six hours each day of the laying period. The earliest a hen was known to leave a nest without being disturbed and after having laid an egg was 11:15. No hen spent the night on the nest during the laying period. Duebbert (1966) reported that eggs in the wild were normally laid between 05:00 and 07:00 at Lower Souris.

Incubation period.—Gadwall incubation periods have been stated to be from 21 or 22 days (Hochbaum, 1944) to 28 days (Witherby et al., 1939). In 1964, 50 eggs in six clutches required an average of 24.0 days incubation (range 22–26) in the hatchery as compared to 25.75 days (range 24–27) for 69 eggs in eight clutches incubated by hens. The difference as determined by an unpaired *t*-test was significant at the one per cent level. Hatchery incubators were kept at 99° F and 90–100 per cent relative humidity. In view of the fact that the total amount of heat above a certain threshold influences the length of the incubation period (Kendeigh, 1963), it is not surprising that such variation in incubation period has been recorded. Dane (1966) has discussed in detail factors affecting the incubation period of the Blue-winged Teal. He found that incubation periods were normally slightly longer in the Delta incubators than they were out-of-doors, but that during extended cold spells, incubation periods outside were considerably lengthened. I did not investigate the influence of weather upon Gadwall incubation.

Hatching, predation, and desertion.—Of 30 wild nests, 14 (46 per cent) produced one or more chicks, 11 (37 per cent) were depredated, and five (17 per cent) were deserted. Other studies have yielded success rates varying from seven per cent (Anderson, 1956) to 92.7 per cent (Duebbert, 1966). Six nests at Delta were apparently depredated by ground squirrels (*Citellus* spp.), four by raccoons (*Procyon lotor*), and one by a striped skunk (*Mephitis mephitis*). It is significant that no instances of avian predation were recorded. Crows (*Corvus brachyrhynchos*) have been exterminated from the Delta area and no gulls (*Larus* spp.) bred nearby.

Two cases of desertion were apparently due to storms, two to human disturbance, and one to predation. A nest containing 11 eggs that I found 8 July 1964 had no eggs the following day. After clearing the area, I found five eggs containing live embryos in three widespread places, all about three meters from the nest. Another nest (9 eggs) located near a construction site was deserted the day I found it. Two nests were deserted in the midst of heavy rains. One held a full clutch, the other two eggs. A nest containing five eggs when I found it, contained a broken egg as well as four intact eggs when I later visited it.

I took the eggs from 3 of 10 captive nests. Another was destroyed by a raccoon. Two of the remaining six were deserted, one on the night of a very severe storm eight days after the start of incubation, the other between the fourth and ninth day of incubation. The remaining four nests hatched a total of 27 young.

Pair bond dissolution.—In captivity, pair bonds were broken at various stages of the breeding cycle. One male left his mate just after she had laid her fifth egg to chase another female whose nest had just been robbed. All other males (7) whose mates incubated eggs, remained with them during some portion of the incubation period. One drake remained until the 23rd day of incubation—the day before the eggs hatched. All of the males (9) deserted their mates between 12 and 22 June. In a pen where six pairs bred, one pair bond was dissolved on 13 June, four 15 June, and one 18 June. Two of the 15 June dissolutions represented nests from which I took the eggs 11 June, at which time the pair bonds were still intact. One of the two pairs just mentioned joined a postbreeding group together; the female of the second pair was won over by a male with whom she had not previously associated.

Gates (1962), Duebbert (1966), and Oring (1962) observed similar variability in desertion times. Gates (1962) felt that although drakes usually left the hens early in the season, before the middle of incubation, some remained until hatching. This is precisely what I observed in captivity. In my opinion, the sight of postbreeding groups may hasten the breaking of pair bonds. In early June, few such groups—all small—are extant. Later, large aggregations are common.

I watched the dissolution of one pair bond closely. Early in the incubation period whenever the hen was flushed from her nest or left it for a break, she immediately joined her mate. He responded by frequent quacks and Head-bobs. By the 10th day of incubation the drake still accepted the hen and chased nearby males but he no longer quacked and his Head-bobs were infrequent. On the 15th day of incubation the hen, when flushed from the nest. joined her mate immediately, following him down the ditch. She was still aggressive toward foreign birds and chased them but the drake ignored strangers and no longer paid attention to her. On the following day (16th day of incubation) I saw the pair together but the male was not in the least aggressive toward other birds and he neither bobbed nor quacked. By the 19th day of incubation the hen made no attempt to join her mate. The attraction between the two was severed.

POSTBREEDING ACTIVITIES

All captive drakes were still with their mates the first week in June. Pursuit flights were frequent though most males were rapidly molting their body feathers. By 5 June. four of seven drakes in one pen had bred and all were obviously molting. A fifth, which later became the last in the pen to breed, had molted considerably fewer feathers than the four mentioned above. The two remaining drakes in that pen were unsuccessful in their attempts to mate. They had no visible feathers of the basic plumage until 20–22 June.

By the end of June pursuit flights in the wild had ceased: hens were deserted. Molting concentrations which had been increasing for several weeks were at maximum size. Duebbert (1966) reported a large number of pursuit flights continuing until mid-July at Lower Souris. At Delta during most of July, wild and captive birds spent most of each day sitting along shorelines preening or sleeping. Most feeding was restricted to the early morning and late evening hours. Not until 23 July did I actually observe a flightless Gadwall, but on that date 10–15 per cent of the birds I saw were flightless; many that I saw or collected had just dropped their remiges; and a wild drake that I collected was almost ready to fly again. By 23 July no adults in any of the breeding pens had dropped their remiges. In two large enclosures housing nonbreeding birds, 3 of 14 wing-clipped females and 8 of 10 wing-clipped drakes had dropped their remiges. In other words, 54 per cent of a nonbreeding population had become flightless, a percentage substantially greater than my estimate of the flightless portion of the wild population. By 5 August, about 50 per cent of the wild adult males were flightless but I saw no flightless females. On the same day, 9 of 10 nonbreeding captive males and 6 of 14 nonbreeding captive females were flightless.

Yearling males are apparently less likely to breed than older birds. In pens where all drakes were yearlings there was little breeding and very few pairs formed. Most two-year-old captive males, on the other hand, bred. Of 15 wild males shot while they accompanied their mates in June (14) and July (1), only three were yearlings as determined by the presence of juvenal upper wing coverts. I have collected just three unpaired drakes in June; all were yearlings. Gates (1962) stated that the first Gadwalls to arrive in Utah in spring were unmated yearling drakes. The drake mentioned above which had almost full grown wings 23 July 1964 may have been just such a yearling which never became involved in courtship. In my opinion, there are a few wild Gadwalls, primarily yearling males, that never participate in courtship activities and these few birds. as well as males thwarted very early in their nuptial efforts, are the first to form postbreeding groups and to molt their remiges. They are followed by early breeding males, by later breeding drakes, by nonbreeding drakes which were not thwarted in their sexual efforts until the season was well along, by early breeding hens. and finally by late breeding hens. The discovery in Louisiana of flightless adult females (Chabreck, 1966) leaves opened the possibility that late breeding hens normally migrate before growing new flight feathers.

One of the captive breeding males became flightless during the third week in June due to badly worn feathers. When these feathers became wet. they absorbed water, and the drake was as incapable of flight as he would have been had he dropped his remiges. Several other males in the pen likewise had badly worn primaries and were able to rise from the water only at very

FIG. 1. Seventh Primaries of Gadwalls in Summer Illustrating Variation in Feather Wear.

gradual angles. I have, on three occasions, taken ducks in the wild showing this same condition. One, an adult female Lesser Scaup (*Aythya affinis*), was so obviously flightless on the water that I didn't realize she actually had a full complement of flight feathers until some time after I had shot her. Another hen scaup that I caught by hand was alert and in fine bright plumage but the flight feathers of her right wing were almost devoid of barbs. A flightless male Gadwall that I collected had many broken flight feathers though none had fallen out. Various degrees of wear in primary feathers are shown in Figure 1.

In the breeding pens only 2 of 21 drakes were flightless by 5 August and neither of these had bred. This may have been due to the fact that I pruned the vegetation of these pens in late July—at about the time the birds would normally have dropped their remiges. The disturbance and lack of suitable cover for hiding may have been responsible for failure of the birds to molt at the normal time. Dense concealing vegetation is, I believe, as essential for suitability of a molting area as are water and proper food. In the Delta Marshes, molting areas all contained dense stands of bulrush (*Scirpus* spp.) or cattail (*Typha latifolia*). Freedom of movement may also be essential. In the large pens where adequate vegetation was available and freedom of movement was guaranteed, birds molted normally. Hochbaum (1944) states that the suitability of a marsh as a haven for flightless dabbling ducks depends upon its providing food, cover, and isolation.

The activity schedule of captives in one pen was studied on 7 August when my assistant and I took turns watching continuously from a blind from 04:30 (1½ hours before sunrise) to 22:30 hours (1¼ hours after sunset). A few days later we watched these same birds from 21:00 to 02:00. Only 2 of 13 adults fed during the early morning hours. Starting at 06:30 there was a half hour period of rapid, nervous swimming back and forth. Otherwise the flock preened and slept until 08:15. Feeding picked up markedly during the middle of the day and reached a peak in early evening. At dark, the nervous swimming recurred. The flock swam back and forth, crawled onto land, re-entered the water, and occasionally flew to the opposite side of the pen only to swim rapidly back to the starting point. There was no evidence of feeding between 23:00 and 02:00.

Perhaps the nervousness exhibited by these captives at dawn and dusk was indicative of *Zugunruhe.* These captives still had old remiges but adults in the wild were testing new wings by mid-August. The wild flocks too were restless, moved about a great deal, and fed throughout the middle of the day.

During the remainder of August and in early September, Gadwall flocks increased greatly in size. These flocks were wary, but they fed throughout the day if undisturbed. Their favorite feeding grounds were areas in which fruit-clusters of pondweed (*Potamogeton* spp.) were numerous. By mid-September Gadwalls were leaving the Delta Marshes; by the end of the month they were rare.

GONAD SIZE

Sowls (1955) collected six female Pintails (*Anas acuta*) which were searching for nest-sites and found their largest ova to be 5–7 mm in diameter. Phillips and van Tienhoven (1962) discussed the development of Pintail ova only from the 6 mm stage on (development past the time of first appearance of yellow yolk) since most ovaries contained many ova smaller than 6 mm but only a few that were larger. Both hen Pintails (Phillips and van Tienhoven, 1962) and hen Gadwalls collected prior to nest initiation had an average of six ova larger than 6 mm in the ovary. These species lay an egg a day. In the Gadwall, I found that seven days were required for ova to develop from the 6 mm stage to the 33–37 mm stage at ovulation. Benoit (1950) estimated the period of total ovarian development to be 5–13 days in domestic fowl (*Gallus gallus*), 14 days in domestic Rock Dove (*Columba livia*), and 10–13 days in domestic Mallard (*Anas platyrhynchos*). At ovulation, Gadwall ova measured 33–37 × 31–33 mm. During the three days preceding ovulation, ova measured 21–28 × 15–27 mm; 16–20 × 16–19 mm; and 10–12 × 10–12 mm. Ova were more or less spherical except during the two days prior to ovulation when they assumed a more oblong shape.

TABLE 1

WEIGHTS OF MALE GADWALLS AT VARIOUS STAGES OF BREEDING CYCLE

Stage of annual cycle	Sample size	Extremes (in grams)	Average (in grams)
Paired, 2+ yrs. old	2	866–1,039	952.5
Unpaired, yearlings	2	744– 771	757.5
With laying or incubating females	12	688– 908	822.1
In postbreeding flock before wing molt	2	930– 965	948.5
In midst of dropping remiges	2	874–1,038	956
With 9th primary 1–50 mm	9	869–1,006	914.4
With 9th primary 51–100 mm	8	840–1,004	912.4
With 9th primary 101–122 mm	10	753– 935	839.3

Males arrived on the breeding grounds with somewhat enlarged testes. Three drakes collected while they were chasing unmated hens had testes averaging 26 × 10.3 mm (left) and 18.3 × 8 mm (right). Fourteen males attending hens had testes averaging 34.4 × 16.4 mm (left) and 27.2 × 13.5 mm (right). In 16 of 17 drakes, the left testis was larger than the right by an average of 6.6 × 2.4 mm. Two not-yet-flightless adult drakes collected from a postbreeding aggregation each had testes less than 8 mm long. The testes of 27 flightless adult drakes were all between 6 and 15 mm long.

WEIGHT

Although weights of Gadwalls have been included in numerous writings, no one has attempted to correlate weight changes during the summer season with breeding and molting as Weller (1957) did so successfully with the Redhead (*Aythya americana*). In Illinois during the southbound migration adult male Gadwalls averaged 990 grams, juvenile males 908 grams, adult

TABLE 2

WEIGHTS OF FEMALE GADWALLS AT VARIOUS STAGES OF BREEDING CYCLE

Stage of annual cycle	Sample size	Extremes (in grams)	Average (in grams)
Not yet laying (ova less than 38 mm)	4	751– 962	842.75
Laying—full sized egg in duct	3	852–1,031	929.3
With eggs incubated 1–12 days	8	625– 757	682.5
With eggs incubated 13+ days	5	574– 685	631.2
With brood 7 days old or less	5	655– 786	695.6
With brood 8–14 days old	4	730– 803	759.5
With brood 15+ days old	4	695– 789	738.75
Flightless; brood deserted with 9th primary 33 mm long	1		796

TABLE 3

WEIGHTS OF GADWALLS DURING SUMMER MONTHS

Sex	Month	Sample size	Extremes (in grams)	Average (in grams)
♂	May	4	744–1,039	855
♂	June	11	674– 908	821
♂	July	17	831–1,038	937
♂	August	15	753– 931	849
♀	May	1		962
♀	June	14	603–1,031	765
♀	July	18	574– 803	698
♀	August	4	658– 796	731

females 849 grams, and juvenile females 808 grams (Bellrose and Hawkins, 1947). Leopold (1919, 1921) reported that Gadwalls (sex and age classes combined) averaged 850 grams during fall and winter in New Mexico and Texas. Kortright (1942) stated that drakes averaged 908 grams (range 709–1135) and females 823 grams (range 596–1021) but he did not mention what season or seasons his data represented. Nelson and Martin (1953), lumping all data, found 104 males to average 908 grams (maximum 1181) and 89 females to average 817 grams (maximum 1362). Tables 1 and 2 categorize, according to stages of the breeding cycle, 81 wild Gadwalls (47 males, 34 females) taken in southern Manitoba. Drakes gained weight rapidly after deserting their mates. Their weight then remained relatively constant until the final stages of wing-molt at which time they lost about 75 grams. Hens lost a great deal of weight during the incubation period but regained weight rapidly while rearing their broods. Females probably lose a good deal of weight while growing new wing feathers but the loss could not be determined from my data. Table 3 presents weight averages for Gadwalls of both sexes during the summer months. These averages reflect the normal activities of Gadwalls during these months.

SUMMARY

In 1963–64, most Gadwalls initiated nests during the last week of May. Nest-sites were usually in dense cover, on dry ground, and near water. First clutches in the wild averaged 10.57 eggs as compared to 8.67 for initial clutches in captivity and 8.25 for renest clutches in the wild. Incubation periods averaged 24.0 days in the hatchery and 25.75 days out-of-doors. In the wild, 46 per cent of 30 nests were successful, 37 per cent were depredated, and 17 per cent were deserted. In captivity, pair bonds were severed at various stages of the breeding cycle but nearly all were broken between 12 and 22 June. In the wild, drakes were with their mates in early June but by the end of the month no pairs were intact.

Nonbreeding drakes that were never active in courtship molted before breeding drakes did, whereas males which did not breed but which attempted to court, molted after breeding drakes. By mid-summer some birds became flightless due to badly worn remiges. Disturbance coupled with lack of cover inhibited wing-molt in captives. Once wild adults regained flight in late summer they were wary and formed large flocks which were soon to depart.

About six days were required for ova to develop from the 6 mm stage to ovulation. Testes of mated drakes were larger than those of unmated drakes that were chasing hens. Testes regressed rapidly once drakes deserted their hens.

Males were heaviest just before dropping their remiges but lost about 100 grams during the flightless period. Females were heaviest during laying, lost weight during the incubation period, and gained weight while rearing broods.

ACKNOWLEDGMENTS

I am especially indebted to George M. Sutton, University of Oklahoma, and to H. Albert Hochbaum and the entire staff of the Delta Waterfowl Research Station for invaluable assistance throughout the course of my study. Hans Lind kindly reviewed the manuscript. Financial aid was provided by the North American Wildlife Foundation and the National Institutes of Health. Were it not for the assistance of John Farrand and Dan Tucker this study would never have been completed.

LITERATURE CITED

Anderson, W. 1956. A waterfowl nesting study on the grasslands, Merced County, California. California Fish and Game, 42:117–130.

Bellrose, F. C., and A. S. Hawkins. 1947. Duck weights in Illinois. Auk, 64:422–430.

Benoit, J. 1950. Organes uro-genitaux. *In* Traité de Zoologie, edited by P. Grassé, 15:341–377. Masson et Cie., Paris.

Chabreck, R. H. 1966. Molting Gadwall (*Anas strepera*) in Louisiana. Auk, 83:664.

Dane, C. W. 1965. The influence of age on the development and reproductive capability of the Blue-winged Teal (*Anas discors* Linnaeus). Unpubl. Ph.D. Thesis, Purdue University, West Lafayette, Indiana.

Dane, C. W. 1966. Some aspects of breeding biology of the Blue-winged Teal. Auk, 83:389–402.

Duebbert, H. F. 1966. Island nesting of the Gadwall in North Dakota. Wilson Bull., 78:12–25.

Gates, J. M. 1962. Breeding biology of the Gadwall in northern Utah. Wilson Bull., 74:43–67.

Hochbaum, H. A. 1944. The Canvasback on a prairie marsh. The Stackpole Co., Harrisburg, Pennsylvania.

Kendeigh, S. C. 1963. New ways of measuring the incubation period of birds. Auk, 80:453–461.

Kortright, F. 1942. The ducks, geese, and swans of North America. Wildl. Mgmt. Inst., Washington, D.C.

Leopold, A. 1919. Notes on the weights and plumages of ducks in New Mexico. Condor, 21:128–129.

Leopold, A. 1921. Weights and plumages of ducks in the Rio Grande Valley. Condor, 23:85–86.

Miller, A. W., and B. D. Collins. 1954. A nesting study of ducks and coots on Tule

Lake and Lower Klamath National Wildlife refuges. California Fish and Game, 40:17–37.

Nelson, A. L., and A. C. Martin. 1953. Gamebird weights. J. Wildl. Mgmt., 17:36–42.

Oring, L. W. 1962. Behavior and ecology of certain ducks during the postbreeding period. J. Wildl. Mgmt., 28:223–233.

Oring, L. W. 1966. Breeding biology and molts of the Gadwall, *Anas strepera* Linnaeus. Unpubl. Ph.D. Dissertation, University of Oklahoma, Norman.

Parnell, J. F., and T. L. Quay. 1965. The populations, breeding biology, and environmental relations of the Black Duck, Gadwall, and Blue-winged Teal at Pea and Bodie Islands, North Carolina. Proc. 16th Conf. S.E. Assoc. Game and Fish Commissioners, 1962:53–67.

Phillips, R. E., and A. van Tienhoven. 1962. Some physiological correlates of Pintail reproductive behavior. Condor, 64:291–299.

Rienecker, W. C., and W. Anderson. 1960. A waterfowl nesting study on Tule Lake and Lower Klamath National Wildlife refuges, 1957. California Fish and Game, 46:481–506.

Sowls, L. K. 1955. Prairie ducks. The Stackpole Co., Harrisburg, Pennsylvania.

Weller, M. W. 1957. Growth, weights, and plumages of the Redhead, *Aythya americana*. Wilson Bull., 69:5–38.

Witherby, H. F., F. C. R. Jordain, N. F. Ticehurst, and B. W. Tucker. 1939. The handbook of British birds. Vol. 3. H. F. & G. Witherby, Ltd., London.

DEPARTMENT OF ZOOLOGY, THE UNIVERSITY OF OKLAHOMA, NORMAN, OKLAHOMA, (PRESENT ADDRESS: DEPARTMENT OF BIOLOGY, UNIVERSITY OF NORTH DAKOTA, GRAND FORKS, NORTH DAKOTA) 3 JANUARY 1967.

THE RADIUS AND RELATIONSHIP OF OWLS[1]

WALTER J. BOCK AND ALLAN McEVEY

WHILE skinning a specimen of *Ninox strenua*, Mr. Michael Traynor of the National Museum of Victoria noticed a "bony spur" on the wing near the wrist. Wing spurs in owls were unknown to Mr. Traynor, and hence he showed it to Allan McEvey. Further examination revealed that this spur lay beneath the skin and that it was attached to the radius, not to the carpometacarpus as is the usual position of the wing spur in birds (Jeffries, 1882*a*; Rand, 1954; only the spur-winged goose, *Plectropterus*, has a spur on the radiale). Initial study disclosed that this structure is not a wing spur, but an enlarged sesamoid bone. The presence of a sesamoid bone associated with the tendon of the M. tensor patagii longus where it bends around the distal end of the radius and its enlargement in some hawks has been known since the middle of the nineteenth century (Giebel, 1866:35; Milne-Edwards, 1867–8: Plate 10, Fig. 1; Alix, 1874:403; Plate 2, Fig. 1; reviewed in Gadow, 1891: 72, 256; Plate 20, Fig. 2). Little significance was given to the presence and configuration of this sesamoid. This radial sesamoid was described and discussed fully for the first time by Shufeldt in the owls (Shufeldt, 1881*a*:615; 1900:600, Fig. 5) and in the hawks (Shufeldt, 1881*b*). He designated it as the os prominens. Jeffries (1882*b*) pointed out that this structure had been described earlier by Milne-Edwards, Mivart and Alix. Both Shufeldt and Jeffries showed that the tendon of the M. tensor patagii longus inserts on the os prominens and discussed its possible functional significance. Lucas (1882*b*), in a brief but characteristically excellent note summarized the knowledge of the os prominens and associated tendons in the hawks and owls. To our knowledge, no significant advance over Lucas' discussion has appeared in the eighty years since his contribution. After the initial series of papers by Shufeldt, Jeffries and Lucas, only a few references to the presence of the os prominens have been published (Pycraft, 1903:32; Hudson and Lanzillotti, 1955:40, Fig. 33).

During the preliminary examination of the radius in owls, our attention was drawn to another peculiar feature of this bone; namely, a small bony arch on the inner side of the shaft. This structure was described as the osseous arch by Shufeldt (1900:679, 680; Fig. 5) very briefly and without additional comments. Pycraft (1903:43) mentioned the bony arch of the radius in passing. The osseous arch of the radius in the owls has again become all but forgotten in the subsequent literature. Nothing had been pub-

---

[1] We dedicate this paper to the late Dr. Tilly Edinger, who had a lifelong interest in heterotopic ossifications, in recognition of her achievements in vertebrate morphology and paleontology.

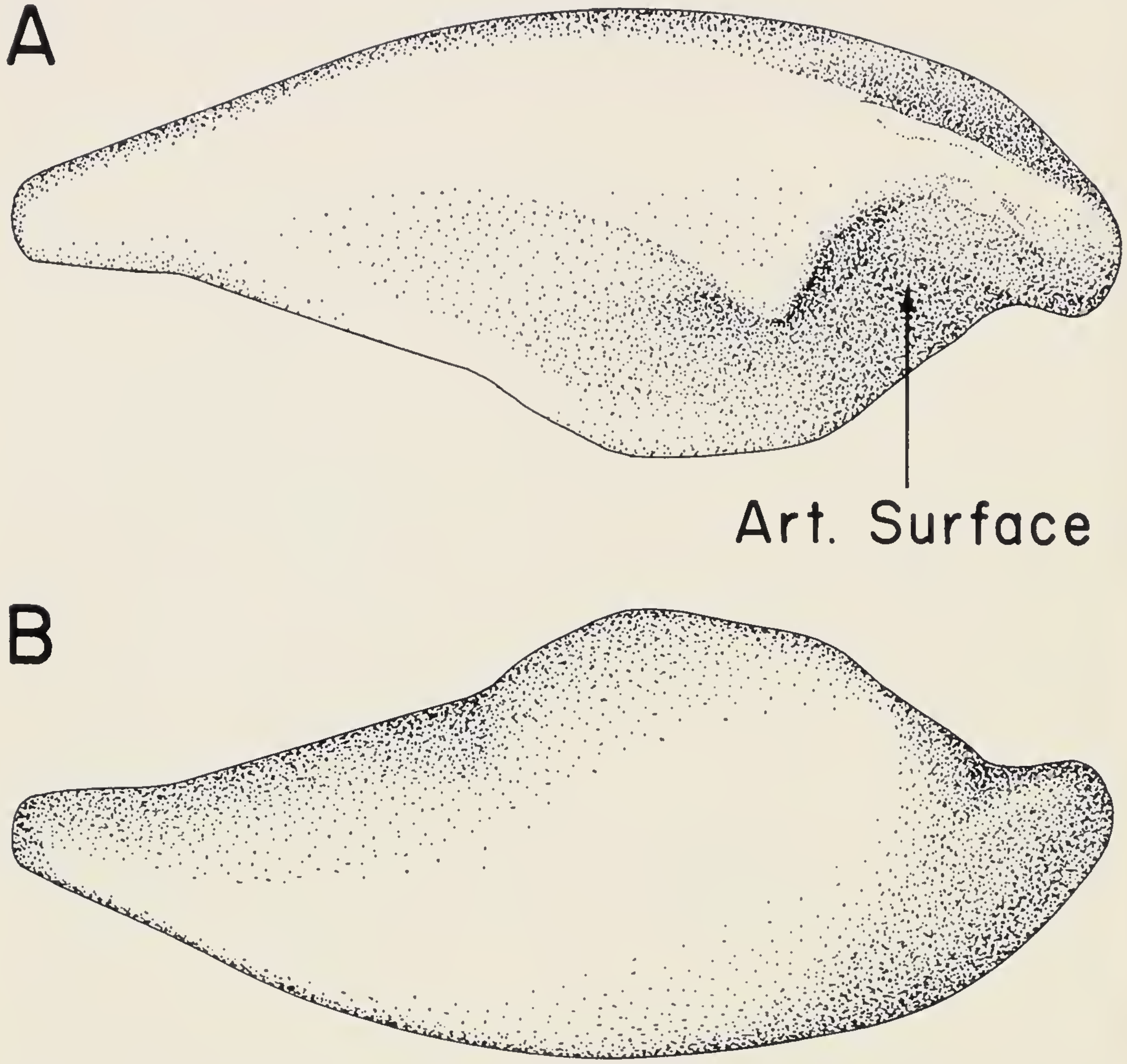


FIG. 1. An isolated os prominens from an immature *Ninox strenua* showing the dorsal surface (A) and the ventral surface (B). The articular surface can be seen on the dorsal surface.

lished on its interrelationships with surrounding soft tissues or on its possible functional significances.

In this paper, we would like to redescribe the os prominens and the osseous arch of the radius, to speculate on their possible functional significance, and to discuss the pertinence of these structures to the relationships of the owls.

DESCRIPTION

The os prominens in owls.—An isolated os prominens from an immature *Ninox strenua* is shown in Figure 1. This heterotopic bone is 20 mm long, 9 mm wide at its greatest width and 4 mm thick. This particular example of the os prominens is much wider than those usually seen in owls. In another specimen of *Ninox strenua* (Fig. 3B), the os prominens is more typical in shape and measures 23 mm long, 8 mm wide, and 7 mm thick. The bone tapers rapidly from its greatest width to a blunt point onto

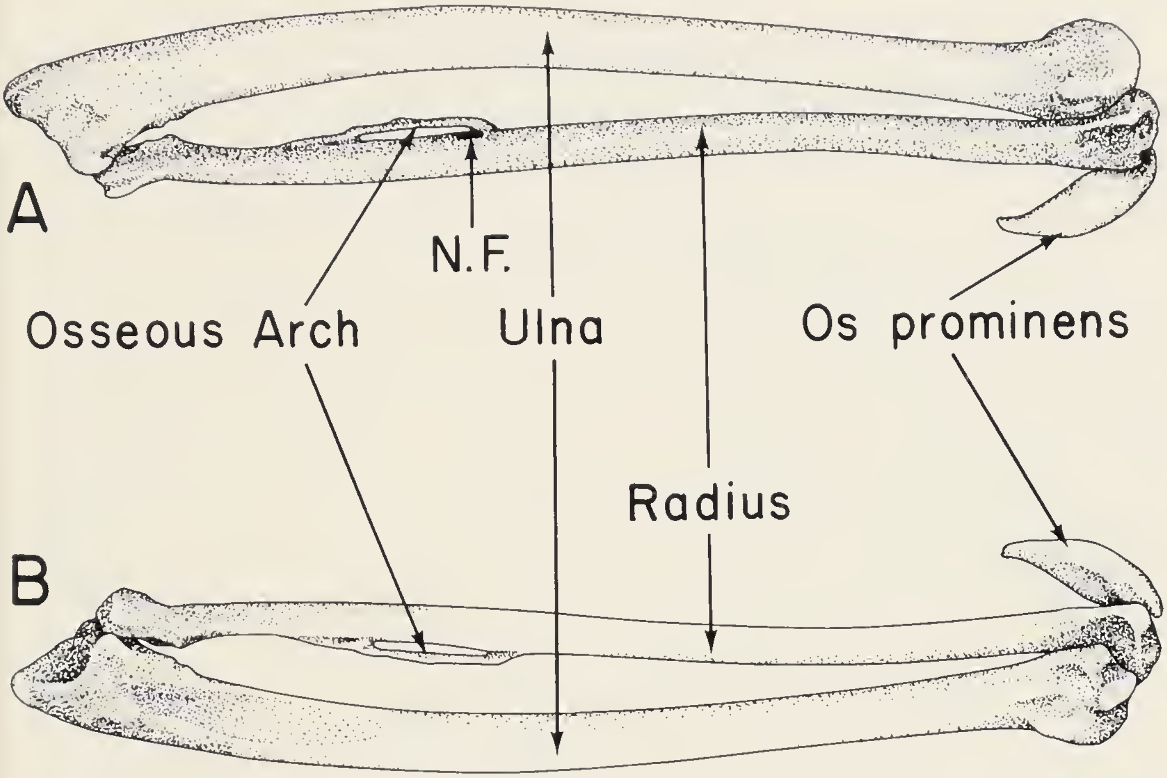


FIG. 2. The forearm of *Ninox strenua* (same specimen as in Figure 1) as seen from below (A) and above (B) to show the os prominens and the osseous arch. The nutrient foramen (N.F.) of the radius can be seen at the distal end of the osseous arch.

which the tendon of the M. tensor patagii longus inserts. Its ventral surface (Fig. 1B) is convex and smooth without any distinctive features, whereas its dorsal surface is concave with an articular surface at its distal end. A slight projection lies along part of the proximal border of the articular surface. The os prominens is attached to the anterioventral surface of the distal external radial condyle. The exact relationship in life of the sesamoid bone to the radius is not necessarily as shown in Figure 2. These bones meet in a moveable articulation, and the os prominens doubtlessly shifts in position with directional changes in the tendon of the tensor patagii.

The os prominens in *Pulsatrix perspicillata* (Fig. 3A), *Ninox strenua* (Fig. 3B, another specimen with the more typical form of the sesamoid), and *Ninox novaeseelandiae* (Fig. 3C) show the more typical configuration of this sesamoid—a hook-shaped bone. It is more elongated and slightly decurved, and in all examples it ends in a blunt point. A thorough survey of the occurrence and configuration of the os prominens in all genera of strigid owls is not meaningful at this time because this sesamoid bone could be easily detached and lost in many osteological specimens. A rough survey indicates that the os prominens is present throughout the strigid owls, even in the smaller species like the Screech Owl (*Otus asio*); its shape is always like that illustrated in Figures 1–3. However, the os prominens is lacking in all specimens of *Tyto* that we have examined. Shufeldt (1900:675) also reported the absence of the os prominens in *Tyto alba* (= *Strix pratincola*) as did Lucas (1882:87).

In strigid owls, such as *Ninox strenua* (Fig. 4B) and *Asio otus* (Fig. 4C), the tendon of the M. tensor patagii longus bifurcates at some point before the distal end of the radius. One branch of the tendon inserts onto the proximal tip of the os prominens.

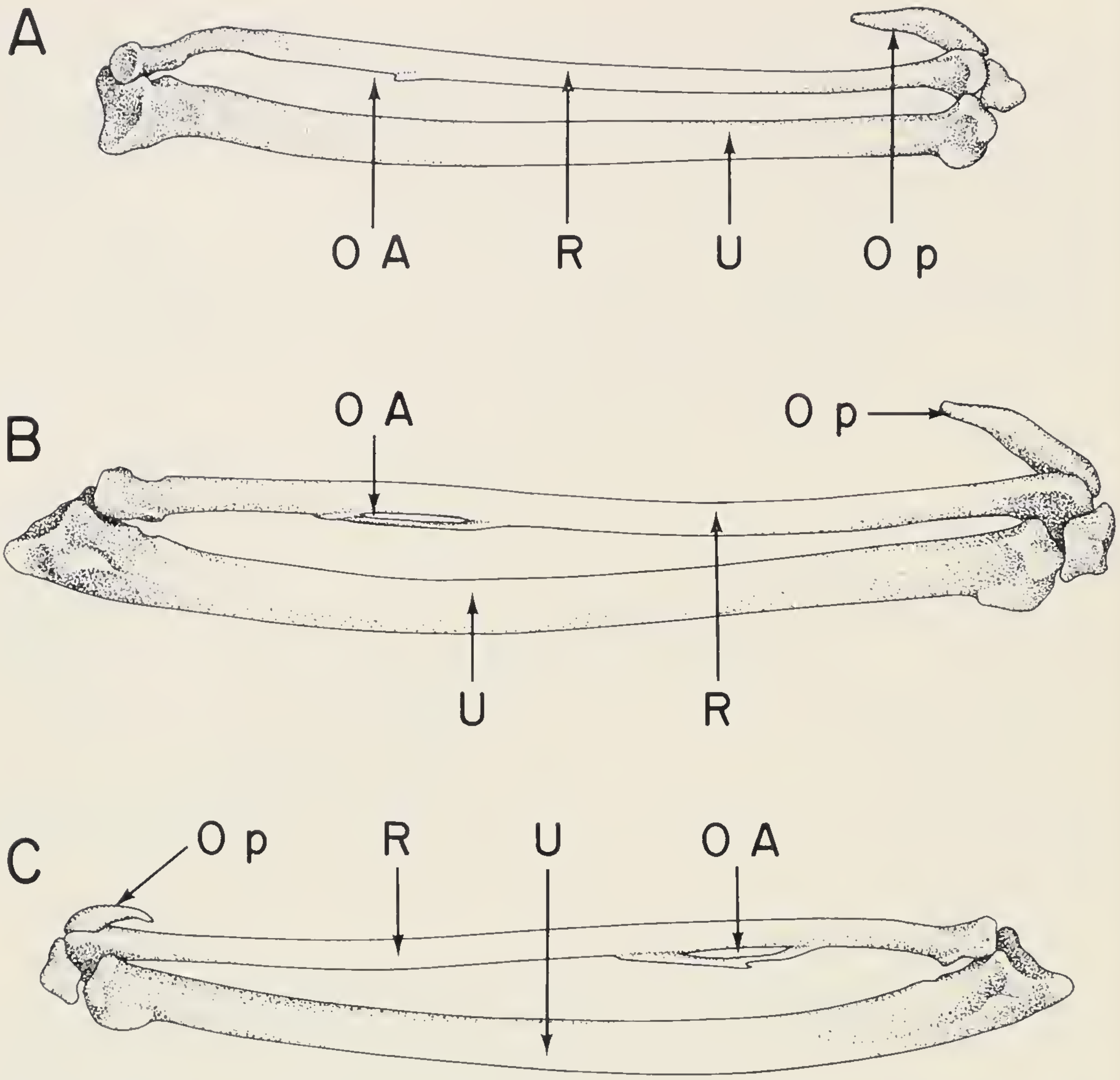
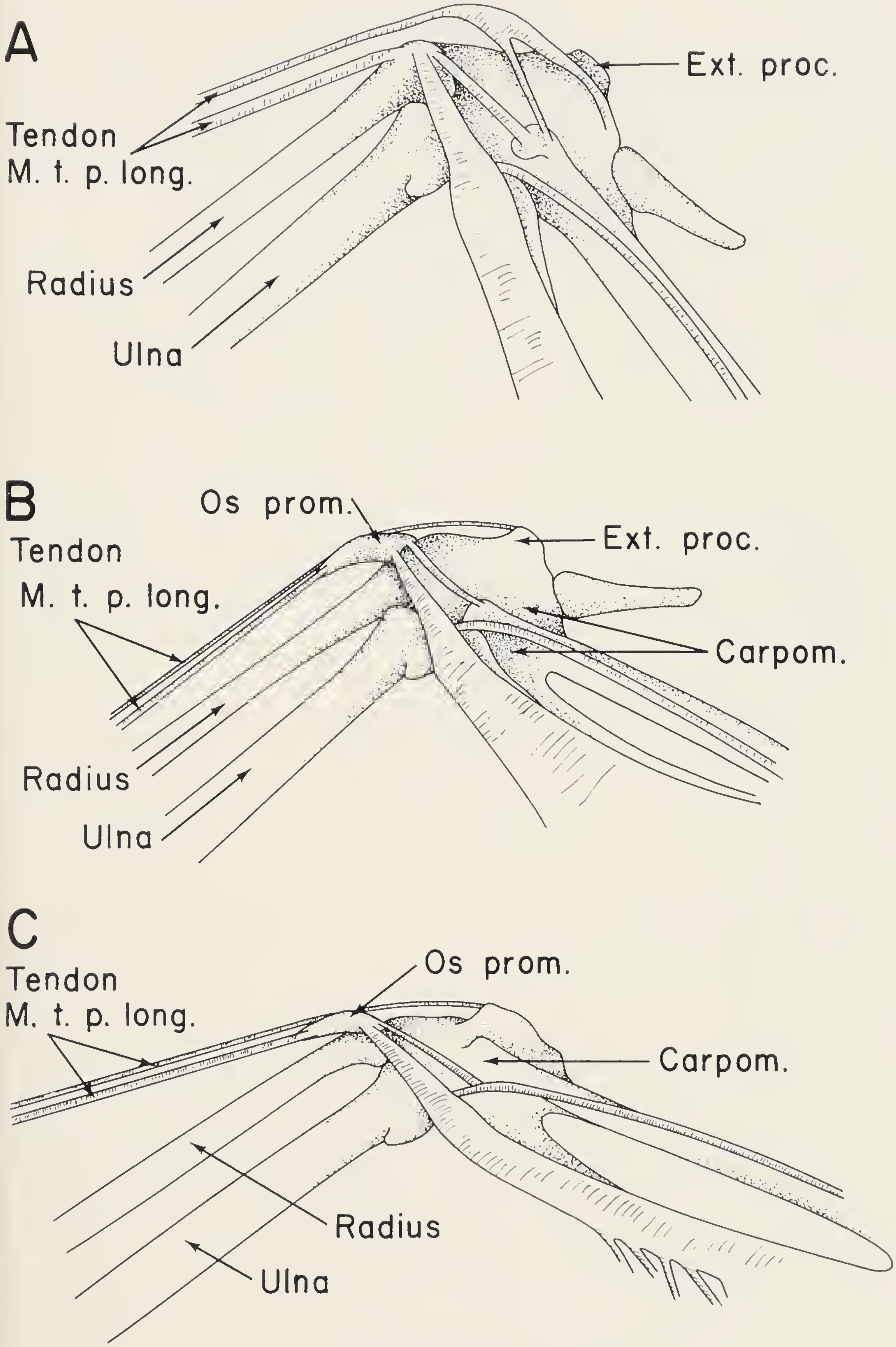


FIG. 3. The forearm of *Pulsatrix perspicillata* (A) *Ninox strenua* (B) and *Ninox novaeseelandiae* (C) as seen from above to show the os prominens (O p) and the osseous arch (O A). The arch is broken in *Pulsatrix perspicillata* with only one end remaining.

The other branch of the tendon passes dorsal to the os prominens and inserts on the extensor process of the carpometacarpus. Our dissections confirm the findings of Lucas (1882:87) who figured these tendons in *Bubo virginianus.* Two ligaments arise from the base of the os prominens. One runs a short distance before inserting on the main body of the carpometacarpus. The other ligament broadens into a flat sheet that runs along the posterior edge of the carpometacarpus and sends off small slips to the

→

FIG. 4. The carpal joint in *Tyto alba* (A), *Ninox strenua* (B), and *Asio otus* (C), to show the attachment of the tendon of the M. tensor patagii longus. This tendon splits with one branch inserting onto the extensor process of the carpometacarpus and the other branch inserting onto the radius or the os prominens. Two ligaments arise from the radius or base of the os prominens and run to the carpometacarpus and the bases of the primaries.


A
Ext. proc.
Tendon M. t. p. long.
Radius
Ulna
B
Os prom.
Ext. proc.
Tendon M. t. p. long.
Carpom.
Radius
Ulna
C
Os prom.
Tendon M. t. p. long.
Carpom.
Radius
Ulna

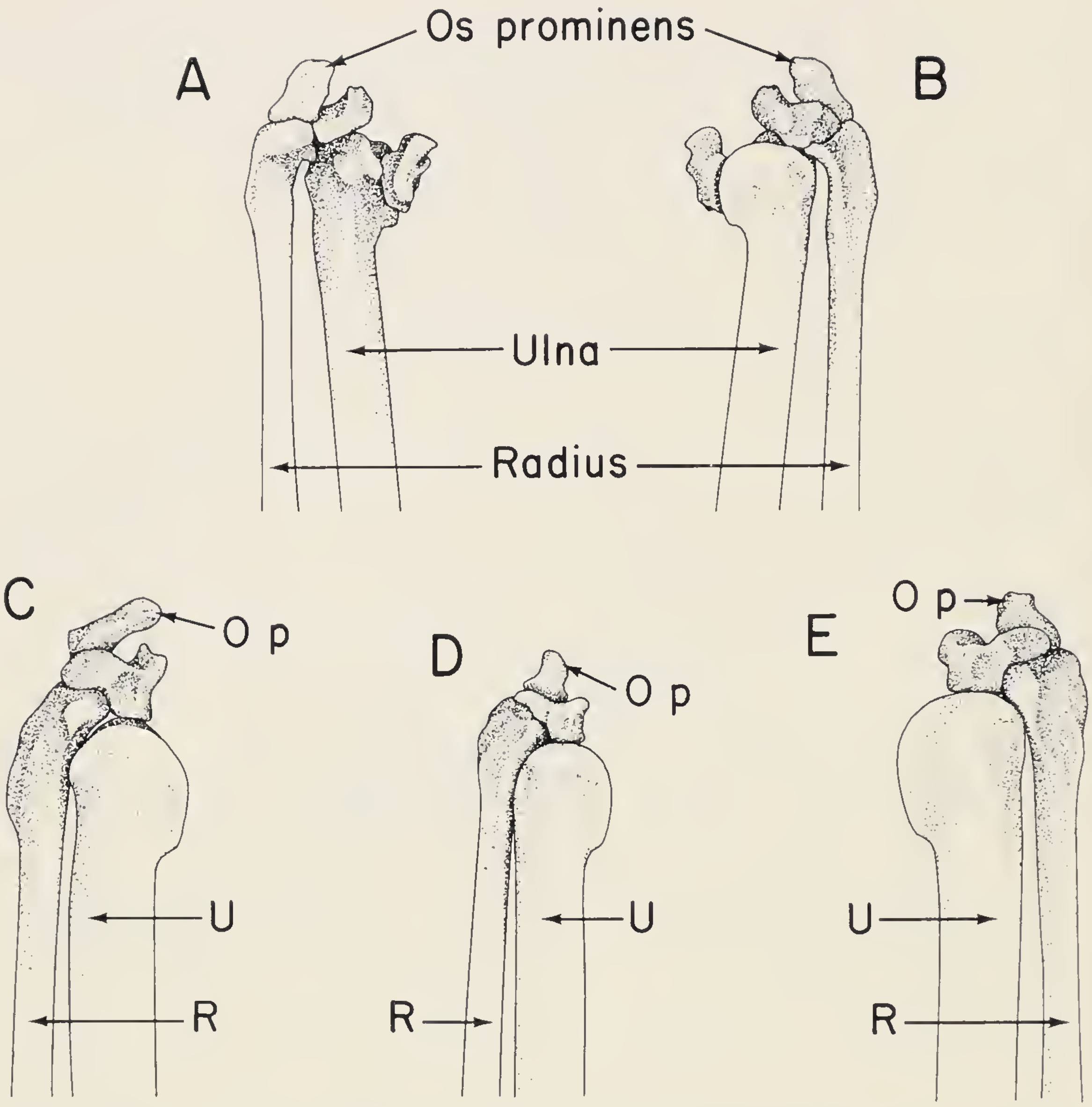


FIG. 5. The forearm of *Accipiter cooperii* (ventral, A and dorsal, B), *Circus cyaneus hudsonius* (C), *Buteo melanoleucus* (D), and *Aquila chrysaetos* (E) to show the os prominens (O p).

bases of the primary quills. These tendons and ligaments are quite similar in *Tyto alba* (Fig. 4A) except for the absence of the os prominens. The tendon of the M. tensor patagii longus splits in *Tyto*, one branch inserting onto the distal end of the radius and the other branch inserting on the extensor process of the carpometacarpus. Two ligaments arise from the radius close to the insertion of the tendon of the M. tensor patagii longus. The shorter ligament inserts on the main body of the carpometacarpus, while the other ligament broadens, runs along the posterior edge of the carpometacarpus and sends off short slips to the bases of the primary quills.

The large size of the os prominens as compared with the size of the M. tensor patagii longus and its tendon is of interest. We did not dissect this muscle in the owls studied, but referred to the description in George and Berger (1966:317–319). The muscle is small, and presumably produces little force compared to the size of the os prominens;

this discrepancy in size of the bone and the muscle is an anomaly and will be discussed below.

The os prominens in hawks.—The os prominens in hawks is a rectangular sesamoid articulating with the anterioventral surface of the external distal radial condyle. Moreover, this sesamoid articulates (probably) with the radiale although the exact relationships between these bones cannot be determined with certainty from dried skeletons. In *Accipiter cooperii* (Fig. 5A and 5B) the os prominens is 5 mm long, 3 mm wide, and 2 mm thick; in *Circus cyaneus hudsonius* (Fig. 5C) it is 8 mm long, 3 mm wide, and 3 mm thick; in *Buteo melanoleucus* (Fig. 5D) it is 8 mm long, 5 mm wide, and 5 mm thick; and in *Aquila chrysaetos* (Fig. 5E) it is 9 mm long, 7 mm wide, and 6 mm thick. The free end of the os prominens is blunt and rounded. In life, the os prominens apparently lies perpendicular to the longitudinal axis of the wrist joint; it is oblique to the longitudinal axis of the radius with its free end pointing toward the tip of the wing.

Again, a detailed survey of the occurrence and configuration of the os prominens in the hawks is not realistic at this time because the sesamoid could be lost in many specimens; alcoholic specimens or carefully prepared skeletons are needed. However, a rough survey was conducted and the results are as follows. This bone appears to be absent in the Cathartidae. A well-developed os prominens as described above was found in many genera of the Accipitridae such as *Accipiter*, *Heterospizas*, *Buteo*, *Circus*, *Aquila*, and *Haliaeetus.* It was not found (presumably absent) in many kites, Old World vultures, and many large hawks and eagles. Lucas (1882:87–88) reported a large, hook-shaped os prominens in *Otogyps* (*Torgos*) *calvus*, describing it as a simple sesamoid in the tendon of the M. tensor patagii longus; we were unable to confirm his report. The os prominens has been reported in *Pandion* (Shufeldt, 1881*b*:201), although we could not find it nor could Lucas (1882:88). It appears to be absent in the Falconidae as a well-developed heterotopic bone, although a small simple sesamoid is present in the tendon of the M. tensor patagii longus in *Falco* (Alix, 1874) and in *Falco mexicanus* (Hudson and Lanzillotti, 1955:40). Dr. George Hudson (pers. comm.) informs us that a simple sesamoid was present in 16 of the 18 genera of hawks dissected; it was absent in *Coragyps* and was only slightly ossified in *Sagittarius.*

Shufeldt (1881*b*:119) reported that the tendon of the M. tensor patagii longus (his extensor plicae alaris) inserts on the free end of the os prominens, as did Milne-Edwards (1867–68; see also Gadow, 1891: Plate 20, Fig. 2, who reproduced Milne-Edwards' figure). Dissection of a specimen of *Buteo swainsoni* (Fig. 6B) confirms these earlier findings. The tendon of the M. tensor patagii longus attaches onto the free tip of the os prominens, after which the tendon continues to the extensor process of the carpometacarpus where it inserts. A short extension of the tendon continues to the pollex. Two ligaments run from the distal end of the radius, one to the main body of the carpometacarpus and one to the bases of the primary quills; these ligaments are similar to those seen in the owls. In *Falco sparverius* (Fig. 6A), the tendon of the M. tensor patagii longus passes over the distal end of the radius to insert on the extensor process of the carpometacarpus. A slight thickening in the tendon may indicate the position of the sesamoid.

The osseous arch in owls.—A low thin bony arch is present on the posterior edge of the radius (facing the ulna) about one-third of the distance from the proximal end of the bone (Figs. 2 and 3). This arch has been described earlier by Shufeldt (1900:673; 680, Fig. 5). Except for a passing mention by Pycraft (1903:43), we have not been able to find any other reference to this feature. In *Ninox strenua*, the arch is 23 mm long (outer dimension), 3 mm high, and 1 mm thick on a radius 125 mm long. The

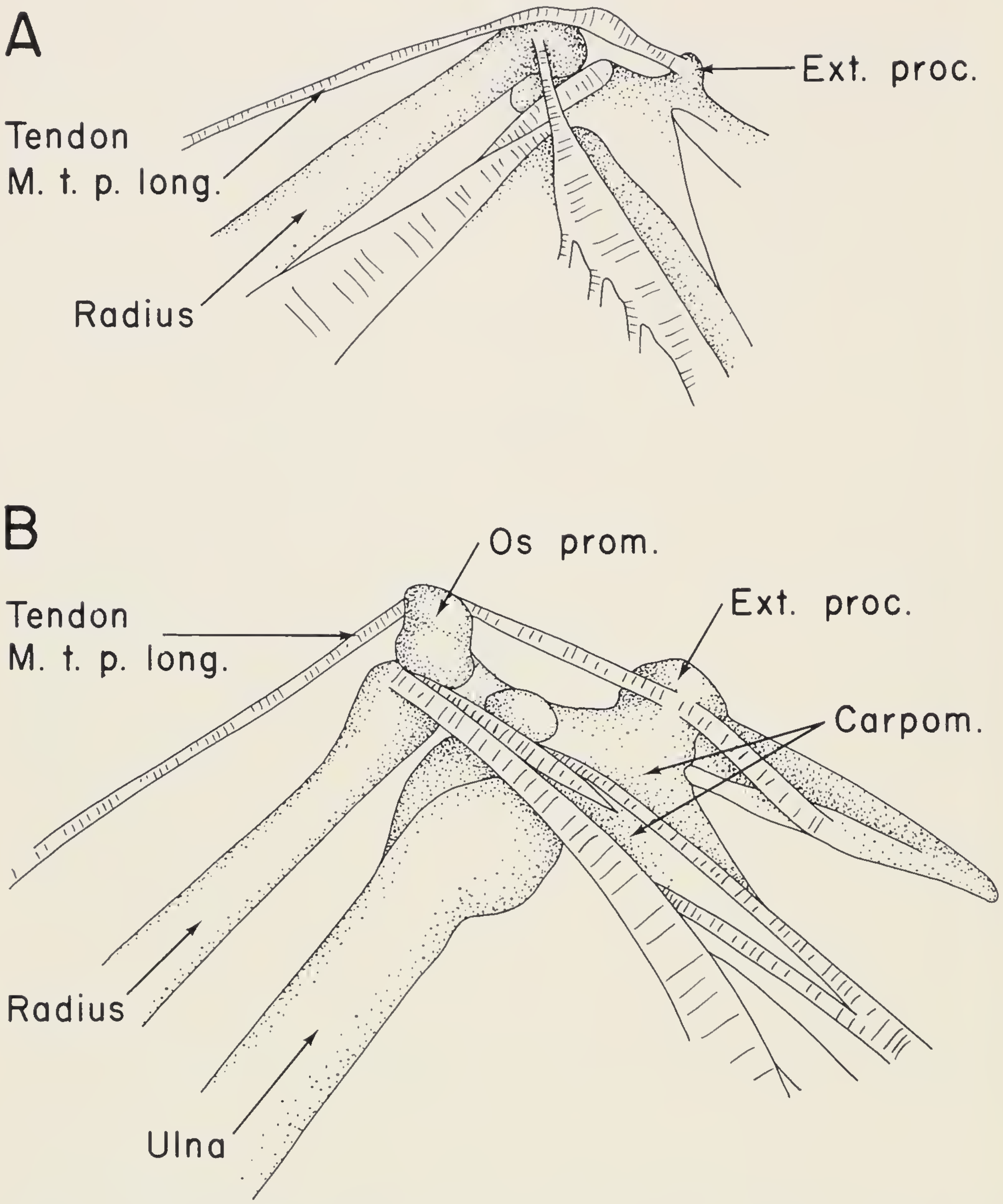


FIG. 6. The carpal joint of *Falco sparverius* (A) and *Buteo swainsoni* (B) to show the attachment of the tendon of the M. tensor patagii longus. In *Falco*, the tendon attaches directly to the extensor process of the carpometacarpus. A small sesamoid may be present in the swelling of the tendon. In *Buteo*, the tendon attaches to the free end of the os prominens before inserting on the extensor process.

inside dimensions of the arch are 9 mm long and 2 mm high. The nutrient foramen of the radius is located at the distal end of the arch; this foramen is very small and may be filled with dried tissue. The radius of some specimens had to be thoroughly cleaned by boiling before the nutrient foramen became visible. The arch is frequently broken

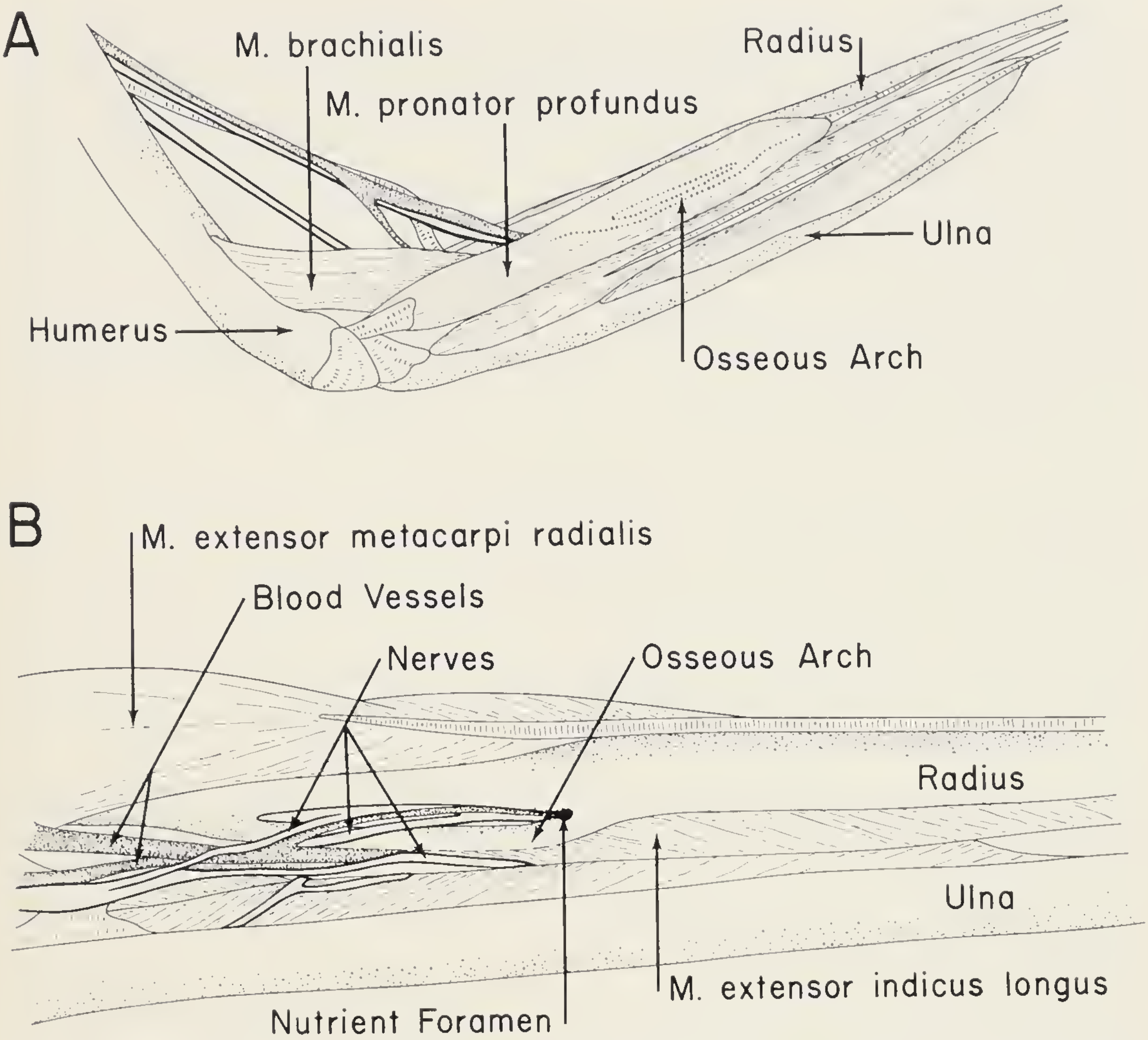


FIG. 7. The forearm of *Asio flammeus* to show the attachment of the M. pronator profundus (A) and of the M. extensor indicus longus (B) to the osseous arch. Nerves and blood vessels pass over the osseous arch to reach the space beneath it. A blood vessel passes through the nutrient foramen.

(as in Fig. 3A) with only the stump of one limb of the arch left; in almost all specimens, at least a remnant of the arch remains. The osseous arch of the radius is present in *Tyto* and in all genera of strigid owls examined. We have not seen a similar structure in any other group of birds, nor do we know of any references to such a structure.

Bony arches such as seen on the radius of owls may serve as the site of muscular attachment or as protection for some feature, such as a nerve or blood vessel, passing beneath it. The forearm of several specimens of Screech Owl (*Otus asio*) and two specimens of Short-eared Owl (*Asio flammeus*; Fig. 7) were dissected to ascertain the relationships of muscles and other structures to the osseous arch. The terminology for the muscles follows George and Berger (1966).

Two muscles attach to the osseous arch of the radius. The more superficial muscle, the M. pronator profundus, originates from the distal end of the humerus, passes over the M. brachialis and inserts on the shaft of the radius distal to the passage of the major nerve trunks and blood vessels from the upper arm to the forearm. The insertion of the M. pronator profundus covers the ventral surface of the osseous arch (Fig. 7A). The deeper muscle, the M. extensor indicus longus, originates from the edge and dorsal surface of the distal limb of the osseous arch and from the inner surface of the radial shaft distal to the arch (Fig. 7B). The origin of this muscle may be slightly ossified resulting in a small keel on the osseous arch. A series of nerves and blood vessels runs over the ventral surface of the osseous arch to reach the space beneath it (Fig 7B). Most of the space beneath the arch is filled with a whitish tissue continuous with and similar to the nerves. An elongated tissue, presumably a blood vessel could be traced through the nutrient foramen into the marrow cavity of the radius. However, it was not possible to trace any nerves through the arch to the muscles on the dorsal side of the radius. A more detailed analysis of the tissues within the osseous arch must await histological study.

DISCUSSION

The functional significance of the os prominens and the osseous arch remains as poorly known as in Shufeldt's day. Although the osseous arch functions as part of the site of attachment for the M. pronator profundus and the M. extensor indicus longus, it is doubtful that this function is associated with the adaptive reasons underlying its evolution. Both of these muscles could attach to the shaft of the radius as they do in all other birds. The intervention of the osseous arch appears to be completely nonessential for the proper attachment of these muscles in the owls. The configuration of blood vessels and nerves at the osseous arch suggests the best possible hypothesis for the adaptive reason for its evolution. The arch could serve as protection for these structures from the forces developed by the surrounding muscles. Our "educated" guess is that protection for the nerves and nerve-like tissues is the main adaptive significance of the osseous arch.

Shufeldt (1881*b*), Jeffries (1882*b*), and Lucas (1882) discussed several possible functions of the os prominens in hawks. We agree in general with their conclusions; namely, that the os prominens displaces the tendon of the M. tensor patagii longus from the surface of the carpus and thereby: (a) increases the moment arm of the force of the M. tensor patagii longus and hence increases the torque of this muscle on the carpometacarpus; (b) increases slightly the surface area of the wing and hence its lifting force; (c) possibly removes some of the force of the M. tensor patagii longus from the carpal bones and thereby protects the carpal bones (we doubt whether friction plays an important role because tendons are usually encased in sheaths with low friction surfaces). The first of these possible functions appears to be the most important and may be associated with adaptive reasons for the evolution of the os prominens in hawks. We have excluded consideration of the small sesamoid in the tendon of the M. tensor patagii longus in this discussion. This sesamoid appears to serve the usual functions of a sesamoid lying in the bend of a tendon around the end of a long bone.

Neither Shufeldt nor Jeffries discussed the function of the os prominens in owls; Lucas alludes briefly to the owls in his discussion. In the owls, one branch of the M. tensor patagii longus runs directly to and inserts on the extensor process of the carpometacarpus. The other branch of the tendon attaches directly to the distal end of the radius (*Tyto*) or indirectly to the distal end of the radius via the os prominens (strigid owls). In *Tyto*, two ligaments run from the distal end of the radius to the body of the carpometacarpus and to the bases of the primary quills. In strigid owls, these ligaments originate from the base of the os prominens. From a consideration of these tendons and ligaments, the major functions of the os prominens in owls appear to be: (a) to displace the tendon of the M. tensor patagii longus from the radius and therefore increase the moment arm of the muscular force; and (b) to couple the action of the M. tensor patagii longus and the ligaments to the carpometacarpus and primary quills directly and independently (or semi-independently) of the action of the radius. Most peculiar is the large size of the os prominens relative to the size of the radius and the size of the M. tensor patagii longus. Quite possibly, this bone experiences substantial bending forces; consequently, it must be large to resist them. Large bending forces would be associated with both possible functions mentioned above. We would suggest that both functions proposed for the os prominens in owls are associated with the adaptive reasons for its evolution in this group.

Shufeldt (1900; 1909:75) and Lucas (1882) imply that the os prominens of the hawks and of the owls is the same feature; *i.e.*, that they are homologous, although neither author makes a definite statement. Because of the continued discusssion of the relationships between hawks and owls (Starck and Barnikol, 1954:58–59; Starck, 1959; Vopio, 1955:128; Sibley[1], 1960; 1965:117), the exact homology of this structure is an important question. We will follow the definition of homology given by Bock (1963) and would like to divide the question of homology into two parts: (A) Is the os prominens in the hawks and in the owls homologous as a sesamoid bone in the tendon of the M. tensor patagii longus? and; (B) Is the detailed configuration of the os prominens in the hawks homologous to the detailed configuration of the os prominens in the owls?

---

[1] Professor Sibley very kindly made available to us the most recent data and interpretations from his work on the electrophoretic patterns of the egg-white proteins and hemoglobins of hawks and owls for which we are most grateful. Both the egg-white proteins and the hemoglobins show differences between *Tyto* and the strigid owls, indicating a separation between these groups of owls, although nothing can be said about degree of relationship. The egg-white patterns of *Tyto* and *Falco* are different, but the hemoglobins of both genera show two components with similar mobilities in starch gel. These results say that these two groups could be related, but they prove nothing one way or the other. Sibley's general conclusions that *Tyto* and the strigid owls are distinct groups, and that the similarities between *Tyto* and *Falco* must be looked upon as of unknown and uncertain significance are in close agreement with our general conclusions (see below).

The answer to the first question is probably "yes" because of the tendency of sesamoid bones to develop in tendons where they curve around the end of a bone and because of the frequent and widespread presence of a small sesamoid in this tendon at the carpal joint, as seen in many hawks and other birds (see Gadow, 1891:72; 256; George and Berger, 1966:318; Hudson, pers. comm.). But the homology of the os prominens in hawks and owls as a sesamoid in the tendon of the M. tensor patagii longus means only that a sesamoid found in this position in any bird would be homologous. This conclusion is of no value in ascertaining the relationships of hawks and owls.

The answer to the second question is clearly "no"; the detailed configuration of the os prominens in these groups is not homologous. We base our decision on the markedly different shape of this bone in the two groups and on the different relationships between the bone and the attached tendons and ligaments. Hence we would conclude that the os prominens in hawks and the os prominens in owls had separate evolutionary histories (evolved from a rudimentary sesamoid in the tendon of the M. tensor patagii longus independently and under the action of different selection forces). Consequently, the presence of this enlarged heterotopic bone in the two groups does not imply affinity. The use of the same name for these two nonhomologous bones is confusing, and we would suggest that some descriptive adjective such as strigid and accipitrid be used to distinguish between them.

The presence of an osseous arch of the radius and the arrangement of the tendon of the M. tensor patagii longus argue against the hypothesis that *Tyto* is related to any group within the falconiformes (*e.g.*, the Falconidae). These features provide strong support for the existing classifications that place *Tyto* in the same order as the strigid owls. Although the insertion of the tendon of the M. tensor patagii longus on the distal end of the radius (directly or indirectly via the os prominens) is not unique to owls, it is unusual for birds and is either unknown or very rare in birds believed to be close relatives of owls. The osseous arch is, to our knowledge, unique to owls and argues strongly for a monophyletic origin of all owls. Sufficient evidence is available to separate *Tyto* from strigid owls no matter what taxonomic rank is assigned to this separation. The absence of the os prominens in *Tyto* provides another bit of evidence supporting this separation as Lucas had mentioned as long ago as 1882.

SUMMARY

1. The os prominens is a large, hook-shaped sesamoid bone in the tendon of the M. tensor patagii longus of strigid owls; it is absent in *Tyto*. A low rectangular os prominens is present in many hawks. The relationships of tendons and ligaments to the os prominens differ in owls and hawks. The functional and adaptive significances of the os prominens could only be suggested.

2. The osseous arch of the radius is a bony arch on the shaft of the radius; it is found in all owls. The M. pronator profundus and the M. extensor indicus attach to the osseous arch. Several nerves and blood vessels run into the cavity beneath the arch, and a whitish tissue (nervous?) fills the cavity beneath the arch.

3. The os prominens in hawks and owls is homologous only as a sesamoid in the tendon of the M. tensor patagii longus. The detailed configuration of this enlarged heterotopic bone in hawks and owls is not homologous and hence does not imply affinity. The presence of the osseous arch and arrangement of the tendons of the M. tensor patagii longus support placing *Tyto* in the same order as other owls. These features do not support relationship between *Tyto* and any hawk.

ACKNOWLEDGMENTS

Above all, we would like to express our appreciation and thanks to Mr. Michael Traynor, preparator at the National Museum of Victoria, for calling our attention to the os prominens. Without his careful surveillance for new and peculiar structures in the material being handled, we would still be ignorant of this feature of owls and could not have done this study. Dr. Tilly Edinger has kindly made available her notes on heterotopic bones in vertebrates for which we are most grateful. We would also like to thank Mrs. Frances Jewel who devoted her usual skill and care in drawing the figures that accompany the text. The officials of the Bird Room, British Museum (Natural History) made available to us several specimens under their care for which we wish to express our appreciation. Special mention and thanks must be given to Major Harold Hall, O.B.E., M.C. and to the Myer Foundation, the Ian Potter Foundation, and the M.A. Ingram Trust, for generously enabling Allan McEvey to spend a month in New York in order to take part in this research. This study was supported by grant N.S.F. GB-3802 from the National Science Foundation to Walter Bock.

LITERATURE CITED

Alix, E. 1874. Essai sur l'appareil locomoteur des Oiseaux. Paris.

Bock, W. J. 1963. Evolution and phylogeny in morphologically uniform groups. Amer. Naturalist, 97:265–285.

Gadow, H. 1891. Vögel. *In*, Bronns' Klassen und Ordnungen des Thierreiches. Leipzig, 6th Bd., 4th Ab.

George, J. C., and A. J. Berger. 1966. Avian myology. Academic Press, New York.

Giebel, C. G. 1866. Über einige Nebenknochen am Vogelskelet. Zeitschr. ges. Naturwissenschaften, 28:29–35.

Hudson, G. E., and P. J. Lanzillotti. 1955. Gross anatomy of the wing muscles in the family Corvidae. Amer. Midl. Naturalist, 53:1–44.

Jeffries, J. A. 1882*a*. On the claws and spurs of birds' wings. Proc. Boston Soc. Nat. Hist., 21:301–306.

Jeffries, J. A. 1882*b*. On the sesamoid at the front of the carpus in birds. Bull Nuttall Ornithol. Club, 7:13–15.

Lucas, F. A. 1882. Notes on the os prominens. Bull. Nuttall Ornithol. Club, 7:86–89.

Milne-Edwards, A. 1867–68. Recherches anatomiques et paléontologiques pour servir a l'histoire des oiseaux fossils de la France. Paris.

Pycraft, W. P. 1903. A contribution towards our knowledge of the morphology of the owls. Trans. Linnacan Soc. London, 9:1–46.

Rand, A. L. 1954. On the spurs on birds' wings. Wilson Bull., 66:127–134.

Shufeldt, R. W. 1881*a*. Osteology of *Speotyto cunicularia hypogaea*. *In*, (1882) Contributions to the anatomy of birds. 12th Ann. Report of the late U.S. Geol. and Geogr. Surv. Terr. (Hayden's), pp. 593–626. (published first in 1881, saw 1882 reprint).

Shufeldt, R. W. 1881*b*. On the ossicle of the antibrachium as found in some of the North American Falconidae. Bull. Nuttall Ornithol. Club, 6:197–203.

Shufeldt, R. W. 1900. On the osteology of the Striges. Proc. Amer. Phil. Soc., 39:665–772.

Sibley, C. G. 1960. The electrophoretic patterns of avian egg-white proteins as taxonomic characters. Ibis, 102:215–284.

Sibley, C. G. 1965. Molecular systematics: New techniques applied to old problems. L'Oiseau, 35 (Berlioz, Volume Jubilaire):112–124.

Starck, D. 1959. Neuere Ergebnisse der vergleichenden Anatomie und ihre Bedeutung für die Taxonomie, erläutert an der Trigeminus-Muskulatur der Vögel. J. Ornithol., 100:47–59.

Starck, D., and A. Barnikol. 1954. Beiträge zur Morphologie der Trigeminusmuskulatur der Vögel (besonders der Accipitres, Cathartidae, Striges und Anseres). Morphol. Jahrb., 94:1–64.

Voipio, P. 1955. Muutuva lintujen järjestelmaä (Das veränderliche System der Vögel). Ornis Fennica, 32:108–129.

DEPARTMENT OF BIOLOGICAL SCIENCES, COLUMBIA UNIVERSITY AND DEPARTMENT OF ORNITHOLOGY, AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK (W.J.B.) AND NATIONAL MUSEUM OF VICTORIA, MELBOURNE, AUSTRALIA (A.M.), 20 APRIL 1967.

RESPONSES OF BLUE-WINGED WARBLERS AND GOLDEN-WINGED WARBLERS TO THEIR OWN AND THE OTHER SPECIES' SONG

Millicent S. Ficken and Robert W. Ficken

Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) are extensively sympatric and hybridize in areas of overlap (Berger, 1958; Short, 1962, 1963). Despite introgression, ethological reproductive isolating mechanisms are operating in this complex (Ficken and Ficken, 1968). Experimental analysis of auditory species discrimination is relevant to an understanding of the reproductive relationships in these since song is probably of some importance in species recognition. Some experiments on auditory species discrimination in Blue-winged Warblers have been conducted by Gill and Lanyon (1964). They found that if Blue-wings were given a choice between Blue-winged primary song and Golden-wing primary song, they responded to their own species' song. We felt that weak responses to the other species song might better be detected by a "no-choice" technique. The purpose of this study was to determine if Blue-wings and Golden-wings would respond to the other species' primary song.

Both species possess a primary and a secondary song. The primary song in both species is given by undisturbed males and predominates early in the nesting cycle, while secondary song is more prevalent after incubation and during and immediately following territorial encounters (Ficken and Ficken, 1966). Thus it is the primary song that is probably important in species recognition. The primary song of the Blue-wing is a short *bee* note followed by a *buzz*, and that of the Golden-wing a *zee* followed by several short *bee* notes. The primary songs of the two species, although distinctive, have some common characteristics (see spectrographs in Ficken and Ficken, 1966). The *bee* notes in the songs of the two species are very similar as are the pitches of the songs and the temporal relationships between notes. The secondary songs are more similar and in both species usually consist of a trill followed by a buzz (Gill and Lanyon, 1964).

METHODS

Studied populations—Experiments were conducted with Golden-winged Warblers on Cheat Mountain (Pocahontas Co.), West Virginia from 19 May to 21 May 1967. Blue-winged Warblers have never been reported breeding in this area, nor have hybrids been reported (Brooks, 1944). An effort was made to test all the singing males that were located on Cheat Mountain.

Blue-winged Warblers were studied in the Catoctin Mountains near Thurmont (Frederick Co.), Maryland on 7 May and 14 and 15 May 1966. Although Golden-wings are found only 20 miles away (Stewart and Robbins, 1958) this was a Blue-wing population. However, during 1958–1965, some hybrids (both "Lawrence's" and "Brewster's" types) were noted in this colony so at least one interspecific mating had probably taken place. In 1966 only phenotypic Blue-wings occurred, but there is the possibility in view of Short's findings (Short, 1962, 1963), that there was introgression in this population.

Males of both species were tested shortly after arrival on the breeding grounds when most had recently acquired mates but nests were probably not yet completed.

Experimental procedure—The experimental procedure was similar to that used by Milligan (1966). First, an initial baseline, which served as a control, was taken. Then the song of the other species was played, another baseline taken, and finally the conspecific song was played. Baselines and playbacks lasted six minutes each. Songs were played at 10 second intervals, with a total of 36 songs of each species. In addition, in experiments with Golden-wings, one minute after cessation of playback of Golden-wing songs, 10 Blue-wing songs were played in an effort to determine if Golden-wings would respond to Blue-wing songs after they had been stimulated by conspecific song. During baselines and playbacks the number of songs given by males and their type (primary or secondary) was noted, as was the location of the male with respect to the speaker. At the time of playback all males were 50 to 100 feet from the speaker.

The stimulus songs were obtained from the Federation of Ontario Naturalists record of warbler songs. Tapes were played at 7.5 i.p.s. with a Uher 4000 S tape recorder. A Nagra DH amplifier-speaker was used. We tried to keep the volume of playback songs similar to that of a bird singing normally.

RESULTS

There were two separate response measures. The number of playbacks spent closer than 30 feet to the speaker, closer than 10 feet and the number of flights over the speaker were tabulated. The category of number of playbacks closer than 30 feet to the speaker also included playbacks closer than 10 feet to the speaker and flights over the speaker, while the number of playbacks closer than 10 feet also included flights over the speaker. The number of playbacks until the first approach to the playback song was also noted. In addition to approach responses, song changes were also noted.

Responses of Blue-winged Warblers—Nine Blue-winged males were tested and seven spent some time closer than 30 feet to the speaker during playback of Golden-wing songs (Table 1). Seven males also responded to Blue-wing primary songs. In addition to the two Blue-wings that responded only to Golden-wing song, one individual responded more strongly to Golden-wing song than to Blue-wing song. All others spent more time closer than 30 feet to the speaker during playback of their own species' song rather than to Golden-wing songs. Totalling the approaches of all males that approached closer than 30 feet, response was significantly stronger to their own primary song than to that of Golden-wings (Using χ^2 tests, $p < 0.001$ for number of playbacks closer than 30 feet and number of playbacks closer than 10 feet). The number of flights over the speaker was similar during playbacks

TABLE 1

APPROACH RESPONSES OF BLUE-WINGED WARBLERS TO PLAYBACK OF GOLDEN-WING SONGS AND THEIR OWN SONGS

	Playback of Golden-wing song				Playback of Blue-wing song			
Male No.	No. of playbacks to first approach	No. of playbacks closer than 30 feet	No. of playbacks closer than 10 feet	No. of flights over	No. of playbacks to first approach	No. of playbacks closer than 30 feet	No. of playbacks closer than 10 feet	No. of flights over
1	4	1	0	0	22	9	8	0
2	22	4	3	1	2	5	0	0
3	4	6	6	0	–	0	0	0
4	–	0	0	0	4	29	12	3
5	2	16	6	3	10	1	1	1
6	8	6	6	0	–	0	0	0
7	–	0	0	0	5	29	25	2
8	12	9	0	0	3	34	11	0
9	1	9	7	1	24	13	11	0
Total	53	51	28	5	70	120	68	6

of both songs, but was too small to test statistically. There was no significant difference ($p > 0.05$) in the number of playbacks until first approach for the two songs.

All songs given by males during the baselines were primary songs. During Golden-wing playback some secondary songs were noted and these were even more frequent during Blue-wing playback (Table 2). There was no change in the total number of songs during the two playbacks as compared to the initial baseline, although there was a significant decline in song following Golden-wing playback ($p < 0.01$).

Responses of Golden-winged Warblers—Three individuals out of the seven tested showed very weak approaches to Blue-wing song (Table 3). However, the approaches were not nearly so marked as during playback of Golden-wing songs to Blue-wings. All seven individuals tested approached the

TABLE 2

NUMBER AND TYPE OF SONGS GIVEN BY MALE BLUE-WINGED WARBLERS DURING BASELINES AND PLAYBACKS

	No. of primary songs	No. of secondary songs	Total songs
First baseline	159	0	159
Playback Golden-wing songs	141	12	153
Second baseline	95	0	95
Playback Blue-wing songs	120	21	141

TABLE 3
APPROACH RESPONSES OF GOLDEN-WINGED WARBLERS TO PLAYBACK OF BLUE-WINGED SONGS AND THEIR OWN SONGS

	Playback of Blue-wing songs				Playback of Golden-wing songs			
Male No.	No. of playbacks to first approach	No. of playbacks closer than 30 feet	No. of playbacks closer than 10 feet	No. of flights over	No. of playbacks to first approach	No. of playbacks closer than 30 feet	No. of playbacks closer than 10 feet	No. of flights over
1	–	0	0	0	2	35	30	14
2	–	0	0	0	2	35	33	16
3	–	0	0	0	3	33	25	20
4	–	0	0	0	2	32	18	7
5	35	2	0	0	8	29	29	6
6	7	5	1	1	6	29	21	20
7	28	2	0	0	2	35	26	2
Totals	70	9	1	1	25	228	182	85

speaker during Golden-wing song playback. No males approached to 30 feet when Blue-wing song was played again after the conspecific song.

Only primary songs were given during both baselines and the playback of Blue-wing song. During Golden-wing playback most of the songs were secondary songs (Table 4). The total number of songs also increased during Golden-wing playback as compared to the baseline ($p < 0.01$) but not during Blue-wing playback ($p > 0.05$).

Comparison of Blue-wing and Golden-wing responses to conspecific song—Golden-wings responded more strongly to playback of their own conspecific songs than did Blue-wings to conspecific song ($p < 0.001$ for number of playbacks closer than 30 feet, $p < 0.01$ for number of playbacks closer than 10 feet, and $p < 0.001$ for number of flights over the speaker). Golden-wings also responded more quickly to conspecific songs than did Blue-wings ($p < 0.001$ for number of playbacks to first approach). Golden-wings gave significantly more secondary songs during playback of conspecific song than did Blue-wings ($p < 0.001$).

TABLE 4
NUMBER AND TYPE OF SONGS GIVEN BY MALE GOLDEN-WINGED WARBLERS DURING BASELINES AND PLAYBACKS

	No. of primary songs	No. of secondary songs	Total no. of songs
First baseline	95	0	95
Playback Blue-wing songs	97	0	97
Second baseline	101	0	101
Playback Golden-wing songs	21	128	151

DISCUSSION

These experiments give some insight into the basis of interspecific song responsiveness in the Blue-wing population. Since males in the Maryland Blue-wing population had not, at least within the last eight years, been exposed to a singing Golden-wing, it seems probable that their responsiveness was not learned but rather had a genetic basis.

Our findings differed from those of Gill and Lanyon (1964) who found that in a choice situation Blue-wings on Long Island did not respond to Golden-wing playback. There are two possible explanations, and the difference in our findings was probably due to a combination of both. Golden-wing contact with Blue-wings on Long Island occurred to a limited extent in the more distant past than in the Maryland colony (e.g. Short, 1963). Although we have no comparative data from our Maryland population, it is probable that introgression there is more marked than the slight introgression Short (1963) found in a Blue-wing population on Long Island. However, it seems unlikely, in view of the history of the Maryland Blue-wing colony, even assuming complete genetic control of song responsiveness, that such a large proportion of the males would be affected by Golden-wing genes for this particular behavior. So while introgression may be partly responsible for their responsiveness to Golden-wing song, it may not be the whole answer. Another reason why we detected responses of Blue-wings to Golden-wing songs to a more marked extent that Gill and Lanyon (1964) is that the no-choice experiment probably detects weak responses more readily than the choice experiment where the bird responds only to the stronger stimulus.

The fact that males in at least some Blue-wing populations are weakly responsive to Golden-wing song may have a bearing on reproductive relationships within this species complex. If females in the population show similar responsiveness, chances of interbreeding would be increased by responsiveness to the other species' song, especially in areas where conspecifics were scarce.

SUMMARY

Blue-winged Warbler males in a population in Maryland, which probably had some introgression of Golden-wing genes, responded weakly but significantly to playback of Golden-wing primary song in a single stimulus test. Golden-winged Warblers, on the other hand, in a population in West Virginia which had probably never been in contact with Blue-winged Warblers showed almost no responsiveness to Blue-wing primary song playback. Each species responded more strongly to playback of its own song. It is suggested that responsiveness to the other species' song probably has at least in part a genetic basis.

ACKNOWLEDGMENTS

This study was supported by National Science Foundation grants GB-3226 and GB-6819. We are grateful to Dr. Douglass H. Morse for his criticisms of the manuscript.

LITERATURE CITED

BERGER, A. J. 1958. The Golden-winged—Blue-winged Warbler complex in Michigan and the Great Lakes area. Jack-Pine Warbler, 36:37–71.

BROOKS, M. 1944. A check-list of West Virginia birds. West Virginia Univ. Agricultural Experiment Station Bull. No. 316.

FICKEN, M. S. AND R. W. FICKEN. 1966. Singing behaviour of Blue-winged and Golden-winged Warblers and their hybrids. Behaviour, 28:149–181.

FICKEN, M. S. AND R. W. FICKEN. 1968. Reproductive isolating mechanisms in the Blue-winged Warbler-Golden-winged Warbler complex. Evolution, 22:166–179.

GILL, F. B. AND W. E. LANYON. 1964. Experiments on species discrimination in Blue-winged Warblers. Auk, 81:53–64.

MILLIGAN, M. 1966. Vocal responses of White-crowned Sparrows to songs of their own and another species. Anim. Behav., 14:356–361.

SHORT, L. L., JR. 1962. The Blue-winged Warbler and the Golden-winged Warbler in central New York. Kingbird, 12:59–67.

SHORT, L. L., JR. 1963. Hybridization in the wood warblers (*Vermivora pinus* and *V. chrysoptera*). Proc. 13th Internatl. Ornithol. Congr., 147–160.

STEWART, R. E. AND C. S. ROBBINS. 1958. Birds of Maryland and the District of Columbia. N. A. Fauna No. 62. Washington, D.C.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF WISCONSIN-MILWAUKEE, MILWAUKEE, WISCONSIN, 6 NOVEMBER 1967.

TERRITORIAL STABILITY IN SHARP-TAILED GROUSE

Roger M. Evans

Return of individual males to the same small "sexual territories" (Nice, 1941) within a lek on successive days of a breeding season has been documented for the Sharp-tailed Grouse (*Pedioecetes phasianellus*) (Grange, 1948) and other closely related lek species (reviewed in Lumsden, 1965). There are fewer reports of individual males utilizing the same territories within a given lek for more than one season. Such a return to the same particular display area implies a high degree of behavioral stability, a condition which, when present, is of relevance to recent suggestions (Wynne-Edwards, 1962; Lumsden, 1965) concerning the possible importance of social organization in the regulation of population density of these species.

In the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*), Copelin (1963) has reported that 15 out of 17 males studied used the same display territories on two successive years, and that some birds also used these same territories during the brief fall display period.

METHODS

Male Sharp-tailed Grouse were trapped on a lek located on untilled pasture land 20 miles southeast of Provost, Alberta, by flushing them into two 3.94 inch mist nets placed along two edges of the area. A numbered aluminum leg band, and a colored neck band made of vinyl plastic and measuring 0.062 × 0.5 × 9 inches, were placed on each trapped male. By fusing one of six different colors of plastic to one end of each neck band, it was possible to provide each male with a different color combination. When in place, the visible ends of the neck bands were approximately one inch long. Ten males, from a total of 20 on the lek, were color marked in the spring of 1959.

Small wooden pegs, placed on the lek in the form of a grid at intervals of 14.3 feet, were used as guides to determine the locations of displaying males. Movements of individual color-marked males were recorded on maps. Points along territory boundaries were determined by the positions taken up by two males when they exhibited threat behavior directed at each other from essentially stationary positions (see Hinde, 1961). A line constituting the outermost margin of all such points for a given male was used to delineate the territory boundary.

Observations were made from a blind set up at the periphery throughout the early morning display periods for a total of 18 days in the spring and fall of 1959 and spring of 1960. The number of points used to plot the spring territories ranged from 51 to 130 in 1959 and 37 to 57 in 1960.

Twenty-six colored boards, measuring 1 inch × 4 inches × 3 feet were distributed over the lek in the spring of 1959. In late May of 1960, these boards, which could have served as territory markers, were displaced laterally, and the subsequent locations of the territories were determined.

RESULTS

Of the 10 males that were color marked in the spring of 1959, five returned to the same lek in the spring of 1960. The other five males were not

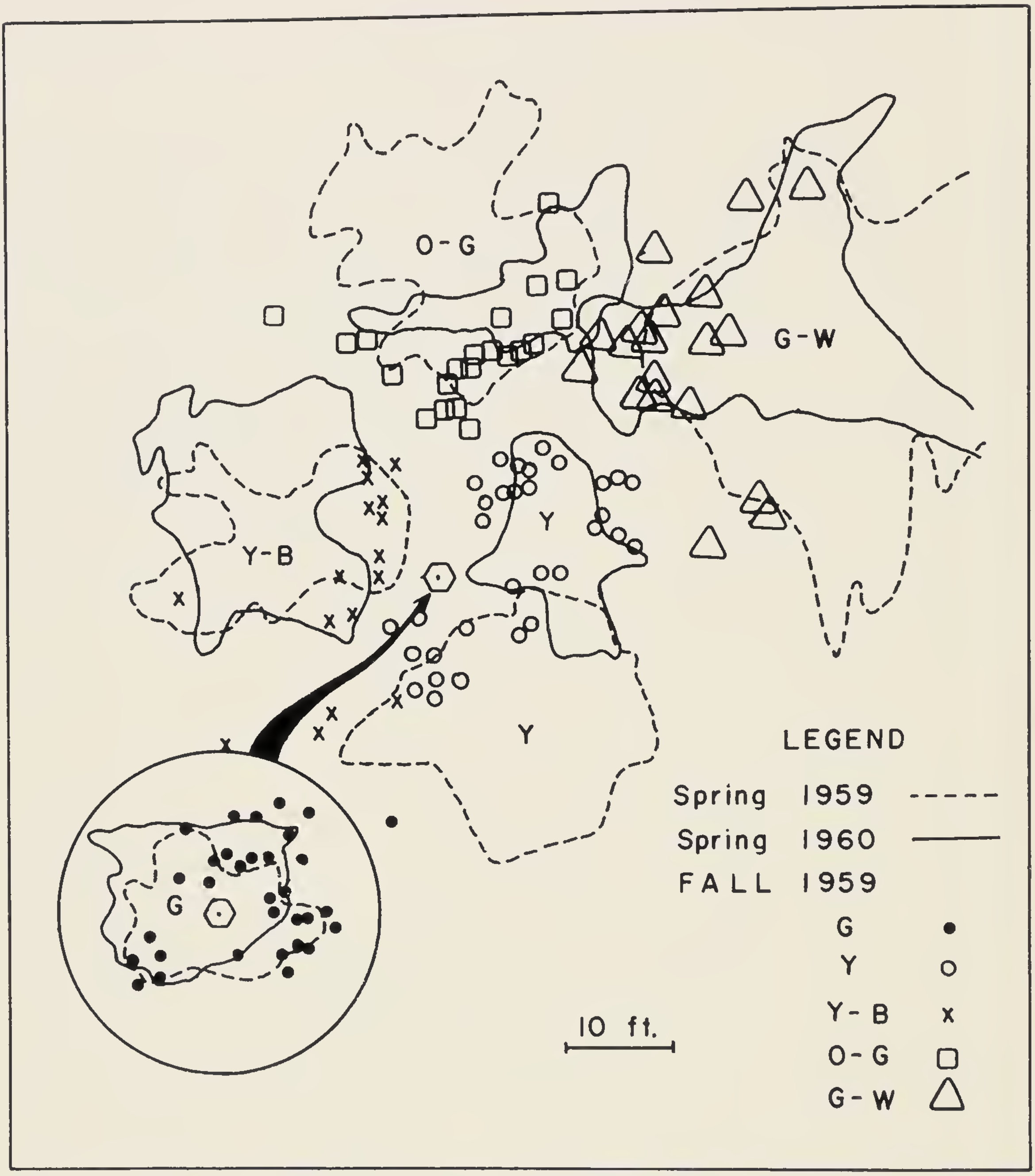


FIG. 1. Territories occupied by five color-marked Sharp-tailed Grouse males on the same lek over two successive years. All territories drawn to the same scale. The arrow indicates the true position of the center of the territory of Male G. Territories were contiguous, each of the five territories shown being surrounded by those of other males (not shown) with the exception of the peripheral portions of the territory of G-W.

seen on any nearby leks in 1960 and so may have suffered over-winter mortality. The territories occupied by the five color-marked males present in the springs of 1959 and 1960 are illustrated by the broken and solid outlines shown in Figure 1. It is evident from Figure 1 that minor variations in the locations of boundaries occurred between years for all males. However, with the exception of Male Y, whose territory shifted approximately 25 feet towards the center of the lek, the positions of the territories, relative to the lek as a whole, were similar in the two years.

The locations of points representing the positions of territorial boundaries in the fall of 1959 are indicated for each of the five males by the various symbols plotted in Figure 1. Although the number of these points was necessarily small relative to the sample sizes obtained in the spring, it is apparent that the males occupied portions of essentially the same territories in both the spring and fall. The data for Male Y indicate that the shift in the territory of this male occurred in part during the fall period.

Displacement of the colored boards was done in late May of 1960, after the above observations were completed. There was no indication that the territories of any color-marked males were altered as a result of this manipulation, which suggests that the colored boards did not constitute the necessary landmarks used by the males in maintaining their territory boundaries.

DISCUSSION

Stability of territories indicates the existence of suitable landmarks that can be used over successive seasons. The lek observed in the present study was located in untilled pasture land which is covered with short tufts of sage interspersed with shallow, narrow depressions apparently denuded by the repeated action of the displaying grouse. Since the displacement of the boards which could have served as artificial landmarks had no effect on the positions of the territories, it is probable that the birds were orienting primarily to the many cues provided by the natural habitat.

It should be emphasized that the stability and permanence of territories described above does not necessarily imply a similar degree of stability on leks of different sizes, or for those located in different types of habitat. For example, Hamerstrom and Hamerstrom (1955) have described an apparent lessening of stable social organization on large leks of the Greater Prairie Chicken (*Tympanuchus cupido*) (see also Grange, 1948; Lumsden, 1965). The territorial permanence observed in the present study cannot therefore be considered typical of all leks. The present results do, however, indicate that a high degree of stability can arise under appropriate conditions of lek size and natural landmarks, and as such provide a basis for comparison with other populations exposed to different conditions of habitat and density.

The lek observed in the present study is apparently an example of what Lumsden (1965) has called the "classical" lek situation, in which the display ground is characterized by a high degree of territorial stability. This author (loc. cit.) has pointed out that the restriction of mating to a limited number of males on such leks tends to decrease the variability of the offspring. In addition, the quality, and hence survival of offspring may possibly be influenced "through selection of certain cocks for mating. . . " (Lumsden, 1965:65). The long-term maintenance of territorial tenure observed in the present study indicates that the territorial stability characteristic of the "classical" lek situation may in some instances extend beyond a single season. Such an extension of territorial stability introduces a strong conservative influence in the social behavior of this species that presumably would act to further reduce the variability of offspring between successive years. Similarly, it would tend to enhance any effects on survival that the highly selective mating system of the "classical" lek might entail.

SUMMARY

The territories of color-marked male Sharp-tailed Grouse were determined by mapping the locations of threats directed across territory boundaries. Of 10 males banded in the spring of 1959, five returned to the same lek the following fall and spring. The positions of territories of these males were essentially the same in both the spring and fall of 1959 and, with one exception, again in the spring of 1960. This stability, which apparently depended on the year to year use of natural landmarks, indicates a conservative tendency in the social behavior of this species that may influence genetic variability and survival.

ACKNOWLEDGMENTS

I would like to thank Dr. V. Lewin for his advise throughout the course of this study, a portion of which was included in a M.Sc. thesis at the University of Alberta. The assistance of R. Webb in various aspects of the field work is gratefully acknowledged. The study was financed by the National Research Council (Ottawa), the University of Alberta, and the Alberta Game Branch.

LITERATURE CITED

Copelin, F. F. 1963. The Lesser Prairie Chicken in Oklahoma. Oklahoma Wildl. Conserv. Dept. Tech. Bull. 6.

Grange, W. B. 1948. Wisconsin grouse problems. Publ. 328, Wisconsin Conserv. Dept., Madison.

Hamerstrom, F. N., and F. Hamerstrom. 1955. Population density and behavior in Wisconsin Prairie Chickens (*Tympanuchus cupido pinnatus*). Proc. XI Congr. Internatl. Ornithol., Basel. 1954., pp. 459–466.

Hinde, R. A. 1961. Behavior, pp. 373–411. *In* A. J. Marshall, Ed., Biology and comparative physiology of birds, Vol. 2. Academic Press, New York.

Lumsden, H. G. 1965. Displays of the Sharptail Grouse. Ontario Dept. Lands and Forests Tech. Series Report No. 66.

Nice, M. M. 1941. The role of territory in bird life. Amer. Midl. Nat., 26:441–487.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd. Edinburgh.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ALBERTA (PRESENT ADDRESS: DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MANITOBA, WINNIPEG, CANADA)
21 APRIL 1967.

HATCHING BEHAVIOR OF THE BOBWHITE

ROBERT A. JOHNSON

THE study of embryonic behavior may contribute greatly to our knowledge of the ontogenetic mechanisms of behavioral development. Synchronization in hatching among certain gallinaceous birds appears to offer a good subject for such study. Vince (1964, 1966) who cites related observations by others, appears to be the first investigator to study the hatching process of the Bobwhite (*Colinus virginianus*) as a coordinated behavioral sequence influenced by environmental factors. She gave special attention to recording the nature of vocal and movement communication and demonstrated that eggs which started incubation 24 hours later than their companions showed a strong tendency to synchronize at hatching time.

The present study was designed to assess the degree of synchronization of hatching of the Bobwhite and to study vocal and movement behavior of incubating embryos as agents in mediating this prehatching synchronization. After the 1964 report by Vince, the plan was enlarged to include observations of the movements of embryos through windows in the shell; and also, to test eggs delayed in incubation 48 hours after that of their companions. The terms "pipping stage," "clicking stage," and "chipping stage" used to denote successive behavioral phases of the total hatching process differ from those used by Vince only for the last phase. In this study the term "chipping stage" is used since Vince's term "hatching stage" seems more appropriately applied to the total process and "chipping stage" denotes that last phase of hatching beginning with the onset of the "surge-pip" behavior resulting in the removal of the shell fragments while turning in the egg and final emergence.

METHODS

Eggs from breeding birds housed in outdoor cages were incubated under bantam hens for 21 or 22 days until the advanced eggs (those placed in incubation one or two days before their delayed companions) began to pip. At this stage all eggs were transferred to the observation incubator operated at a temperature of 101–102 F (except one test observed at 95–98 F). Twelve hatchings were recorded during the seasons of 1965 and 1966 as outlined in Table 1. Segregated eggs were placed in small padded trays apart from larger trays containing clutches (Fig. 1). Successive hatchings were kept under continuous observation throughout day and night. A stop watch was used to record intervals between rhythmic pipping movements of the "chipping stage" (behavior consisting of successive "surge-pip" movements). The behavioral movements of the prehatched bird during the chipping movements phase of hatching were studied as follows: A. After these movements started,

TABLE 1
INCUBATION PLAN AND HATCHING DATA

Tests		Eggs pipped	Test plan	Number hatched	Stage at death	Average incubation time	Spread in hours
1965	1966						
1		5	all in clutch	5		561.6	2
1a		6	clutch	5		577.0	3
	1b	8	clutch	6	pipped	601.0	6
	1c	5	clutch	3	clicking	585.0	1
2		6	single egg segregated	3	clicking		22
	2a	5	single egg segregated	2	clicking	600.2	26.5
3		12	in pairs, one	3 early	clicking	572.7	3.5
			24 hours delayed*	6 delayed		551.8	3.1
4		24	in pairs, one	10 early		558.8	30
			48 hours delayed*	8 delayed#		528.8	43
		5	control group in clutch delayed date	5		561.5	2
5		11	one clutch				
			5 advanced	5 early		571.8	3.7
			6 delayed 48 hours	5 delayed		524.3	0.5
	5a	20	one clutch				
			9 early	7 early			1.0
			11 delayed 48 hours	11 delayed			6.8
	5b	16	one clutch				
			5 early			585.5	1.0
			11 delayed (temp. 95–98 F) 48 hours			587.0	3.3

* Eggs started incubation 24 or 48 hours later than their "early" companions.
\# *T* is significant beyond 0.01 level in Wilcoxon matched-pairs signed rank test.

parts of the shell around the beak and head were removed to facilitate observations of the head movements and responses (Craig, 1912); B., egg caps were detached to be set out slightly from the main body of the egg where they were secured in place by narrow strips of tape in a manner to allow the rotating embryo freedom to continue without having the egg tooth contact the shell or shell membrane: and C., using preparations described above, four eggs were further treated by extending first one and then both feet

FIG. 1. Showing observation incubator with eggs hatched in a clutch in the large tray, and eggs in pairs (one advanced and one delayed) in each small tray.

through a window in the small end of the shell. Thus, analysis of the rhythmic movements of feet, body and head were observed.

RESULTS

In tests 1, 1*a*, 1*b*, and 1*c* where eggs were hatched in clutches simulating natural conditions, the average incubation time for the four clutches varied from 561 hours to 601 hours, but the spread between the first and last egg to hatch of any one clutch was only six hours, usually much less (Table 1). This high degree of synchronization is a result agreeing with that reported by Vince.

In tests 2 and 2*a* where eggs were hatched in isolation after pipping, the data are too meager to be more than suggestive. The few chicks that did hatch in these tests came out over a long period of time (22 hours to 26.5 hours). The number of deaths in the pipped and clicking stages, after isolation in the early pipped stage, was high. This tendency continued among the advanced eggs matched with 24 hour delayed eggs. Vince apparently did not get this result. She, referring to eggs kept in isolation says (1966), "these eggs all hatched normally but, if the embryos stimulate each other the development of isolated eggs could differ from that of eggs hatched in clutches."

In test 3 where 12 eggs isolated in pairs with one of each pair 24 hours delayed at the beginning of incubation, half of the early eggs died in the clicking stage. Those that hatched required an average of 572.7 hours incubation time whereas the six delayed companions, one of each pair, all hatched in an average of 551.8 hours, and the average of the hatching time for the delayed eggs was only 3.1 hours behind that of the early companions.

In test 4 where 29 eggs were placed in the incubator, 24 were arranged in isolated pairs so that one of each pair started incubation 48 hours later than its companion. Five eggs started on the delayed date were retained together in a clutch as a control group. The hatching data show synchronization with the delayed eggs of isolated pairs brought forward in their hatching time. Results show 528.8 hours average for the delayed eggs compared to 558.8 hours for the advanced companions; whereas, the control clutch of delayed eggs was comparable in total hatching time to the average for the advance members of the isolated pairs. The Wilcoxon matched-pairs signed rank test shows the delayed birds have a speeded incubation period. The results gave * T significant beyond 0.01 level. Applying the T-test to the same data, the result * T is significant beyond the 0.001 level.

In tests 5 and 5*a*, eggs were hatched in clutches with a part of each clutch delayed 48 hours. A marked degree of advancement in the hatching time for the delayed eggs is shown in each test. In test 5b where 16 pipped eggs were incubated at a temperature of 95–98 F, eleven of which were 48 hours delayed and kept continuously with the five advanced companions in one clutch no synchronization occurred between the early and the late ones. But those of each incubation date synchronized within their group. The average for the early was 585.5 hours and for the delayed 587.0 hours.

DISCUSSION

In all eggs placed in incubation either 24 or 48 hours after their companions and transferred from bantams to an observation incubator operated at 101–102 F, the delayed eggs showed a tendency to advance their hatching and to synchronize with their earlier companions. Vince (1964) obtained this result for eggs delayed 24 hours but she did not report trials with the longer 48 hour delay period. Records of the time spent in the three hatching stages—pipping, clicking, and chipping, indicate that the greatest degree of stimulation of delayed embryos came during the clicking of their early companions. Vince (1966) has shown that there is vocal sound and movement with rhythmic sequence during all stages of hatching and that its expression is strong and rhythmically regular in the last two phases of hatching.

The third behavioral phase in hatching, which I have called "chipping stage." is made up of a series of spasmodic muscular movements involving the leg, trunk, and head muscles. Each "surge-pip" begins with the leg push and progresses through the trunk region ending with a strong downward tipping of the head after the upper thrust which pushes the egg tooth through the shell. This movement, like clicking, is rhythmic in operation. Each new "surge-pip"

TABLE 2

HATCHING DATA (SAMPLE)

Egg mark	Incubation status	Hours pipped	Hours clicking	Minutes chipping	Number of rotations in shell	Intervals in seconds between "surge-pip" movements
A^2	advanced	33	12.25	17/60	2.25	7-6-7-7-7-7-7-7-7-7
N^2	delayed	*		25/60	1.0	5-4-7-4-5-5-6-6-6-7-7-5-5-5-5-5-5-5-5-7-5-6
K^2	delayed	13	19	20/60	1.75	4-4-4-4-5-5-5
G^2	delayed	9	2.5	15/60	1.50	8-6-7-9-6-6-1-9-8-7
Q	delayed		15.0	33/60	3.50	7-15-10-13-5-5-5-6-6-5
L^2	delayed		17.0	30/60	1.75	8-6-7-8-4-8-3-5-7-3-6-7-6-7-6-7
O^2	delayed			20/60	2.50	8-8-8-8-7-8-8-4
H^2	advanced	27	11.0			6-6-7-67-7-8-6-5
D	advanced	20	17.0	20/60	3.50	
E	advanced	20	9.6	20/60	2.50	
H^3	delayed	8	10.75	30/60	6.50	
E^2	delayed	16	11.0	45/60	6.40	
G	delayed	29	11.50	27/60	2.50	
I	advanced	15	9.0	18/60	3.50	

* Data not recorded.

movement comes generally after six, seven, or eight second intervals (Table 2).

The final triggering of the "surge-pip" movements ending the chipping stage appears to be the infectious factor in starting the same advancement in adjacent eggs. Thus, we may hypothesize that there are two levels of stimulation of delayed embryos influenced through sound and movement communication and that activity characteristic of the clicking stage stimulates delayed embryos to act earlier than they would otherwise, and that the first embryo of the clutch which begins to "surge-pip," jarring its companions, stimulates them to begin similar action. Embryos may have been in the clicking stage for hours, yet when one in a clutch of eggs begins the "surge-pip" effort, they usually all soon begin, and then emerge within 20 to 30 minutes.

Clicking begins slowly and works up to a crescendo. Vince (1966) has shown that it develops independent of lung ventilation and breathing. One might expect a time requirement for its maturation, yet some of the delayed eggs in the 48 hour delay test completed all three of the hatching phases in about 4 hours. Other advanced eggs remained in the clicking stage for 26 hours.

In test 5*b* where there was no ill effect on the quantity of hatch at the lowered temperature, and no synchronization between early and late eggs we may find a suggestion for exploring operational thresholds of stimulation

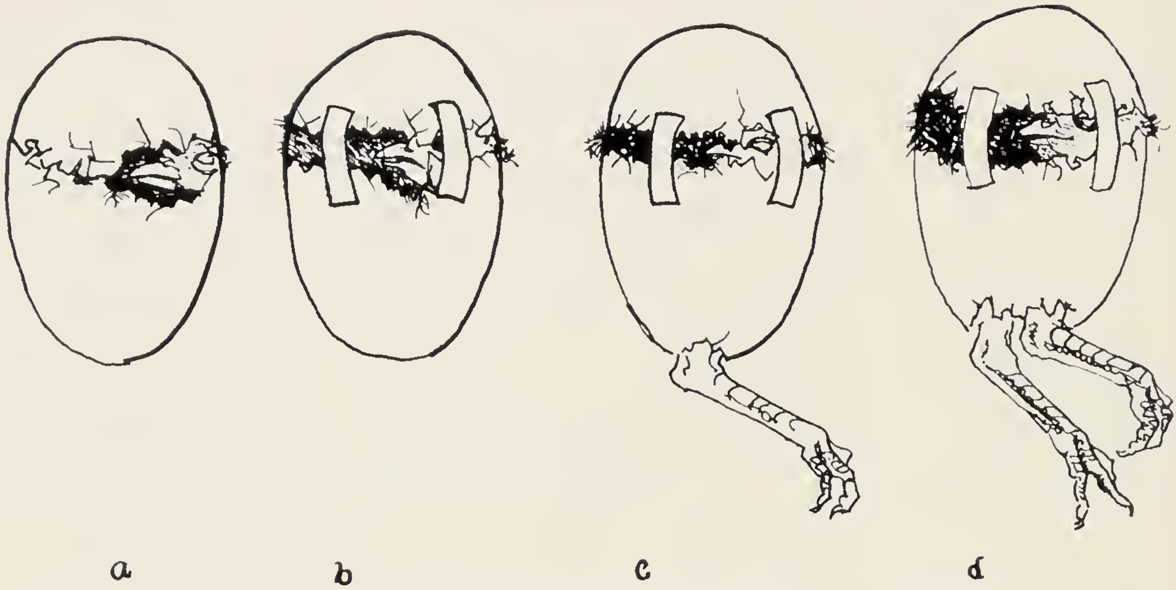


FIG. 2. Showing method of preparing eggs for observation of prehatching behavior.

factors; but, further investigation of the role of temperature levels is needed.

The feet and neck of the quail chick are proportionally longer than those of domestic chickens and occupy relatively different positions within the shell. In the Bobwhite chick the left leg lies with the heel against the small end of the shell but the long tarso-metatarsus extends ventrally and upward to bring the toes near the pipping location. The right foot lies more to one side with the toes folded back of the wing. Observations made through a shell opening made by extending the egg cap (Fig. 2b), indicated at first, that the left leg and foot might be responsible for the chicks rotary movement within the shell. But, when the small end of the shell was removed and the left leg extended outside the egg (Fig. 2c) the "surge-pip" continued as before, although at first the rotary progress stopped. After a few minutes that progress was resumed at a slower than normal rate. Following this discovery the right foot was also extended from the shell (Fig. 2d) which did not effect further change in behavior or progress. With the cap of the shell extended so that the egg tooth made no contact with the shell, the entire rhythmic movement of the "surge-pip" action became clear. Each effort began with a strong push on the left heel and foot attended by a weak scratching movement with the right foot. Then trunk muscles expanded with inhalation which exerted strong pressure on the upper curvature of the shell in the region of the lower cervicals. While this pressure was being applied the head made a strong tip-up movement causing the tooth to penetrate the shell. Then suddenly, all pressure was relaxed except the contact of the skull against the shell. The last component of this coordinated "surge-pip" action was a deep strong depressing movement of the beak which because of contact of the top of the head and the hatching muscle with the shell (Fisher, 1958) gripped the shell sufficiently to rotate it a small distance in a counter-clockwise direction. Thus, when the next "surge-pip" seizure occurred, 6 to 8 seconds later, a new advanced location on the shell was pierced. Any slight amount of drying of the pierced membrane caused it to shrink, which slowed or stopped the rotary advancement of the hatching process. In these cases, "surge-pip" movements continued for some time although death in the shell was imminent. Under normal conditions strong embryos leave unpierced spaces in the shell membrane as they progress with one "surge-pip" movement after another, and these may require from three to six rotations within the shell to cut the egg cap free and allow the chick to emerge. Ordinarily, two or three times around frees the cap and allows the bird's head to extend free. As soon as the neck straightens from its coiled position within the egg all "surge-pip" movements cease.

It may be significant to note that these "surge-pip" efforts are actually a series of coordinated movements which originate in the caudal region of the embryo and advance to the head region. This appears to be a development which was not seen by Kuo (1932) for domestic chickens. He states, "The development of embryonic behavior in the chick begins from the head and progresses caudal. Every embryonic movement, after its first appearance, tends to persist throughout embryonic life or even after hatching, unless it is interfered with, or modified by, structural or environmental changes."

SUMMARY

Eggs from Bobwhite in incubation tests at 101–102 F indicated synchronization at hatching when placed in clutches and/or segregated pairs with 24 or 48 hour delay periods for matched eggs. One test at temperature 95–98 F and 48 hour delay period failed to show these results. Statistical treatment in the case of test number 4 (matched pairs with one 48 hours delayed) is given and showed *T* significant beyond 0.01 level in the Wilcoxon matched-pairs signed rank test.

The behavioral characteristics of three phases of hatching are discussed and the term "chipping stage" is used to denote the last of these successive stages. The term "surge-pip" is given to the rhythmic behavior repeated during the chipping stage. Elements of this behavior are discussed in relation to the anatomical parts involved and the events leading to the chick's emergence.

ACKNOWLEDGMENTS

Appreciation is due Dr. D. S. Farner for valuable suggestions in connection with the manuscript. My daughter, Elizabeth, assisted with recording data and made the sketches in Figure 2. Editorial suggestions for revision are gratefully acknowledged.

LITERATURE CITED

Craig, W. 1912. Behavior of the young bird in breaking out of the shell. J. Anim. Behav., 2:296–298.

Fisher, H. I. 1958. "The hatching muscle" in the chick. Auk, 75:391–399.

KUO, Z. Y. 1932. Ontogeny of embryonic behavior in Aves. The chronology and general nature of the behavior of the chick. J. Exp. Zool., 61:395–430.

VINCE, M. A. 1964. Social facilitation of hatching in the bobwhite quail. Anim. Behav., 12:531–534.

VINCE, M. A. 1966. Potential stimulation produced by avian embryos. Anim. Behav., 14:34–40.

R.R. 11, BOX 188, BLOOMINGTON, INDIANA, 16 JANUARY 1967.

JOSSELYN VAN TYNE AWARD

A sum of $1,194.82 is available in the Josselyn Van Tyne Memorial Fund for research grants in 1969. Of this amount, $185.00 is earmarked for research in systematics. Any student of birds is invited to apply for research grants. Young men and women just starting their careers or others not eligible for government grants are encouraged to apply.

Applicants should prepare a brief but comprehensive description of their research projects specifying the objectives and proposed plans of procedure. Particulars of the type and amount of financial assistance needed must be included. A brief statement of the applicant's ornithological background should be appended. Letters of recommendation from one or more recognized ornithologists would be helpful.

Applications should be submitted not later than 1 April 1969 to the Chairman of the A.O.U. Research Committee, Dr. Richard C. Banks, Bird and Mammal Laboratories, U. S. National Museum, Washington, D. C. 20560.

BEHAVIORAL ONTOGENY OF THE MOCKINGBIRD

ROBERT H. HORWICH

THE reconstruction of behavioral phylogenies stems mainly from comparisons among existing animals since behavior leaves almost no fossil record. These comparisons seldom include ontogenetic development. This paper describes the development of behavior in the Mockingbird (*Mimus polyglottos*) and incorporates this ontogeny into Nice's (1962) useful scheme of five stages based on the age of first appearance of behavior patterns and on dominant behaviors. The Mockingbird ontogeny is also compared with Rand's (1941) study of the Curve-billed Thrasher (*Toxostoma curvirostre*).

METHODS

Observations were made of the behavior of 38 captive Mockingbirds (35 obtained as nestlings and three as fledglings) raised in laboratory cages and fed an artificial mixed diet (Horwich, 1965). Some notes on wild nestlings were also kept. A chronological ontogeny was developed on the basis of birds of known ages. Other birds were aged according to their feather development (Horwich, 1966). In the compilation, the day on which a behavior was first or last seen represents the day when at least one individual was seen to have performed or have ceased to perform the action.

RESULTS

Begging—(see Horwich, 1965)—A change in begging behavior takes place from day one to day 12. This transition in the development is from an initial, unsteady, upward stretching of the whole body on the tarsometatarsus (day 1) to a position in which the front of the body is lowered at an angle of 45° to the horizontal, and the flexed legs are planted firmly on the ground (day 12). A few wing movements and a tail component occur within this developmental transition of behaviors. In addition, on the ninth day, a co-ordinated foot component is integrated into the sequence. In this movement the weight of the body shifts, so that the young bird moves first one foot and then the other, usually taking four to eight steps in the same position.

Three vocalizations accompany begging. After day three low intensity "contentment" cries are given after feeding, and muted begging vocalizations are emitted. On day seven, the latter single syllabled call becomes louder, harsher, and more distinct. Gage (1961) noted this change in the voice two to three days before fledging with the possible function of aiding the parents in locating the young.

The stimuli that elicit begging change gradually. On day one a tapping on the nest elicits a stretching of the neck upwards and gaping, which is maintained for only a few seconds. Then there occurs a refractory period during which the response cannot be elicited for some seconds. By the fourth day tapping also elicits a vocalization. This total begging response continues to the sixth or seventh day.

On the sixth to eighth days, sleeping captive birds respond to tapping; however, if their eyes were open they responded to the sight of my hand. In the wild, young of this age may initially respond to the tapping by raising up and gaping without vocalizations. Then upon further, rougher vibrations and/or the sight of an intruder (human) they will assume the crouching posture described below.

This suppression of begging vocalizations in a strange situation was also shown when three individuals were taken from the nest at nine days. They continually crouched and had to be initially force-fed by inserting food into the closed beak with a forceps, after which they would swallow the food. After a number of feedings in this manner they began to beg by gaping only; the begging vocalizations and the other components were not present until a day later.

By the fourteenth day sight is the most important stimulus to elicit begging by the fledglings and they now orient to the human feeder.

Wing-flashing—(see Horwich, 1965)—Wing-flashing, the jerky extension of both wings dorso-laterally in hitches, first appears usually on day 10 or 11.

Fear crouching and escape—On about the seventh day the young birds no longer beg when the nest is tapped. Instead, they withdraw all parts of their body, pull their head within their shoulders and remain crouched and quiet. On day 12 a tendency to run away in similar fear situations develops and this appears definitely on day 13, fledging day. Occasionally escape was noted on day 12 when I attempted to take nests in the field. These individuals crouched at first but upon further disturbance, some of the birds hopped out of the nest and attempted to escape capture by hopping away.

Defecation—In a three-day old chick, defecation consists of turning the body around and moving it backwards, usually to the edge of the nest. Then it wiggles the tail rapidly from side to side, elevating the cloaca, and ejecting a fecal sac over the nest lip. This pattern wanes by day 16, by which time only tail wiggling and cloacal elevation still occur with defecation. On day 17 some tail wiggling occurs but it was also on this day that the defecating pattern of the juvenile and adult first appears: lowering of the body (usually on a perch), opening of the ventral feather tracts, defecating, closing the feathers, and rising to the normal perching position. In all cases past day eight, when the captive young were precociously out of the nest, the nestling defecation pattern was seen, independent of the nest stimulus.

Stretching—Three types of stretching appear on day nine and persist thereafter. The leg-stretch consists of extending both legs full length almost vertically by pushing them against the perch. This extension pushes the body up and causes it to assume a slanted position with the head lower than the tail. A second stretch which usually precedes the first, is the backward and sideward stretching of the wing and leg on the same side of the body. In performing this movement the primaries and secondaries of the wing are extended and spread. The tail is often twisted slightly in the direction of the spread wing, and it is also spread. Although the former two movements are usually done together, sometimes the order is reversed and sometimes either is done without the other. A third stretch consists of raising both wings up and back to a 90° angle with the horizontal and then lowering them again at about the same rate.

Hopping—On day eight captive birds first hopped to the rim of and often outside of the laboratory nest. Such "premature fledging" appears to be an artifact of laboratory conditions. Since it occurred in the morning, such "fledging" was probably due to the birds not having been fed early enough.

The characteristic walking of the adults probably occurs at about two weeks after fledging, but my records are incomplete. Mockingbirds conform to the ontogenetical pattern of hopping first and later developing the adult walk (Daanje, 1950).

Preening—The first motion thought to be preening occurs on day one: uncoordinated movement of the bill about the lower breast. By day three actual breast-preening does occur. The femoral tract is the next area in which preening is noticed; these two regions are the first to develop feathers. On day seven preening on top of the wings occurs. By day 10 direct preening of the underwing (inserting the bill under the wing from the anterior end), and indirect preening (inserting the bill under the wing from the posterior border) appear. Preening of the uropygial region also appears at this time.

Pecking and paper-tearing—Paper-tearing consists of pecking a hole in the newspaper lining the cage floor and pulling a strip of paper from this hole or other frayed paper edges. Often the bird then carries the strip in its bill. Both pecking and paper-tearing occur by day 13, and the pecks are first oriented at small moving objects or small specks on the cage floor. In the case of one male, paper-tearing increased in March at age nine months. This activity is later part of nest-building. The paper strips were used as nest lining materials by both sexes in captivity (Horwich, MS).

Head-scratching—Indirect scratching of the posterior portion of the head is first observed on the ninth day. Because of the balance involved, this action necessitates a well co-ordinated neuro-muscular system. One case of direct head-scratching was noted, but in this case I believe the bird had a vitamin deficiency. It was unable to maintain its balance well even on two feet. In this one instance the wing was lowered even though the bird scratched directly. Hailman (1960*a*) also observed a fledgling Mockingbird to scratch directly as well as indirectly. In both of these observations the scratching seemed to cause the bird to be off balance. In light of the rarity of these direct scratches I would accept his observation as being an abnormal occurrence rather than any developmental transition.

Bathing—Bathing is often preceded by a partial or full bathing sequence performed before entering the water. Bathing movements superficially resemble the begging of the fledgling. The bird assumes an angle of 45° with the horizontal with its breast and head lower than its posterior end. It then flips its wings out and up, slightly out of phase with each other, in a very agitated manner, a movement that flips water over its body. It continues this motion as it alternately raises and lowers its head and body in and out of the water. When the head and body are out of the water, the bird flips its wings rapidly, and alternately rolls its body and ruffles its contour feathers. The rolling effect seems to be produced by the alternating wing flipping. After bathing the bird goes through a sequence of drying movements. These incorporate many of the same bathing movements without the forward bending of the head and body. In addition, the feathers are ruffled and the whole body is shaken. The wings are usually drooped during this ruffling. Often the bird flutters its wings synchronously at an angle below the horizonal and intermittently preens under them directly. The fluttering consist of spreading the primaries and sometimes the secondaries and extending the manus. The fluttering then takes place while the feathers are half spread. The tail is also spread and it seems to vibrate as the wings are fluttered and as the body rolls. The head may be rubbed on a branch and the breast is preened. The whole body seems to move at once with the wings alternating to give the ruffling and rolling effect. Sometimes after the shaking of the body the bird wags its tail rapidly from side to side on the horizontal.

The whole bathing and drying sequence was first seen on day 11, when the birds were first given a large water dish. In nature this behavior would probably only occur before fledging in the context of rain bathing although I have never seen rain bathing in Mockingbirds. A sequence similar to drying occurs following close contact between two individuals (Horwich, MS).

Song—A subsong which consisted of a low intensity, disorganized, continuous sound (often sung with the bill closed) was first heard on day 27. On day 48 a song, still considered to be a subsong, was given with the mouth open. These vocalizations became much louder around day 65 and approached the loud "surety" of the true song on day 80. One bird which was caught as a fledgling began singing but stopped between 90 to 100 days of age, possibly due to the loud singing of the other remaining male. He was not heard again until six months later (in February, 1964) when he resumed singing a true song.

Socialization—At about two weeks after fledging the young birds may show a tendency to rush at and chase other Mockingbirds or other species of birds. Two birds at this age showed what might have been the precursor of the "hostile dance" (see Hailman, 1960*b*). First one hopped toward the second who hopped toward the first and the first retreated from the second. Agonistic behavior gradually increases until day 42 when chasing may become so intense that the birds have to be separated. In one case in which two siblings were left together for 45 days, one was found dead in the cage and was believed killed by the other. A few days after this, the remaining bird began to sing.

DISCUSSION

Nice (1962) has proposed a series of ontogenetic periods which standardize the dimension of time for comparisons among species. As the developmental histories of more species are developed and fit into this basic series of behavioral age classes, a phylogenetic classification can be based on the characters of seven age groups instead of the adult animal alone. This will give additional characters which are not now used in the comparison of species (i.e. relative rates of behavioral development, correlations of structural and behavioral developments, relations of precursors of behaviors, etc.).

The behavioral patterns of the Mockingbird fit quite well into Nice's categories, although the Mockingbird differs in having a slightly slower rate of development than the Song Sparrow (*Melospiza melodia*) which served as the basis for these categories.

The following list gives a comparison of the behavioral development of the Mockingbird and the Curve-billed Thrasher (adapted from Rand, 1941) using Nice's system of behavioral age classes. (Numbers in parentheses refer to the age in days when the behavior was first noted; (h) means at hatching; (R) refers to additional observations of Ricklefs (1966); (–) means the behavior possibly occurred earlier.)

I Post-embryonic Period

Mockingbird—(0–4 days)—Nestling begging: neck and body extension, gaping (h), wings extended out and down at the sides (1); soft vocalizations beginning (4); begging response to tapping on the nest (0–5); eyes just begin to open; low intensity contentment calls; nestling defecation (h); preening of the ventral tracts; embryo resting position in the nest (h).

Thrasher—(0–4 days)—Begging by standing on the belly and feet with its wings directed out and down (4) and gaping; start to stand on the tarsi; embryo resting position (h).

II Preliminary Period

Mockingbird—(5–6 days)—Preening of the ventral tracts with initiation of femoral tract preening (3); eyes open; standing on tarsi (5).

Thrasher—(5–6 days)—Eyes open; stand on tarsi (4); head drawn in to rest on nest; wings aid in righting (5); freezing (5).

III Transition Period

Mockingbird—(7–9 days)—Maturation of the begging wing movements: fluttering wings (7); begging in response to a visual stimulus (6–8); change to a harsher begging cry (7); fear crouching (7); stretching (9); wing-flicking; scratching (9); tail component in begging; hopping; alarm chips (7); perching; fanning wings (flight maturation) (7).

Thrasher—(7–13 days)—Eyes wide open; hopping (11); some escape; absence of random movement (7); squealing injury cry (10); stretching (9-R); scratching (22 R); fanning wings (9-R); alarm chip (18 R).

IV Locomotory Period

Mockingbird—(10–17 days)—Landing (15?); perching (8–10); flying (15); sleeping with bill in scapulars (13–14); completes preening; fledgling begging: bowing (12); orient to feeder (14); beg to siblings (14); tail-flicking; wing-flashing (10–11); escape (12); scream (13); flight; pecking (13); paper tearing (13); adult defecation (17); food capture (13); bathing (11–); drinking (11–); intraspecific pecking; landing on others (19?); leaving nest (11–13); bill wiping (13).

Thrasher—(14–20 days)—Escape (12–15); shrinking (17); fits of wildness (18R); flight (19); landing (awkward 14–18) (24–25); walking (14–18); perching (16); exploratory pecking (19); tail flicking; digging (19); pick up food (21); preening; stretching; sleeping with bill in scapulars (18–19); bill wiping (16 R); juvenile defense; leave nest (14–18); orient to feeder (15R); snake display (17–18); kuks.

V Socialization Period

Mockingbird—(18–30$^+$ days)—Self-feeding; dependent on adult (13–37); beg to each other (22); subsong (27); indications of aggression (15$^+$); chasing (25); flight perfection; walking (26–27?).

Thrasher—(21–40 days)—Self-feeding; singing (21, 18R); sun bathing (21); flight perfection; dig holes; no actual aggressive behavior for the first 10 weeks.

VI Juvenile Period

Mockingbird—(40-? days)—No data on precocial sexual behavior; true song (80); completely independent of parental care; sunning (late).

Thrasher—(70? days)—Mobbing (89–92).

VII Adult Period

Mockingbird—(270 + days)—Nest building; aggression; sexual activity; etc.

The first two chronological categories are similar in the two mimids but during the Transition Period at about seven days, the thrasher's relative rate of behavioral development becomes slower. The Mockingbird is much more precocial in the development of the preening movements, starting as early as three days to preen its ventral tract. There was no mention of any maintenance activities in the thrasher (Rand, 1941) until late in the Locomotory Period at which time preening, stretching, and bill wiping occurred.

The feather development is also slower in the Curve-billed Thrasher. All locomotory activities were concentrated within about three days before and after fledging in the mockingbird but in the thrasher these activities were more dispersed. For example, in the thrasher, hopping on the nest lip was seen at 11 days but flight was not really perfected until day 25, although it did occur by day 18 or 19. As locomotion improved in the thrasher it developed pecking and digging movements. This was much later than in the Mockingbird, but in both it occurred at about the time of fledging or a little after. Digging may show some correlation with the bill development. Independence and self-feeding also occurred later in the thrasher as did the "snake display," a probable homolog of wing-flashing. In addition, the the thrashers showed no actual aggressive behavior for the first 10 weeks whereas Mockingbirds show indications of agonistic behaviors during the Socialization Period.

SUMMARY

The behavioral development of the Mockingbird is established from observations of 38 young birds. Each behavior is described including its modifications with aging, and the initiations and cessations of the behavior are noted. Using the age classification periods and criteria of Nice, an effort was made to compare two related species; the Mockingbird and the Curve-billed Thrasher. This comparison shows a general slower developmental rate in the Curve-billed Thrasher after seven days of age relative to that of the Mockingbird.

ACKNOWLEDGMENTS

I am grateful to Drs. Robert W. Ficken, Wolfgang Schleidt, Douglass Morse, and Jack Hailman for their corrections of the manuscript and to Susan Horwich for her editing and typing of the manuscript. This study was financed by Frank M. Chapman Fund of the American Museum of Natural History.

LITERATURE CITED

Daanje, A. 1950. On locomotory movements in birds and the intention movements derived from them. Behaviour, 3:48–98.

Gage, G. 1961. A pair of Mockingbirds at Clemson. Chat, 25:47–50.

Hailman, J. P. 1960*a*. Direct and indirect scratching by a fledged Mockingbird *Mimus polyglottos*. Ibis, 102:129–131.

Hailman, J. P. 1960*b*. Hostile dancing and fall territory of a color-banded Mockingbird. Condor, 62:464–468.

Horwich, R. H. 1965. An ontogeny of wing-flashing in the Mockingbird with reference to other behaviors. Wilson Bull., 77:264–281.

Horwich, R. H. 1966. Feather development as a means of aging young Mockingbirds (*Mimus polyglottos*). Bird-Banding, 37:257–267.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York, 8:1–211.

RAND, A. L. 1941. Development and enemy recognition of the Curve-billed Thrasher, *Toxostoma curvirostre.* Bull. Amer. Mus. Nat. Hist., 78:213–242.

RICKLEFS, R. E. 1966. Behavior of young Cactus Wrens and Curve-billed Thrashers. Wilson Bull., 78:47–56.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MARYLAND, COLLEGE PARK, MARYLAND (PRESENT ADDRESS: 5-27 4TH STREET, FAIR LAWN, NEW JERSEY) 12 DECEMBER 1966.

REQUEST FOR INFORMATION

As part of a study on the morphological variation and biosystematics of North American Peregrine Falcons only 68 museum specimens, from a total of 1,217 examined, are known, or thought to have been, from the population that formerly bred in the eastern portion of the U.S. and Canada. Most of these have been accessible because they were in large museums. Specimens from other regions in North America are well represented, however. After placing the specimens into sex and age categories the samples become pitifully small for a statistical treatment. As the eastern population of peregrines is now apparently extirpated this problem has increasing importance. The literature is full of accounts of falcons being collected at aeries and mounted or prepared as specimens by "so and so" but many of these specimens can not now be located. Perhaps they are on someones' fireplace, attic, in a high school collection etc. Information is needed as to the whereabouts of peregrines taken at known breeding stations, or taken from April through August at cliffs from the mid-west to the east coast in the U.S., southern Canada, and the Maritime Provinces. Information should be sent to Dr. Clayton M. White, Section of Ecology and Systematics, Langmuir Laboratory, Cornell University, Ithaca, New York 14850.

GENERAL NOTES

A case of Turkey Vulture piracy on Great Blue Herons.—One of the parent Turkey Vultures (*Cathartes aura*) in a nest that I studied near Huntington, Ohio had an unusual method of obtaining food for its two, two-week-old young. In the swampy, Elm-Maple woods where the vultures nested, there was also a small heronry containing about 20 nests of the Great Blue Heron (*Ardea herodias*). On 9 June 1964, the adult vulture twice flew into the heronry for a short time and then returned to its own nest where it fed its young. On 10 June I watched this activity from a vantage point with a view of the heronry, and the reason for the vulture's visits became clear. After landing on a heron's nest which contained two, three-week-old young, the vulture beat the young herons with its wings and jabbed at them with its beak. This caused the young herons to regurgitate their last meal. The vulture then stopped beating them, ate the mass of semi-digested food, and returned to its own nest to feed its young. This behavior was repeated once more during the day but at a different heron nest. This was not the only method used to obtain food for the young since the adult also made longer foraging trips and returned with food which was obviously carrion. The adult herons were never at their nests while the vulture was present.

Mehner (Wilson Bull., 64:242, 1952) has speculated about the possible effect Turkey Vultures might have in causing the abandonment of heron nests. In the heronry under observation, the landowner noticed a steady decline in the number of herons nesting during the previous two years. Perhaps repeated attacks by the vulture caused the death of many young herons by starvation or injury. Turkey Vultures are also known to kill and eat young herons on the nest (Pearson, Bird Lore, 21:321, 1919). It is possible that the vulture could seriously affect the heron's nesting success by such activities and thereby cause the abandonment of nests.

The vulture could have acquired its piratic behavior from experiences it had while attempting to kill a young heron on the nest. If the heron was too large for the vulture to kill easily and regurgitated during the struggle, the vulture may have been satisfied to take the regurgitated food. After several incidents like this, the vulture may have learned that it could get an easy meal by merely beating the young herons.—Stanley A. Temple, *Laboratory of Ornithology, Cornell University, Ithaca, New York 14850, 22 December 1967.*

Unusual cases of re-nesting Mallards.—The importance of re-nesting in waterfowl as compensation for losses caused by nest destruction has been much discussed. One question dealt with is in what way the stage of incubation at the time of destruction affects the interval to the new attempt. Hochbaum (The Canvasback on a prairie marsh. Amer. Wildl. Inst., 1944) doubted that re-nesting would be possible if the destruction occurred after the incubation had started. Sowls (A preliminary report on re-nesting in waterfowl. Trans. N. Amer. Wildl. Conf., 14, 1949) investigated this by removal of eggs at various stages of egg laying and incubation and found that the re-nesting interval (the time from the destruction of the first nest to the laying of the first egg in the second), as observed in 6 species of Anatinae, mainly Pintail (*Anas acuta*), Gadwall (*A. strepera*), and Blue-winged Teal (*A. discors*), was directly proportional to the time spent on the first nest. Every female waited at least 4 days and for each additional day of incubation on the first nest before destruction, an average of 0.57 day was added to the re-nesting interval. Later these figures were modified to 3 and 0.62 day respectively (Sowls, Prairie ducks. Harrisburg, Pa., 1955). Based upon observations on Ring-necked Duck (*Aythya collaris*), Lesser Scaup (*A. affinis*), and Cinnamon Teal (*Anas cyanoptera*) Hunt and Anderson (California Fish and Game, 52:1, 1966) concluded that only for the teal did their figures correspond to this rule. For Gadwall, Gates (Wilson Bull., 74:43–67, 1962) found that the re-nesting interval lengthened with a later nest destruction only during the first 10 days of incubation and that the interval was highly variable thereafter. As very few figures seem to be available for the Mallard (*Anas platyrhynchos*) and as most of the information comes from nests destroyed during the first 15 days of incubation, the following observations of female Mallards laying a second clutch after having successfully hatched the first one, might be of interest. The observations were made during 1967 and 1968 at Öster-Malma, a field station of the University of Stockholm.

In the first case in 1967 a marked female and 10 ducklings left the nest, an artificial nest-box, on 5 May with one unhatched egg remaining. The nest was situated on an island in a small pond within a fenced area. The brood was immediately attacked by a male Canada Goose (*Branta canadensis*) which had his female incubating about 10 m away from the duck nest. In order to protect the ducklings the whole family was evacuated to a larger pond situated about 40 m away. The ducklings could walk through the fence and the female fly over it. On one of the three following days the family was seen together in the new pond. On 18 May there was still only one egg in the old nest, but on the following day two eggs were found there. From now on, and until 3 June, at least 5 of the ducklings were regularly seen on the larger pond, while the female stayed within the fenced area. As a matter of fact they were never seen together during this period. On 4 June the female was caught on the nest, which now contained 11 new eggs and 8 days later she was still incubating. Shortly afterwards, however, the nest was robbed, probably by a Jackdaw (*Corvus monedula*) and 5 eggs left in the nest were all infertile. The ducklings were not seen after 3 June and probably did not survive.

In 1968 this female nested in the same nest-box. On 12 May she left the nest followed by 13 ducklings. As in the previous year the family was seen together on the following day, but later on several occasions the ducklings were found alone. Within the first month 2 of them died but the remaining 11 fledged and were seen together in the middle of August. On 10 June the same female was incubating a complete second clutch of 11 eggs in the box. Ten of these eggs hatched on 26 June which means that the incubation started on 30 May and thus the egg-laying not later than 20 May. This time the family kept together in a perfectly normal manner. Despite this the brood was seriously reduced and on 16 August contained only 3 ducklings all of which however fledged.

In the second case in 1967 two females incubating in the same nest, hatched in all 13 ducklings on 14 May and left the nest on the following day. A new clutch with 6 eggs, incubated by one of these females, was found in the same nest on 17 June. These eggs hatched on 4 July which means that the incubation probably started on 7 June.

Thus Mallard females have been found to be able to lay a second clutch after having successfully hatched a first one. This has previously been reported for Mallard in cases where the entire brood has been lost within 48 hours or so after hatching (Burger, Northeast Fish and Wildl. Conf., 1964) and for Wood Duck (*Aix sponsa*) when however the fate of the ducklings has been unknown (McGilvrey, Auk, 83:303, 1966). At least in two of the three cases described here, part of the brood was still alive when the female started her second clutch and the reason for this abandonment of the brood is unknown. The re-nesting interval in these cases was 13, 8, and 17 days respectively, thus below the 20 days that could be expected from figures calculated by Sowls.—ANDERS BJÄRVALL, *Dept. Zoology, University of Stockholm, Rådmansgatan 70 A., Stockholm Va, Sweden. 29 September 1967 (additions 22 October 1968).*

Build-up of grit in three pochard species in Manitoba.—Grit from the esophagus, proventriculus, and gizzard of 305 of 345 Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), and Lesser Scaup (*A. affinis*) examined for food contents was measured as part of an investigation of the summer foods and feeding habits of diving ducks in Manitoba (Bartonek, unpubl. Ph.D. thesis, Univ. Wisconsin, Madison, 1968).

The average volume of grit, as measured by water displacement, in the esophagi of the 305 birds, juveniles and adults combined, was only 0.007 ± 0.004 ml (95 per cent C.L.). Some trichoptera larvae, Molannidae in particular, incorporate particles of sand and gravel into their cases, and when consumed by the ducks indirectly contributed to the amount of grit ingested. Among juveniles, the quantity of grit in the gizzards increases with the age of the birds (Table 1). Juvenile ducks were classified to age according to the method of Gollop and Marshall (Mississippi Flyway Council Tech. Sect. Rept., 1954). The gizzards of juvenile Lesser Scaup contained more (but not always significantly more) grit than those of Redheads and Canvasbacks. Among adults, the gizzards of Redheads contained significantly more (95 per cent C.L.) grit than those of either Canvasbacks or Lesser Scaup.

Grit and other mineral matter varied in size from gravel (> 2 mm) to clay (colloidal). Four juveniles, three of which were 2–3 days old and the other 2 weeks old, did not have grit in their gizzards.

That gizzards retain grit longer than food is evident by the grit to food ratios for these three segments of the digestive tract: 1:122 in the esophagus, 1:7 in the proventriculus, and 1:1 in the gizzard.

Of the 345 waterfowl examined, only 6 contained lead shot in their gizzards. Two juvenile Canvasbacks, one juvenile Redhead, and two adult Canvasbacks had one lead shot each in their gizzards; another juvenile Canvasback contained three lead shot. The incidence of shot among these birds collected on the breeding ground is lower than that summarized by Bellrose (Illinois Nat. Hist. Surv. Bull., 27:261–262, 1959) for

TABLE 1

AVERAGE VOLUMES (ML) OF GRIT IN THE GIZZARDS OF CANVASBACKS, REDHEADS, AND LESSER SCAUP (With 95 Per Cent Confidence Limits and with Sample Sizes in Parentheses)

Species	Average volume of grit in gizzards				
	Juveniles			Adults	
	Class I	Class II	Class III and flying	Female	Male
Canvasback	0.32 ± 0.17 (22)	1.19 ± 0.25 (47)	1.52 ± 0.33 (37)	1.45 ± 0.43 (23)	1.60 ± 0.37 (18)
Redhead	0.46 ± 0.20 (27)	1.25 ± 0.34 (15)	1.86 ± 0.54 (10)	2.71 ± 0.53 (19)	3.06 ± 0.56 (22)
Lesser Scaup	0.83 ± 0.26 (21)	1.72 ± 0.30 (11)	2.05 ± 0.39 (11)	1.62 ± 0.51 (11)	1.33 ± 0.42 (11)

birds taken during the hunting season in the United States and Canada, where he reported percentages of Canvasbacks, Redheads, and Lesser Scaup containing lead shot to be 13, 20, and 10 per cent, respectively.

One juvenile Canvasback's gizzard contained a bent, much-eroded nail. The nail had neither caused apparent damage to the gizzard nor impaired the bird's health. Olney and Beer (Wildfowl Trust Ann. Rept., 12:169–170, [208], 1961) report five ducks that either became sick or were killed after various ingested metal objects pierced the digestive tracts.

Support during during field studies and preparation of the manuscript was given, in parts, by the Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin, the Delta Waterfowl Research Station, Delta, Manitoba, and the Bureau of Sport Fisheries and Wildlife.—James C. Bartonek, *Northern Prairie Wildlife Research Center, Bureau of Sport Fisheries and Wildlife, Jamestown, North Dakota 58401, 14 February 1968.*

Time frequency between successive drumming performances of Ruffed Grouse.—Drumming counts have been and continue to be used in two ways: by game biologists to census Ruffed Grouse (*Bonasa umbellus*) intensively on small areas where observers tally individual birds, and extensively where the frequency of drumming at several listening stations during predetermined time intervals constitutes a population index. The latter method is usually used during a roadside census.

Petraborg, et al. (J. Wildl. Mgmt. 17:292, 1953) while attempting to establish criteria for running roadside drumming counts timed the intervals between successive drums of individual males, apparently to the nearest one-half minute, and concluded the mean to be slightly over 4 minutes. These same workers also noted that "... in the morning drumming begins shortly after 4 A M, reaches a maximum between 5 and 6 A M, then levels out to a plateau between 5 and 10 A M. After 11 A M drumming falls sharply to approximately zero." A minor drumming activity period in late afternoon was also noted.

During an approximate 3-week period in the spring of 1961 I noted the time of day, to the second, that Ruffed Grouse started individual drumming performances on 4-160-acre study units of the Gratiot-Saginaw State Game Area, Michigan.

In early April I found an active drummer and for several mornings well before daybreak, I set up a tape recorder within about 30 yards of the drumming log, turned the device on, and departed to work elsewhere. The time of start was recorded and when I later monitored the tapes, the precise time of drumming and therefore the time interval between drums was recorded. While engaged in locating other drumming sites, I simply noted the precise time that individual performances began.

Altogether, I was able to record 415 time intervals between successive drums of 11 individual male Ruffed Grouse that spring. In no instance did I record the last drum of the morning for any bird. The data presented here represent drumming during the early morning period only, and represent the behavior of a composite of cocks located throughout the habitat being studied. These data are pooled for all mornings and represent a variety of climatic conditions, although I did no field work on very windy or rainy mornings.

The mean interval between drumming performances was 4.05 ± 0.28 minutes (confidence limits are expressed as 2 standard errors of the mean).

I subdivided the morning period into 10, 15-minute intervals related to sunrise time as follows: 1 hour or more before sunrise; between 1 hour and 45 minutes before

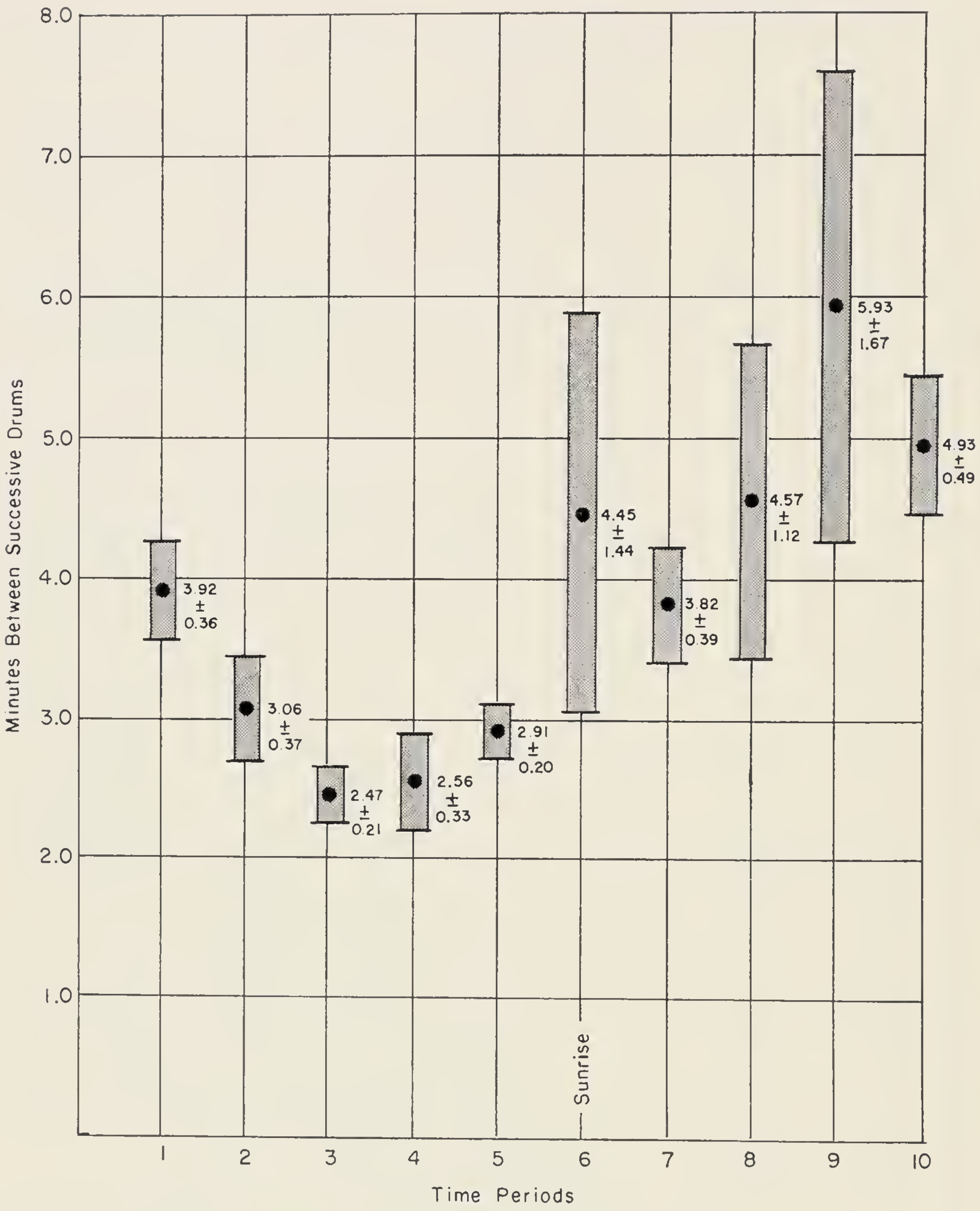


FIG. 1. Time interval between 415 successive morning drums of 11 Ruffed Grouse by 10 arbitrary time periods. (Bars depict means and 2 standard errors of the mean).

sunrise; between 45 and 30 minutes before sunrise; etc. The frequency of drumming by time intervals is graphically presented in Figure 1.

The first drumming in the morning generally begins some time prior to an hour before sunrise. These data indicate that intensity increases (or conversely the interval between successive drums decreases) and appears to peak about 30 minutes before sunrise. Thereafter, intensity tapers off quite rapidly. Significant differences in drumming frequencies between successive 15-minute intervals were not apparent except between the first three intervals. The wide confidence limits for certain of the 15-minute time intervals viz. sunrise to 15 minutes post sunrise, are due to a relatively few very long intervals between drums. During the early morning period prior to sunrise, birds at established drumming sites probably actively drum.

Apparently, birds established on drumming sites actively drum at regular frequencies during the period prior to sunrise. Most variation occurs after sunrise.

In intensive studies on small study areas where individual birds are located through repeated daily checks, the intensity of drumming is not a critical factor, although longer time intervals between drums make it easier to miss birds. On the other hand, when making roadside or other extensive counts in which the number of drums heard per unit time is the parameter used, it is obvious that surveys should be started an hour before sunrise.

The relationships between drumming behavior, population density and climatic conditions need much more study.

This study is a contribution from Pittman-Robertson Project W-117-R, Michigan.—Walter L. Palmer, *Rose Lake Wildlife Research Station, Michigan Department of Conservation, Route 1, East Lansing, Mich. 48823, 17 February 1968.*

Increase in Herring Gull colony in Cape May, New Jersey.—Ornithologists have been interested in the southward movements of the Herring Gull (*Larus argentatus*) along the east coast of the U.S. (Hailman, Auk, 80:375, 1963; Bull, Birds of the New York area, Harper & Row, 1964). The interest stems from the question of what conflicts might occur when the Herring Gull establishes a new colony in an area where another species of Laridae has been nesting. If the two species compete for the same resources, we should expect by the competitive exclusion principle to see a local demise of one.

A profile of a typical coastal marsh in Cape May, New Jersey is given in Figure 1. The vegetation is mostly *Spartina alterniflora* (included also are: *S. patens*, *Salicornia* sp., and *Distichlis spiccata*). In some places the Army Corps of Engineers dredged the intercoastal waterway pumping large quantities of sand and fill onto *Spartina* marshes. The resulting higher marsh table engenders subsequent succession of the vegetation to the woody bush *Iva* sp. (W. Bourn and C. Cottam, Research Report 19, Fish and Wildlife Service, 1950; E. Rosenwinkel, Bull. New Jersey Acad. Sci. 9:1–20, 1964).

For three summers (1964–1966) we studied the ecology and habitat responses of breeding Laughing Gulls (*Larus atricilla*) on Ring Island (39° 03′ N, 74° 47′ W), Cape May, New Jersey. The Laughing Gull colony is situated on the marsh covered by *S. alterniflora* and not on the higher fill areas. In 1964 we noted a few Herring Gulls circling over a stand of *Iva* on an island adjacent to Ring Island, but did not investigate. On 1 June 1965 we visited the stand of *Iva* and counted 17 Herring Gull nests. On 15 and 16 June a northeast storm hit the coast. Three study areas in the Laughing Gull colony containing 79, 36, and 516 nests lost respectively 100, 95 and 60 per cent of their nests. At the same time all the nests in the Herring Gull colony remained intact. The storm tide did not inundate the higher fill area as it did the lower *Spartina* marsh. Clearly, in a storm the Herring Gulls of this colony fared better than the neighboring Laughing Gulls. On 3 June 1966 we again visited the Herring Gulls and counted 42 nests. While recording their contents, we noted a higher proportion of clutches with three eggs (at the time about 10 per cent of the eggs had already hatched) compared to those of the Laughing Gulls ($\chi^2 = 5.51$; $P < 0.05$).

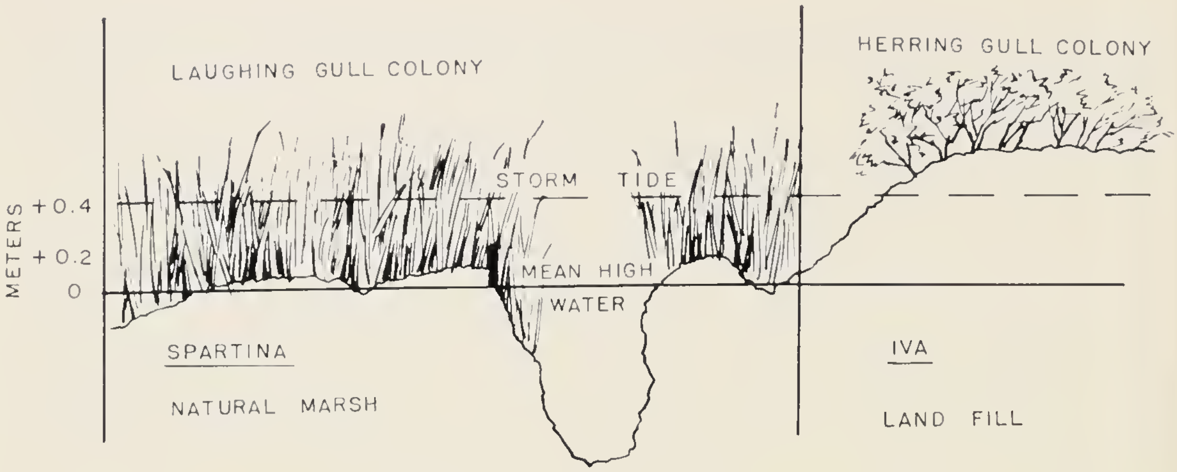


FIG. 1. A generalized profile of the salt marsh and land fill area in Cape May, New Jersey.

If the present trend is maintained this difference can become significant if the Herring Gull colony increases further. The greater number of clutches with three eggs among the Herring Gulls could result from higher initial productivity, reduced loss of nest contents or some combination of the two.

At present, we think the Herring Gulls are not yet in direct competition with Laughing Gulls for nesting habitat since the former build nests on higher sites (G. Nobel and M. Wurm, Ann. New York Acad. Sci. 45:179–220, 1943 reported similar findings for those two species on Muskeget Island, Mass.) while the latter are exploiting the lower *Spartina* marsh. However, and this is of consequence, changes wrought by man either in dredging or filling usually result in destruction of prime marshes (*Spartina*) for the Laughing Gull and an increase in the areas which support *Iva* thus laying open the possibility of more Herring Gull intrusion. As yet there was little evidence of predation by Herring Gulls on the Laughing Gull colony, nor any evidence of food competition.

We acknowledge Mildred Miskimen, Donald Kunkle and Jon Greenlaw. These observations result from work supported by the Ecology Training Grant 3343.—SALVATORE F. BONGIORNO AND JEFF SWINEBROAD, *Zoology Department, Rutgers University, New Brunswick, New Jersey, 21 February 1968.*

Barred Owl feeds on crow.—On 2 December, 1965, at about 07:00 I found on the highway near Plainfield, Wisconsin a dead Barred Owl (*Strix varia*) and about 12 feet away a dead Common Crow (*Corvus brachyrhynchos*). Although sunrise occurred at about 07:14 it was still quite dark since the sky was completely overcast and thick ground fog existed. I had passed there on the previous night at about 22:00 and neither of these birds was on the road at that time. At this point along the highway there are pine plantations on both sides of the road offering many possible roosting sites for crows.

It appeared as though the birds were killed at or at about the same time. The owl was limp, still warm, and showed little external damage. It had 63 grams of crow in its stomach. The crow was badly damaged and due to a much exposed and flattened surface area was no longer warm. The exposed tissue of the crow was not frozen, however, and the freshness of the blood indicated it had been recently killed. The temperature at the Stevens Point Municipal Airport, 20 miles north, at 06:40 was 27° F.

Steinke (Wisconsin Conserv. Bull., 18:7–10, 1953) lists 23 crows found during 3362 miles driven in Wisconsin over a six-year period (1947–52) and Schorger (Passenger Pigeon, 16:53–55, 1954) listed 11 crows as road-killed over a 16 year period (1932–47). But only one of these observations was made during December.

Since crows are apparently seldom killed by cars during this time of year, and since the incident took place at night, it seems unlikely that the crow was killed by a motor vehicle. The evidence suggests that the crow was killed by the owl, which was either feeding on it on the road, or was flying across the road with its prey when it in turn, was killed by a passing car. There is, however, the possibility that the crow was carrion.

The only reference I can find of Barred Owls eating carrion is by Forbush (Birds of Massachusetts and other New England States, Vol. II, 1929, p. 206). The only reference I can find of crow being recorded as food for Barred Owls is in Bent (U.S. Natl. Mus. Bull., 170:189, 1938).—Charles R. Sindelar, *1865 S. West Avenue, Apt. 5, Waukesha, Wisconsin, 2 February 1966.*

Behavior of a Ruby-throated Hummingbird in a room.—An immature male Ruby-throated Hummingbird (*Archilochus colubris*) was observed while confined in a room at Western Illinois University in Macomb, Illinois, 18 September 1967. The room in which observations were made is 15 feet square and 21 feet high. The north and south sides of the room open to 10-foot-wide corridors, and 18-foot-tall windows comprise about one-half of each of the east and west sides. Five-foot-wide doorways (without doors) open from the east and the west sides to the exterior. The walls and ceiling of the room are white except brownish where some paint is flaking off. The ceiling is without fixtures or wires suitable for perching.

The day was overcast and humid, becoming partly cloudy. At 10:30 CDT the hummingbird was called to my attention. I watched it for the following hour and then for several minutes each hour until 17:00 that afternoon. It hovered and darted nearly at the level of the ceiling with its crown and bill tip usually less than an inch from the ceiling. The bill was inclined slightly upward, and the body hung at about a 60° angle from the ceiling. The bird did not approach the walls of the room, even where the windows came within three feet of the ceiling, nor did it move along the ceiling into the somewhat darker north corridor.

The dartings of the hummingbird were directed toward many small insects, probably dipterans and hymenopterans, resting on the ceiling or hovering immediately under it. The hummingbird caught and appeared to eat immediately several insects shorter than 5 mm in length; many attempted captures failed. If an insect were not caught as soon as it took flight, the hummingbird sometimes chased it several inches. Ruby-throated Hummingbirds normally capture flying insects (Tyler, *In* Bent, U.S. Natl. Mus. Bull., 176:342, 1940; Forbush, Birds of Massachusetts, 1927), but it seems noteworthy that the confined bird was catching insects rather than obviously seeking an escape route.

The bird continued flying just under the ceiling for at least six and one-half hours and presumably found its way out through one of the doorways between 17:00 and 19:00 that evening. Because it seems unlikely that the hummingbird would stay in the room for so long just to feed on the insects, its continued presence in the room probably indicates that it could not find its way out. But if it were trying to escape, why did it keep hovering near the center of the white ceiling rather than investigating the large, unshaded windows nearby? A hypothesis that it was responding to the brightest area as the potential escape route was rejected, for the ceiling was only one-fourth as bright as the terrain which was visible through the windows. Nor was it staying in the darkest area, for the ceiling of the north corridor was much darker.

If the Ruby-throated Hummingbird possessed an innate drive to fly upward when meeting a vertical obstruction, this would explain its constancy in flying only inches below the ceiling, its failure to investigate the windows three feet lower than the ceiling, and its failure to find the doorways 13 feet below the ceiling. An innate drive of this sort would be of selective advantage in natural situations.—Edwin C. Franks, *Department of Biological Sciences, Western Illinois University, Macomb, Illinois, 4 December 1967.*

Egg measurements of California and Ring-billed Gull eggs at Miquelon Lake, Alberta, in 1965.—During a study of the breeding biology of the California (*Larus californicus*) and the Ring-billed Gulls (*Larus delawarensis*) on two islands in Miquelon Lake, Alberta (53° 15′ N and 112° 55′ W), egg measurements were taken

Table 1

Distribution in Length and Width of California and Ring-billed Gull Eggs at Miquelon Lake, Alberta in 1965

	Number of eggs					
	California Gull			Ring-billed Gull		
Length in mm	I egg	II egg	III egg	I egg	II egg	III egg
71.9–70.0	1	1				
69.9–68.0	9	2	1			
67.9–66.0	13	12	3			1
65.9–64.0	20	27	11	2		
63.9–62.0	8	8	24	2	5	2
61.9–60.0	3	5	10	9	9	1
59.9–58.0	1		5	14	14	17
57.9–56.0			1	14	11	11
55.9–54.0				2	3	6
53.9–52.0					1	4
51.9–50.0						1
Mean in mm	65.42	64.95	63.09	58.88	58.79	57.22

	Number of eggs					
	California Gull			Ring-billed Gull		
Width in mm	I egg	II egg	III egg	I egg	II egg	III egg
51.9–50.0	1					
49.9–48.0	13	9				
47.9–46.0	26	30	16			
45.9–44.0	15	15	29	2	1	1
43.9–42.0		1	9	23	25	7
41.9–40.0			1	16	15	30
39.9–38.0				2	2	5
Mean in mm	46.82	46.61	45.07	41.98	42.06	41.13

TABLE 2
MEAN LENGTH AND WIDTH OF EGGS I, II AND III, IN MM, IN EIGHT GULL SPECIES

Authority	Location	Gull species	No. of clutches measured	Mean length of eggs in mm			Mean width of eggs in mm		
				I	II	III	I	II	III
Harris (Ibis, 106: 432–456, 1964)	England	Great Black-backed Gull	35	76.0	75.8	71.6	51.2	51.6	52.2
"	"	Herring Gull	100	68.7	68.7	66.5	48.3	48.4	46.3
Paludan (Vidensk. Medd. Dansk. Naturh. Foren., 114: 1–128, 1951)	Denmark	"	57	72.44	72.10	69.16	50.58	50.53	49.18
"	"	Lesser Black-backed Gull	62	66.94	66.31	63.74	46.45	46.56	45.32
Harris (loc. cit.)	England	"	59	67.1	66.5	65.8	46.7	46.9	45.8
Behle and Goates (Condor, 59:235–246, 1957)	U.S.A.	California Gull	93–100	66.5	66.7	65.9	46.7	46.7	45.5
This study, 1965	Canada	"	55	65.42	64.95	63.09	46.82	46.61	45.07
"	"	Ring-billed Gull	43	58.88	58.79	57.22	41.98	42.06	41.13
Coulson (Proc. Zool. Soc. London, 140: 211–227, 1962)	England	Kittiwake	33	55.29	54.27	55.00	40.73	40.57	39.32
Preston and Preston (Ann. Carnegie Mus., 33:129–139, 1953)	U.S.A.	Laughing Gull	15	55.32	54.56	54.33	39.45	39.29	38.38
Ytreberg (Nytt Mag. Zool., 4:5–106, 1956)	Norway	Black-headed Gull	105	52.05	51.45	50.34	36.56	36.65	36.10

of the first (I egg), second (II egg) and third eggs (III egg) laid in the clutches of these species (Table 1). In both species the third egg of the clutch is smaller on the average than the first two eggs laid. This appears to be a common phenomenon in gulls (Table 2).—KEES VERMEER, *10015-103 Avenue, Edmonton, Alberta, 5 February 1968.*

House Sparrow occupancy of Cliff Swallow nests.—Bent (U.S. Natl. Mus. Bull., 179:468, 1942), and Burleigh (Auk, 47:48, 1930) reported occupation of Cliff Swallow (*Petrochelidon pyrrhonota*) nests by House Sparrows (*Passer domesticus*). Buss (Wilson Bull., 54:153, 1942), Stoner (Wilson Bull., 51:221, 1938) and Brewster (Mem. Nuttall Ornithol. Club, 4:1, 1906) noted that sparrows in taking over nests not only destroyed swallow eggs, but also young nestlings. However, direct observation of such interactions have not been reported, nor has it been determined whether House Sparrows affect Cliff Swallow populations.

During the summers of 1967 and 1968 I observed House Sparrows taking over Cliff Swallow nests near Bruceton Mills, West Virginia. In one case in 1967, five pairs of swallows had nests completed or nearly completed by 13 May, in a row along a girder within a barn-door entrance. Around noon on 23 May a pair of sparrows began to defend nests Number 2 and 5 of the row of five nests. The sparrows perched on a power line near the barn entrance, but would enter and defend the nests when any of the 10 swallows tried to enter them. The two sparrows occupied only two of the five nests at one time (the male in one, the female in another), but during a three-hour period, none of the swallows successfully entered their nests. The sparrows were then driven away for one hour with a pellet gun and in their absence the swallows returned. When the shooting was stopped, the pair of sparrows again resumed their position within the nests. The swallows were not aggressive, and only occasionally gave an alarm call. Within 24 hours the swallows abandoned the nest site; their movements to new nest sites have been reported (Samuel, EBBA News, 30:5, 1967). Within three weeks, House Sparrow eggs were found in three of the five nests. Similar House Sparrow behavior was recorded at three other barns involving the complete abandonment of two, three, and four swallow nests.

On the six-square mile study area, 10 barns and sheds contained 48 swallow nests in 1967. Twenty-three of these were lost to House Sparrows; 15 nests were taken over before eggs were laid, seven had contained eggs, and one had held nestlings. During the summer of 1968, Cliff Swallows had greater success, with 10 of 41 nests taken by House Sparrows, all before eggs were laid.

The number of Cliff Swallows in each barn may be important in survival. Of the 42 nests built in 1968, 26 were in one barn and only 4 of these (15.4 per cent) were lost to sparrows. The other 15 nests were divided among 4 barns and 6 of these (40 per cent) were lost to sparrows. It must be pointed out however, that the farmer whose barn contained the 22 successful nests, regularly shot House Sparrows. In all other barns where swallows were observed, sparrows were abundant. The time of original occupancy of the nests may determine future Cliff Swallow populations in an area. If the nests are taken over immediately after they are built, the Cliff Swallow may be able to re-nest. However, Samuel (EBBA News, 30:5, 1967) has indicated that such re-nesting may also be unsuccessful. In West Virginia, where the Cliff Swallow is found in low numbers, any delay in nesting would appear to be a limiting factor. During two summers, 33 of 90 (36.6 per cent) Cliff Swallow nests built in 11 barns were lost to House Sparrows.

Financial support during the period in which these observations were made was provided by a National Science Foundation summer traineeship and a Frank M. Chapman Memorial Fund Grant provided by the American Museum of Natural History.— David E. Samuel, *Department of Biology, West Virginia University, Morgantown, West Virginia 26506, 31 July 1968. (Originally submitted 22 January 1968.)*

Factors influencing breeding range expansion of the Azure Bluebird.—Until recently the Mexican form of the Eastern Bluebird, known as the Azure Bluebird (*Sialia sialis fulva*), was thought to breed in the United States only in the Huachuca, Santa Rita, and Pajaritos Mountains of southern Arizona (American Ornithologists' Union, Check-list of North American Birds, Fifth Ed., 1957:444). Neither Brandt (Arizona and its bird life, 1951) nor Tanner and Hardy (Amer. Mus. Novitates No. 1866, 1958) recorded it from the Chiricahua Mountains, Cochise County, Arizona. In 1960 a single breeding pair was found near the Southwestern Research Station of the American Museum of Natural History (Phillips et al., The birds of Arizona, 1964), which is located in Cave Creek Canyon of the Chiricahuas. Since that time its population has increased there and it is now a regular breeding species in the vicinity of the Research Station (Ligon and Balda, Trans. San Diego Soc. Nat. Hist., 15:41–50, 1968).

During the summer of 1965, in the course of my study of the Elf Owl (*Micrathene whitneyi*), I recorded the following observations which suggest that nest sites may be in short supply for this bluebird. On 29 May 1965 I accidentally destroyed the nest cavity (13 m from the ground in the dead limb of a living sycamore) of a pair of Elf Owls. On 30 May I placed a bird box at the site of the destroyed cavity, hoping that the owls would re-nest in it. Within two days a pair of bluebirds had occupied the box. On 7 June 1965, at another site a female Elf Owl deserted her nest, located 6 m up in a dead sycamore, after I had opened the cavity. This hole also was occupied quickly by bluebirds. In both instances young were successfully reared.

There are 12 common species of hole-nesting birds in the Chiricahuas, not including woodpeckers, most or all of which begin nesting prior to the dates given above. The rapid occupancy of the above-described nest sites by the bluebirds, after many or most of the other hole-nesters had begun breeding, suggests that they do not fare well in interspecific competition for nest holes, possibly because they begin breeding activities later than most of the other hole-nesters. Scarcity of nest sites may help to explain the rarity of the Azure Bluebird in the mountain ranges from which it has long been known (Bent, Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull., 170, 1949). Specialized nesting requirements are thought to be a probable cause of population decrease in the Mountain Bluebird (*Sialia currucoides*) (Power, Condor, 68:351–371, 1966).

Ecological requirements other than nest sites may also serve to limit this species. Marshall (Proc. Tall Timbers Fire Ecology Conf. 2:135–141, 1963) found the Azure Bluebird to be more common in the open parklike forests of northern Mexico, where fire is of regular occurrence, than in the mountains of southern Arizona, where fire has been excluded. The resulting heavy undergrowth and dense foliage in Arizona may influence the numbers of this bluebird. Heavy grazing by cattle near the research station has destroyed much of the undergrowth, producing a more open woodland than is found in areas where both fire and cattle have been excluded.

Another possible factor influencing the Azure Bluebird is the presence of the Western Bluebird (*Sialia mexicana*). In the Chiricahua Mountains this species is found in open areas of higher altitudes where ponderosa pine (*Pinus ponderosa*) is common. Azure Bluebirds were never seen in areas occupied by Western Bluebirds. Marshall (Pacific Coast Avifauna, 32:62, 1957) states that intense competition between the two species of bluebirds is suggested by their distributions.

The observations reported above were made during a study supported by the Frank M. Chapman Memorial Fund of the American Museum of Natural History and the National Science Foundation Training Program in Systematics and Evolutionary Biology (GB-3366) through the University of Michigan Museum of Zoology.—J. David Ligon, *Department of Biology, Idaho State University, Pocatello, Idaho. (Present address: Museum of Southwestern Biology, Department of Biology, University of New Mexico, Albuquerque, New Mexico 87106), 20 November 1967.*

Plastic device causes gull mortality.—While driving down the beach at Michigan City, Indiana, on 28 January 1967, I found a dead Herring Gull (*Larus argentatus*) with a plastic device, such as is used to hold a six-pack of beer together, locked about its head (Figure 1). Mr. James Landing of Michigan City has found several dead gulls in similar condition, and as of 1 October 1967, three Herring Gulls with these devices were in the Michigan City harbor. Gulls have also been seen at Benton Harbor, Michigan, with the same object, in the mouths or around the necks. Mr.

Fig. 1. Herring Gull with plastic device looped behind the head and cut into the upper mandible.

Frances Van Huffel of Mishawaka, Indiana, has suggested that they may look like fish entrails and consequently attract the gulls.—Scott C. Rea, *952 Riverside Dr., South Bend, Indiana, 6 December 1967.*

Distraction display of a pair of Black-throated Green Warblers.—Distraction displays of birds have been reported by many observers. They appear widespread in the wood warblers (Parulidae), having been recorded from at least 34 species (Ficken and Ficken, Living Bird, 1:103, 1962). However, most such displays reported in the literature are ones that have been directed toward human subjects. Hence, a series of distraction displays that I observed on 5 July 1966, at Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln Co., Maine, directed at another potential predator appear worthy of note.

Immediately prior to the observations reported below I was studying a territorial encounter between two pairs of Black-throated Green Warblers (*Dendroica virens*), apparently resulting from one pair with two or more young straying over a territorial boundary. This intense encounter, punctuated by chases, fights, Moth Flights (see Ficken and Ficken, Wilson Bull., 77: 363, 1965), and loud harsh chipping by both adults and young, had been under way for 15 minutes when two Blue Jays (*Cyanocitta cristata*) flew suddenly and silently into the midst of the fighting birds. Almost immediately one male Black-throated Green Warbler virtually dropped from approximately 40 feet in small limbs of a red spruce (*Picea rubens*) to limbs of a small balsam fir (*Abies balsamea*) at a height of about five feet above the ground, followed immediately by one of the jays. Within 15 seconds of this chase the jay flew to where it and its associate had landed originally, and these two birds then moved about in the branches for approximately five minutes, periodically giving musical *wheee* notes. During this time several or all of the adult warblers uttered nearly constant chip notes, though the vocalizations of the young nearly ceased. At this point a female Black-throated Green Warbler also virtually dropped toward the ground, giving only sporadic flutters during its descent. It dropped to a level of three to four feet in another small balsam fir, and I would have mistaken it for a young bird unable to fly adequately, had it not landed in a position directly in front of me. One of the jays immediately pursued this warbler down to a low level, alighting only a few feet from the bird. In neither instance did the behavior of the warblers directly following this drop change appreciably from that preceding the action. They recommenced chipping at this low level and proceeded to ascend the tree via short flights to the immediate vicinity of the young. Within 30 seconds of the second chase both jays moved away in the direction from which they had come originally. Following the departure of the jays the hostile encounters between the two pairs of Black-throated Green Warblers, which had nearly ceased in the presence of the jays, increased to their former intensity and still were continuing when I left the area 10 minutes later.

The similarity between the dive-display of both Black-throated Green Warblers and motions of a young fledgling that is scarcely able to fly was striking. It would appear that the jays had responded initially to these performances as they would to that of a young bird; as soon as the adult warblers terminated the behavior, the jays ceased to pay attention to them.

At the time of this encounter both adult and young warblers were conspicuous as a result of both their vocalizations and movements. The young remain conspicuous during the extended period of dependency or partial dependency upon the adults (probably in excess of one month in some instances) as a result of the nearly constant loud begging notes that they produce. Hence, they would appear to be vulnerable to predators at this time. The Blue Jay, along with the red squirrel (*Tamiasciurus hudsonicus*) probably is one of the most important predators of eggs and nestlings of small birds in the spruce forests. These observations, as well as those of Lamore (Wilson Bull., 70:96, 1957) and Chase (Wilson Bull., 11:57, 1899) suggest that Blue Jays will also take newly fledged individuals.

Cruickshank (Auk, 53:480, 1936) reported a display similar to the two reported here given by a Black-throated Green Warbler when he approached its nest. The general lack of observations of this particular behavior may be due to the fact that young seldom are approached by a human when high enough in a tree for adults to respond as described above. These are the only records of this precise behavior that I have noted during six years of intensive study upon this and a large number of other species of wood warblers.

Financial support for the study of warblers was provided by the National Science Foundation (GB-3226 and GB-6071). I thank M. S. and R. W. Ficken and J. P. Hailman for comments upon the manuscript.—Douglass H. Morse, *Department of Zoology, University of Maryland, College Park, Maryland, 12 January 1968.*

Meadowlarks feeding on road-kills.—On the afternoon of 17 December 1967, we obtained information which showed meadowlarks (*Sturnella magna* and *S. neglecta*) to be feeding on the carcasses of road-killed birds. The area was along New Mexico State Highway 26 between the towns of Hatch and Deming in Dona Ana and Luna counties. The date marked the third consecutive day of near-blizzard conditions in southwestern New Mexico, and at the time we passed, most of the terrain, including the road, was covered with 6 to 10 inches of snow. The temperature was in the low twenties, and there were cloudy skies with occasional snow flurries and a strong southwesterly wind. The only snow-free areas visible to us were in the sets of tire tracks that traversed the highway. In the tracks were gathered many birds, including mainly Mourning Doves (*Zenaidura macroura*), Horned Larks (*Eremophila alpestris*), Lark Buntings (*Calamospiza melanocorys*), and meadowlarks.

Although traffie was sparse through the area, many birds had been killed or injured by automobiles, and their bodies littered the highway and roadside. We stopped frequently to identify these carcasses and to salvage specimens. During one of these stops we observed a meadowlark fly up from the badly mangled carcass of another meadowlark. Alerted to the possibility that the bird might have been feeding on the road-killed carcass, we subsequently noted the frequent association of meadowlarks with road-kills as we drove along. We noted this association at least 10 times with carcasses of various species. On one occasion, while we were stopped, a meadowlark was actually observed pecking at a carcass. None of the other species of small birds we saw appeared to be feeding on carcasses, nor did they appear to be associated with them. Hence it appeared that only meadowlarks were involved in this behavior.

Later, the stomachs of two meadowlarks (one each of *S. magna* and *S. neglecta*) we salvaged were examined and found to contain numerous feathers and some skin, along with stones and a few seeds. In each case the identifiable feathers proved to be those of Mourning Doves, which were almost certainly two different individuals. Interestingly, the stomachs of other birds obtained at the same time (3 *Eremophila alpestris*, 1 *Spizella breweri*, and 1 *Zonotrichia leucophrys*) were found to contain only numerous seeds and stones, which again suggests that they were not feeding on road-kills.

Although the habit of feeding on road-kills is commonplace in the area among hawks (e.g., *Buteo jamaicensis*, *B. lagopus*, *B. regalis*, *Circus cyaneus*), ravens (*Corvus cryptoleucus*, *C. corax*), and the Turkey Vulture (*Cathartes aura*), we have not previously observed it in meadowlarks. In fact, there seems to be only one other reference to such behavior, that of a *S. magna* feeding on the partly-smashed carcass of another of its kind near Bath, New York, on 5 July 1939 (Terres, Auk, 73:289–290, 1956). Normally, the highly animalian diet (63 to 74 per cent) of meadowlarks is confined to arthropods, but occasionally small vertebrates such as amphibians are also eaten (Bent, Life histories of North American blackbirds, orioles, tanagers, and allies, U.S. Natl. Mus. Bull., 211, 1958).

Nevertheless, it is not particularly surprising that meadowlarks will turn to road-kills for food, particularly under conditions which make the procurement of normal food items difficult. In fact, since meadowlarks winter much further north and in areas where adverse weather is more prevalent, one wonders whether or not this type of behavior is more commonplace than suspected. Even before the advent of road-kills, such sources as predator kills may have furnished food under adverse conditions and allowed meadowlarks to survive until normal food was again available. One also wonders whether the stimulus to be carnivorous is primarily from exposed or mangled carcasses, or whether intact bodies, such as might result from deaths due to disease, starvation, or freezing, are also attacked.

We are very grateful to Mrs. Roxie Laybourne of the Smithsonian Institution for identifying the feathers from the stomachs of the two meadowlarks.—John P. Hubbard and Claudia L. Hubbard, *Rockbridge Alum Springs Biological Laboratory, Goshen, Virginia 24439, 5 February 1968.*

ORNITHOLOGICAL NEWS

We want to remind those people who plan on attending the Annual Meeting of The Wilson Ornithological Society in Williamsburg, Virginia on 1 May to 4 May, that reservations for accommodations should be made at once. Williamsburg is normally a crowded place during the spring months and suitable accommodations will be in short supply. A highlight of the papers session on Friday and Saturday will be a symposium on present and future research in ornithology to be arranged and chaired by H. B. Tordoff. Kenneth C. Parkes has agreed to act as toastmaster for the Saturday evening banquet. A special feature of the banquet will be a showing of a color film entitled, "The Birds of Africa and Asia" produced by M. P. Kahl of the National Geographic Society and made available through the courtesy of that Society.

As a result of the generosity of an anonymous donor who contributed a sum of $500, the Wilson Society announces the initiation of a new award of $100 annually to be known as The Margaret Morse Nice Award. The award will be made to the candidate whose project is adjudged by the Research Committee to have the best potential of adding to the sum of ornithological knowledge, with the candidates to be limited solely to persons not having college or university affiliation. A high school student would be eligible, however. Persons interested in applying for this award should write the Chairman of the Research Committee, Dr. H. B. Tordoff, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

Dr. Raymond A. Paynter, Jr. has retired from the Editorial Board of *The Wilson Bulletin.* Dr. Paynter has served on the Board since it was founded in 1956, and the Society and the Editor extend their deep appreciation for his many services to the *Bulletin.*

We report the deaths of the following members: Lewis McIver Terrill, a founder of the Province of Quebec Society for the Protection of Birds on 22 December 1968; Hugh C. Land on 23 December 1968; Fred T. Hall, a former secretary of The Wilson Society on 11 January 1969; and Mrs. Arthur A. (Elsa Guerdrum) Allen on 31 January 1969.

The following publication will be of interest to many members. Adams, Jean Larson and Howard H. Michaud, *A Selected List of Filmstrips on the Conservation of Natural Resources,* The Interstate Printers and Publishers, Inc., Danville, Illinois 61832, 42 pp., 1968. Single copy 50 cents; 2—99 copies, 40 cents ea.; 100 or more copies, 35 cents ea.

The booklet is Key No. 5 of a conservation series sponsored by the Conservation Education Association through a grant from the Conservation Foundation and published by the Interstate Printers, Inc.

ORNITHOLOGICAL LITERATURE

LIFE HISTORIES OF CENTRAL AMERICAN HIGHLAND BIRDS. By Alexander F. Skutch. Publications of the Nuttall Ornithological Club, No. 7. Cambridge, Massachusetts, 1967: 6¼ × 9¼ in., vi + 213 pp., 1 table, 6 figs. $6.00 (obtainable from N.O.C., c/o Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138).

Excluding the work of Alexander Skutch, life history studies of Central American birds are seldom seen in the literature. Scientists from North America and elsewhere, whose time in the field generally is limited to a season or two, are reluctant to study a particular bird whose nest, breeding season, and habitat may be uncertain or even unknown. The possibility of wasting much valuable time in a fruitless search is too great. For this and other reasons, past work in the tropics has consisted largely of general collecting or ecological studies of a particular community where the objectives of the study could be broad and adjustable, and nearly any information obtained could be a meaningful contribution. This has been especially true of graduate students whose degree plans and financial limitations might allow for only one or two visits to the tropics.

Alexander Skutch, however, by establishing permanent residence at a farm near San Isidro del General in Costa Rica, has been able to accumulate data on tropical birds in one area for over a quarter of a century. He has studied also for considerable periods in other parts of Costa Rica and in other Latin American countries. While one season may bring him little or no useful information on many birds of the area, in his accumulated notes the general pattern of breeding and behavior of more and more species is becoming clear. In the "Life Histories of Central American Birds," volumes I and II (Pacific Coast Avifauna, Cooper Ornithological Society, Nos. 31 and 34), plus numerous shorter papers, Skutch has put together life history reports on many tropical species. The present work is the continued fruition of these years of study.

Thirty-nine species are included in this book, all characteristic of the highlands at elevations above 1,300 m (4,000 ft). As Skutch indicates, rather complete biographies are given of some birds, while others that are less well studied are included because of some interesting aspect of their life cycle. Notable here is the vivid description of the singing of the Brown-backed Solitaire (*Myadestes obscurus*). In the introduction Skutch describes in detail the nine localities at which most of his highland work was done. Six of these are in Costa Rica, two in Guatemala, and one in Ecuador. He spent about a year on the Sierra de Tecpam in Guatemala and at Montaña Azul in Costa Rica, and three to six months at several of the other localities. In writing of these areas Skutch takes space to describe the climate, vegetation, birds, and his own work there in very readable terms. His lucid prose gives a real sample of the flavor and excitement of highland birding.

Also included in the introduction is a section on altitudinal and local migrations, a subject which has not been worked out carefully for most tropical species. Some birds that Skutch studied apparently move to a lower elevation after breeding, some to a higher elevation. In the last part of the introduction an excellent discussion is given on altitudinal distribution. In describing the Tropical Zone, Subtropical Zone, Temperate Zone, and Paramo as they occur in Costa Rica, Skutch emphasizes the great amount of overlapping that can occur between these areas and thus the difficulty of defining their limits clearly. He also points out that in southern Central America, not unexpectedly, increasing elevation usually goes along with a decrease in the number of species and, possibly, a decrease in the abundance of each species as well. The reduced number of birds in colder areas may be due to slower growth and lower reproductive rates of the organisms in the lower part of the food chain, the plants and poikilothermic animals upon which birds feed.

The life histories included in this volume cover five hummingbirds, six tyrant flycatchers, four thrushes, six wood warblers, seven fringillids, and eleven other birds of nine families. A good job has been done of ferreting out the work of others who may have studied any of these species from Mexico to South America. One of the more complete studies is on the Green Violet-ear (*Colibri thalassinus*). It emphasizes the singing of the male; the timing of the nesting season, which extends in one area or another from July to March; and the rearing of the young. After observing at length the tireless singing and intermittent feeding of a male, Skutch concludes that the bird is "a highly efficient machine for turning nectar into squeaks."

Many interesting details are brought out in the accounts, including: the way in which the male and female Blue-throated Toucanet (*Aulacorhynchus caeruleogularis*) share incubation; the nest structure of the Spotted Barbtail (*Premnoplex brunnescens*); the courtship display of the White-ruffed Manakin (*Corapipo leucorrhoa*), and comparisons with the display of other Central and South American manakins; the pugnacity of a Mountain Elaenia (*Elaenia frantzii*); the mellow song of the Rufous-browed Pepper-Shrike (*Cyclarhis gujanensis*); the nest building of the Flame-throated Warbler (*Vermivora gutturalis*); the feeding of the Common Bush-Tanager (*Chlorospingus ophthalmicus*) on the nectar of the *Salvia* blossoms despite their deep corolla tubes; the unique song of the Large-footed Finch (*Pezopetes capitalis*); and the hitch-hiking of some Rufous-collared Sparrows (*Zonotrichia capensis*) that showed up at sea level in Puerto Limón, Costa Rica.

Notable throughout the book is the vast botanical knowledge Skutch, a botanist by training, brings to his discussions. Plants are seldom mentioned without being identified to family or beyond. Accounts of hummingbird feeding are made more meaningful by the naming and description of such plants as *Salvia nervata*, with its long, furry, crimson corolla tubes, and the large scarlet passion flowers (*Passiflora vitifolia*), in which only the longer billed hummingbirds can reach the floral nectaries.

Though there is much valuable information in every account, few are so complete as to discourage additional work. Detailed studies on behavior, territoriality, social relations, the nesting cycle, and other topics are still needed for most of these species. However, even the briefest of the Skutch accounts is a usful starting point for any detailed study and, most importantly, can often answer the questions of when, where, and how to look for the bird and its nest. For most readers, who will not be planning an immediate trip to the tropics or additional work on any of these species, this book offers a chance to share some rewarding experiences with one of Central America's great naturalists.—Hugh C. Land.

The Wild Turkey and Its Management. By Oliver H. Hewitt, Editor. The Wildlife Society, Washington, D.C., 1967: 9 × 6 in., xiv + 589 pp., 3 col. pls., 2 fold-out maps. $6.00.

This is a large book (589 pages), but of high quality, both in make-up and content. The 18 individual chapters are authored by specialists in the various aspects of the history and life history of the Wild Turkey. Chapter 1, on historical background, is brief, but adequate. A more thorough coverage can be found in "The Wild Turkey: Its History and Domestication" by A. W. Schorger (University of Oklahoma Press, 1966). There is little to quarrel with in Chapter 2 on taxonomy, distribution, and present status. In discussing the distribution of the eastern Wild Turkey, however, one reads through 22 lines of distributional notes including recent introductions in Wisconsin only to find the next paragraph gives the "much more restricted" range as of 1967.

Physical characteristics and physiology were covered in one chapter. The physiology section included a weak section on the various senses and ended with comments on "behavioral characteristics." The latter could have been better handled in the chapter on behavior. In general, this chapter is well done and, by omission of detail, points up what is still to be investigated.

The chapter on behavior is short on comparative behavior with other birds and some of the flat but important or interesting assertions could have been strengthened by documentation (e.g., shelter-seeking, investigative and imitative behavior, orientation, homing, and sex and age relationships). The brief section on the stimulus for molting dangles since it is too brief to be comprehensive and its relationship to behavior obscure. The conclusion is inadequate for a chapter with much fine information.

The section on population dynamics touches all the standard statistical bases. The data, however, come in the main from the Eastern and Florida Turkey and only two tables (6.2 and 6.7) use data from western subspecies. The text does not push the data excessively, but makes them available for those who may wish to do so. A closer tie-in with the relationship of the statistics to on-the-ground management would have enhanced the section.

Feeding habits and foods of Wild Turkeys are well treated and the literature on the subject well covered. Most data come from the hunting season collections (e.g., spring-fall). Late spring and summer information comes largely from dropping analysis. Such analysis requires difficult separation and measurement procedures. The section is well written but could have had a summary statement.

The section on limiting factors points out the time, place, or activity that could limit population size. Weather, habitat destruction, and hunting appear to be the most important factors bringing about reductions in Wild Turkey populations. Other factors such as diseases, parasites, accidents, introductions, etc. are described with qualifiers indicating that documentation (as a limiting factor) is meager or lacking. The most carefully worded paragraphs are found under predation and predator control (e.g., "Control may occasionally be warranted on limited areas" (p. 209)). The text, concluded by this statement, did not require so guarded an attitude toward either predation or predator control.

The brief but well-stated chapter (9) on highlights of management acts as an abstract for the next seven chapters that deal with management problems and programs of various geographic areas.

In general, the management chapters give a good insight into regional problems associated with the maintenance of Wild Turkey populations. Multi-authored books suffer in part from repetition. For example. after reading in great detail about food habits in an earlier chapter (7) we encounter much the same treatment on a local level in Chapter 14 (Table 14.1).

The role of the transplanted turkey, including failures and successes, is documented; a plea for forest management is made in reviewing Wild Turkey habitat in the Ozarks. The concluding remark underscores the difficulty facing both the wildlife and forest managers. It reads (p. 400): "Therefore, before any substantial increases can be made in over-all habitat improvement for forest game species, management must have access to the 90 per cent of forest lands in private ownership."

Some of the "limiting" factors are dealt with on a regional level. The chapter on the Rio Grande turkey sums up the basic limiting factor for most turkey range (p. 492): "The future of the [Rio Grande] turkey depends primarily on land use programs on ranches within its range."

Turkey hunting means just what it says. One must know his quarry, place himself in the proper place at the proper time, entice his prey into gun range (a feat requiring more than a little skill) and finally to bag his bird. The brief chapter (17) on hunting covers these salient points.

The final chapter (18) begins thus: "The wild turkey has responded so well to modern management that it has become the outstanding success of wildlife management in this decade."

In the same two and one-half pages are found these statements: "There yet remains a monumental task in gathering information on many facets of the turkey's requirements which may vary widely from one range to another," and "A discussion of research needs would consume volumes." One wonders if these researches are academic or are the *needs* to be met in order to make the management of the turkey an outstanding "outstanding success." Research will always be needed on game animals in order to achieve adequate management because the biology and social factors affecting a hunted animal are never static. To overstate the case for research may cause legislatures and public administrators to become either skeptical or antagonistic and certainly gun shy of researchers.

An appendix of scientific names of organisms listed in the text follows the last chapter. The literature cited section covers 24 pages and the index requires seven pages. Chapter authors and personal communication contributions are included in the index.

The photographs are excellent and plentiful. Three colored plates by Ned Smith, George M. Sutton, and L. A. Fuertes enhance the volume. The two folded maps on life areas and Wild Turkey distribution are informative and do not physically encumber the book.

There is a sprinkling of split infinitives and an occasional lapse into the mid-Victorian passive. All aspects considered, however, this is a thorough, well-documented work. There should be no doubt in the mind of the reader that he has been enlightened by a group of experts.

A compilation by numerous authors is a difficult chore for an editor. Dr. Hewitt has done a fine job. The book will appeal to the administrator, researcher, ornithologist, hunter, and layman. The Wildlife Society has sponsored a winner. I recommend this reasonably priced volume for all who are interested in the Wild Turkey.—ROBERT A. MCCABE.

SEABIRDS OF THE TROPICAL ATLANTIC OCEAN. By George E. Watson. Smithsonian Publication 4680, Smithsonian Press, Washington D.C., 1966; 8⅛ × 10¾ in., xxx + 120 pp., 12 bl. and wh. pls. by Tina Abbott Clapp; map by William A. Risley. $3.75.

With the present growing interest in the biology of tropical seabirds, there has been a need for a single work on the identification and distribution of those occurring in the tropical Atlantic as a whole. The author and publishers of the present manual are to be congratulated on the manner in which they set about their task. In March 1965, following a commission from the Bureau of Commercial Fisheries for illustrated keys to identify seabirds encountered during tuna surveys, a preliminary edition of the manual was issued "for immediate test use at sea and for critical appraisal by specialists in seabirds." The present edition was then prepared, incorporating the corrections, comments, and criticisms that resulted, and should be invaluable not only in assisting observers at sea but also by improving the standard of seabird identification generally. In particular, it is to be hoped that fishery personnel will now feel equipped and encouraged to make available those ornithological records that they are in a unique position to provide. Publication costs have been kept down by reproducing the original—and impeccable—typescript itself as the main text and this arrangement should enable the manual to be kept up-to-date and even further improved by subsequent editions.

The main area covered in detail extends approximately between 35 degrees north and 35 degrees south—that is, from Bermuda and Madeira in the North Atlantic to the mouth of the River Plate and the Cape of Good Hope in the South Atlantic. Reference is also made to the Azores and the Tristan da Cunha group (including Gough Island) which lie in slightly higher latitudes. A double-page map shows the area and all place names mentioned, together with the direction—though not the limits—of the main ocean currents.

The introductory section opens with a useful outline and discussion of seabird distribution in relation to water conditions, with particular reference to nutrient enrichment and the availability of food. Species are then classified (Tables 2 and 3) according to the relevant surface water zones (polar, subpolar or temperate, tropical) in which they occur and their oceanic habitat (coastal, offshore, pelagic). The long-held belief that frigatebirds occur only rarely far from land (p. xvi) must now be seriously questioned, for evidence is accumulating—see, for example, Bourne, Ibis, 108:187–188, 1957)—that these incredibly aerial birds may be extremely pelagic at certain stations but are overlooked because they soar so high. The author next gives instructions on the use of the manual as an illustrated key, together with brief comments on various seabird characters. Although information on these is to be found in the species accounts later, it would have been valuable at this point if further tables had been compiled classifying the seabirds along the lines already offered under surface water and habitat zonation; in particular, size, plumage-type, manner of flight, and feeding could well have been covered. Suggestions are also given for preserving and shipping specimens, and the introduction closes with a comprehensive list of references to important works on seabird identification and biology.

The plates, executed mainly in line and wash, follow next. Though simple the plates adequately fulfill their object and are certainly better for the most part than anything yet available in this particular field. All except the last (topography of a seabird) consist of a double-page spread, with the drawings alone on one half and the explanatory text on the other, overlaid in the case of Plates 2 through 11, on faint, "shadow" versions of the figures. On Plate 1, there are 15 highly effective silhouettes of characteristic types of seabirds in flight, plus a cormorant and gull on the water; these usefully establish the relative sizes of the birds—though no scale is given, either here or on any of the plates—while the accompanying captions supply the identification points. Plate 11 compares the bills of seven species of albatrosses, three jaegers, five prions, three shearwaters, and a gadfly petrel.

The majority of the plates, 2 through 10, illustrate the various families of seabirds, mainly in flight and often grouped with other families with which they might be confused at sea: Plate 2, albatrosses, large petrels, gannets and boobies; 3, shearwaters and petrels; 4, frigatebirds, pelicans, and birds of prey (Black Kite and Osprey); 5, cormorants, alcids, and penguins; 6, adult gulls; 7, immature gulls; 8, tropic-birds and some terns; 9, remaining terns (including the noddies) and skimmer; and 10, skua, jaegers, phalaropes, and storm petrels. The groupings are mostly sound but, in Plate 2, the necessity of showing so many large species on a single page has resulted in overcrowding and too small a scale—the gannets and boobies would have been better placed on a separate plate, perhaps together with the pelicans. For this reviewer, the gannets and boobies are particularly disappointing. On this tiny scale, it was obviously difficult to show adequately their differing sizes and proportions, both specific and (in the case of the two smaller boobies) sexual. The Masked Booby is drawn the same size as the larger gannets and its neck is too short and thick-set. The distinctive plumage of the juvenile form of this species, with its dark head and back but white collar and underparts, should also have been included—also the various immature plumages of the gannets and the dark, white-tailed-only, adult phase of the Red-footed Booby. The upper facial area of the latter species is incorrectly shown as feathered instead of bare. The frigatebirds are another group that would have benefited from more space. The choice of the so-called "light phase" to illustrate the Ascension Frigatebirds is unfortunate in a species that is typically all-dark in both sexes; moreover, the "immature" of this species has a much wider and darker upper-breast band than figured.

The bulk of the book is devoted to a systematic account and, though planned primarily for identification purposes, it also collects together a surprising amount of information of wide biological interest that is otherwise scattered through an extensive literature. A diagnosis of characters is given for each family, followed by a key to species, with cross reference to the keys of similar groups where necessary. The species accounts themselves are organized under the following headings: (1) Characters (overall length and wingspread, descriptions of most distinctive plumages and appendages, comparisons with related or otherwise confusing species); (2) flight (manner of flying, height above sea, relation to ships); (3) food (type of prey taken, hunting behavior, flocking and relation to schools of predatory fish); (4) habitat (zones frequented), and (5) distribution (breeding and dispersal ranges, migrations, and vagrancy). Shorter accounts appear separately of a few species that occasionally enter the fringes of the tropical Atlantic from high latitudes or breed only in the Tristan group. In an appendix, there are distributional lists of breeding and non-breeding species for the various islands and coasts, together with local references and egg and migration dates (where known). Schedules of species likely to be seen during selected ocean transects would also have been welcome but probably difficult to compile accurately.

A few inaccuracies still remain in the text, of which the following may be mentioned. Audubon's Shearwater is given as a breeding species at Ascension, unequivocally on page 13 and with reservations on page 102, yet there is in fact no direct evidence of breeding and the bird has only once been recorded there (on Boatswainbird Island in March 1959). The Madeiran Storm Petrel is said to follow ships regularly (p. 20) but this was not the reviewer's experience during three transects to or from Ascension (see also "Handbook of North American Birds" (1:237, 1962)). The "immature" Brown Booby is characterized as having a "greenish yellow" bill on page 27 and a "conspicuous straw colored" one on page 30. In fact, the situation is more complex than this: at Ascension (at least) the juvenile form has a dark slate-gray bill and facial skin, the latter being the first to change to shades of cinnamon or yellow and then the bill itself to a fleshy-mauve—but at no time is the bill ever yellow (or green) in life. Only the adult male of this species has the facial areas and feet bright yellow (nuptial stage) or greenish (non-nuptial). It must be added here that a certain amount of confusion is caused throughout the book by imprecise terms for the plumage categories below the adult—e.g. "young" and "immature." In some cases it is the true juvenal dress that is described (or figured), in others not. On page 50, the characters of the Slender-billed Gull are wrongly stressed for, as shown by Wallace (Brit. Birds, 57:242, 1964) and others, the bill of this species is not slender at all but, compared with that of the Black-headed Gull, is "clearly longer, deeper and heavier looking with a markedly decurved upper mandible." Because of local turbulence and upwelling, seabirds are said to be more numerous around Ascension than St. Helena (p. 102) but this statement overlooks the former existence of a large and varied petrel fauna on the latter island (see Ashmore, Ibis, 103B:390–408, 1963). Further, the Ascension Frigatebird is given as occurring formerly on St. Helena whereas the extirpated frigatebird there was almost certainly *Fregata ariel*, as correctly stated on page 38. Finally, as pointed out by Bourne (Ibis, 108:426, 1966), a number of vagrants to the Canaries—the Razor-billed Auk, Puffin, Dovekie, Great Skua, Great Black-backed, Common, and Mediterranean Gulls—have been listed in error under the Cape Verde Islands (p. 109), though not in the species accounts themselves.

The book closes with an index of colloquial names, containing scientific names and colloquial synonyms, but there are no separate indices to scientific or place names. The nomenclature followed is up-to-date and uncontroversial for the most part. The suggestions of Alexander et al. (Ibis, 107:401–405. 1966), to which the author himself was a signatory, for that difficult group, the Procellariiformes, have been followed in the main, including the use of the generic names *Calonectris*, *Procellaria*, *Bulweria*, and *Hydrobates*—though *Adamastor* is maintained. Among the few questionable colloquial names, one wonders particularly why Dove Prion was preferred to the much more familiar Fairy Prion for *Pachyptila turtur*.

In brief this well-produced book is warmly recommended to all workers on seabirds. both as a guide to the identification and distribution of these fascinating birds in the tropical Atlantic and, also, as a compendium of much information on their general biology—K. E. L. Simmons.

Birds of South Vietnam. By Philip Wildash. Charles E. Tuttle Co., Rutland, Vermont. 1968: 6 × 9 in., 234 pp., 25 col. pls., 21 bl. and wh. illus., map. $7.50.

A short foreword by Jean Delacour, the expert on birds of Vietnam, is followed by the author's preface, an account of the geography and history of the region, a linear list of species to be found east of Laos and Cambodia and south of 17° N, and a figure explaining the indicative terms used in describing a bird's plumage. With his preface the author modestly, and one hopes permissively, quotes Roger Ascham (1515–1568), an expert on archery of his day, as follows: "If I have said amisse I am content that any man amende it, or if I have sayed too little any man that will to adde what him pleaseth to it."

Mr. Wildash is a British diplomat, attached to the embassy in Saigon for some time; he has done an admirable job in preparing this first field guide for the birds of southern Vietnam. He has described 586 species and illustrated 215 in color himself.

Sixty-nine families are briefly characterized. Perhaps it might be said that some of these remarks are not particularly helpful to the birdwatcher. True cuckoos are "Parasitic birds which lay their eggs in the nests of others" is an example. Descriptions of species will be found most helpful, although there is no indication of size nor are the birds drawn to scale. To these descriptions are added brief notes on habits (which sometimes include notes on status and habitat) as well as distribution within this restricted area— for example: "southern South Vietnam" or "throughout South Vietnam."

It is certainly true that "ecology and behaviour of birds [of Vietnam] have been ignored by most naturalists in the rush to collect new species," as the author remarks. To be sure, after a long walk Deignan's "Birds of Northern Thailand" and Stuart Baker's "Fauna of British India" (2d ed.) may be consulted after reaching home, for they are bulky books. For example, Mr. Wildash says of *Garrulax leucolophus*: "Frequents lowland forest and brush. Sings most strikingly in unison. Sociable. Unafraid of human habitation. Very common." Both Baker and Deignan correctly observe that these birds are extremely curious. It could be said that they come to look at you and when they see you they set up a babble, a strident, almost hysterical cacophony resembling laughter. A day's walk in any part of the world will reward you with no more fascinating bird.

Subspecies have been omitted, presumably in order to restrict the size of a book designed to be used out of doors. The author correctly points out in his preface that many of such subspecies are quite different to their representative counterparts in China, Siam, and India. For example, Number 536, "Red Headed Tit," has a gray head in Vietnam. Here it might properly be said that Mayr characterized 803 species and subspecies in his "Birds of the Southwestern Pacific" in a volume smaller and lighter than this one.

"If I have sayed too little any man that will to adde," said Sir Roger Ascham. It appears that a good many species such as *Plegadis falcinellus*, recorded as a migrant in Cambodia, and *Botaurus stellaris*, taken just north of 17° N, might well be taken in southern Vietnam soon.

Advertised on the dust jacket, and claimed in the preface, is the statement that this book should be useful in ten countries and islands in southeastern Asia. A count of the species of the genus *Garrulax* in both northern and southern Vietnam reveals that fourteen species have been omitted from this book because they have not been recorded south of 17° N. And so it seems doubtful that the book would be altogether adequate even in northern Vietnam. It would be useful, in fact presently indispensable, to the bird-conscious traveler to Vietnam and Thailand, and there is no doubt about it.—JAMES C. GREENWAY, JR.

PENGUINS. By John Sparks and Tony Soper. David & Charles, Newton Abbot, 1967. 263 pp., 33 photos, 24 main text illus. by Robert Gillmor. 45s ($4.95 in Great Britain; $8.95 from Taplinger Publishing Company in United States).

To write a popular yet accurate book on penguins can be a difficult task. For the sake of popularity, the temptation is to emphasize anthropomorphic interpretations of penguin stance and behavior. John Sparks and Tony Soper have admirably converted "cute" penguins to real birds. Inaccuracies tend to be minor and limited to missing decimal points (on page 60, only 1.5 per cent of territory-holding Adélie Penguins change rookeries, not 15 per cent), erroneous temperature conversions (on page 76 we find –40°C converted to –30°F), perhaps some unwarranted generalizations about thermoregulation and finally a few confusing phrases (on page 212, Adélie Penguins "nest at the foot of gentle ice-cliff slopes").

After a brief introduction, the authors thoroughly convince their readers that penguins are birds supremely adapted to an aquatic way of life. The two following chapters on breeding behavior and movements seem too brief and ignore many fascinating problems concerning social behavior and population dynamics. In the discussion of feeding habits and predation, the reader finds good illustrations of high-latitude food chains and the depredations of South Polar Skuas, leopard seals, and man. I most enjoyed the final chapters concerning evolution, discovery, and exploitation. Here the authors rely heavily on obscure and exciting accounts by early sailors and explorers.

Although there are severe inequalities in what we know about the various species of penguins, the book "Penguins" presents a well balanced picture of all penguins, both their differences and similarities. The combination of easily understood language and wonderfully correct illustrations by Robert Gillmor make this a fine book about a popular group of birds.—R. L. PENNEY.

THE SUNBIRDS OF SOUTHERN AFRICA: ALSO THE SUGARBIRDS, THE WHITE-EYES, AND THE SPOTTED CREEPER. By C. J. Skead, assisted by Cecily M. Niven, J. M. Winterbottom, and Richard Liversidge. Published for the Trustees of the South African Bird Book Fund, by Balkema, Cape Town and Amsterdam, 1967: 7½ × 9¾ in., vii + 351 pp., 10 col. pls., 12 bl. and wh. pls., 41 line drawings. $12.00.

The interest of South Africans in their bird life can be gauged by the sale of Austin Roberts' "The Birds of South Africa." This excellent, well-illustrated guide, with synopsis of habits, was published in 1940, and had already sold 28,000 copies before its revision in 1957. The present volume on sunbirds, etc. is the second of a pioneer series (the first published in 1960, covering the canaries and buntings), and invites comparison with Bent's "Life Histories" and the A.O.U. "Handbook." It aims at covering all that is known about the life histories of South African birds, and in addition, discusses some of their taxonomy and nomenclature.

There is a mine of information in this volume, especially on nectar, flower structure, and flower-feeding habits, and the role of this in pollination by sunbirds and sugarbirds. The sunbirds (20 of the more than 100 known species occur here) despite their adaptation in tongue and bill for flower-feeding, emerge as active, energetic, acrobatic birds, part of the hop-and-flit brigade. They may glean insects from leaf and twig, fly out to snap them up on the way, and eat berries, as well as feed at flowers. Of especial interest is the unique habit of some sunbirds in building their pendant, domed nest by first making "a hanging rope" of material into which the female forces her way. As she pushes out the walls of the cavity she adds material to the inside. Within a species, nest-building may be accomplished in two days, or prolonged to thirty, apparently not a matter of necessity but of motivation.

The sugarbirds, here kept as the family Promeropidae, peculiar to South Africa and with two species, have two striking behavioral differences compared with sunbirds. They have a display flight and build an open, cup-shaped nest. But the main reason for keeping them separate from the species-rich honey-eaters (Meliphagidae) of the Australian area is one of geography.

The three white-eyes (family Zosteropidae) are rather "ordinary" birds, with a predilection for fruit and nectar, but also they eat many insects. This is a family that has its center of abundance in the Indo-Malayan area.

The single African creeper, *Salpornis spilonota* (family Certhiidae), does creep on tree trunks, and is brown, but aside from this has little to indicate relation to the Brown Creeper. However, nothing has been found in its life history to indicate other surer relationships, and it is retained in Certhiidae for lack of a better place for it.

As I have said, this book is a mine of information, but it needs digging out. Skead's readable, narrative text, used for a multitude of detail, at first palls as reading, and then seems an encumbrance to finding information. For the sake of the general reader, references are usually omitted to avoid the destruction of the "flow of the narrative." This is combined with an encyclopedic approach, synonymies, and color descriptions keyed to Ridgway's color standards. These seem strange bedfellows. I cannot help wondering if more synthesis and succinctness would not have been advisable; to state clearly, even in synoptic form, in places where such would be useful, and then where appropriate, as for general behavior and habitats, use Skead's smooth-flowing narrative prose.

The following illustrates the arrangement and coverage. Each family has an introductory section, varying from seventy-eight pages for the sunbirds to two pages for the creepers, followed by species accounts with such headings as: Local Names (English and others), Distribution in South Africa, Field Characters, Habits, Habitats, Food, Voice, Song, Call Notes, Breeding Season, Courtship, Territory, Nest Site, Description of Nest, Nest Building, Clutch Size, Egg Color, Egg Size, Incubation Period, Nesting Period, Nest Sanitation, Post Nestling Period, Breeding Success, Parasitism, Sundry, and Taxonomy (with synonymies, description and subspecies with diagnosis where appropriate). There is also a bibliography, a gazetteer, and an index.

There are ten very attractive color plates showing male, and occasionally female, and an egg of each species; 12 monochrome plates showing such things as habitats and nests; and 41 line drawings illustrating such things as tongues, bills, feeding habits, poses, and displays. There are also maps of the ranges of each species. In a pocket inside the back cover is a phonograph record of sunbird and white-eye voices.

As a practical point, it is interesting to project the completion of this series if it is to cover all the 813 species listed for South Africa. The first volume, covering the 17 species of canaries and buntings, was published in 1960, this second volume, covering 26 species, in 1967.—Austin L. Rand.

LETTERS TO THE EDITOR

SHARP-SHINNED HAWK MIGRATION IN THE NORTHEASTERN UNITED STATES

Sir:

Mueller and Berger's (Wilson Bull., 79:50–63, 1967.) criticism of my (Wilson Bull., 76:257–264, 1964.) interpretation of Sharp-shinned Hawk migration in the northeastern United States requires comment. However, neither my time nor your space will permit a full answer.

Our interpretations differ concerning the role that wind plays in causing concentrations at points along the Atlantic coast. A part of all hypotheses proposed by Trowbridge (1895, 1902), Stone (1922, 1937), Allen and Peterson (1936), and now, Mueller and Berger (1967) is that wind drifts hawks off course and that northwesterly winds drift hawks from inland to the coastal region, where they continue southward until they are concentrated by the large bays. My hypothesis is that the wind's direction differentially affects the hawks' migratory behavior, northwesterly winds being most effective in causing the passing hawks to divert, that is, to drop to a lower altitude and to fly along the shorelines, while a varying proportion of hawks continues across the bays.

(1) Mueller and Berger contend that a correlation exists between hawk concentrations and northwesterly winds. Such a correlation cannot distinguish between the two hypotheses because each hypothesis states that a northwest wind is most effective in causing concentrations; the one, by drifting hawks, the other, by diverting hawks.

(2) Mueller and Berger attempt to show that there are too many hawks at Cape May to be accounted for by any hypothesis that does not include wind-drift as a component. Their analysis is faulty. First, Mueller and Berger assume that hawks are

uniformly dispersed across the broad front. This is not necessarily so; hawks may become concentrated for reasons other than wind-drift. Perhaps the hawks from New England and the Maritime Provinces (east of the NE-SW line in my Figure 3), once reaching the southern New England coast, continue their migration southward in the coastal region and over Cape May. Perhaps hawks reaching the Delaware Bay shore several miles west of the Cape May peninsula divert eastward and continue southward on the peninsula rather than cross the widest part of the bay. Second, Mueller and Berger assume that only one mile of a 2,500-mile-long front is intercepted at Cape May Point. Actually, Cape May Point is the small end of a funnel that is at least 10 miles wide at its mouth (the north end of the peninsula). Thus, the hawks entering the peninsula may be concentrated at least 10 times when they reach the point. Third, Mueller and Berger assume that each hawk is counted only once. Most counted hawks at Cape May are heading northward. If these northward-flying hawks are remaining on the peninsula until wind conditions permit their crossing the bay, as thought by Stone (1937), then it is possible that some hawks are counted more than once. These possibilities are not mutually exclusive.

I agree with Mueller and Berger that the observations at Cape May are of concentrations, but I do not agree that concentrations are proof of wind-drift.

Mueller and Berger point out the difficulties involved in obtaining evidence for drift. Perhaps we can never get unquestionable evidence without expensive instrumentation. Until unquestionable evidence is obtained, I think it is wise to recognize the inadequacies of the data and the tentativeness of our speculations.

I am grateful to James T. Tanner and Robert C. Frohling for permitting me to examine unpublished data and to Stephen T. Emlen for reading an earlier draft of this letter.—BERTRAM G. MURRAY, JR., *Section of Neurobiology and Behavior, Division of Biological Sciences, Cornell University, Ithaca, New York. (Present address: Department of Natural Science, University College, Michigan State University, East Lansing, Michigan 48823).*

Sir:

We remain in disagreement with Dr. Murray. If there remains a reader interested in this controversy, we should be happy to correspond with him.—HELMUT C. MUELLER, *Department of Zoology, The University of North Carolina, Chapel Hill, North Carolina,* AND DANIEL D. BERGER, *Cedar Grove Ornithological Station, Route 1, Cedar Grove,* Wisconsin.

This issue of *The Wilson Bulletin* was published on 26 March 1969.

SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subsequently identified. Summaries of major papers should be brief but quotable. Where fewer than five 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 "Style Manual for Biological Journals" (1964. AIBS). Photographs for illustrations should be sharp, 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. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A WORD TO MEMBERS

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

PLAN TO ATTEND THE 1969 ANNUAL MEETING

The 1969 meeting of the Wilson Ornithological Society will be held at the College of William and Mary, Williamsburg, Virginia from Thursday, 1 May to Sunday, 4 May 1969. The meeting will be a joint session with the Virginia Society of Ornithology and will be sponsored by that organization and the College of William and Mary. All regular sessions will be held in the John Millington Hall of Life Sciences on the campus.

A special program on Thursday evening will consist of an exhibit of some of the work of Mark Catesby, the Colonial Naturalist, and a film on his life which also shows much on the natural history of Tidewater Virginia will be presented.

Approximately 100 species of resident and migratory birds should be available at this season in the area immediately around Williamsburg. Among the more common species are Brown-headed Nuthatch, Yellow-throated Vireo, Blackpoll Warbler, Pine Warbler, Louisiana Waterthrush, Hooded Warbler, and Summer Tanager.

Early morning field trips on Friday and Saturday will be conducted to local areas, including the Yorktown Battlefield and Jamestown Island. These areas, in addition to the birding, are of considerable historical significance and interest.

On Sunday there will be two major field trips, one to Seashore State Park and one to Craney Island, an artificial impoundment in Hampton Roads. Emphasis at the first site will be on its botanical features as well as resident and migratory birds. Spanish moss and a number of other plant species reach their northern distributional limits in Seashore Park and typical birds would include Prothonotary Warbler, Yellow-crowned Night Heron, Yellow-throated Warbler, Seaside Sparrow, and Sharp-tailed Sparrow. Emphasis at Craney Island will be on shorebirds which reach their peak of migration about the first week in May.

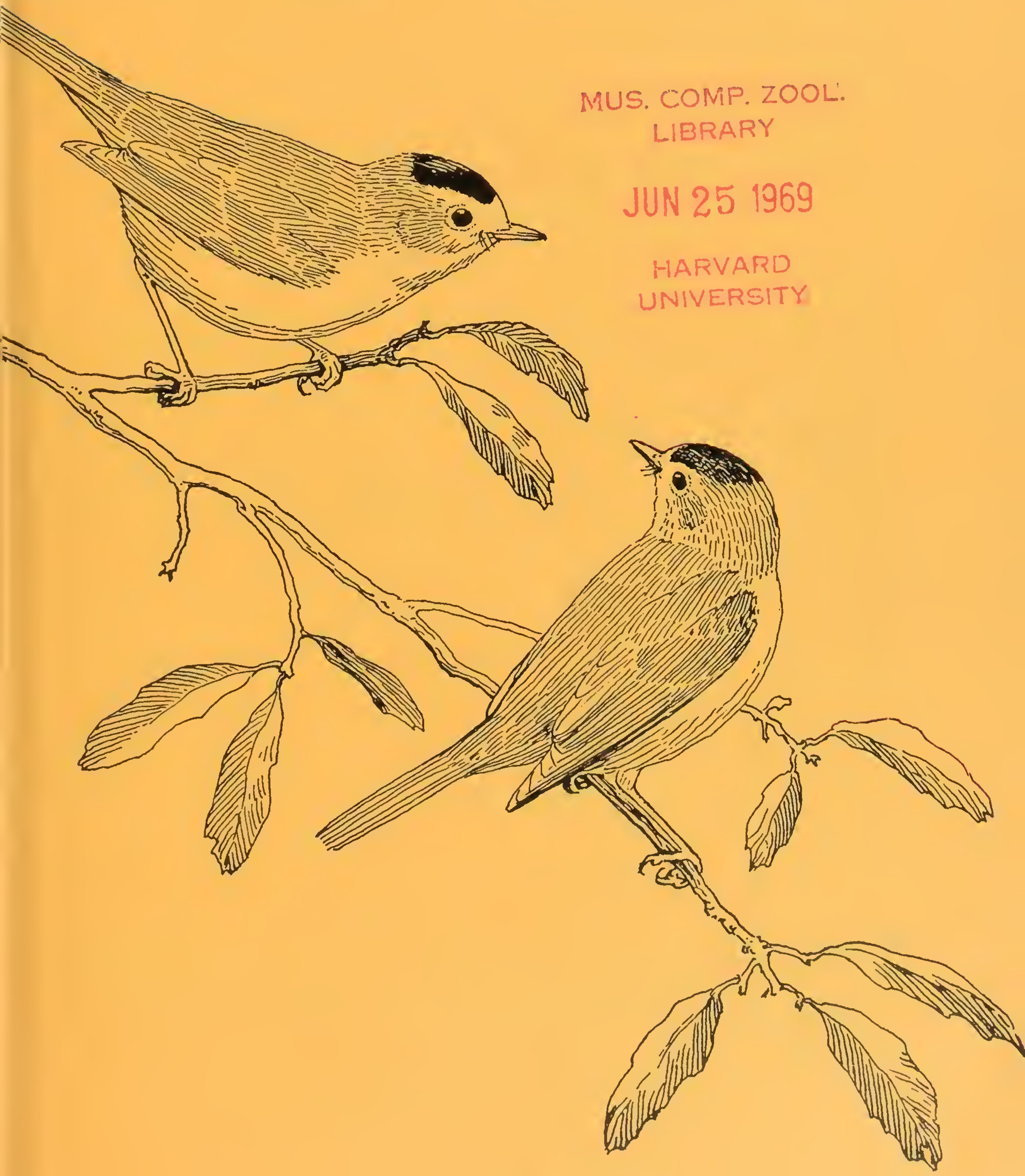
If demand is sufficient, a third trip on Sunday will be arranged to Cedar Island, one of the barrier islands off the Eastern Shore of Virginia. This trip would feature thousands of migrating shorebirds, colonies of Black Skimmers, Common, Royal, and Gull-billed Terns, and one of Virginia's largest heronies in which Glossy Ibis and Cattle Egrets are becoming common nesting species.

Colonial Williamsburg is particularly known for the elaborate restoration of a portion of the city to its eighteenth century appearance. This extensive undertaking consists of an area nearly one mile in length in which approximately 140 buildings have been restored or reconstructed on their original sites. There are nearly 100 formal and informal gardens which are open to the public. Members and friends of the W.O.S. who expect to attend the meeting should plan to avail themselves of the opportunity to visit as much of this historical heritage as possible. Special trips will be arranged for those not attending the papers sessions.

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY
WEST VIRGINIA U. • MORGANTOWN, W. VA.

VOL. 81 No. 2 JUNE 1969 PAGES 121–232



THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—William W. H. Gunn, Apt. 1605, 155 Balliol Street, Toronto, Ontario.

First Vice-President—Pershing B. Hofslund, Dept. of Biology, University of Minnesota Duluth, Duluth, Minnesota 55812.

Second Vice-President—Kenneth C. Parkes, Carnegie Museum, Pittsburgh, Pennsylvania 15213.

Secretary—Jeff Swinebroad, 8728 Oxwell Lane, Laurel, Maryland 20810.

Treasurer—William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107.

Elected Council Members—Andrew J. Berger (term expires 1970); C. Chandler Ross (term expires 1971); Ernest P. Edwards (term expires 1972).

Membership dues per calendar year are: Sustaining, $10.00; Active, $5.00.
Life memberships, $150 (payable in four installments).
THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 104 periodicals as gifts and in exchange for *The Wilson Bulletin.* With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to "The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan." Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically.

THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December, at Morgantown, West Virginia. The subscription price, both in the United States and elsewhere, is $6.00 per year. Single copies, $1.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $1.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan.

Second class postage at Lawrence, Kansas, U.S.A. 66044

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by The Wilson Ornithological Society

Vol. 81, No. 2 June 1969 Pages 121–232

CONTENTS

A Study of the Rufous-fronted Thornbird and Associated Birds. Part II. Birds which Breed in Thornbirds' Nests *Alexander F. Skutch* 123

Some Aspects of the Ecology of Migrant Shorebirds. II. Aggression *Harry F. Recher and Judy A. Recher* 140

Movements, Population Fluctuations, and Mortality Among Great Horned Owls *Paul A. Stewart* 155

Notes on Song Structure in Townsend's Solitaire *Donald J. Borror and K. C. Halafoff* 163

Reproductive Behavior of Hairy Woodpeckers. III. Agonistic Behavior in Relation to Courtship and Territory *Lawrence Kilham* 169

Life History of the Red Warbler *Bruce G. Elliott* 184

Sexual and Agonistic Behavior of the Common Rhea *Robert J. Raikow* 196

General Notes

juvenal plumage of the spotted rail (*rallus maculatus*) *Robert W. Dickerman and Kenneth C. Parkes* 207

porcupine quills found in foot of sharp-shinned hawk *Alice Kelley and Neil Kelley* 209

the migration of the american golden plover through surinam *F. Haverschmidt* 210

mew gulls in ontario *Robert F. Andrle and Harold H. Axtell* 211

color aberrations in some alcids on st. lawrence island, alaska *Spencer G. Sealy* 213

flicker incubates pink plastic balls, on a lawn, for five weeks *Sally Hoyt Spofford* 214

HOODED WARBLER IN TRINIDAD, WEST INDIES .... *C. Brooke Worth* 215
RECORD OF FEMALE CARDINALS SHARING NEST .... *Orville O. Rice* 216
RELATIONSHIPS AMONG SOME SOUTH AMERICAN SEEDEATERS (*SPOROPHILA*) WITH A RECORD OF *S. HYPOCHROMA* FOR ARGENTINA *Lester L. Short, Jr.* 216
STATUS OF LINCOLN'S SPARROW IN JAMAICA, WEST INDIES .... *Michael Gochfeld* 219
APPENDICULAR MYOLOGY OF PASSERINE BIRDS .... *Andrew J. Berger* 220

ORNITHOLOGICAL NEWS 224

ORNITHOLOGICAL LITERATURE 225

Lester L. Short, Jr. Three papers on variation in flickers (*Colaptes*); *Hybridization in the Flickers* (Colaptes) *of North America*; *Variation in West Indian Flickers* (*Aves*, Colaptes); *Variation in Central American Flickers*, reviewed by Ned K. Johnson; H. J. Frith, *Waterfowl in Australia*, reviewed by Paul A. Johnsgard; David F. Parmelee, H. A. Stephens, and Richard H. Schmidt, *The Birds of Southeastern Victoria Island and Adjacent Islands*, reviewed by George A. Hall.

PUBLICATION NOTES AND NOTICES 195, 232

A STUDY OF THE RUFOUS-FRONTED THORNBIRD AND ASSOCIATED BIRDS

ALEXANDER F. SKUTCH

PART II: BIRDS WHICH BREED IN THORNBIRDS' NESTS[1]

THE open nests in which the majority of birds lay their eggs are rarely attractive to birds of other kinds, although a poor builder, such as a dove or a cuckoo, may use an abandoned nest as the foundation for its own crude construction. Closed nests, however, are eagerly sought by many kinds of birds that cannot build them, but either wait until such a structure is abandoned or forcibly evict the rightful occupants. Nests so massive and well enclosed as those of the Rufous-fronted Thornbird (*Phacellodomus rufifrons*) have many claimants, some of which are mild and inoffensive while others are mercilessly aggressive toward the industrious builders.

TROUPIAL

The melodious Troupial (*Icterus icterus*), or *turpial* as it is called in its native land, the national bird of Venezuela, is a large oriole about 10 inches long. Its head, throat, chest, back, wings, and tail are black, with a broad white longitudinal band on each wing. The rest of the plumage is bright orange. The sharp bill is black, with the basal half of the lower mandible bluish gray. Behind each clear yellow iris is a large triangle of bright blue skin, from which a narrow extension passes forward over the eye. The legs and toes are plumbeous. The sexes are difficult to distinguish by their appearance and even by their voices.

The Troupial inhabits more or less arid, open country, with scattered trees or light woodland, in northern and central Venezuela, northern Colombia, and the islands of Curaçao and Aruba. Popular as a cage bird, it has been carried to many lands, especially the Antilles, where it has become established in Puerto Rico and St. Thomas and has been recorded in the wild in a number of other islands. On the mainland, it ranges from sea level up to about 4,250 feet (Phelps and Phelps, Jr., 1963:349). Considering the fame of this bird, surprisingly little has been published about its habits in the wild state. Todd and Carriker (1922:475) reported that it was fairly common on the Goajira Peninsula, where it often perched on the giant cactus, upon the fruit of which it fed almost exclusively when in season. In northeastern Venezuela it was rather common throughout the year along the borders of the seasonal deciduous woods (Friedmann and Smith, 1950:528).

In the vicinity of Pirapira, a region of fairly high rainfall, Troupials

---

[1] Part I of this paper appeared in The Wilson Bulletin, 81:5–43, (1969).

were rare. Here I found them in the rows or clumps of trees with bushy undergrowth that interrupted the extensive pastures. They were always in pairs, and seem never to flock in the manner of many other icterids. They subsist upon fruits and insects which they find amid foliage. They hang back downward while investigating clusters of leaves or old inflorescences, and they hold the larger edible objects beneath a foot while they tear them apart with their sharp bills.

The song of the Troupial is notable for its full, mellow notes rather than for intricate structure or continuous flow, as in the thrushes. Although the phrases tend to be short and repetitious, they enchant us by their rich tones. *Come right heere* (the last syllable higher and long drawn out), *come right heere*; and *come heere come heere*; and *here come here come*, are verses that I often heard. Except in the morning twilight, I rarely heard long-continued, freely flowing song. When the Troupial sings, the long, aculeate feathers of its throat stand out like a bristly black beard.

Available accounts of the nesting of the Troupial are brief and confusing. One of the most detailed is that of Cherrie (1916:207), who wrote:

> "A nest and set of eggs was collected at Caicara [Venezuela] May 4, 1907. The nest had as its foundation the half decayed mass of grasses that once served, most probably, as a nest of *Pitangus sulphuratus rufipennis.* Repairs had been made in the roof and a lining of soft grasses had been placed on the bottom of the nest cavity. From the outside there was nothing to indicate that it was more than an old nest long since abandoned. The entrance, the original one, was on one side but completely hidden from below by surrounding foliage. In the same tree were three other deserted nests of *Pitangus*, each of which was in a much better state of preservation than the one that the trupial had selected."

Phelps (1953?:75) states that sometimes Troupials construct their own nests in the form of a pouch, but generally they take advantage of old nests of other birds, making certain repairs to them. Bond (1960:222) reports that in the West Indies the Troupial nests in a deep, purse-shaped, pendant structure, built like that of the Jamaican Oriole (*Icterus leucopteryx*). Smith (Friedmann and Smith, loc. cit.) was told that the Troupial uses the nests of the Rufous-fronted Thornbird instead of building for itself. He would not vouch for this belief; but in April he did observe Troupials, on two occasions in different localities, entering thornbirds' nests. Schwartz (*in* Gilliard, 1958, color fig. 192) published a photograph of a Troupial at the entrance of a thornbirds' nest. He told me that, in his long experience in Venezuela, Troupials breed only in thornbirds' nests in regions where the two species occur together. (They were not sympatric at Caicara, where Cherrie found the Troupial using a nest of the Great Kiskadee.) It is not evident that anyone has ever watched Troupials construct the pouches in which they sometimes nest; they may have been made by some other bird. My

FIG. 1. A large nest of the Rufous-fronted Thornbird in which Troupials raised a brood. The entrance to the chamber occupied by the Troupials can be seen in the lower part of the nest. The constriction in the middle of the nest was later made much more pronounced. Pirapira, Carabobo, Venezuela, April 1966.

own experience of the nesting of the Troupial, limited as it is, makes me doubt that it could build competently.

Establishment of a pair in thornbirds' nests.—The first wild Troupials that I ever saw were a pair that on 3 April visited a thornbirds' nest that I was watching, clinging to it here and there and peering into its chambers, all in silence. During a day on the *llanos* of Cojedes, the only Troupials that I noticed were a pair at a thornbirds' nest. The only pair that I discovered breeding at Pirapira did so in a thornbirds' nest.

This large nest (Fig. 1), containing five compartments, hung, at a height of 12 feet, from a small leguminous tree (*Gliricidia sepium*) in the midst of a pasture, close by a much larger mango tree. When I first noticed the nest at the beginning of April, six thornbirds slept in it. As I approached this nest on the evening of 9 May, a Troupial flew from it. Soon thereafter the six thornbirds entered. I withdrew to a greater distance and stood half-concealed. Presently the Troupial returned and, with some hesitation, entered a chamber below that in which the thornbirds rested. As the larger bird went in, some of the thornbirds came out, but they soon re-entered their dormitory. I noticed no antagonism between the two kinds of birds. Subsequent examination showed that the Troupial had made, in the side of the chamber where it slept, an opening much wider than the original doorway. It had not yet laid an egg there.

On the following evenings, the thornbirds and the Troupial entered the large nest without paying much attention to each other. Once, when the Troupial arrived while the thornbirds were retiring, the four who had just entered flew away with the other two who were still outside; and this caused the Troupial to fly off, too. The thornbirds returned first; and after all six had entered, the Troupial went into its compartment without causing them to emerge.

Meanwhile, the thornbirds had been building a new nest in the same tree, eight feet from the old one. By 18 May two thornbirds were sleeping in the new nest; and before the end of the month all six had moved to it, leaving the old one to the Troupial. This long structure was growing thinner in the middle, just above the chamber occupied by the Troupial. Although the thornbirds had transferred many sticks from it to their new nest, they removed these sticks chiefly from the top and did not seem responsible for this constriction in the middle of the old nest. One morning I surprised a Troupial clinging to the side of the nest, apparently pulling out sticks; but the bird was very shy and would not continue its activity in my presence. not even after I had hidden myself in a neighboring thicket. By the time the Troupial had finished remodeling the thornbirds' nest, it had roughly the shape of an hour-glass. The sticks that had been pulled from its side littered the ground below.

On the evening of 1 June, while from concealment I watched the thornbirds retire into their new nest, mellow whistles announced the arrival of the pair of Troupials. After clinging to the old nest here and there, one of them entered the compartment which for at least three weeks had been serving it or its mate at a dormitory, while the other continued to move among the surrounding branches. Presently the Troupial emerged from this dormitory, tried several other compartments, and finally stayed in one in the constricted middle of the nest, from which the outer layers of the wall had been torn away. This bird's mate then entered the room which the first had just vacated, so that now the two Troupials occupied chambers that adjoined each other vertically. In a little while the bird in the higher compartment, evidently not feeling at ease there, came out and tried to join its mate in the lower chamber. It forced itself most of the way in, but in the end was obliged to return to the higher compartment. Either the lower chamber was too small to hold two Troupials, or the one already within repulsed its mate. From this evening's watch I learned two important facts that were later fully confirmed: (1) that both sexes of the Troupial use thornbirds' nests as dormitories; and (2) that adult Troupials sleep singly.

As I approached these thornbirds' nests in the dim, misty dawn of 2 June, a stag was eating the ripe fallen fruits beneath the neighboring mango tree. He raised his antlered head to look at me, then trotted off toward the nearest thicket with his white tail raised above his back. The male Troupial was already looking forth from the higher chamber, singing in his velvety voice *Here come, here come*, and *come right here, come right here.* After continuing to sing for about five minutes, he emerged and repeated his mellifluous notes while he clung to the outside of the nest or flitted among the surrounding branches, waiting for his mate to come forth. When at last she darted from the lower chamber, the two flew away together.

That evening the Troupials arrived at the nests before the thornbirds, and one entered the lower of the two chambers which they had occupied on the preceding night. After it was well settled, its mate came and clung in the doorway, as though wishing to enter; whereupon both flew out, to rest a while in neighboring trees. This happened three times. The fourth time that one entered this lower chamber, the other followed it inside. For a few minutes, both remained out of sight; then one appeared in the doorway and slowly emerged, as though being pushed or pecked from behind and reluctant to go. When finally outside, it climbed up and entered the higher compartment. But in a little while it came out and again tried to join the other below. Repulsed once more, it re-entered the less desirable upper chamber and stayed while the dusk deepened. I was now fairly certain that it was the female who occupied the lower chamber with the wide doorway and would not permit her mate to sleep with her, but I am not sure which of the two lodged here at the beginning. Possibly the female had claimed her mate's dormitory for breeding.

On the following evening, again, the male joined the female in the lower chamber but stayed only a few minutes, then entered the upper chamber. Soon after this, he provided a more satisfactory bedroom for himself by opening the side of the lower chamber of the nest which the thornbirds had newly built in the same small tree. The wide gap that he made was below the entrance which the thornbirds had provided for this chamber. They had already begun to incubate, and I found a broken white shell on the ground below their nest. Doubtless the Troupial had devoured the contents of the egg. By this time, the female had laid and started to incubate in the older nest, in the chamber where I had first found a Troupial sleeping a month earlier. Throughout the incubation period, and until the young Troupials were almost ready to fly, the female slept in the brood chamber, while he mate lodged nightly in the newer nest nearby.

Where did the poor thornbirds sleep after being evicted from both of their nests? While I watched in the evening from a neighboring thicket, the male Troupial entered the new nest, so early that the long ridge across the valley was bathed in bright sunshine from base to crest, although the nest itself had long been in shadow. After a while, the female Troupial came and clung in front of the compartment with the eggs, but, shyer or more suspicious than the male, she would not enter. As she flew off, her mate emerged from his dormitory and followed her. Soon he re-entered; then the female alighted in front of her nest, only to leave without entering; and again he came out to join her. This happened over and over, while the shadows crept to the summit of the eastern ridge. Although the male Troupial apparently could not see the female from inside his bedroom, somehow he sensed her departure and emerged to learn what was wrong. Retreating then to a more distant observation post, I had the satisfaction of seeing both Troupials settle down for the night in their respective chambers. Then, peering through my binoculars in the deepening dusk, I saw the six thornbirds, or most of them, arrive and enter the compartment above the incubating female Troupial, where far a while her mate had reluctantly slept. The male Troupial and the thornbirds had, unwillingly on their part, exchanged dormitories. The thornbirds were back again in the chamber where they had slept before the Troupials had torn away the outer layers of the wall.

For a week or more, the thornbirds lodged above the incubating Troupial. Sometimes the male Troupial chased them as they left in the morning. Meanwhile, the thornbirds were building a third nest, on the farther side of the spreading mango tree, 65 feet from their first nest. Nevertheless, they occasionally visited the old nest where the Troupials had eggs, bringing a twig to it, or climbing over it to arrange the sticks of which it was composed. When a Troupial found one of them there, it chased the smaller bird. One morning I saw a Troupial drive a thornbird from the old nest or near it. The brilliant bird hotly pursued the dull one through the crown of the large mango tree, thence to a smaller tree, then across 25 yards of open pasture into a thicket. Even here the aggressive Troupial did not relent, but continued to chase the poor fugitive through the close-set bushes until I lost sight of its glowing plumage. Rarely have I seen one bird pursue another so long or with such fierce persistence. Since I heard no outcry from the thornbird, who in the dense thicket had the advantage over the bigger assailant, I believe that it escaped. Soon thereafter the thornbirds moved to their newest nest and had fewer encounters with the Troupials.

The eggs.—On 6 June, nearly a month after I discovered that a Troupial was sleeping in the thornbirds' nest, I for the first time found one member of the pair inside in the daytime. Next day I brought a ladder and found three eggs, the full set. They differed considerably in shape and pigmentation. One was long and strongly tapering, the others shorter and relatively broader. On a dull white ground, they were irregularly speckled, blotched, and scrawled over the whole surface, but most heavily on the thicker end, with shades of brown and pale lilac. A few of the heavier spots were almost black. These eggs measured 28.3 × 17.8, 26.0 × 18.1, and 25.5 × 17.8 mm. The three eggs in a set found by Cherrie (1916:208) at Caicara, Venezuela, on 4 May 1907 were similar but slightly larger.

The eggs in the thornbirds' nest rested on a thick pad of finely shredded, light-colored vegetable material, which the Troupials had placed over the sparser lining originally applied by the thornbirds. At the rear of the chamber, where the wall of sticks was thin, it had been covered with coarse grass stalks and the like, shutting out most of the light. The nest chamber was 4½ to 5 inches in diameter by 5 inches high. The opening that the Troupials had made in the front was 4½ inches wide by 3½ inches high. Recalling how difficult I had found it to open a thornbirds' nest with my fingers, I marvelled that the Troupials had succeeded, with their slender, sharply pointed bills, in making this wide gap in the wall. This, and the removal of sticks from the part of the nest immediately above their chosen chamber, represented by far the major part of their labor in preparing a receptacle for their eggs and young. The application of a bit of lining was, for an oriole, a paltry effort at nest making.

Incubation.—While incubation was in progress, I passed two mornings watching the Troupials' nest from a blind. Although I could not distinguish the sexes of this pair, my failure to witness a change-over during 13 hours of watching makes it almost certain that only the female incubated, as in all other icterids for which information is available.

On 10 June I began my vigil at 05:55, while the waning moon still shone brightly. The earliest birds had just started to sing. I did not see the male Troupial fly from his dormitory, but presently I heard him singing superbly. Then five or six thornbirds emerged from the compartment above the incubating female and spent many minutes climbing over their ruined nest, passing from chamber to chamber (except the one where the Troupial was incubating) until, at 06:25, the last of them flew away. The female Troupial did not leave her eggs until 06:32. By 12:43 she had taken nine sessions, ranging from 12 to 45 minutes and averaging 28.9 minutes, and the same number of recesses, ranging from 4 to 23 minutes and averaging 12.3 minutes. She was in the nest for 70 per cent of the morning.

Five days later, on 15 June, the male Troupial left his dormitory and began to sing at 06:03. Then he chased the thornbirds as they sallied from the chamber above his incubating mate. She first flew out at 06:33, for a recess lasting 13 minutes. When she returned at 06:46, her partner accompanied her and entered the compartment where the thornbirds had slept, remaining about two minutes. By 13:06 the female had taken nine sessions, ranging from 15 to 61 minutes and averaging 31 minutes. Her longest session began just after noon; the next longest was 43 minutes. Her nine absences ranged from 5 to 22 minutes and averaged 12.7 minutes. She incubated for 71 per cent of the morning. The similarity of the records for the two mornings, both of which were sunny, is noteworthy.

Sometimes, after leaving the nest, the female sang and was answered by her mate in the distance. Occasionally she sang loudly as she was about to enter. Once she returned to her nest with something small, probably a particle of food, in her bill. She seemed to be anticipating the hatching of the nestlings. After she had entered, the male followed her into the nest, where he stayed for less than a minute. I could not see whether he carried anything. Although the male sometimes escorted the female back to the vicinity of the nest, he rarely went as far as the doorway. Evidently the sight of food in his mate's bill stimulated him to look for nestlings. This observation suggests one of the means by which a male bird who does not incubate discovers that the eggs have hatched and it is time to begin feeding them. Since the male Troupial found only eggs in the nest, he did not again enter it during the next four hours. Five more days passed before the eggs hatched.

The nestlings.—By the morning of 21 June there were two newly hatched Troupials. The third egg contained a small dead embryo. The nestlings' pink skin bore sparse gray down. The interior of their mouths was red, and the flanges at the corners were white. When they were only three or four days old, the nestlings were heavily infested with *tórsalos*, the white larvae of a dipterous insect that formed relatively huge swellings under the skin. One nestling bore 10 of these parasites, including three on its head and three on one leg. When the young Troupials were a week old, their eyes were open. The sheaths of their remiges had already become long, and the feather rudiments in other tracts were sprouting through the skin. When the nestlings were 10 days old, their plumage began to expand. The *tórsalos* that had infested them had gone, leaving superficial scars that were already disappearing; but the nestling who had fewer of these larvae was far ahead of the more heavily parasitized one in size and the development of its plumage. When two weeks old, the more advanced of the young Troupials was fairly well feathered, but it remained in the nest for another week.

These nestlings were fed chiefly on insects, larval and mature, with a liberal admixture of fruit pulp. As they grew older and the items delivered to them became larger, it was evident that orthopterons, resembling grasshoppers and crickets, formed an important part of their diet. Some of the larger articles brought by the parents were too badly mangled for identification. The fruit given to the nestlings seemed never to come from the neighboring mango tree, although sometimes a parent visited the ripening fruits that it bore, sticking its sharp bill far into the juicy pulp. Both parents fed the young, seeming to take fairly equal shares in this task. When the two nestlings were five days old, they received 51 meals during four hours of the morning. Some of these meals were delivered while the parent clung in the doorway, back outward; but on other occasions the parent went inside, even when it did not stay to brood. Apparently it was the female who entered, sometimes pushing past her mate who stood in the doorway, feeding, in order to deliver her billful inside. When the two nestlings were 12 days old, they received only 38 meals during four hours of the morning; but now the items given to them averaged larger. Seventeen was the greatest number of feedings in a single hour that I recorded on either morning. To feed the 12-day-old nestlings, the parents always stood in the doorway, often side by side. Frequently they sang while coming with food in their bills.

During four hours of the morning when the nestlings were five days old, they were brooded 10 times, for intervals ranging from 5 to 16 minutes and totalling 106 minutes. Evidently only the female covered the nestlings. Sometimes she ended a session of brooding by pushing past her mate while he clung in the doorway to feed them, but after delivering the meal he never stayed. When 12 days old, the nestlings were brooded through the night, but not after the parent flew from the nest at dawn. Thornbirds of the same age are still brooded much by day.

At first excessively shy, the parent Troupials became bolder after their eggs hatched. When the nestlings were five days old, their mother entered the nest to brood them while I set up the blind in the open pasture about 40 feet in front of the nest; and later that same morning the parents continued to feed the nestlings while I folded up the blind. After a few more days, at least one of the parents would deliver food while I stood exposed only 30 feet away. When I climbed a ladder to look into the nest, the parents would come into the small tree that supported it, alighting a few yards above me and singing rather than scolding with harsh notes. This reminded me that many years before, in Honduras, a Black-cowled or Lesson Oriole (*Icterus prosthemelas*) would intersperse his nasal scolding notes with song when I visited his nestlings. Although the Troupials' vocabulary included nasal notes similar to those of other orioles, they did not use such notes to protest my intrusion at their nest.

I never touched the nestlings after they were feathered. One left the nest on 11 July, while the other, doubtless the one who had had the heavier infestation of *tórsalos*, remained two days longer. The first departed at the age of about 21 days, the second at 23 days. Like the adults, they already had bare skin behind and above the eyes, but it was of less intense blue. I last saw these young Troupials, with a parent who fed them, 10 days after their first flight. The pattern of their plumage was much the same as in the adults, but the colors were less intense. The parts of the body which on the adults are bright orange were on them pale yellow. The prominent longitudinal band on their wings was an impure white. They flew well and soon vanished into a patch of woods.

The female parent continued to pass the night with the nestlings until they were at least 17 days old and well feathered, but during their last nights in the nest they were alone. The other parent still slept in the newer thornbirds' nest in the same tree. About this time, I noticed a wide gap in the lower chamber of a thornbirds' nest situated about 250 feet from the Troupials' nest. This nest did not belong to the large family of thornbirds which the Troupials had hitherto persecuted, but to another family, consisting of a single pair. The nestlings which this pair of thornbirds had been feeding a few days earlier had vanished, and they were trying to repair the breach in their wall. A few days later, however, the hole gaped as widely as before, and I suspected that a Troupial was sleeping here.

Watching in the evening, well concealed in a thicket, I saw the thornbirds bring sticks to their nest, spend some time arranging the top of the structure, then enter their upper chamber, which they were now building up. Presently a Troupial arrived and, after much hesitancy, went to the nest, removed a stick from the wide opening and dropped it to the ground. Finally, it entered to sleep in the lower chamber, while the two thornbirds remained in the upper one.

The last of the young Troupials had just flown, and their nest remained vacant after nightfall. I could not discover where they slept. Probably they roosted in the open until mature enough to capture a thornbirds' nest for their dormitory. Although many birds that sleep in dormitories, including Rufous-fronted Thornbirds, some wrens, some woodpeckers, certain barbets and jacamars, lead their newly fledged young to a suitable nest, other dormitory-using birds, such as Bananaquits (*Coereba flaveola*) and a number of woodpeckers, carelessly leave their fledglings to spend the night in the open while they themselves take shelter in the nest.

After the middle of July, I could find the sleeping place of only one Troupial, an adult who now occupied the chamber whence the young had flown. To my great surprise, it remained within, staring at me, while I directed the beam of my flashlight into its dormitory in the deepening twilight. Two brightly gleaming eyes, like those of some nocturnal creature, reflected the rays from the darkness of the chamber. I was amazed to find such an intense eye gleam in a bird which, as far as I know, is never active by night.

I am aware of no other member of the oriole family that sleeps in a dormitory instead of roosting amid foliage. This pair of Troupials had taken possession of three thornbirds' nests, in all of which they slept and in one of which they later raised nestlings. Their two young were reared at the price of two broods of thornbirds, representing, probably, six young thornbirds. If Troupials were more abundant, they would certainly be one of the chief enemies of thornbirds. Fortunately, these brilliant rascals are, in many parts of their range, far less abundant than the obscure, industrious birds whose nests they steal.

It is evident from this account that the Troupial is not typical of the American orioles currently classified in the genus *Icterus*, of which technically it is the type. In external morphology, it differs in having bare skin around the eye and lanceolate neck feathers. Behaviorally, it differs in stealing the nest of some other bird instead of weaving a deep cup or pouch for itself, and in sleeping in a closed chamber instead of roosting amid foliage. No other oriole that I am familiar with is so aggressive.

PIRATIC FLYCATCHER

The thievish ways of the small, vociferous Piratic Flycatcher (*Legatus leucophaius*) are well known. It appears never to build a nest for itself but captures a covered structure made by some other species. In an earlier work (Skutch, 1960:453–455), I listed nine kinds of birds in whose nests it has been found breeding; and I have no doubt that when the habits of

Neotropical birds have been more extensively studied, the number of its known hosts will be greatly increased. While the prospective victim is industriously building, a pair of Piratic Flycatchers perches nearby, calling breezily and from time to time chasing the builder. To persecute it more vigorously would defeat the Piratic Flycatchers' purposes; but after the nest has been finished and the maker has laid in it, the pirates throw out the eggs, thereby causing it to abandon the nest. Occasionally Piratic Flycatchers even pull out nestlings; once I watched them tear the young from a retort-shaped nest of the Sulphury Flatbill (*Tolmomyias sulphurescens*). This seemed an act of wanton destruction, as the pirates never used the nest.

Although I was aware of no record of the Piratic Flycatcher breeding in a nest of the Rufous-fronted Thornbird, from my long familiarity with this rogue in Central America I was not surprised when, on 26 March, I found a pair of these birds clinging to the front of a thornbirds' nest. This was a large structure, with three of four compartments, hanging 50 feet up in a *Cordia* tree in a pasture. Three thornbirds slept in it, and at least two of them were building a new compartment at the top. While the thornbirds worked, laboriously carrying sticks to this great height by flitting from branch to branch, the pair of flycatchers perched nearby, calling *pee-e-e-e* and *pee-de-de-de* in their usual irritating fashion, and often displaying their yellow crown patches. Frequently they clung, singly or together, in front of the next-to-lowest compartment, which they seemed to have selected to receive their eggs, and occasionally one of them entered it for a few minutes. From time to time, a flycatcher chased a thornbird as it flew down for another stick or ascended with its burden. More rarely, a thornbird chased a flycatcher from the nest, with sometimes the second flycatcher pursuing the pursuer. But neither kind of bird hurt the other, and much of the time they ignored each other.

On the evening of 26 March, I watched the thornbirds retire. After one of the flycatchers flew away, the other remained clinging in front of the nest, calling. The three thornbirds reached the top of their nest from the rear, where the foliage screened their approach. As they came down the front of the structure to enter one of the lower chambers, the pirate attacked but did not stop them. For ten minutes after they retired, the flycatcher remained clinging in front of the nest, then flew off in the dusk.

As daylight faded on 5 April, the thornbirds ascended inconspicuously through the foliage of the *Cordia* tree, and coming over the top of the nest, entered the new compartment without being molested by the flycatchers—perhaps without being noticed by them. The pirates remained clinging to the nest for many minutes, while the thornbirds stayed out of sight in the topmost chamber. At last, in the failing light, one flycatcher flew away, but the other still clung to the doorway of their chosen chamber. Of a sudden, in the twilight, a thornbird emerged from the upper compartment, came down over the side of the nest, and pushed into the lower chamber right in front of the flycatcher, who spread its wings over the entrance in a vain effort to block the way.

The other two thornbirds followed, likewise forcing their way into the opening in front of the flycatcher. The latter remained clinging there while it faded from vision in the gathering darkness. Soon I could hardly distinguish even its light head markings through my binoculars. Finally, when it was nearly dark, I though I saw the bird fly away, not clearly enough for certainty.

By 12 April, the flycatchers seemed to be incubating in the next-to-lowest compartment; and now the thornbirds slept in their newly built chamber at the top of the nest. By 29 April the flycatchers were feeding nestlings, and by 23 May the young had gone. The number of thornbirds who slept in the upper chamber was now reduced to two. By 8 June, when the flycatchers were incubating their second brood, the thornbirds had at last begun to incubate in the chamber above them. On 28 June and 6 July, both kinds of parents were feeding nestlings. Occasionally a flycatcher would dart perfunctorily at a thornbird arriving with food, but mostly each of the four parents minded its own business. I last watched this nest on the evening of 18 July. The flycatchers had vanished, and there was no way of telling whether they had successfully raised their young, for these birds do not return to their nest to sleep. But when only two thornbirds entered the nest in the twilight, I knew that they had somehow lost their brood.

OTHER SPECIES

Jinete Flycatcher.—Machetornis rixosa has been variously called the Short-winged Tyrant (Hudson, 1920, I:161) and the Fire-crowned Tyrant (Phelps and Phelps, Jr., 1963:174), neither of which names serves to distinguish it from a dozen other species of Tyrannidae. Surely the Venezuelan name *Jinete*, or *Atrapamoscas Jinete*—the Horseman, the Mounted Flycatcher—is more distinctive; for the first thing that one is likely to notice about this seven-inch, brownish gray, yellow-breasted bird is its curious habit of riding on the backs of quadrupeds—horses, cattle, pigs, or dogs. This penchant has been noticed by various writers, from Argentina to Venezuela; and the first Jinetes that I ever saw, on the extensive salt meadows at Chichiriviche on the coast of the state of Falcón, were resting on the backs of the half-wild asses so numerous there. When hunger prompted them to leave these comfortable perches, they dropped down to the ground, over which they walked or ran with alternately advancing feet, catching insects stirred up by the grazing animals, much in the manner of anis. Hudson was impressed by how swiftly they ran over open ground. Friedmann and Smith (1955:506) noted the increase of these flycatchers in the well-watered camps of the oil companies in northeastern Venezuela. Here they took to following men mowing the laws, also like anis, and to capturing disabled or freshly killed insects at parked automobiles, as likewise insects that were attracted to lights during the preceding night.

These authors state that *Machetornis* builds bulky nests of grass under the eaves of houses and in the axils of the stout petioles of palm fronds. In Argentina, it often breeds in a hole in a tree trunk, where it builds a neat nest of slender twigs and leaves, lined with horsehair. It also takes possession

FIG. 2. A nest of the Rufous-fronted Thornbird in which a pair of Blue Tanagers built their nest. The photograph was taken in the dry season when the tree was temporarily leafless. Pirapira, Carabobo. Venezuela, April 1966.

of the bulky nests of sticks built by the Firewood-gatherer (*Anumbius acuticaudatus*), to retain which it must often battle fiercely with other claimants, such as the Bay-winged Cowbird (*Molothrus badius*) (Hudson, 1920, I:94, 163). In Venezuela, where *Anumbius* and its nests are absent, the Jinete finds a similar site in the nests of the Rufous-fronted Thornbird. Schwartz published a photograph of a Jinete at a thornbirds' nest (*in* Gilliard, 1958, color fig. 126). I saw no Jinetes at Pirapira; but during a day on the *llanos*, I found a pair of these flycatchers at a thornbirds' nest that hung in the midst of a small colony of Yellow-rumped Caciques (*Cacicus cela*). While one of the flycatchers guarded in front, the other disappeared inside; but I could not stay long enough to learn whether they were breeding or only preparing to do so. Another pair of Jinetes alternately visited two thornbirds' nests hanging in the same tree, at one of which the thornbirds were building.

Blue Tanager.—In South America, as in Central America, the common, widespread Blue Tanager (*Thraupis episcopus*) usually builds its neat, cup-shaped nest amid the foliage of a tree or tall shrub. Occasionally, however, it prefers a more sheltered situation, as in the midst of a bunch of green bananas hanging in the plantation, on a beam beneath the thatched roof of an open shed (Skutch, 1954:192), or in a thornbirds' nest (Fig. 2). Early in the morning of 23 May, I stood watching a pair of thornbirds going over their large nest, entering and leaving the chambers. A pair of Blue Tanagers perched in the branches above the nest and repeatedly darted down at the thornbirds. Each time the aggressors bore down on them, the thornbirds slipped into a chamber for safety, soon to reappear. Later in the morning, when no thornbird was in sight, both tanagers arrived with nest material in their bills. Although earlier, when in an aggressive mood, they had paid no attention to my presence below them, now they showed their habitual wariness and would not come to the thornbirds' nest to deposit their loads, even after I had withdrawn a good distance to watch. In the evening I again found the tanagers at the thornbirds' nest, but they flew away before the thornbirds arrived. As far as I could learn, the tanagers never finished their nest in this inaccessible structure.

Later in the same morning, 23 May, I noticed a second pair of Blue Tanagers building in another thornbirds' nest. The bottom of this large structure was falling away, exposing the interior of a chamber. Here, sheltered by the whole mass of sticks above them, but with easy access on the open side, the tanagers were completing their cup. Both sexes brought fine fibers for the lining. On later visits, I failed to find the tanagers incubating or attending nestlings here; but in mid-June, when the supporting tree was felled for posts, I extracted their well-made nest from the ruins of the thornbirds' home.

On 25 May I noticed a third pair of Blue Tanagers carrying material into a thornbirds' nest. Apparently they never laid in this structure, which hung conspicuously from a mango tree, above the edge of a pond.

Sayaca Tanager.—The Sayaca Tanager (*Thraupis sayaca*) resembles the Blue Tanager but is paler, and in Venezuela it prefers more arid country. On 22 July I noticed one of these birds carrying nest material into a small, apparently unfinished nest of the thornbird, in a low, exposed tree standing on the bank of a stream in the *llanos.* Once the tanager entered through the doorway in the side and emerged through the top of the nest.

Saffron Finch.—The Saffron Finch (*Sicalis flaveola*) breeds in a variety of holes and crannies, ranging from a natural cavity in a tree, an old woodpecker's hole, or a space beneath a roof, to the closed nest of some other bird, such as an abandoned structure of an oriole, a cacique, a flycatcher, or a spinetail (Cherrie, 1916:191–193; Mitchell, 1957:226–227; etc.). This finch's habit of nesting beneath roof tiles is responsible for its Venezuelan name, Canario de Tejado (Phelps, 1953?:92). It lines its chosen cranny with various soft materials. At Pirapira the Saffron Finch was far from abundant and I found no nest. Paul Schwartz told me that one June he discovered a pair of these finches breeding in a thornbirds' nest which earlier had held an active Troupials' nest.

Striped-backed Wren.—The Striped-backed Wren (*Campylorhynchus nuchalis*), a member of the cactus-wren group, sometimes uses an old thornbirds' nest as a foundation for its own bulky structure. I noticed such a nest above the busy old highway between Valencia and Maracay.

Great Kiskadee.—Although the Great Kiskadee (*Pitangus sulphuratus*) usually builds in the fork of a tree, sometimes it welcomes a broader foundation for its bulky, domed nest of straws. In mid-April I found a kiskadee incubating in such a structure that it had built atop a thornbirds' nest hanging from a mango tree, about 20 feet above the margin of a small pond.

Thick-billed Euphonia.—On 21 July, long after the kiskadees had abandoned the above-mentioned nest, I noticed a pair of tiny Thick-billed Euphonias (*Tanagra laniirostris*) building their own nest inside its ample chamber. As in other species of euphonias, the male and female were taking fairly equal shares in the work, usually arriving and leaving together. They did not sing while they built.

Striped Cuckoo.—Paul Schwartz told me that he once saw thornbirds feeding a fledgling Striped Cuckoo (*Tapera naevia*). This cuckoo parasitizes chiefly, if not exclusively, members of the Furnariidae, species of *Synallaxis* and *Certhiaxis* being its usual dupes.

Some account has been given of nine species of birds which, in their breeding season, derive more or less benefit from the thornbirds' massive nests. Some of these birds, such as the Troupial, appear, at least in certain regions, to be largely dependent on the thornbird for chambers in which to nest, as likewise to sleep. Although the Piratic Flycatcher is known to breed only in closed nests made by other birds, it has a wide variety of hosts, some of which it appears to prefer to thornbirds. For still other birds, such as the Jinete Flycatcher and the Saffron Finch, the thornbird's nest is an alternative to a natural or man-made hole or cranny or the nest of some other species of bird. Blue Tanagers occasionally seek the shelter afforded by a thornbird's nest instead of following their usual practice of building their open cups amid foliage, and probably the same is true of the Sayaca Tanager. For Striped-backed Wrens and Great Kiskadees, the thornbird's nest is hardly more than a foundation for their own bulky structures. For a pair of Thick-billed Euphonias, a thornbird's nest was only the support of a support.

The relations of these tenants of thornbirds' nests with the thornbirds themselves are various. Troupials do much harm to thornbirds, often destroying eggs or nestlings in the nests they covet for breeding or sleeping. Although the thornbirds may continue to lodge in compartments adjoining those occupied by Troupials, I doubt that they could raise a brood in the same nest with these aggressive icterids. Piratic Flycatchers and thornbirds may, as we have seen, simultaneously incubate or feed nestlings in different compartments of the same nest; yet these aberrant flycatchers are potentially dangerous neighbors, for sometimes they wantonly throw eggs or nestlings from nests that they do not need. Little is known of the relations of the Jinete with its thornbird hosts. The remaining tenants of thornbirds' nests are probably not injurious to the builders. Blue Tanagers prefer old chambers so open that the thornbirds would not use them. Much remains to be learned of the interrelations of all these birds and the thornbirds. Likewise, more extended observations will certainly lengthen the list of species that breed in thornbirds nests. I should be greatly surprised if the Southern House Wren (*Troglodytes musculus*) does not at time occupy them. And not only birds, but animals of other kinds, find a lodging in these barracks of sticks. Mitchell (1957:133) quotes earlier writers who found mice established in the older parts of thornbirds' nests.

SUMMARY

Nine species of birds are known to make more or less use of thornbirds' nests for breeding. Most of these birds do so only occasionally, and they may occupy only old nests or abandoned parts of nests, so that they are hardly injurious to the thornbirds. The Troupial, however, appears regularly to breed in thornbirds' nests wherever the two species occur together, and it also uses them as dormitories. The nesting of a pair of Troupials was followed from beginning to end.

The Troupials did not use the entrances provided by the much smaller thornbirds, but tore a wide gap in the side of each chamber that they occupied. This pair of Troupials opened in this way two nests built successively by one family and one nest of a neighboring family, destroying one set of eggs and one brood of nestlings.

A month before laying began, a Troupial started to sleep in the chamber where the brood was reared. The male of this pair, repulsed whenever he tried to join his mate in this dormitory, slept in another chamber of the same nest and later in the replacement nest of the same family of thornbirds. While there were eggs and nestlings, he lodged alone in this nest close by the breeding nest.

The Troupials' preparation of their breeding nest consisted in lining it with fibrous materials more liberally than the thornbirds had done and in pulling many sticks from the part of the elongated structure above their chosen chamber, causing it to become constricted in the middle. The Troupial's three eggs, laid in early June, were incubated by the female, for periods ranging from 12 to 61 minutes, with a constancy of 70.5 per cent.

Both parents fed the nestlings with larval and mature insects, including many grasshoppers and crickets, and fruit pulp. Only the female brooded. Two young were reared and flew from the nest when about 21 and 23 days old. They did not return to sleep in the nest, which was now used as a dormitory by a single parent.

Neither in external morphology nor in habits can Troupials be considered typical of the group of birds commonly included in the genus *Icterus*.

Thornbirds may sleep in a chamber adjoining that occupied by a sleeping Troupial, but it is doubtful whether they could rear a brood in a structure where Troupials are breeding, as the latter become fiercely aggressive toward the builders of their stolen nest.

A pair of Piratic Flycatchers and a pair of thornbirds simultaneously incubated and fed nestlings in different chambers of the same thornbirds' nest. The latter failed to raise their brood.

In late May, three pairs of Blue Tanagers were found building in as many thornbirds' nests, but none succeeded in rearing a brood.

Other birds known to breed in thornbirds' nests include the Jinete or Fire-crowned Flycatcher, Sayaca Tanager, and Saffron Finch. The Striped-backed Wren and Great Kiskadee sometimes use thornbirds' nests to support their own bulky structures. A pair of Thick-billed Euphonias built in a kiskadee's nest atop a thornbirds' nest.

LITERATURE CITED

Bond, J. 1960. Birds of the West Indies. Collins, London.

Cherrie, G. K. 1916. A contribution to the ornithology of the Orinoco region. Mus. Brooklyn Inst. Arts and Sci. Bull., 2:133a–374.

Friedmann, H., and F. D. Smith, Jr. 1950. A contribution to the ornithology of northeastern Venezuela. Proc. U. S. Natl. Mus., 100:411–538.

Friedmann, H., and F. D. Smith, Jr. 1955. A further contribution to the ornithology of northeastern Venezuela. Proc. U. S. Natl. Mus., 104:463–524.

Gilliard, E. T. 1958. Living birds of the world. Doubleday and Co., Garden City, New York.

Hudson, W. H. 1920. Birds of La Plata. J. M. Dent and Sons, London and Toronto.

Mitchell, M. H. 1957. Observations on birds of southeastern Brazil. Univ. of Toronto Press, Toronto.

Phelps, K. D. de 1953? Aves venezolanas: cien de las más conocidas. Creole Petroleum Corporation, Caracas, Venezuela.

Phelps, W. H., and W. H. Phelps, Jr. 1963. Lista de las aves de Venezuela con su distribución. Tomo I, parte II. Passeriformes. Segunda edición. Bol. Soc. Venezolana Cien. Nat., 24:1–479.

Skutch, A. F. 1954. Life histories of Central American birds. Pacific Coast Avif., 31.

Skutch, A. F. 1960. Life histories of Central American birds II. Pacific Coast Avif., 34.

Todd, W. E. C., and M. A. Carriker, Jr. 1922. The birds of the Santa Marta region of Colombia: a study in altitudinal distribution. Ann. Carnegie Mus., 14:1–611.

EL QUIZARRÁ, SAN ISIDRO DEL GENERAL, COSTA RICA, 3 OCTOBER 1966.

SOME ASPECTS OF THE ECOLOGY OF MIGRANT SHOREBIRDS. II. AGGRESSION

HARRY F. RECHER AND JUDY A. RECHER

THE behavioral patterns of migrant shorebirds differ considerably from those of the same birds on the breeding grounds. The dynamic character of migration and the formation and maintenance of flocks contrasts with the fixed location of the nest site and the lower population densities on the breeding grounds. Population density greatly increases during migration. Species with different breeding ranges or from different habitats join together forming dense multispecific aggregations and frequenting habitats within which all foraging individuals must resort to the same horizontal plane (Recher, 1966).

Aggressive interactions between shorebirds can be observed during both the breeding and the non-breeding seasons, but may occur for very different reasons and have very different effects. During the breeding season aggression is primarily associated with territoriality and courtship. During migration and on the wintering grounds, aggression is primarily associated with interactions between foraging individuals. The density of foraging aggregations and the restriction of individuals to the same horizontal plane creates situations in which some birds may find it difficult to maintain individual distance through avoidance movements and in which the availability of food organisms may be restricted by the presence of competing individuals. Thus it is not surprising that frequent and often prolonged aggressive interactions are a distinctive characteristic of shorebird foraging aggregations during migration.

In this paper we describe the patterns of aggression observed among migrant shorebirds and relate these patterns to prevailing environmental conditions. Some consequences of aggression are also discussed. Descriptions of individual encounters, postures and movements associated with shorebird aggression will be presented elsewhere.

PROCEDURE

The conclusions presented here are based upon observations made between August 1961 and December 1966 along the East, West, and Gulf Coasts of North America. They are primarily concerned with behavior observed in coastal habitats, but probably the conclusions reached are applicable to birds frequenting inland regions.

To provide a quantitative basis for the comparison of aggression under different environmental circumstances, aggressive interactions were scored as to the frequency of occurrence and the intensity of individual events. Intensity is necessarily a subjective evaluation, but to provide a basis for the quantitative comparison of aggressive behavior each display and movement was scored on the basis of time and energy expended and

TABLE 1

INTENSITY VALUES ASSIGNED AGGRESSIVE DISPLAYS AND MOVEMENTS

Intensity Value	Displays and Movements
1.0	Threat display; intention movement; simple supplanting movement (e.g., foraging displacement)
2.0	Displacement movements other than simple supplantations (e.g., defense of individual distance)
3.0	Displacement movements followed by pursuit; displacement movements in which the attacked bird is forced to flight; stand-off displays; pursuit
4.0	fighting

assigned an "intensity value" of from one to four (Table 1). The greater the time and apparent energy expenditure, the higher the assigned value. Because aggressive interactions between individuals might involve any number of separate displays and movements, each interaction was recorded as a series of numbers representing each separate display and movement involved—for example: a threat display followed by a fight and then pursuit would be scored as 1, 4, 3 giving the entire interaction an intensity value of 8. When an interaction involved three or more individuals, the displays and movements of each interacting pair were scored separately—for example: a bird attacked by two others in immediate succession might result in the sequence 1, 3 : 2, 4, 3 giving intensity values of 4 and 9 for each pair's interactions. Translated the 1, 3 might indicate a threat display followed by displacement and pursuit, and the 2, 4, 3 might indicate displacement resulting in a fight followed by pursuit. Appropriate notations were used to keep individuals separate if, for example, the attacked individual became the pursuer.

During periods of observation, censuses were made at a maximum of 5 minute intervals. Whenever possible, the area censused was measured and any noticeable patchiness recorded. (We use the words "patchy" and "patchiness" to indicate the distribution of environmental resources (food and space) as discrete packets or patches.) In the habitats studied, patchiness results primarly from the intermixture of different kinds of substrates, from variations in water content or distribution, and from topographical irregularities.

OBSERVATIONS

Differential Species Aggressiveness.—The frequency of aggression observed during migration varies considerably between species. In part, this is a result of the variable abundance of species—one would not expect to frequently observe aggression between individuals of very rare or uncommon species. But it remains true even among species which are abundant during migration and which form dense foraging aggregations that certain of these (i.e., Red-backed Sandpiper (*Calidris alpina*)[1] and dowitcher (*Limnodromus* spp.)

---

[1] In this paper we have chosen to follow the current B.O.U. Check-list in merging the genera *Ereunetes* and *Erolia* with the genus *Calidris* and the genus *Totanus* with the genus *Tringa*. A variety of behavioral and ecological observations leads us to conclude that this is a more realistic classification than that used in the 1957 A.O.U. Check-list.

are only infrequently aggressive whereas with others (i.e., Western Sandpiper (*Calidris mauri*) and Semipalmated Sandpiper (*Calidris pusillus*)) aggressive interactions are common.

As a result of these species differences, the ideas presented here are based primarily upon observations of Western Sandpipers and Sanderlings (*Crocethia alba*) on the West Coast and of Semipalmated Sandpipers, Sanderlings, and Semipalmated Plovers (*Charadrius semipalmatus*) on the East Coast. Instances of aggression observed between individuals of other species (particularly: Marbled Godwit (*Limosa fedoa*), Willet (*Catotrophorus semipalmatus*), Lesser Yellowlegs (*Tringa flavipes*),[1] Greater Yellowlegs (*Tringa melanoleucus*), Least Sandpiper (*Calidris minutilla*), White-rumped Sandpiper (*Calidris fuscicollis*), Ruddy Turnstone (*Arenaria interpres*), Black-bellied Plover (*Squatarola squatarola*), and Avocet (*Recurvirostra americana*)) have helped in understanding the ecology of aggression. Observations on the infrequent occurrence of aggression among such abundant species as Red-backed Sandpiper and Dowitcher were also of considerable value. They provide a background against which the aggressive behavior of other species stands in bold contrast.

Interspecific Aggressive Interactions.—Aggressive interactions between individuals of different species are normally infrequent and of lower average intensity than intraspecific aggressive interactions occurring simultaneously. Of 926 aggressive interactions scored involving Semipalmated Sandpipers in situations where other species were present, only 4.3 per cent were interspecific. The interspecific interactions observed during the course of this study are presented in Table 2. Undoubtedly, others occurred of which we were not aware and not all of the interactions observed between Semipalmated Sandpipers and Least Sandpipers or between Western Sandpipers and Least Sandpipers were recorded, but the small number of interactions observed for other species pairs do serve to show the infrequency with which interspecific aggression occurs. It most often appears that individuals of different species, if not ignorant of, are at least indifferent to each other's presence. Where interspecific aggression does occur it is usually between morphologically similar individuals in situations of intense intraspecific conflict, as for example, occurs in territorial defense. Sixty-five of the 138 interspecific interactions recorded in Table 2 involve one or more territorial individuals and 88 of 138 involved congeneric birds. Of 126 interactions scored for Western Sandpipers defending feeding territories within multispecific aggregations, 26 per cent were interspecific. All involved the morphologically similar Least Sandpiper.

Despite the increased frequency of interspecific aggression observed to occur during instances of territorial behavior, the average intensity of these

TABLE 2

INTERSPECIFIC AGGRESSIVE INTERACTIONS

Attacking Bird	Attacked Bird	Number Observed Interactions	Average Intensity
Charadrius semipalmatus	*Charadrius vociferous*	1	1.0
Charadrius semipalmatus	*Calidris pusillus*	1	1.0
Catoptrophorus semipalmatus	*Tringa melanoleucus*	1	1.0
Catoptrophorus semipalmatus	*Crocethia alba*	1	1.0
Catoptrophorus semipalmatus	*Limosa fedoa*	8	1.0
Tringa flavipes	*Tringa solitaria*	5	2.0
Calidris melanotos	*Calidris pusillus*	2	1.0
Calidris fuscicollis	*Charadrius semipalmatus*	2	2.0
Calidris fuscicollis	*Calidris pusillus*	24	1.9
Calidris bairdii	*Calidris mauri*	4	1.0
Calidris minutilla	*Calidris pusillus*	2	2.0
Calidris minutilla	*Calidris mauri*	4	2.5
Calidris alpina	*Calidris minutilla*	3	1.0
Calidris alpina	*Calidris pusillus*	3	1.0
Calidris alpina	*Calidris mauri*	1	1.0
Calidris pusillus	*Charadrius semipalmatus*	1	1.0
Calidris pusillus	*Calidris melanotos*	1	1.0
Calidris pusillus	*Calidris fuscicollis*	4	1.0
Calidris pusillus	*Calidris minutilla*	12	1.9
Calidris pusillus	*Calidris alpina*	3	1.0
Calidris pusillus	*Crocethia alba*	2	1.0
Calidris mauri	*Calidris minutilla*	31	1.0
Calidris mauri	*Lobipes lobatus*	2	1.0
Limosa fedoa	*Catoptrophorus semipalmatus*	5	1.0
Crocethia alba	*Calidris minutilla*	4	1.8
Crocethia alba	*Calidris pusillus*	2	1.0
Crocethia alba	*Calidris mauri*	4	2.0
Crocethia alba	*Calidris alpina*	5	1.6

interactions remains less than simultaneously occurring intraspecific territorial interactions. The average intensity of interactions between Least Sandpipers and territorial Western Sandpipers was only slightly greater than 1.0 whereas the average intensity of intraspecific (Western Sandpiper) interactions occurring simultaneously was 2.5. Of the 41 interspecific aggressive interactions scored involving Semipalmated Sandpipers, 31 occurred in situations where Semipalmated Sandpipers were defending territories. The average intensity of these 31 was 2.0; of the remaining 10, only 1.0. Contrast the average intensity of 2.0 for interspecific interactions involving territorial Semipalmated Sandpipers with an average intensity of 3.0 for 106 intraspecific territorial interactions between Semipalmated Sandpipers.

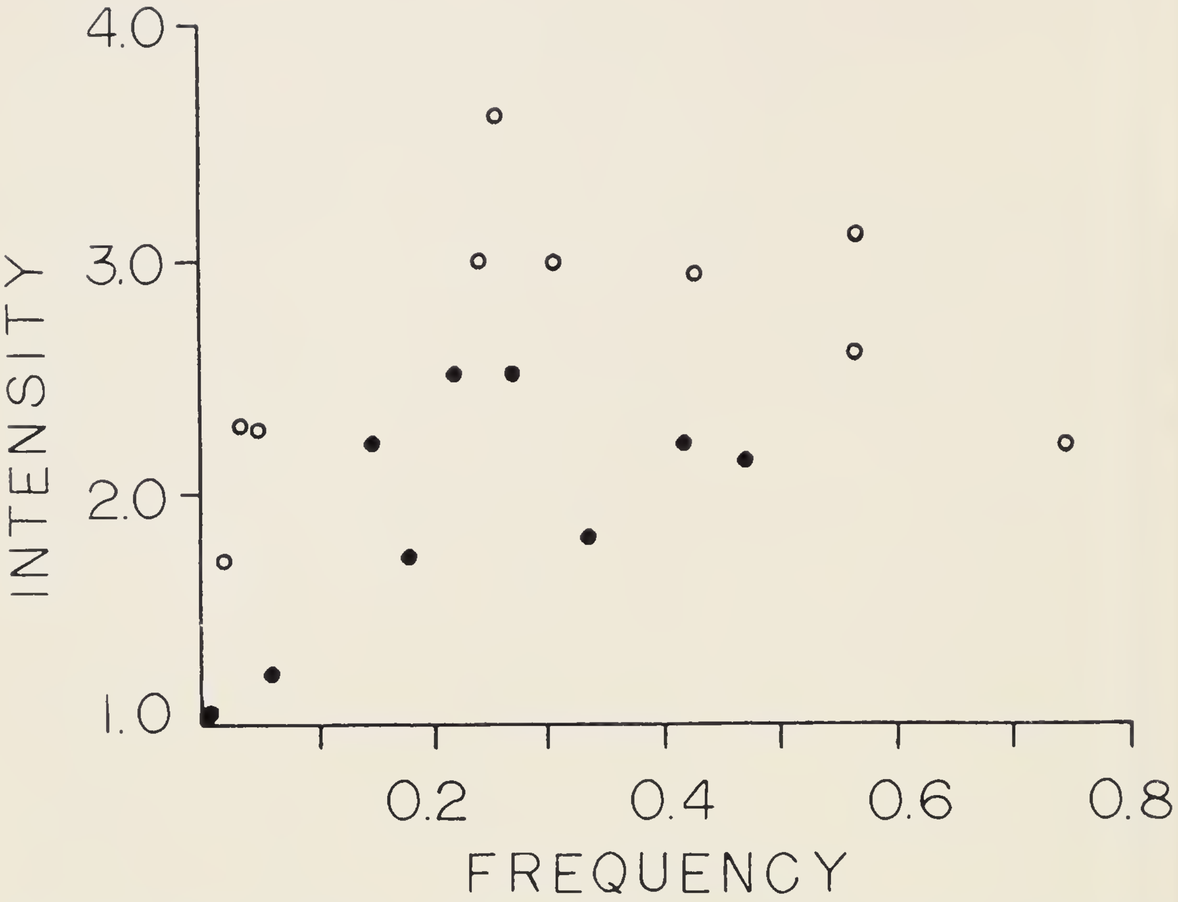


Fig. 1. Relation between frequency and intensity of aggressive interactions. Legend—● Frequency and average intensity of aggressive interactions between non-territorial Semipalmated Sandpipers (*Calidris pusillus*) at Jamaica Bay, New York during August, 1965. Each point represents a minimum of 30 minutes of scored observation. ○ Frequency and average intensity of aggressive interactions between Semipalmated Sandpipers in situations where at least two of the individuals in the observation area were territorial. Each point represents from 5 to 45 minutes of scored observation. Frequency is plotted as the number of interactions observed per minute of observation per individual.

Intraspecific Aggression.—As stated previously, most aggressive interactions occur between conspecific individuals. Species differ in aggressiveness and even between aggregations of species in which aggression is most often observed, the frequency and intensity of aggression varies widely. Within most aggregations of foraging shorebirds, aggressive interactions are limited to low intensity threat displays or supplanting movements, but at any time one may also observe prolonged interactions involving movements and displays assigned high intensity values (e.g., fighting).

In part, the intensity of aggression can be correlated with the frequency of aggressive interactions, while frequency appears to be determined by various environmental conditions.

The Relation between Frequency and Intensity of Aggression.—As the

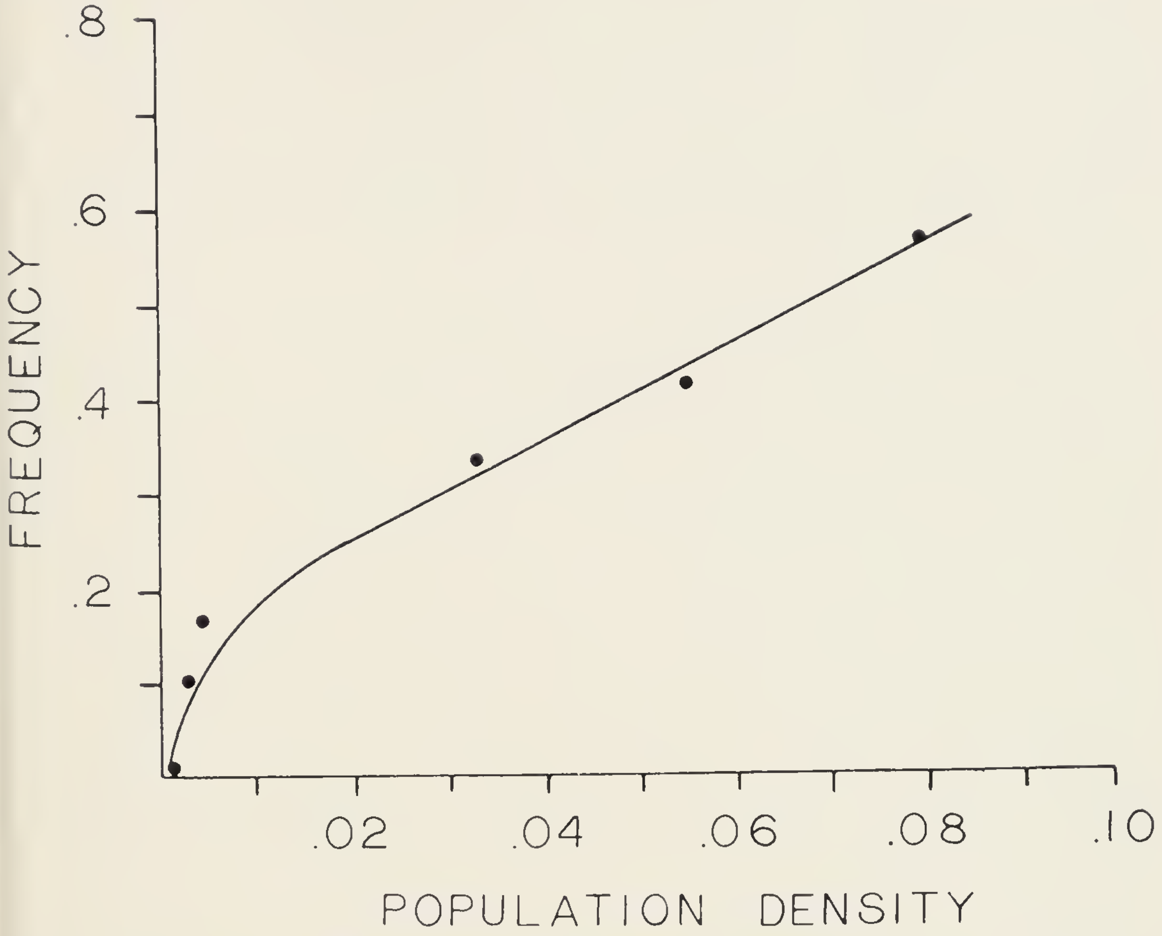


Fig. 2. Relation between frequency of aggressive interactions and population density. The frequency of aggressive interactions (per individual per minute) between non-territorial Semipalmated Sandpipers (*Calidris pusillus*) at Jamaica Bay, New York has been compared to population density as density increased through migration between 20 and 31 August 1965. The observation site and the area of the observation site remained constant throughout the observation period. Each point represents a minimum of 30 minutes of continuous observation. Population density is represented as individuals per square foot.

frequency of aggression changes or when we compare situations with different interaction frequencies, we find that the average intensity of the interactions observed also changes or differs (Fig. 1). In general, the average intensity of the interactions observed increases as the frequency of aggression increases. However, there is a point beyond which there appears to be a slight but definite decrease in average intensity with a continuing increase in the frequency of interactions. This pattern is also observed in situations where at least some individuals are territorial (Fig. 1).

The observed decrease in average intensity with high frequencies of aggression does not necessarily result from any decrease in interactions assigned high intensity values (for example, fighting or lengthy sequences of displays and movements), but follows from a relative increase in the number of displays and movements assigned low intensity values (for example, threat displays and supplanting movements). As the frequency of aggression increases a greater number of individuals become involved. Indicative of the greater involvement of individuals is an increase in the number of birds displaying threateningly or bumping and supplanting others within the group. Thus, interactions are more frequent, but of average lower intensities.

Frequency and Population Density.—Normally, the frequency of aggressive interactions is greatest at high population densities and decreases as the population density decreases. In Figure 2, the frequency of aggressive interactions among non-territorial Semipalmated Sandpipers has been compared over a succession of days. The area on which these birds were foraging remained unchanged throughout the period of observation, but the overall population density increased as a result of migration. As may be seen from the figure, the frequency (and consequently the intensity) of aggression increased as the density of the population increased. (The brief span of time covered by these observations makes it unlikely that the observed changes in the frequency of aggression are the result of temporal changes in behavior.) However, there are exceptions to this general rule. Aggression is suppressed at very high population densities and may be reasonably frequent at very low population densities if some of the individuals present are territorial.

Gradual changes in population density such as occurred in the example presented above (Fig. 2) demonstrate quite nicely the overall relation between the frequency of interactions and population density. However, a more frequent situation is the rapid increase in population density following an influx of new individuals or the reduction of the foraging area available on rising tide. In both these instances, the frequency of aggression changes abruptly as the population density rapidly increases as is shown, for example, in Figure 3.

Most often the initial aggressive response to increasing population densities results in the dispersion of individuals, a consequent reduction of population density and a reduction in the frequency of aggression. If population density remains at a higher level than that preceding the influx of new individuals the frequency of aggression may also remain higher, but is invariably lower than that prevailing during the initial aggressive response.

Perhaps the greatest and most consistent concentrations of migrant shorebirds occur along the water's edge on a falling tide. Yet, despite the large numbers of birds aggregated within this relatively narrow zone, aggressive interactions are relatively infrequent. Similarly, large numbers of birds are occasionally seen to aggregate and forage within exceedingly limited areas—presumably they are attracted by an extreme concentration of food

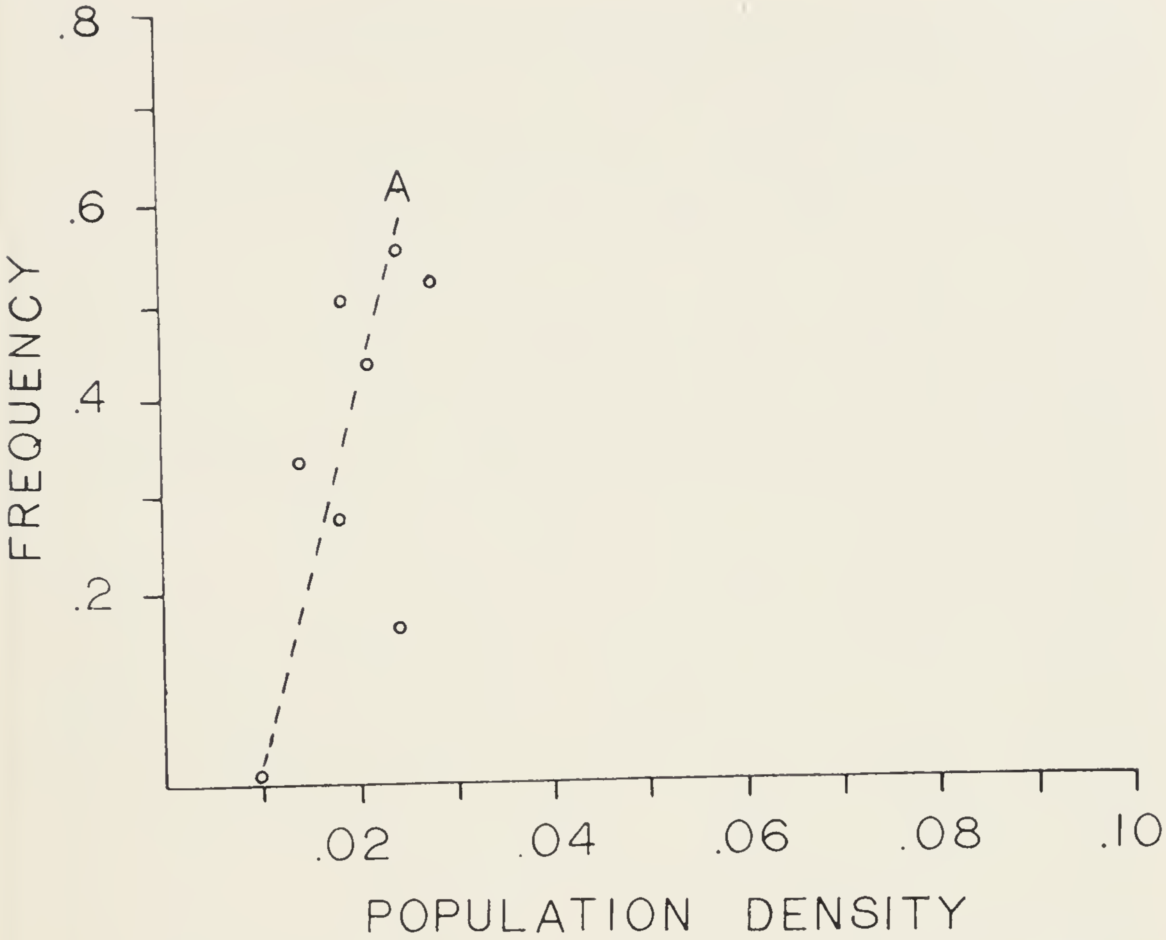


FIG. 3. Relation between frequency of aggressive interactions and population density. Changes in the frequency of aggressive interactions (per individual per minute) between Semipalmated Sandpipers (*Calidris pusillus*) as population density changes abruptly with a decrease in available foraging space on the rising tide at the Brigantine National Wildlife Refuge, New Jersey on 4 August 1964. The points plotted represent consecutive 5 minute scores over a 40 minute period.

organisms—in much the same way as individuals aggregate at a receding water's edge. Here also aggression is suppressed, but may be observed during the initial stages of aggregation and again during dispersal. It is likely that both the extreme population density of these aggregations and the abundance of available food act together to suppress aggression. Brawn (1961) in a study on cod (*Gadus callarias*) observed that the frequency of aggression was depressed while the fish were actually feeding, but shortly after all food was consumed aggression would reappear with "greatly increased vigour."

It is reasonable to presume that once the frequency of aggression exceeds a certain level being aggressive is no longer of benefit to the individual. The individual is therefore confronted with two choices, he may either leave the area or he may cease responding aggressively to the presence of others. If food is particularly abundant (as it is along a tide edge) it is unlikely the individual will find as good foraging elsewhere and the second choice becomes the better strategy.

Patterns of Intraspecific Aggression.—The local distribution and abundance of migrant shorebirds is, in part, a result of the mutual attraction and repulsion of individuals. Attraction is evident by the failure of individuals to occupy uncrowded or empty areas, preferring instead, to join or remain with others. In contrast, repulsion is represented by the maintenance of individual distance and territoriality. Attraction, like aggression, is most pronounced among conspecific individuals. In multispecific aggregations of foraging shorebirds, individuals tend to associate conspecifically. Single individuals or small groups may temporarily associate with other species, but movements and distribution are normally determined by the physical environment and other conspecific individuals.

Individual Distance.—There is an area around each bird—individual distance—within which other individuals are not tolerated (Conder, 1949). The radius of this area varies, and among migrant shorebirds aggression appears to result when the individual cannot maintain individual distance by avoidance movements and still remain in a suitable feeding area. Aggression is infrequent among shorebirds foraging on very uniform and extensive expanses of tidal mud or sandflat. Where the distribution of suitable foraging area is patchy or restricted as along a water's edge or in a drying marsh, aggressive interactions are more frequent. In the latter situations, individual movements are partially restricted by the patchiness of the habitat and avoidance of other individuals becomes difficult without leaving the foraging area. Patchy environments are also conducive to the establishment of feeding territories.

Avoidance of other individuals becomes increasingly difficult as population density increases. Thus, even when individuals are able to remain in a suitable foraging area, an increase in the level of aggression usually results as population density increases. Population density stabilizes as individuals adjust the extent of individual distance defended with a consequent decrease in the frequency and intensity of aggressive interactions. Because they can adjust the extent of distance defended, individuals are able to forage in areas of higher population densities without being involved in continuous aggression. The ultimate population density which results, depends upon the extent to which individual distance is restricted. It seems likely that the extent of individual distance defended is, in turn, determined by the distribution and abundance of available food organisms. If food is abundant and uniformly distributed, an individual can probably forage efficiently within areas of very high population density. In such circumstances, an individual will restrict the extent of individual distance defended and the frequency of interindividual aggressive interactions will be less than in an area where the available food supply is limited or patchily distributed. In the latter situation, individuals will maintain a greater individual distance and may establish feeding territories. Individuals in such are area will respond aggressively to any increase in population density and except when "overwhelmed" by an influx of a large number of new individuals, will maintain population density at a relatively low level.

Territoriality.—During the non-breeding season, individual shorebirds frequently establish and maintain feeding territories. The establishment and defense of these territories follows a pattern similar to that used by many birds in the establishment and defense of breeding territories. The boundaries of feeding territories are well defined and territorial birds "advertise" their territory by a combination of displays and calls. Individuals defending adjacent territories "recognize" their mutual boundaries and each is "dominant" within his own area. How long a territory is maintained depends in part upon where it is established and in part upon the environmental stimulus initiating territorial behavior. It is obvious that territories established below high tide line cannot be maintained beyond the duration of exposure by low tide. Territories established in non-tidal areas may be maintained for long periods of time being re-established from one day to the next. We have recorded instances in which Western Sandpipers and Willets continuously defended territories in excess of five hours and in which a territory was re-established at the same site for at least three days. Unfortunately, we were not able to determine whether with Western Sandpipers the same individuals were involved in re-establishing territories, but are certain that the same Willet returned each succeeding day of observation. Hamilton (1959) in a study of migrant Pectoral Sandpipers (*Calidris melanotus*) found that territorial individuals returned to their territories each day over a number of weeks. He also observed that only a small percentage of the individuals in the area actually established territories and that these were all male birds. Of five territorial Western Sandpipers collected at Palo Alto, California during fall migration of 1963, three were males and two were females. Our observations on Western Sandpipers, Semipalmated Sandpipers, Sanderlings, Willets, and Semipalmated Plovers indicate that the same individual may be territorial or non-territorial and that territoriality depends largely upon environmental conditions. It is not unusual to observe a territorial bird leave his territory, forage elsewhere and then return to re-establish the abandoned territory.

There are two general situations in which we have observed territorial behavior. The first and by far the most common is in patchy environments where either foraging sites are limited or food organisms patchily distributed. Sanderlings, for example, will defend small patches of substrate turned over by humans digging on tidal flats for worms or clams. On shallow, drying puddles territories established by Western and Semipalmated Sandpipers are invariably located on the downwind shore whenever the breeze has been sufficiently intense to pile up food organisms along the shoreline. Territories are also established along water edges when the zone suitable for foraging is narrow and, in this sense, the available foraging space is restricted. A second situation conducive to territorial behavior has only been observed with Sanderlings though it should apply to other species as well. Sanderlings foraging along open sandy beaches most frequently form foraging flocks which move along the beach as integrated units. If however, food organisms are scarce, Sanderlings disperse and individuals establish territories. It is predictable that a sparse food supply would elicit territorial behavior. The probability of obtaining the occasional food item appearing at the surf edge decreases as the number of Sanderlings foraging at that point increases. The concentration of food in one situation and its scarcity in another are both readily apparent to the human observer and the advantage gained by the territorial bird despite the expenditure of time and energy necessary for territorial defense seems fairly obvious. (Aggressive interactions involved in territorial defense are generally of greater duration and involve a greater number of displays and movements assigned higher intensity values than are associated with non-territorial interactions (Fig. 1).

Though quantitative evidence is difficult to obtain, an indication of the advantage territorial individuals have over non-territorial individuals was secured in a series of observations made on a group of Sanderlings foraging along a water's edge where *Limulus* were spawning. The spawning area had been subdivided into feeding territories with the result that there were a small number of territorial birds within the spawning area and a larger number of non-territorial birds around the periphery making frequent attempts to cross territorial boundaries and forage within the spawning area. Aggressive interactions between territorial and non-territorial birds were frequent and relatively intense (average intensity 2.4). Both groups of birds expended considerable time and energy in aggressive interactions (the two territorial individuals scored spent 32.4 per cent of their time defending their territories and the four non-territorial birds scored spent 38.8 per cent of their time in actual aggressive interactions), with the important difference being that territorial birds were able to forage between aggressions in an area with a very dense concentration of food (*Limulus* eggs literally covered the substrate surface) whereas non-territorial individuals expended *all* the time between aggressions in non-foraging movements about the periphery of the spawning area. Eventually, non-territorial individuals left this area and resorted to less suitable sites (no concentration of *Limulus* spawn).

Tolerance of Neighbors.—There are situations in which shorebirds (especially Semipalmated Sandpipers, Western Sandpipers, and Semipalmated Plovers) may be very tolerant of other individuals (neighbors) foraging in the same area (i.e., individual distance may not be defended), but in which new individuals (strangers) entering the area are attacked and driven off. We have observed this behavior most frequently in small aggregations (less than 15 individuals) foraging in non-tidal situations where suitable foraging areas are small and patchily distributed. *In effect,* the situation is one in which a number of individuals are defending the same territory—tolerant of each other, but intolerant of strangers. However, there is no co-ordinated group action nor is the composition of the group stable so that the area *cannot* be considered a group territory in the sense of Carrick (1959).

Of 104 aggressive interactions scored involving Semipalmated Sandpipers in situations like that described in the preceding paragraph in which the attacked bird was driven from the group area, 70 involved newly arrived birds. Yet, it appears that this is not a case of individuals "recognizing" one another, but of attacking and driving off any conspecific bird landing within the area. Thus, the few non-group birds who happen to walk into the area are generally tolerated and group individuals flying up and relanding within the area are attacked. Each of the 34 interactions scored between group individuals in which the group bird attacked was driven off involved an individual who had flown up and relanded. Group individuals relanding in the area and attacked were frequently able to defend themselves successfully and remain within the area. In only five instances was a non-group individual able to remain within the area after flying in and being attacked. Generally individuals are attacked by one group member after another until driven from the defended area. A result of this response to strangers and the tolerance of neighbors is a remarkably constant population size within the defended area. In a typical series of five-minute censuses for a group of Semipalmated Sandpipers defending a wet area on a drying marsh at Brigantine, New Jersey, the recorded group size was 7, 7, 6, 7, 6, 7.

DISCUSSION

In an ecological sense, aggression among migratory shorebirds is essentially a response dictated by prevailing environmental conditions whether these be population density or the distribution and abundance of food organisms. It is predictable that aggression should occur in those situations in which the individual benefits from being aggressive.

Presumably for individuals of "non-aggressive" species, aggression does not result in any consistent or significant advantage. Species in which aggression is infrequent tend to be birds which forage by probing into the substrate. They also tend to forage below the water's edge. In contrast, most aggressive species forage above the water's edge and tend to visually locate prey found on the substrate surface. It is possible that probing birds foraging below the water's edge are utilizing a more abundant or more uniformly distributed food supply. Certainly they have access to a wider vertical zonation of prey than do birds restricted to taking prey from the substrate surface. That individuals which locate prey visually may also compete more directly for food organisms seems also likely. Visual predators will almost certainly be alert for prey over a greater area immediate to themselves than will species which locate prey by probing. Because of this, one should expect visual predators to maintain a greater extent of individual distance and to be more aggressive in the maintenance of this distance.

Alternatively, it may be that probing birds must expend proportionally greater amounts of time and energy in the location of prey than do visual birds. If this is true, then the difficulties associated with relocating a patch of prey and in determining the boundaries of this patch so that it might be effectively defended may so reduce the chance of any possible benefit from aggression as to result in its essentially complete suppression among probing species.

The diversity of the habitats frequented by shorebirds appears inadequate to permit the ecological segregation of morphologically similar species (Recher, 1966). The general lack of interspecific conflict among morphologically dissimilar species, but its relatively high incidence among the morphologically similar Least and Western Sandpipers on the West Coast and Least and Semipalmated Sandpipers on the East Coast bears this point out. Grant (1966) in an experimental study of three morphologically similar sparrows, *Zonotrichia spp.*, found interspecific aggression to be most pronounced between the two most morphologically similar species even though the two species normally frequented different habitats. Such interspecific behavioral interactions may be important in the ecological segregation of species. Of the three sandpipers mentioned above, the Least and Semipalmated and the Semipalmated and Western have broadly overlapping bill measurements, but the Least and Western do not. The Semipalmated and Western Sandpipers occur together in only a small portion of their respective migratory ranges. Unfortunately, where they do cohabit we have no information as to how they interact behaviorally. The relationship of the Least Sandpiper to each the Semipalmated and Western Sandpipers is, however, of considerable interest and one reasonably well worked out. The ecology and behavior of these two species pairs illustrate some of the ways in which interactive behavior may determine species relationships.

On the West Coast, the intrahabitat distributions of Least and Western

Sandpipers broadly overlap whereas on the East Coast Least and Semipalmated Sandpipers tend to occupy different habitats and occur together relatively infrequently (Recher 1966). When they are found together aggressive interactions between Least and Semipalmated Sandpipers tend to be more intense (though probably no more frequent) than aggressive interactions between Least and Western Sandpipers in similar habitats on the West Coast (Table 2). It is well known among amateur ornithologists that along the East Coast the Least Sandpiper is a bird of the marshes while the Semipalmated Sandpiper "prefers" the more open tidal flats. Similarly, on the West Coast Least Sandpipers are more often encountered in marshy situations than are Western Sandpipers, but available marshland is considerably more limited along the West Coast than it is in the east. Therefore, we suggest that on the West Coast Least Sandpipers are "forced" to utilize tidal flats more frequently than conspecific birds migrating along the East Coast. Consequently, contact an interaction between Least and Western Sandpipers cannot be so easily avoided by habitat segregation as it can be between Least and Semipalmated Sandpipers. The greater morphological differences and the lesser intensity of interindividual aggression between Least and Western Sandpipers may be tangible measures of the degree to which these two species have interacted in the past. The greater intensity of aggressive interactions between Least and Semipalmated Sandpipers demonstrates the intensity of the interaction between morphologically similar species and may be a prime mechanism in causing habitat segregation. Since they may segregate ecologically by habitat, Least and Semipalmated Sandpipers remain morphologically similar. Undoubtedly, interindividual aggressive interactions have not been the exclusive mechanism in bringing about or maintaining habitat or morphological differences between shorebird species, but as Grant (1966) also suggests, they may be important in initiating and maintaining species differences.

SUMMARY

Frequent and often prolonged aggressive interactions between conspecific individuals are characteristic of shorebird foraging aggregations during migration and on the wintering grounds. Aggression does occur between individuals of different species, but is normally infrequent and of lower average intensity than simultaneously occurring interspecific interactions. Population density and the patchiness of available food and foraging space appear to be the main features of the environment determining the frequency of aggressive interactions. The average intensity of aggressive interactions appears in turn to be determined by the frequency with which individuals interact. Aggression does act as a population spacing mechanism, but individuals are aggressive only because it is a means by which they may appropriate for their own use a portion of the environment (food or foraging space) which would otherwise be unavailable to them.

ACKNOWLEDGMENTS

We would like to thank Paul Ehrlich, Gunther Hadersberger, John Ogden, Michael Soule and John Wourms for their advice and comments. At various times during the course of this research the senior author has received support from the National Science Foundation and the National Institute of Mental Health. That portion of the research done while the senior author was a predoctoral student at Stanford University received support from United States Public Health Training Grants 5T1 GM—365—01 and 02.

LITERATURE CITED

Brawn, V. M. 1961. Aggressive behaviour in the cod (*Gadus callarias* L.) Behaviour, 18:107–147.

Carrick, R. 1959. The contribution of banding to Australian bird ecology, Monograph. Biologicae, 8:369–81.

Conder, P. J. 1949. Individual distance. Ibis, 91:649–655.

Grant, P. R. 1966. Preliminary experiments on the foraging of closely related species of birds. Ecology, 47:148–151.

Hamilton, W. J. 1959. Aggressive behavior in migrant Pectoral Sandpipers. Condor, 61:161–179.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology, 47:393–407.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF SYDNEY, SYDNEY, N.S.W., AUSTRALIA (PRESENT ADDRESS: DEPARTMENT OF ENVIRONMENTAL STUDIES, THE AUSTRALIAN MUSEUM, SYDNEY, N.S.W., AUSTRALIA, 22 MAY 1967.

MOVEMENTS, POPULATION FLUCTUATIONS, AND MORTALITY AMONG GREAT HORNED OWLS

Paul A. Stewart

In his studies of the survival of banded birds, Hickey (1952) used certain recovery records of Great Horned Owls (*Bubo virginianus*) available on 30 July 1946 for development of a life table and other statistics. However, Hickey considered his analysis of the mortality rate of Great Horned Owl to be preliminary and indicated that a further analysis should be made when more data would have accumulated. The present paper includes some more recent data in a life table and in addition summarizes available information on travels of the birds, population fluctuations, and causes of mortality.

This analysis of North American recovery records of Great Horned Owls is based on data from 434 banding recoveries on file with the U.S. Fish and Wildlife Service on 30 November 1962. The birds were banded in 45 states and provinces and recovered in 46. Banding and recovery localities extended from Nova Scotia to California and from central Alberta to Florida. Relatively large numbers of birds were banded in Ohio, Wisconsin, Saskatchewan, New York, and Michigan. Eighty-nine of the 434 birds were banded as adults, 82 as immatures, 205 as juveniles, nestlings or locals, and 58 were unidentified as to age at banding.

For the development of a life table, a class of young birds was formed from those identified as juveniles, nestlings, and locals, the immatures being excluded because of uncertainty of the identification and meaning of this age class. Some birds were undoubtedly identified as adults when they were in fact less than one year of age. The term "direct recovery" is used in this paper to indicate that no more than one migration season intervened between banding and recovery dates. A bird constituting an indirect recovery could have participated in both a departing and returning migration. Arbitrarily, recoveries less than 50 miles from the banding places were dismissed as insignificant local movements, in part because of occasional uncertainties as to the exact locations of banding or recovery.

Data from the Christmas bird counts for 1949–65 as published in Audubon Field Notes (1950–66) were examined in search of evidence of cyclic fluctuations in Great Horned Owl populations, although Stewart (1954) indicated limitations to usefulness of the Christmas bird count data. Granting that these counts leave much to be desired as a scientific method for examining bird population trends, it seems that the data should be sensitive enough to indicate the presence or absence of cycles or major fluctuations in the population.

MOVEMENT

The locations of the recovery records of banded Great Horned Owls suggest that it is relatively unusual for these birds to make long-distance flights, but some such flights are made. Of the 434 recovery records, 405 (93 per cent) were of birds taken within 50 miles of the banding sites. Of the 29 birds recovered more than 50 miles from the banding sites, 16 had traveled more than 100 miles, 7 more than 200 miles, 5 more than 300 miles, 3 more than 400 miles, 1 more than 800 miles. The longest recorded flight was approximately 860 miles from central Alberta to southeastern South Dakota. Some of the 434 birds, however, were killed so soon after banding that they had little opportunity to travel. Of the 434 birds, 379 (87 per cent) were still alive at the end of one month after banding; 330 (76 per cent) were alive at the end of three months. Of the 330 birds surviving at least three months after banding, only the 29 (9 per cent) were recovered more than 50 miles from the banding sites.

In the case of birds recovered after two or more migration seasons passed, recovery at the banding sites, of course, does not mean that the birds had not participated in a migration. It seems likely, though, that only a part of the birds moved southward in any one winter. In central Alberta, 21 recoveries were taken with all seasons represented as follows: winter, 2; spring, 7; summer, 3; fall, 9.

Fewer southern than northern birds made long-distance travels. Of 23 birds banded in central Alberta, 6 (26 per cent) traveled more than 50 miles; of 43 banded in central Saskatchewan, 9 (21 per cent) traveled more than 50 miles; of 48 banded in Ohio, 2 (4 per cent) traveled more than 50 miles; of 32 banded in Michigan none traveled more than 50 miles. In the area south of 50° N and west of 80° W there were 202 birds banded, and only five traveled more than 50 miles between the banding and recovery sites. Of these five birds only two traveled more than 100 miles.

Of the 15 Great Horned Owls traveling 50 miles or more after being banded in central Alberta and Saskatchewan, four traveled in a north-south direction; ten traveled in a northwest-southeast direction; one traveled in an east-west direction. Of four birds traveling 50 miles or more after being banded in New York, all traveled in an east-west direction. Two birds traveled more than 100 miles after being banded in the central United States, but they traveled in the wrong season or direction so that migration was not indicated. Great Horned Owls appear not to perform regular north-south migrations but rather to disperse in all directions (Fig. 1).

Young Great Horned Owls may be more prone to travel than adults, for all except two of the ten direct long distance recoveries were of young birds. It must be recalled, however, that a total of 89 birds were banded as adults and

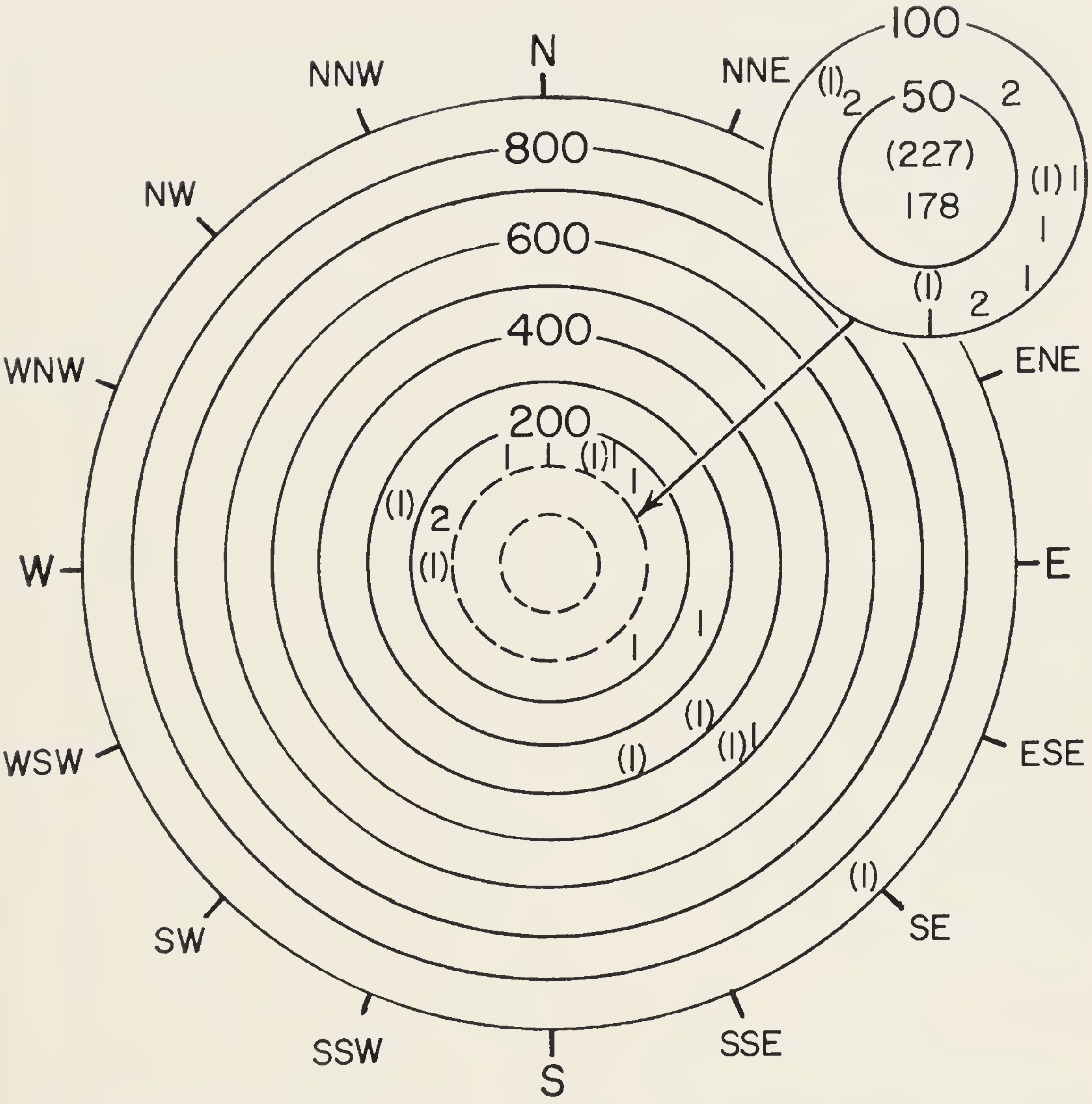


FIG. 1. Movements of Banded Great Horned Owls in Relation to their Banding Places. Distances of movement in miles are indicated by the concentric circles. The numbers of birds moving the various directions are indicated by the numbers between the circles. Numbers for direct recoveries are inclosed in parentheses; indirect recoveries are unmarked.

287 as young birds, so the probability of recoveries was different for the two age groups. All owls taken as direct recoveries and making fairly long-distance movements from central or southern Alberta and Saskatchewan were young birds. In Alberta and Saskatchewan six birds were banded as adults and 61 as young, so again the probability of recoveries of birds banded as adults was much smaller than for young. Only direct recoveries are considered here because when sufficient time had elapsed to get indirect recoveries all of the birds would have attained adult status.

Among the indirect recoveries of Great Horned Owls banded as young in central and southern Alberta and Saskatchewan, there was one bird recovered in central Minnesota on 17 December 1957, 500 miles southeast of the site where it was banded on 24 May 1956. This bird could have made its southward flight in either its first or second year, but if the flight were made in the second year, this would be the only adult making such an extended trip.

That there may have been unusually heavy southward movements of Great Horned Owls during 1916–18 was suggested by Bowles (1918) who reported large numbers in Washington in the falls of 1916 and 1917, by Brockway (1918) who reported large numbers in Connecticut in the winter of 1917–18, and by Soper (1918) who reported large numbers in southern Ontario in the winter of 1917–18. Apparently, none of these reports involved subspecies more northern than those native to the respective regions.

Taxonomists recognize ten races of Great Horned Owls in North America (A.O.U. 1957:277–279) and the fact that this species shows such diversity suggests that either it is relatively sedentary or has a tendency to return to its hatching place to breed. In observations in Kansas, Baumgartner (1939: 282) found that Great Horned Owls remained at their nesting sites throughout the year, except possibly for a few months in late summer and fall. In Michigan, Craighead and Craighead (1956:82) made observations indicating that birds paired during the fall and early winter and then remained at their nesting sites throughout the prenesting period.

POPULATION FLUCTUATIONS

Southland invasions by northern birds of prey usually are assumed to be associated with food scarcity in the North. The chief food of the Great Horned Owl in Canada is the varying hare (*Lepus americanus*) (Errington, et al., 1940:785), and North American populations of this cyclic species were at a low level in the period 1916–18 (Leopold, 1933:65). Speirs (1939:412) reported southward flights of Great Horned Owls during 1916–18, 1925–27, and 1936–38. A 9–11 year cycle was thus suggested. Presumably following Speirs, other authors (Hickey, 1943:76–77; Lack, 1954:209; Dasmann, 1963:148) have reported cyclic fluctuations in the Great Horned Owl population. However, differences of opinion are recorded in the literature as to whether Great Horned Owl populations actually are cyclic. Van Tyne and Berger (1959:178) indicated that the Great Horned Owl is one of several species making "great southward invasions at intervals without evidence of regular cycles."

The Christmas bird counts show no indication of a 9–11 year cycle in the Great Horned Owl population during 1949–65. Likewise no "great southward

TABLE 1

DYNAMIC LIFE TABLE FOR 97 GREAT HORNED OWLS BANDED AS NESTLINGS, JUVENILES AND LOCALS BEFORE 1951 AND RECOVERED BEFORE 30 NOVEMBER 1962

Age in years	Alive at start	No. deaths	Per cent mortality per year
0–1	97	45	46
1–2	52	21	40
2–3	31	9	29
3–4	22	7	32
4–5	15	4	27
5–6	11	2	18
6–7	9	2	22
7–8	7	2	29
8–9	5	2	40
9–10	3	2	67
10–11	1	0	0
11–12	1	0	0
12–13	1	0	0
13–14	1	1	100
Total and mean		97	32

invasion" was shown. While more than three times as many birds were observed in the Christmas bird counts during 1963 as during 1951, much of the difference between low and high levels resulted from a steady increase in numbers of birds observed each year. This steady increase in totals of Great Horned Owls observed on the 51 Christmas bird counts that were examined probably resulted chiefly from a growing increase in efforts of observers to run up large totals of birds to be reported, rather than from population increase. Chandler S. Robbins (pers. comm.) confirmed that there has been increasing effort to find Great Horned Owls in at least two of the counts used in this study.

MORTALITY

A life table was constructed from recovery records of 97 Great Horned Owls banded before 1951 as juveniles, nestlings, and locals. Of these 97 birds, 45 (46 per cent) died within the first year after banding. The mean annual mortality rate after the first year was 31 per cent (Table 1); the mean annual mortality rate after the second year was 30 per cent. With a sample of 58 recoveries, Hickey (1952:116) determined a first-year mortality rate of 51 per cent and an average annual mortality rate after the first year of 23 per cent.

In comparing Hickey's calculated mortality rates with rates calculated in this study, it must be pointed out that slightly different methods of analysis were used. Hickey used an abridged life table constructed from banding totals of all banders who had banded later-recovered nestling Great Horned Owls. The subsequent fates of banded birds were followed through the recovery reports. Data of banders not obtaining recoveries were ignored, thus giving a slight bias toward a higher mortality rate. Hickey's base sample was of birds banded, some of which were not recovered. I used a dynamic life table, as described by Hickey (ibid.:10). My sample included only birds which were recovered, the recovered sample being classified as to the length of life of the birds.

Adult birds appear to have a higher probability than young of being recovered soon after banding. Nine of 80 adults (11 per cent) were recovered in the first week after banding; 4 of 205 young (2 per cent) were recovered in the first week. In the first two months after banding, 39 per cent of the adults and 13 per cent of the young were recovered. These data suggest either that the adult birds may have had some attribute of health or behavior which made them susceptible to capture, first for banding and subsequently for recovery, or that the initial capture for banding made them more easily captured a second time.

One of the banded Great Horned Owls lived 4 years longer than any of the others, or until it was 13–14 years of age. This bird was banded in Iowa on 23 April 1939 and recovered near the banding site on 6 October 1952. Even this 13–14 years of life was less than half the potential life span for the species, for Bent (1938) reported a male Great Horned Owl kept in captivity for 29 years. A captive Eagle Owl (*Bubo bubo*) in Europe was reported by Gunston (1964:114) to have reached the age of 68 years—seemingly the age record for an owl. The loss of bands is undoubtedly an important factor limiting the recorded life spans of wild-living Great Horned Owls.

Information on the causes of death was available for 374 Great Horned Owls. As the deaths of all of these 374 birds were reported by humans and thus each bird came into human hands, this is a biased sample of mortality causes. Shooting was clearly the chief cause of death of birds in this sample, 52 per cent being reported shot. In addition to these, another 8 per cent were reported as injured when found, and most of the injuries may have resulted from shooting. Still another 99 birds (27 per cent) were found dead, and some, perhaps most or all of these, may have been shot—perhaps shot by one person and found dead by another. As many as 322 of the 374 birds (86 per cent) may have died from shooting. Another 37 birds (10 per cent) were trapped and killed. One bird was caught by hand and killed. Of the 374 birds, 360 (96 per cent) may have died from intended killing by man.

Among factors each responsible for death of 2 per cent or less of birds in the sample, being killed by an automobile was the leading factor, accounting for the deaths of six birds (2 per cent). Entanglement in string or wire was responsible for the deaths of two birds and electrocution for one. Only 4 birds (1 per cent) were killed in ways that appeared to have been natural; flying into an object (2 birds), starved (1 bird), avian predator (1 bird).

SUMMARY

A study was made of movement and mortality of Great Horned Owls through use of 434 recovery records of banded birds on file with the U.S. Fish and Wildlife Service on 30 November 1962. Population trends were studied with use of the Audubon Field Notes Christmas bird counts from 51 localities for the period 1949–65.

The banding data indicate that some Great Horned Owls disperse in all directions in the fall and winter, but most remain near their hatching and breeding places throughout the year. Banding recoveries from the northern part of the bird's range were available only from Alberta and Saskatchewan, and movement from this region was chiefly southeastward. The longest flight was approximately 860 miles. Movement was confined to young birds. There was less movement in the southern than in the northern part of the range.

Most recovered Great Horned Owls were intentionally killed my man, chiefly by shooting. First year mortality of young birds was 46 per cent; mean annual mortality after the first year was 31 per cent. The oldest bird lived to be between 13 and 14 years of age. The Christmas bird count data give no indication of major fluctuations, cyclic or otherwise, in the Great Horned Owl population during 1949–65.

ACKNOWLEDGMENT

I am grateful to Allen J. Duvall for making available to me all of the banding recovery records of Great Horned Owls and for a critical reading of this manuscript. Joseph J. Hickey, Brooke Meanley, Helmut C. Mueller, and Chandler S. Robbins also read the manuscript and offered valuable suggestions for its improvement. The help of Alfred J. Godin in preparing Figure 1 is gratefully acknowledged. The feasibility of using statistical tests for analysis of data in this paper was discussed with Robert G. Heath, and he is to be credited with the adopted procedure. The U.S. Fish and Wildlife Service aided in the typing of the manuscript. The many persons who banded Great Horned Owls or reported the owls' recoveries to the U.S. Fish and Wildlife Service performed services essential to this study, but space limitations clearly forestall individual acknowledgment. Likewise, the necessary contribution of a host of observers on Christmas bird counts cannot be individually acknowledged.

LITERATURE CITED

American Ornithologists' Union. 1957. Check-list of North American birds. 5th Ed. Baltimore, Maryland.

Audubon Field Notes. 1950–1966. 4–19 (2).

Baumgartner, F. M. 1939. Territory and population in the Great Horned Owl. Auk, 35:351–352.

Bent, A. C. 1938. Life histories of North American birds of prey (Part 2). U.S. Natl. Mus., Bull., 170.

Bowles, J. H. 1918. Northern owls again visit Washington. Condor, 20:45.

Brockway, A. W. 1918. Large flight of Great Horned Owls and Goshawks at Hadlyme, Connecticut. Auk, 35:351–352.

Craighead, J. J. and F. C. Craighead, Jr. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg and Wildlife Management Institute, Washington.

Dasmann, R. F. 1963. The last horizon. Macmillan Co., New York.

Errington, P. L., F. Hamerstrom, and F. N. Hamerstrom, Jr. 1940. The Great Horned Owl and its prey in north-central United States. Agr. Exp. Sta., Iowa State College of Agr. and Mechanic Arts, Research Bull., 277:759–850.

Gunston, D. 1964. Methuselahs are rare in the wild. Mass. Audubon, 48:110–114.

Hickey, J. J. 1943. A guide to bird watching. Oxford Univ. Press, New York.

Hickey, J. J. 1952. Survival studies of banded birds. U.S. Fish and Wildlife Service, Spec. Sci. Rept.:Wildl. No. 15.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press.

Leopold, A. 1933. Game management. Charles Scribners, New York.

Soper, J. D. 1918. Flight of Horned Owls in Canada. Auk, 35:478–479.

Speirs, J. M. 1939. Fluctuations in numbers of birds in the Toronto region. Auk, 56:411–419.

Stewart, P. A. 1954. The value of the Christmas bird counts. Wilson Bull., 66:184–195.

Van Tyne, J. and A. J. Berger. 1959. Fundamentals of ornithology. John Wiley and Sons, New York.

U.S. DEPARTMENT OF AGRICULTURE, AGRICULTURAL RESEARCH SERVICE, ENTOMOLOGY RESEARCH DIVISION, OXFORD, NORTH CAROLINA. 11 OCTOBER 1967 (ORIGINALLY RECEIVED 12 JANUARY 1966.)

NOTES ON SONG STRUCTURE IN THE TOWNSEND'S SOLITAIRE

Donald J. Borror and K. C. Halafoff

Studies of bird song structure with a sound spectrograph are generally based on sonagrams made with a wide-band filter; such sonagrams exaggerate the frequency spread of a sound, but reveal minute features of tempo. Sonagrams made with a narrow-band filter are seldom used because they exaggerate the timewise spread of a sound, even though they reveal details of frequency more precisely than wide-band sonagrams. Most song structure studies have been concerned primarily with temporal patterns and only general features of frequency, which are best shown by wide-band sonagrams.

Songs of the Townsend's Solitaire (*Myadestes townsendi*), like the songs of many other birds, contain elements that appear in wide-band sonagrams to be abrupt slurs, sometimes ranging over half an octave or more in less than 0.01 second. Since the mark on the sonagram is continuous, the assumption is that the abrupt rise or fall in pitch is continuous, hence the term *slur* appears to be appropriate for such a sound.

In the course of graphing Solitaire songs we made some sonagrams using a narrow-band filter, and it was noticed that some of the slurs had a banded appearance in these sonagrams; this suggested that the abrupt pitch change was stepwise rather than continuous—in the nature of a glissando.[1] Repeated graphing of these "slurs" and studies of the resulting sonagrams have revealed some interesting things about song structure in this bird.

METHODS

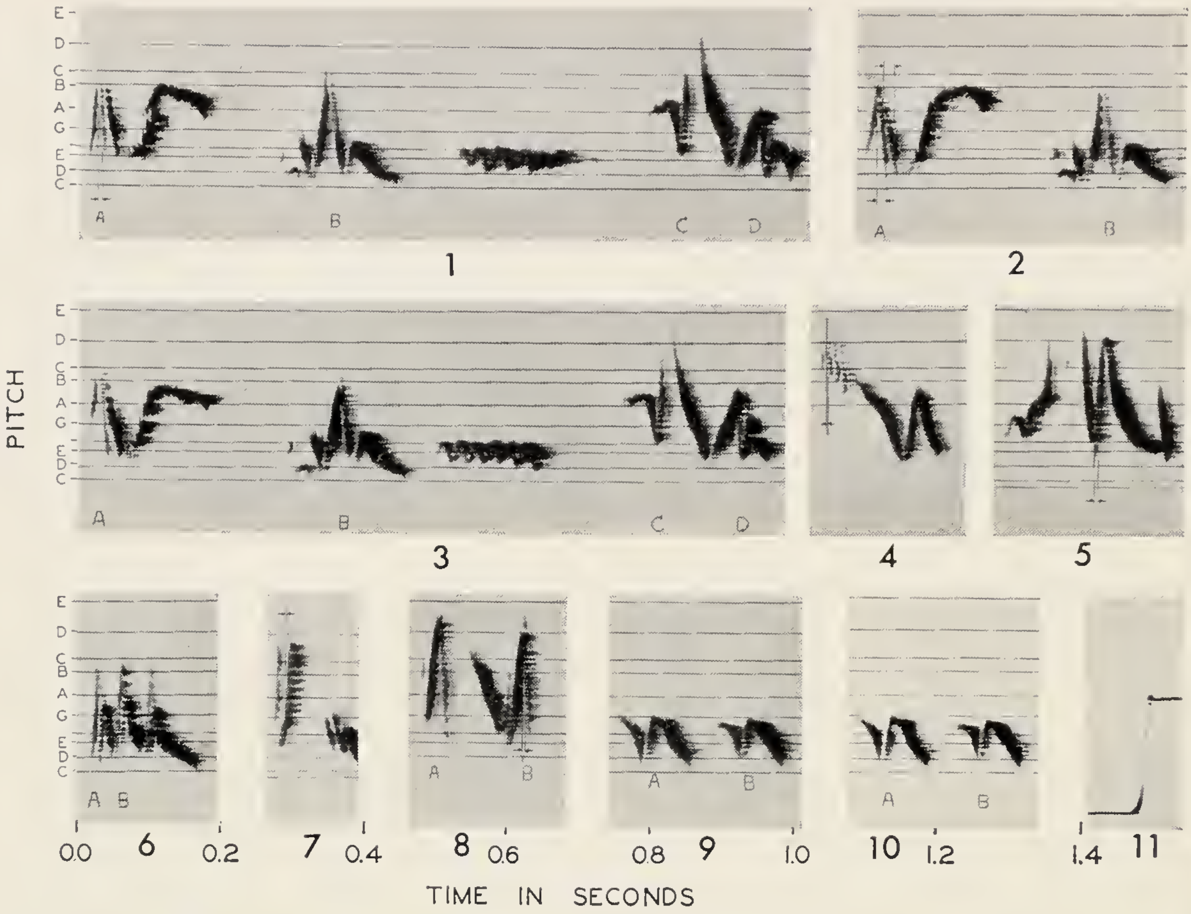
This study was made of the songs in a single recording (with 14 songs), OSU recording no. 7931, made on the north rim of Crater Lake, Oregon, 24 July 1965; the recording was made by D. J. Borror, using a Nagra III recorder, a tape speed of 15 ips, and a D33 American microphone mounted in a 24-inch parabolic reflector. The sonagrams were made with a Vibralyzer sound spectrograph.[2]

We have been particularly interested in the elements of these songs in which there is a rapid and stepwise change in pitch. Since our analyses are based on the banded character of these elements, one may well wonder how accurately the sonagrams portray the true character of the sound. If the pitch change is actually stepwise rather than continuous, this fact would be revealed to the ear in a playback at a reduced tape speed. With our equipment a reduction in tape speed is accompanied by a corresponding

---

[1] Webster's dictionary defines a glissando as "a rapid series of consecutive notes played on a piano, harp, or other similar instrument by sliding one or more fingers across adjacent keys or strings."

[2] A tape copy of one of the songs in this recording was sent to the Kay Electric Company, Pine Brook, N. J. (manufacturers of the Vibralyzer); their study of a glissando in this song showed the same things our studies did. We wish to thank Mr. George Smith, of the Kay Electric Company, for their study of this tape.



Figs. 1–10. Sonagrams of portions of Townsend's Solitaire songs, made with a narrow band filter from songs in OSU recording No. 7931 (Crater Lake, Oregon, 24 July 1965). The lowest *C* in the pitch scale has a frequency of 2093 cycles per second, except in Fig. 7; in Fig. 7 the lowest *C* has a pitch of 1046.5 cycles per second, and the time scale is twice that shown at the bottom of the figure. TF, tonal fraction; I, average time interval between the start of successive steps in the glissando; letters indicating pitch are in italics.

Fig. 1. Four phrases from song 5. Each of the glissandos marked (A, B, C, and D) is immediately preceded by a continuous slur in the opposite direction. In the glissandos at A and B TF decreases with the fall in pitch, from about 1/3 above *C* to 1/6 between *F* and *E* in A, and from about 1/5 between *C* and *B* to 1/6½ between *A* and *G* in B; in C TF decreases with the rise in pitch, from about 1/2½ between *F* and *G* to about 1/4½ between *G* and *A*. The glissando at A is 0.00456 sec in length, with I = 0.00022 sec.

Fig. 2. Two phrases from song 4 (the same phrases as the first two in Fig. 1, but from a different song); note the continuous upslur immediately preceding the downward glissando in B and the first one in A. There are two glissandos at A, the first 0.0123 sec in length, and the second 0.0158 sec; TF between *A* and *G* is 1/5 in the first glissando, and about 1/3½ in the second. TF in the glissando at B varies from about 1/6 to 1/8.

Fig. 3. A portion of song 3, showing the same phrases as Fig. 1; the first two phrases here are the same as those in Fig. 2. The steps in A are fairly distinct between *A* and *C*, a little less so between *G* and *A*; TF between *A* and *C* is about 1/6, and between *G* and *A* is about 1/7. At C there are 4½ steps between *G* and *A* (TF = 1/4½). TF in D

reduction in pitch, and at tape speeds lower than 1/32 normal the sounds are unintelligible; only the slowest of the "slurs" studied (e.g., that shown in Fig. 7) appear stepwise to the ear when played at 1/32 normal speed. Many are preceded or followed by a slur that in narrow-band sonagrams *does* appear continuous; if there is horizontal banding in one of two adjacent "slurs" and not in the other, the two must be different. Sonagrams of a fast shift in frequency of an oscillator tone (Fig. 11) show a continuous mark, with no banding. All of these slurlike passages have been graphed a number of times, forward and backward, and over intervals of several months, and the banding remains the same (see Figs. 9 and 10). We therefore believe that this banding is not an artifact; some of the rapid pitch changes in these songs appear to be glissandos, in which successively higher or lower frequencies are initiated in a stepwise fashion.

We have been primarily interested in two features of these stepwise "slurs" or glissandos, the tonal fractions of successive steps, and the rates at which successive steps appear. Data on tonal fractions were obtained by superimposing on the sonagrams horizontal lines representing notes of the musical scale (omitting, for the sake of clarity, the black notes of the piano); such lines have been put on the sonagrams in Figs. 1–10. Data on step rate were obtained by measuring the time interval between the beginning of the first step and the beginning of the last one (shown in Figs. 1-A, 2-A, 4, 5, 7, and 8-B) and counting the steps it contained. We have obtained some data on step duration from wide-band sonagrams (since the duration of a sound is exaggerated in narrow-band sonagrams), measuring at about the middle of the passage (see legend of Figs. 3 and 4).

←

decreases with the fall in pitch. The duration of the steps in A is about 0.003 sec, and about 0.010 sec for those in B.

FIG. 4. A phrase from song 4. Of the four downslurs at the beginning of this phrase, the first is continuous and the other three are stepwise. The uniform spacing of the steps in the glissando marked means an increase in the TF with decreasing pitch; this glissando is 0.00193 sec in length, with 12 steps; I = 0.00016 sec (the shortest found). The step duration is about 0.002 sec.

FIG. 5. A portion of song 6, with an upward glissando immediately preceded by a continuous downslur. TF decreases with a rise in pitch, from about 1/3 between *F* and *G* to 1/9 between *B* and *C*. I = 0.00021 sec.

FIG. 6. A phrase from song 4; note that the first upward glissando (at A) is preceded by a continuous upslur. TF in the glissando at A is about 1/5 between *E* and *A*, and between *F* and *G* in the first glissando at B it is about 1/3½.

FIG. 7. A portion of song 2; note the continuous upslur immediately preceding the glissando. I = 0.00078, with 9 steps; TF is constant at about 1/3 tone. This was the slowest of the glissandos examined. (The pitch in this sonagram is an octave lower than in the other sonagrams, and the time scale is twice that of the others.)

FIG. 8. A portion of song 5. Each of the two downward glissandos is immediately preceded by a continuous upslur. TF in both A and B decreases with the fall in pitch, from about 1/6 to 1/9 in A, and 1/6 to 1/7 in B. B is 0.00386 sec in length; I = 0.00024 sec.

FIGS. 9 and 10. A portion of song 6, the two sonagrams made several months apart; note the similar banding in the glissandos marked. In A and B TF decreases with the rise in pitch, but the steps in the two (which appear to be renditions of the same sound) are not quite the same.

FIG. 11. Sonagram of a fast shift in frequency of an oscillator tone (from the Kay Electric Company). Note that there is no indication of banding in this abrupt slur.

TONAL FRACTIONS

Most early analyses of bird songs (e.g., Mathews, 1921; Arlton, 1949), which were based solely on aural observations, consisted of musical scores; some modern analyses, based on audiospectrographic studies as well as aural observations (e.g., Hall-Craggs, 1962), have also used musical scores. These scores all use our half-tone musical scale,[3] with the implication that the tonal fractions used by birds were the same as those in this musical scale. Some workers (e.g., Howard, 1952) have suspected that smaller tonal fractions are sometimes used by birds, but little attention has been given this point by modern workers using audiospectrographic methods of song analysis.

Our studies of Solitaire songs have yielded numerous instances of tonal fractions less than a half-tone; some examples are shown in Figs. 1–10 (tonal fraction is abbreviated TF in the figure legends). These fractions varied from about 1/2 to 1/9, and usually changed in size through a given glissando. Increases or decreases in the tonal fractions occurred during both rises and falls in pitch, but as a rule there was no reversal of the direction of the change in a given glissando; a diminishing tonal fraction continued to diminish, and an increasing one continued to increase, until the end of the passage. Only rarely did the tonal fractions remain constant through a passage (e.g., at 1/3 tone in Fig. 7). The fractions often differed in different renderings of what appeared to be the same phrase or figure—in different songs, and in different parts of the same song (cf. A in Figs. 1, 2, and 3; and A and B in Fig. 9). The tonal fractions in two or more glissandos uttered in succession usually differed. In parts of these songs where the pitch was sustained for a short period it was not constant; at the end of the figure in Fig. 3, for example, the pitch falls about 1/4 tone.

STEP RATES IN THE GLISSANDOS

Data on step rates in four of the glissandos shown in the figures are given in Table 1. The time intervals (I) between the beginning of successive steps (the horizontal bands in a narrow-band sonagram) varied from 0.00078 to 0.00016 second; these figures correspond to rates of 1282 to 6211 per second, and represent the rates at which successive steps in the glissandos appear. Measurements of the duration of the steps ranged from 0.002 to 0.010 second; these figures, and the configuration of the steps in narrow-band sonagrams, indicate that successive steps overlap in time—producing a sound with a complex frequency content, but with the successive frequencies beginning in a stepwise fashion rather than all at the same time. It should be noted that our figures on the duration of the steps necessarily includes the reverberation

---

[3] American Standard Pitch, in which the *A* above middle *C* has a frequency of 440 cycles per second, and there are 12 half-tone steps (tonal fraction = 1/2) in an octave.

TABLE 1

DATA ON SOME SOLITAIRE GLISSANDOS

Glissando in Fig.	Length (sec)	Steps No.	Steps Pitch Limits	I*	Steps Initiated per sec.
1A	0.00456	21	E–C#	0.000217	4608
4	0.00193	12	B–D#	0.000161	6211
7	0.00702	9	G–D	0.000780	1282
8B	0.00386	16	G–C	0.000241	4149

* I is the average length of time between the start of one step and the start of the next.

time, which cannot be separated from the actual duration of the sound (as emitted by the bird) once the recording has been made. On the other hand, the values of the time intervals between the start of adjacent steps in a glissando are free from reverberation, as none occurs at the very start of a sound.

Published sonagrams of bird songs do not show note rates higher than about 200 to 250 per second; compared with such figures, our rates of the steps in Solitaire glissandos—up to several *thousand* per second—are fantastically high. The Solitaire is initiating sounds of successively higher or lower pitch at extremely rapid rates; we do not know how the bird is able to produce sounds at these rates.

To date we have found similar glissando-like passages in songs of the Wood Thrush (*Hylocichla mustelina*); it is probable that some abrupt slurs in songs of other birds are also stepwise rather than continuous.

PROBLEMS OF MUSICAL NOTATION

Our musical scale is based on a half-tone musical interval as the smallest tonal fraction. It is possible to modify this scale, using some other fraction (e.g., 1/3 or 1/4 tone), but all such modifications would presume that the minimum tone unit is constant; it is impossible to do this if the tonal fraction is variable, as it is in these Solitaire glissandos. The only way to write down such fractional-tone bird music would be to indicate each note by its frequency figure (attempts to use such notation in modern music have been made), but such a score would be so difficult to read tonally that it would hardly make sense, and no musician would be able to play it.

Time intervals between adjacent sound units in a bird song can be measured with considerable precision, but it is questionable whether these irregular intervals could be indicated accurately in a musical score, even with the smallest musical units. The time between successive steps in Solitaire glissando passages is extremely short, and it would be very difficult to exactly indicate this time in a musical score. Thus the prospect of the universal use of conventional musical notation, even in an amended form, for writing down bird song must be ruled out.

With our present electronic tools, a sonagram with notes of our musical scale superimposed on it (as in Figs. 1–10) is probably the closest to a musical representation of a song that can be obtained. Such a graph could easily be read, both tonally and along the time scale (provided the overtones can be recognized—by their harmonic relation to the basic notes, and by checking through retarded replay and thus separating them from the melody itself); it contains all the sound elements, including loudness (indicated by the darkness of the mark) and timbre (indicated by the harmonics).

SUMMARY

Sonagrams made with a narrow-band filter of abrupt slurs in songs of the Townsend's Solitaire (*Myadestes townsendi*) show some of the slurs to have a characteristic banding, indicating that the pitch change is stepwise (a glissando) rather than continuous. Tonal fractions in these glissandos varied from about 1/2 to 1/9 tone; they usually decreased toward the end of a glissando, and often differed in different renderings of the same phrase or figure, and in two or more glissandos uttered in succession. Measurements of the time intervals between the start of successive steps indicated that these steps were begun at rates of 1282 to 6211 per second. Conventional musical scores are inadequate for representing such elements of a bird's song; a sonagram with notes of the musical scale superimposed on it is probably the closest to a musical representation of a song that can be obtained.

LITERATURE CITED

Arlton, A. V. 1949. Songs and other sounds of birds. Eklund Printing Co., Hoquiam, Washington.

Hall-Craggs, J. 1962. The development of song in the Blackbird *Turdus merula*. Ibis, 104:277–299.

Howard, L. 1952. Birds as individuals. Doubleday & Co., Inc., New York.

Mathews, F. S. 1920 (rev. ed.). Field book of wild birds and their music. G. P. Putnam's Sons, Inc., New York. (Reprinted in 1967 by Dover Publications, Inc., New York.)

DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, OHIO STATE UNIVERSITY, 1735 NEIL AVE., COLUMBUS, OHIO 43210, AND 12 JOHN ST., UPPER FERNTREE GULLY 3156, VICTORIA, AUSTRALIA, 17 NOVEMBER 1967.

REPRODUCTIVE BEHAVIOR OF HAIRY WOODPECKERS.
III. AGONISTIC BEHAVIOR IN RELATION TO COURTSHIP AND TERRITORY

Lawrence Kilham

THIS report describes the agonistic behavior of Hairy Woodpeckers (*Dendrocopos villosus*), which may take place at any time of year and with either sex, but which reaches a peak when rival males display against each other on winter mornings from mid-January to early March. Other examples of this behavior include conflicts between females in the fall, interspecific conflicts, and abnormal situations such as defeat of a mated male on his territory, stemming from inadequacies of local environment.

Present observations, like those of preceding reports, were begun in Maryland (Kilham, 1960, 1965, 1966*a*, 1968). They were carried on primarily, however, in Tamworth and especially in Lyme, New Hampshire over the course of nine years.

DISPLAYS ASSOCIATED WITH AGONISTIC BEHAVIOR

Some displays described in part elsewhere (Kilham, 1960, 1966*a*) are included below to give a more complete outline.

Threat display.—(a) Bill-waving Dance. A Hairy Woodpecker of either sex points its bill upward and at times even backward (Fig. 1), then swings its bill back and forth like a conductor's baton, while jerking head and body and making half-starting motions with its wings. The bird on the offense does the dancing. These displays are also used in interspecific encounters as against a Starling (*Sturnus vulgaris*) near a nest hole. Skutch (1955) gives some additional description.

(b) Display of white breast. This can occur briefly as an isolated performance (Fig. 1) apart from the Bill-waving Dance of which it is a main component. I saw it, for example, on several occasions when an owning male faced another male who was unresponsive to challenge, possibly due to immaturity. It is conceivable that the white breast of the Hairy Woodpecker serves a signaling purpose, since it shows up well in the bare woods of late winter when agonistic and courtship behaviors are at a peak.

Actual Conflict.—(a) Combat pose. A Hairy Woodpecker ready to strike or to meet blows holds itself with bill opened, wings held out slightly from the body, and tail well-fanned outward (Fig. 2). Outer tail feathers sometimes twitch independently of the rest of the tail.

(b) Direct clash. When antagonists grapple with each other, they use bills to seize and pull feathers rather than to strike blows.

(c) Head feathers. These are usually pressed down, giving a sharp outline

FIG. 1. Male Hairy Woodpecker in full threat display, a pose basic to the Bill-waving Dance.

to the head in conflict. Hairy Woodpeckers may raise their head feathers in mixed situations, where they are curious in regard to an intruder, whether specific or non-specific, while still holding themselves in readiness for combat.

Defense.—When threatened or about to be attacked a Hairy Woodpecker may (a) hold a frozen pose with head and bill pointed straight forward (b) spread wings out horizontally (c) swing around a trunk or branch with wings fully outstretched upward.

Displacement pecking.—A woodpecker in conflict may start pecking assiduously on places such as the bark of sound, healthy trees. This reaction is more frequent toward the end of long conflicts.

Vocalizations.—These are divisible into four groups.

(a) *Wick-a-wick-a-wick.* I have heard these notes only in male-male conflicts. They resemble a vocalization of the Yellow-shafted Flicker (*Colaptes auratus*). (Kilham, 1959*a*.)

(b) Speaks as well as Sputters are expressions of excitement from any cause; a Sputter being basically a Whinny, which due to its intensity carries a connotation of alarm, at least to a human ear.

(c) *Queek, queek, queek* and *chewi, chewi, chewi.* The notes express exuberance in courtship and may sound incongruous when given in conflict situations. Conflicts, however, are stimulating to courtship when both sexes are present, as they frequently are.

(d) *Teuk, teuk*; *chewk chewk*; *chewki, chewki*; *queek, queek* and a variety of other short, rubber-doll-like, notes may accompany bill-waving displays, giving the effect of a performance by marionettes. Excitement of the moment may explain the diversity of vocalizations used.

CONFLICTS OF MALES IN LATE WINTER

Early breeding season encounters of Pairs A and B were favorable for observation in taking place along a restricted area of territorial boundary (Fig. 3) in two successive years. Three of the four woodpeckers involved

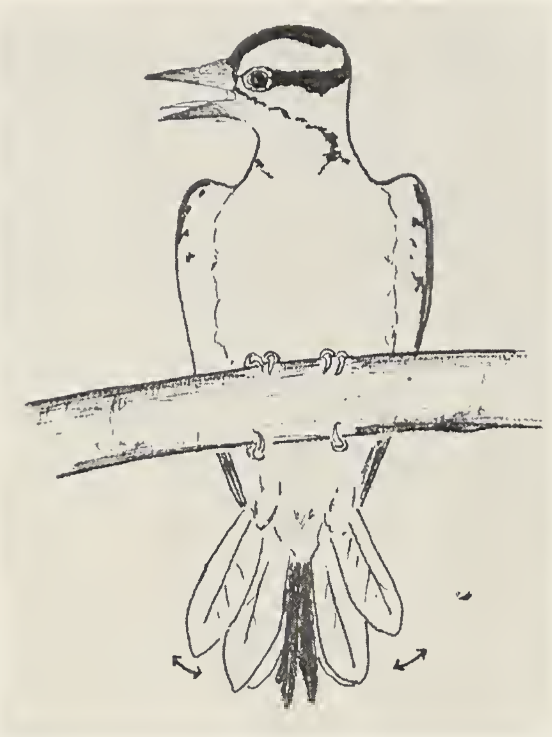


FIG. 2. A Hairy Woodpecker in combat readiness as it faces an intraspecific opponent.

were present in both years. Female A (FA), however, acquired a new mate MA′ in 1965. Events which involved FA and MA′ were the more representative of the agonistic behavior of *D. villosus.* They fell into the following phases:

Phase I was brief for MA′ when, new to both mate and territory on 31 January, he fled as if in terror on meeting neighboring Male B (MB) who was trespassing across the border. Within a month, however, MA′ had become a match for MB as could be seen in displays which lasted from 07:25 to 08:30 on 28 February. Events began when MB crossed the border at 07:00 (Fig. 3). FA was alone at the time. She made many *speaks* as if nervous but did not attack MB. MA′ was drumming 200 yards away. Displays began immediately when he arrived at 07:25. The two males resembled puppets operated by strings as they faced each other, a short distance apart on a limb, with bills up and tails spread, then started jerking heads to and fro, half-starting their wings and making toy-like *chewk, chewk* notes. Such bursts of activity might last for several minutes. The two would then rest for a time in strained postures until conflict was precipitated again, usually by one of the females making Speaks or Sputters, from positions that each held back from the displaying males (Fig. 3). One male might then float to another tree on out-stretched wings followed by his opponent. A common tactic was for one to get below the other on the tree. Thus the male higher up might swoop down on the one below, as the latter evaded by swinging around the tree trunk with wings outstretched. Such maneuvers brought the

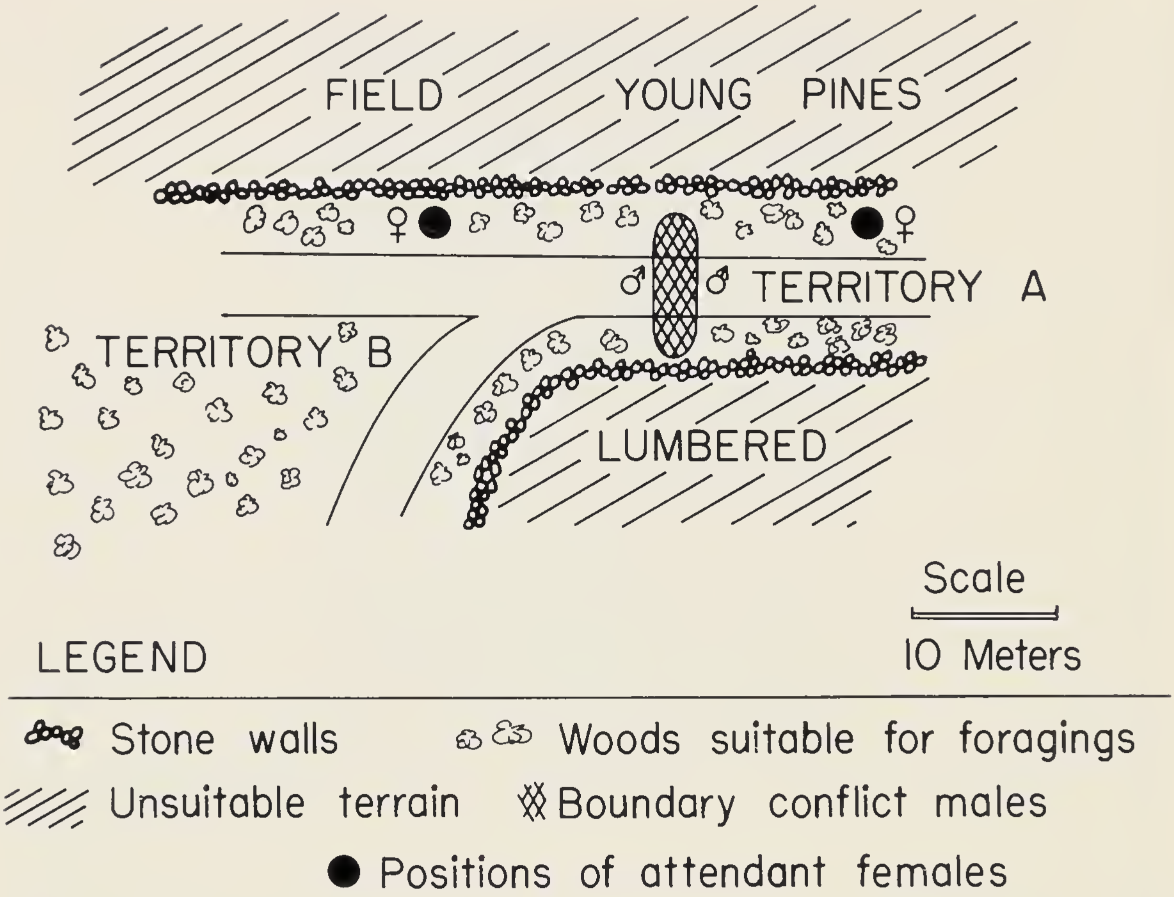


Fig. 3. The site of ritualized, early morning conflicts of two male Hairy Woodpeckers in February along a portion of their common territory boundary, showing positions of attendant females. (Pairs A and B, 1964.)

two close to the ground. Signs of fatigue began to appear as the conflict wore on, with the contestants flying more from tree to tree and taking longer pauses to peck in nervous fashion.

Conflicts in early March marked a third phase in which conflicts tapered to a close. Those on 2 March, for example, lasted only from 06:45 to 07:05. MA′ swooped repeatedly at MB. He now appeared the more aggressive of the two. The two males spent much time resting motionless. FB flew toward her mate in one such pause in fluttering, gliding flight, making *chewki* notes, and this precipitated a renewal of displays. At the end of the encounter FB assumed an invitatory pose, crosswise on a limb (Kilham, 1966*a*). MB came within a few feet. The two, however, flew off without copulating, although the conflict had obviously aroused FB in this direction.

Pairs A and B came to their mutual border again on 4 March. On this occasion they did no more than idle about for a short while, each remaining on its own side. They left by 07:15 and this was the last time I saw the four woodpeckers together.

Conflict of females, 1965.—I saw no further conflicts between Pairs A and B in the spring of 1965, but on 24 July FA and FB had an encounter in the border zone used by the males in February (Fig. 3). The two females were resting motionless three feet apart when first observed. They soon started Bill-waving Dances accompanied by doll-like *queeks* which continued for only a few minutes. FB then flew back to the vicinity of MB who, accompanied by a juvenile, was back from the boundary in his own territory and did not participate.

I have observed a total of four such conflicts between female Hairy Woodpeckers in New Hampshire, of which three took place in September and October. One on 8 October 1961 resembled the one described above in that FX in Tamworth was accompanied by MX at the time she faced her rival at what had been the boundary of the breeding territory. The males in both situations remained back from the encounter and uninvolved.

Disequilibrium between males A and B in 1964.—MA, who was FA's mate in 1964, appeared to be atypical in at least three aspects of his behavior which were, a) failure to reciprocate in full to the courtship advances of his mate FA (Kilham, 1966*a*); b) hyper-excitability in the nesting period (Kilham, 1968) and, c) lack of interest in either territory or in the challenge of neighboring males.

Observations on MA began in mid-December when I located his roost hole 150 meters within Territory B and 15 meters from that of FB. The two woodpeckers belonging to different pairs paid little attention to each other on emerging in the morning. Male B began to seek out his mate soon after dawn by the end of the month, but it was not until 25 January 1964, that he became aggressive toward the intruder MA. By this time FB had gone to roost elsewhere. MB came to the wood at 07:05 and took a position above the roost hole of MA who first put his head out at 07:16. MA emerged the day before and the day after at close to 07:12, but on 25 January he remained within until 07:26. MB meanwhile, preened, scratched, and drummed demonstratively as if waiting for his rival to come out. When MA finally did so, MB put on a full display, with bill back and white breast rounded forward (Fig. 1). MA kept well away, however, and soon flew off to his own territory pursued by MB.

MB sought a conflict again on 13 February, for he invaded territory A at 07:20 and, coming to an aspen where MA was resting 40 meters beyond the boundary, he made the same exaggerated breast display as on 25 January (Fig. 1). Neither the trespassing nor the display aroused MA. He moved away, pecking on places of no special interest as he did so and MB. returned to his own territory.

MB came to the border again on the following morning. This time he did no more than cling to a tree trunk and look across for several minutes. He then gave a Sputter and flew back the way he had come. On 19 February both MB and FB came to tree on the border at 07:30 and remained there, either motionless or preening for 20 minutes. Such occasions suggested that the borderline, defined by conflicts in 1965, was recognized, at least by Pair B, and I believe by FA as well, in 1964.

MA was not only indifferent to the intrusions of MB, but also about moving into Territory B to feed, which he did on 7 and 22 February. FB met him on both days. She attacked him by advancing rapidly up the trunk or along the limb where he happened to be, without displays, but moving directly at him. MA's only response was to fly to another tree. FB desisted after several such attacks.

One might assume from MA's unresponsiveness that he lacked a will to fight. Two observations, however, indicated that he was aggressive in other situations. One was at a time, 25 December 1963, when FB approached his roost hole in Territory B after he had emerged. MA popped inside hurriedly and faced her at the entrance. The two woodpeckers then had three sharp exchanges of blows, with MA striking so hard from within that FB lost her hold on the bark several times. A second instance of MA's aggressiveness was at a suet holder, two kilometers away, where FB was feeding on 22 February. MA drove her off and when a Starling attacked him a minute later, he swung under a limb in a full-wing threat display, then attacked and drove this bird away as well.

MA was possibly an immature male, less than a year old. This might explain his lack of agonistic and courtship behavior, as well as sense of territoriality. These deficiencies did not keep him from successful nesting later on. Here two further explanations are conceivable; one, that he matured as the season progressed and second, that his mate, FA, had a territorial sense established by occupancy dating from the preceding fall, if not from a longer period beforehand, and this was sufficient to hold the pair together in the early breeding season. The unusually prolonged courtship endeavors of FA in relation to MA are described elsewhere (Kilham, 1966*a*).

Intense conflict followed by coition.—The territory of Pair E lay on the east and that of Pair F on the north slope of Lyme Hill, with an area of continuous woodland in between. Above this was a small, more open area where winds swept around a shoulder of the hill, which was attractive to the pairs of Hairy Woodpeckers for at least two reasons; one, the blown-down or broken trees provided a supply of wood-boring insects and second, it was the only piece of terrain between their territories which had well defined topographical features. Both causes may have operated to make this segment of border, roughly 10 meters in extent, the scene of conflicts between Males E and F. ME and FE, for example, had worked on the wind-blown trees from 08:15 to 08:35 on 13 March 1965. These quiet activities were interrupted at 08:35 when ME began giving Speaks, then flew at Male F who had just arrived. The two males now engaged in a Bill-waving Dance accompanied by *wick-a-wick-a-wick* vocalizations. They separated after a few minutes to feed near their respective mates. This momentary quiet was broken when MF suddenly flew at ME and knocked him from his feeding place, the males then falling through the air as they grappled together. The rival males had several more of these clashes during the next three to four minutes. Female E had meanwhile flown to a tall dead stub and drummed, as well as giving Whinnies. When MF flew to her directly from his last clash with MF, she broke into a medley of exuberant *teuk, teuk* notes, moved out to take a copulation pose by crouching low on a limb, then broke into a frog-like *quare* as ME mounted in what appeared to be full coition. There was thus a rapid change, within seconds, from agonistic to sexual behavior. It was as if a drive built up for one was directly transferable to the other.

I observed that ME and FE moved uphill toward the wind-blown area on four other mornings in March, between 06:00 and 07:00. The only other conflict with their neighbors, however, was a brief one on 22 March. It seemed possible that this early morning movement toward the border area was actually appetitive behavior, in which displays with rivals were sought, as if the male and female of the pair felt a need for these activities.

Comment on territory and terrain in relation to sites of conflicts.—The territories of Hairy Woodpeckers are large, being roughly 500 meters in length as figured in two previous publications (Kilham 1960, 1966*a*) and having borders that are ill-defined in most directions in New Hampshire where much terrain consists of young woods, fields, or other unsuitable habitats. There is thus no crowding of pairs but rather the reverse. If conflicts were random affairs under such conditions they might be comparatively infrequent. This is especially true in the early breeding season when unfavorable weather may interrupt courtship and agonistic activities for days or even weeks at a time. The fact that pairs seek conflicts in the first hour or two after dawn on favorable mornings and at a set section of the boundary where conflicts have taken place before may thus have importance. The border sections were about 10 meters in length. As observed for Pairs A and B, and for Pairs E and F, in two successive years, the section in each case was an area of woodland favorable to feeding. For Pairs A and B, the area consisted of large maples bordering a dirt road (Fig. 3) while for Pairs E and F, the strategic meeting place was an area along a ridge where high winds had killed or weakened trees and thus increased the supply of wood-boring prey. Each of these places was where the woodpeckers would have been likely to meet when feeding. Once contact was made, they may have returned when seeking conflict at other times. This tendency of *D. villosus* to have successive conflicts in one segment of boundary was also noted in Maryland (Kilham, 1960).

TERRITORIAL DRUMMING

The larger part of the drumming of Hairy Woodpeckers in winter and spring appears to be related to courtship, while drumming made in response to territorial neighbors is less frequent. Examples of this territorial drumming are as follows:

ME and FE were feeding well within their territory at 08:00 on 21 March 1965, when a member of Pair A began drumming across the valley. ME became excited immediately as indicated by Speaks and Sputters. He flew 100 or more meters to a position on his boundary opposite to where the sound was coming from, then started drumming in reply. After a few minutes, he began preening between bouts as if having no sustained interest. This brief episode brought out features of territorial drumming. One was that it was not related to FE, since ME had flown directly away from her, and second, it was precipitated by the action of the neighboring woodpecker. An interpretation of events was that ME had flown to the border as if eager for a conflict, presumably with Male A′, but the nature of the terrain was unfavorable to any direct encounter since fields and a highway separated Territory E from Territory A.

An almost identical episode took place with MB on 4 March 1965. He was working on the entrance of a potential nest hole at noontime, with FB not far away, when drumming began in Territory C. MB gave a Whinny, then flew to some tall basswoods which grew along his border and began drumming in reply. The terrain separating the basswoods from Territory C was of an indifferent nature, in terms of places to feed since it consisted of small pines and a field. MB drummed at a leisurely rate of four bursts a minute. One would have thought, to see him fly to his border so promptly, that he was eager for an encounter, but, as in the case of ME, the nature of the terrain made an actual conflict unlikely.

I have been unable to determine by sound whether a male or a female Hairy Woodpecker is drumming and possibly a Hairy Woodpecker cannot either when the sound comes from outside its own territory. This may make no particular difference in regard to territorial drumming. Males such as E and B appeared to have a high level of eagerness for conflict as judged by their prompt and excited response. Drumming by either member of a neighboring pair might, therefore, be enough to bring male woodpeckers to opposite borders, well separated though these might be.

TERRITORIAL INTRUSIONS OF AN UNMATED FEMALE

In March and April 1965 an unmated female (UNF) wandered about in portions of territories A, B, and C arousing responses from the respective mated pairs, as may be illustrated by an encounter on 5 April. MA′ and FA had reached a quiet phase of breeding behavior at this time. FA had been inspecting a birch stub as a potential nest site when she flew to the ground among some low pines to face UNF, who had appeared suddenly. The intruder was seemingly unconcerned as FA came within a few feet. FA did not attack, but pecked indifferently on a dead limb, then gave shrill *chewkis* and flew up to rest on a limb in a crosswise pose, inviting coition, as MA′ arrived. He came within a few inches of her, then turned to swoop down to the intruding female. UNF continued to be unconcerned as MA′ approached in a Bill-waving Dance, then flew at her, giving shrill *chewkis* as he did so. FA joined her mate. She remained to one side, however, and uninvolved in the displays. All three finally flew off together.

On 10 March, UNF invaded Territory E. FE had been drumming and preening in leisurely fashion at 08:50 when she suddenly made *queek*, *queek* vocalizations as UNF alighted on a neighboring tree. FE pursued the intruder up the tree trunk, but in quiet fashion, without displays. Both females then rested motionless until UNF departed.

A feature of these episodes was the lack of agonistic response to the invading female shown by owning females A and E. Male A′, on the other hand, had immediately resorted to a Bill-waving Dance, then a direct attack. These events suggested that female Hairy Woodpeckers are not much concerned about the defense of breeding territories in the first half of the year when males are the active partners, but become so only subsequent to the breeding season when males are no longer interested.

CONFLICTS IN NESTING PERIOD

Conflicts between two male Hairy Woodpeckers in May 1963 were unusual, a) in being carried on at a time when pairs are normally occupied with nesting and b) in that an intruding, unmated male (MZ) ultimately defeated a mated male (MX) in the latter's territory in Tamworth.

Defeat of a male on his own territory.—4 May. Speaks and sputters attracted my attention at 07:00 to a series of Bill-waving Dances going on between males X and Z close to their common boundary (Fig. 4). The conflict was a mild affair, carried on in silence, and ending with departure of intruder MZ.

5 May.—MX and his mate FX were feeding close together on the following morning when MX suddenly became alert, then flew through woods to meet MZ who had invaded his territory again. There was a brief encounter before MZ left. MX flew back to his mate and copulation followed as if an emotional intensity engendered by the conflict had carried over directly.

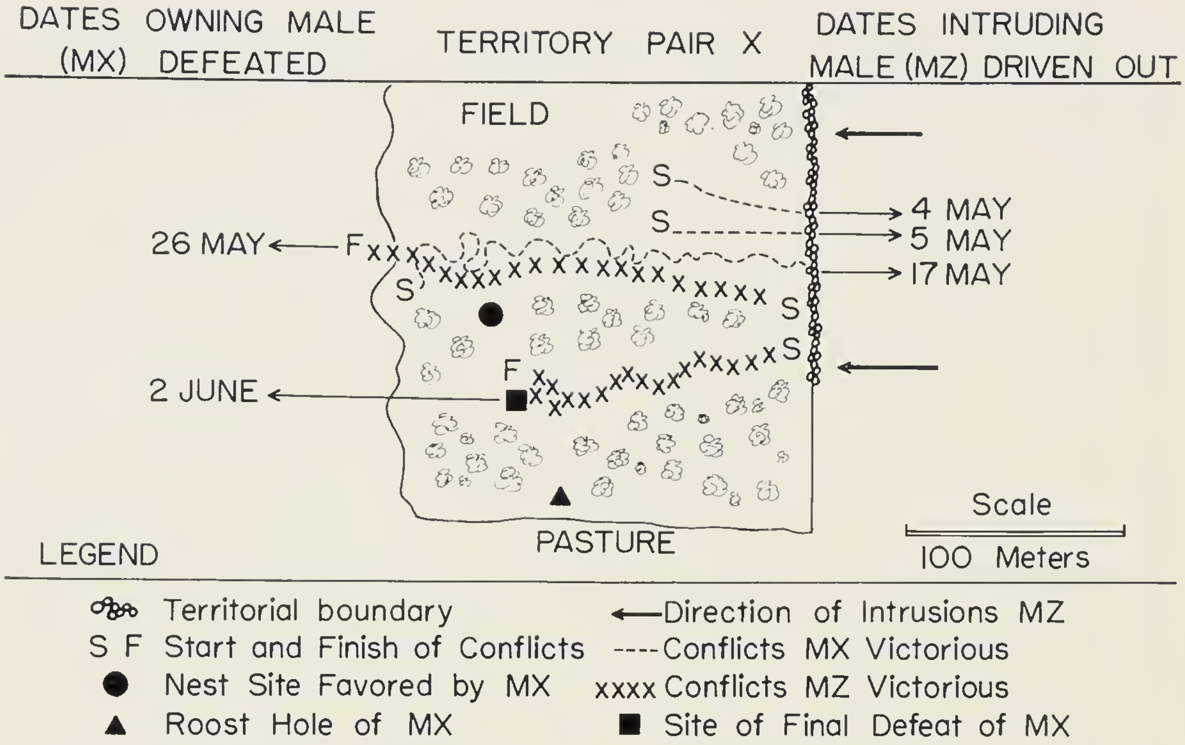


FIG. 4. Diagrammatic view of five invasions of intruding male Hairy Woodpecker MZ into territory of mated male MX, showing manner in which MX was ultimately defeated on his own territory in May and June, 1963.

17 May.—MX was resting as I watched him for 20 minutes in the center of his territory. He stretched himself out on a dead limb in a sunbath, with head back and wings relaxed, scratched his head directly (Kilham, 1959*c*), and preened. MZ interrupted these activities at 08:30 by appearing in woods below. I was thus present at the onset of a conflict which lasted for one hour. It involved a gamut of activities ranging from Bill-waving Dances and full-wing threat displays to bodily clashes with loss of feathers, all accompanied by occasional *wick-a-wick-a-wick* vocalizations. The two males appeared to be evenly balanced. It was only by a slight margin that MX drove his rival backward the way he had come (Fig. 4).

25 May.—This was an extraordinary day in which MX in one part of the wood and his mate FX in another carried on duets of drumming, answering each other with regularity at rates of about six times a minute. The duets began at 05:45 and were still continuing, off and on, at 19:45. FX tapped a number of times at a potential nest stub of poor quality. It appeared as if she were trying to get her mate to come and inspect it. If he started to approach, she would cease drumming and wait. The fact that he did not actually come gave an appearance of strained relations between the two. This was the final day that I observed efforts by either of them to find a possible nest site.

26 May.—The course of this encounter, which began at 09:30, was the reverse of that described for 17 May (Fig. 4), for MX was driven back to the center of his territory which he finally abandoned to his rival MZ.

2 June.—MX precipitated the final conflict observed when his drumming brought MZ to the boundary at 05:30. As on 26 May, MZ forced MX back to the center of Territory X. Much of the fighting was done close to the ground. MX had enough after a half hour for he worked to the bottom of a brush pile to hide, but MZ followed and a spasmodic beating of wings accompanied this final clash of the two males. MZ came out after a few minutes, rapped on a dead branch, and flew off. MX did not appear until five minutes later. He gave a few Speaks and a Sputter, then flew in a direction away from that taken by MZ.

Comment.—One may ask why intruder MZ was able to defeat owning male MX on the latter's own territory and why MZ should have been so persistently aggressive. Conceivable answers to these questions lie in a combination of circumstances. If MZ had lost his mate, as appeared to be the case, a drive built up in months of courtship may have found outlet in destructive aggression, a situation which I have observed among woodpeckers in an aviary when efforts to nest finally broke down (Kilham 1959*a*, 1962).

The failure of MX to defend his territory rested on a different type of situation, ecological in nature. Thus a feature of the conflicts was that MX won encounters with MZ up until 25 May. On this date he and his mate FX had duets of drumming carried on in what to an observer was an agonizing fashion, over a day of 15 hours. After this time the two woodpeckers, MX and FX, made no further attempts to nest. Their pair bond had broken and from then on MX did not have the will to fight he had before. The psychological advantage now went to the intruder.

I might not have appreciated the ecologic background of this situation had I not been following the succession of forest trees in these woods, which were my own. Thus a combination of hurricanes and lumbering operations had provided a supply of stubs favorable to nesting woodpeckers in previous years. No living larger trees remained, however, which might die and keep adding to a supply of nest sites. The best stubs either rotted in time or their potential as nest sites waned. They gradually gave way to a succession of vigorous young trees offering no dead wood such as might be suitable for excavating. The environment had thus become depleted of a resource of crucial importance to nesting woodpeckers.

My first appreciation of this depletion of habitat came from observations of Pair A of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) which had nested in the same area of woodland (Fig. 4) in 1958 (Kilham, 1962). Pair A failed to nest in the following year, however, when efforts to find a suitable tree were unsuccessful. An end result was that the male sapsucker with no nest to attend to in May and June flew around and around his territorial borders seeking to precipitate conflicts with males of four neighboring pairs, then occupied in raising young. Pair A of the sapsuckers and Pair X of Hairy Woodpeckers might have been able to nest had the birds moved elsewhere. Both species, however, remained attached to their territories.

INTERSPECIFIC CONFLICT

Interspecific competition is rarely observable in nature. A series of encounters between Pair F of Hairy Woodpeckers and a male Yellow-bellied Sapsucker observed in April 1963, however, revealed that competition exists between these two species for a crucial resource; for optimal nesting both require living trees with rotten centers of identical diameters. This idea, first suggested by the interspecific encounters, has been substantiated in continuing observations. A second point of interest about the conflicts was the insight given into the fighting potential of the male as compared with that of the female Hairy Woodpecker in the breeding season.

The members of Pair F had been excavating a nest hole 15 meters up in a hop hornbeam (*Ostrya virginiana*) in Lyme when the male sapsucker began excavating a hole 75 centimeters above. The sapsucker had appeared in the area three days before and had inspected the hornbeam. Female F paid little attention to this initial intrusion as she rested before her excavation. The intruder began an excavation of his own on the following day. By this time he was more aggressive and able to drive the female Hairy Woodpecker away. The main conflicts came on 21 April. I had begun watching the female of *D. villosus* at 06:30, when the sapsucker arrived and attacked her at her excavation. Both birds fell grappling to the ground. They lay there momentarily, and when the two had reascended the tree trunk, the woodpecker renewed the conflict, thus precipitating a second episode of grappling and fall. The female Hairy Woodpecker was beaten in this encounter. The male sapsucker pursued her from tree to tree, then returned to inspect her excavation unmolested. He finally left for a round of drumming on various trees. FF remained at a spot 70 feet away for the next 15 minutes, preening in a nervous manner and making an unusual number of *jeek* notes as if disturbed. Meanwhile her mate, who had been absent during the conflict, arrived at the nest excavation. He tapped at the entrance as if trying to get her to return, but she remained at a distance. The Yellow-bellied Sapsucker now returned to the hornbeam and immediately swooped on the male Hairy Woodpecker hitting him so forcefully that the two fell grappling to the ground where they remained clutching for nearly a minute. On this occasion the male Hairy Woodpecker was decidedly the victor. He chased the sapsucker away so effectively that the intruder did not return nor did its incipient nest excavation become any larger.

DISCUSSION

Hairy Woodpeckers are birds of marked individuality living, in New Hampshire, in woodlands which are forever changing due to lumbering, diseases and other factors; to nest successfully under such circumstances requires close adaptation not only to environment but also between the two members of a breeding pair. Cooperation comes to be of the closest kind, once a nest site has been selected and excavation begun. It develops progressively in the early breeding season when two types of activity engender social bonds. One type relates to courtship in which Hairy Woodpeckers display, even in February when woods are deep in snow, by exchanges of intimate notes, pseudo-coition, and activities about a symbolic nest hole and the other type, to agonistic encounters with rival pairs. This latter behavior takes place between January and March. A schematic view of these events is that if the male is new the female attracts him by her drumming or presence to sections of the territorial border where he is likely to encounter the male of the neighboring pair. He may flee from initial conflicts. As he gains familiarity with his new territory and mate, however, encounters with rival males become rituals serving a number of functions. A male Hairy Woodpecker, for example, has superabundant energy and aggressiveness in the early morning of a favorable day, and this might well be directed against his mate were it not channeled off in ritualized conflicts with rival males. Hence the energy serves to strengthen rather than weaken the pair bond, as may happen under conditions in an aviary where no rival is present. Males with energy to expend may enjoy doing so. A conflicting desire to flee has not been apparent in encounters observed. In fact an analogy which came to mind in watching the woodpeckers was rather of a vigorous tennis match in which both male contestants were satisfied with the boundary (the net) staying where it was, and both were driven on by the presence of their mates who attended the performance, but back at a distance and without direct participation (Fig. 3). If the actual displays continued for an hour, both males might show signs of fatigue. Now one and now the other, might start pecking as if desirous to start feeding, which was natural, since neither male may have fed since emerging from its roost hole at dawn. Sometimes a female would incite her mate to attack his rival by coming closer and giving vocalizations. This in turn initiated a further bout of displays. The suggestion was that these encounters were joint enterprises. The females became aroused sexually by attending them as well as the males by the contesting, as was evidenced when a female assumed a coition pose crosswise on a limb at the moment her mate flew from an encounter. Copulation may take place in such circumstances, within seconds. This close association of agonistic and sexual behavior is also observable among Pileated Woodpeckers (*Dryocopus pileatus*) as described elsewhere (Kilham, 1959*b*).

Other aspects of the lives of Hairy Woodpeckers may also serve to obviate male aggressiveness. Among these are occupation of territories in the fall by the females who establish boundaries to some extent in conflicts with other females. The female is thus on familiar ground by the onset of the breeding season in mid-winter, a circumstance giving her a psychological advantage counteracting male dominance, at least initially. And again, in later months when members of a pair feed together in woodlands, sexual differences in feeding behavior may further serve to forestall male aggressiveness arising from dominance at food situations. It should also be emphasized that Hairy Woodpeckers are mated for life. Familiarity with mate and terrain thus acquired may further contribute to the intimate pair bond characteristic of *D. villosus* but not of all woodpeckers (Heinroth and Heinroth, 1958, Kilham, 1966*b*).

Agonistic behavior among Hairy Woodpeckers is a constructive force under usual circumstances. It may, however, become destructive in situations which are abnormal or unbalanced, such as loss of a mate or tenacity to habitat which has become depleted of some essential requirement. Illustrations given of this situation were (1) the persistent territorial invasions of an unmated male Hairy Woodpecker (MZ) and his ultimate defeat of a mated male (MX), as described from Tamworth in May, 1963 (Fig. 4), and (2) the excessively aggressive behavior of a male sapsucker which had failed to nest successfully in the same area in a previous year (Kilham, 1962).

In conclusion I would agree with Hinde (1956) that "the ways in which territorial fighting is specialized" may vary with each species. The balance of selective forces for Hairy Woodpeckers, occupying large, ill-defined territories with comparatively little competitive pressure, may be quite different than that for colonial-nesting species such as gulls (Tinbergen, 1960). This may explain why I have not noted displacement activity, and the simultaneous arousal of the tendency to attack and a tendency to flee, as being features of their agonistic behavior.

SUMMARY

The agonistic behavior of Hairy Woodpeckers in relation to courtship and territory takes place on favorable days in winter when neighboring males, attended by their mates, seek encounters along a section of territorial borders held in common. Occasions when pre-copulatory behavior followed conflicts within seconds suggested that both sexes were aroused by such conflicts, even though the females did not participate directly. The greater aggressiveness of the males was revealed in other types of conflict in spring. Thus a male took the lead in driving an unmated female intruder from his breeding territory and in an interspecific encounter in April, a male Hairy Woodpecker defeated, whereas his mate was defeated by, a male Yellow-bellied Sapsucker. An unusual series of conflicts were observed in May in which an unmated male intruder finally defeated a mated male in the latter's own territory. This abnormal situation appeared related to the fact that the mated pair remained attached to a territory in which suitable nest trees were no longer available. A situation was observed in the case of a mated male, who appeared to have no territorial sense and took little interest in either agonistic or courtship activities, yet nested successfully later on. Hairy Wood-

peckers have large, often ill-defined territories in New Hampshire. What is surprising is the degree of individuality shown in their agonistic and other behavior. They appear able to develop close, intimate pair bonds under a wide variety of circumstances.

LITERATURE CITED

HEINROTH, O., AND K. HEINROTH. 1958. The birds. Univ. Michigan Press, Ann Arbor.

HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis, 98:340–369.

KILHAM, L. 1959*a*. Early reproductive behavior of flickers. Wilson Bull., 71:323–336.

KILHAM, L. 1959*b*. Behavior and methods of communication of Pileated Woodpeckers. Condor, 61:377–387.

KILHAM, L. 1959*c*. Head-scratching and wing-stretching of woodpeckers. Auk, 76:527–528.

KILHAM, L. 1960. Courtship and territorial behavior of Hairy Woodpeckers. Auk, 77: 259–270.

KILHAM, L. 1962. Breeding behavior of Yellow-bellied Sapsuckers. Auk, 79:31–43.

KILHAM, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. Wilson Bull., 77:134–145.

KILHAM, L. 1966*a*. Reproductive behavior of Hairy Woodpeckers. I. Pair formation and courtship. Wilson Bull., 78:251–265.

KILHAM, L. 1966*b*. Nesting activities of Black-backed Woodpeckers. Condor, 68: 308–310.

KILHAM, L. 1968. Reproductive behavior of Hairy Woodpeckers. II. Nesting and Habitat. Wilson Bull., 80:286–305.

SKUTCH, A. F. 1955. The Hairy Woodpecker in Central America. Wilson Bull., 67: 25–32.

TINBERGEN, N. 1960. Comparative studies of the behavior of gulls (Laridae: A progress report). Behaviour, 15:1–70.

DEPARTMENT OF MICROBIOLOGY, DARTMOUTH MEDICAL SCHOOL, HANOVER, NEW HAMPSHIRE, 23 MARCH 1967.

LIFE HISTORY OF THE RED WARBLER

Bruce G. Elliott

The Red Warbler (*Ergaticus ruber*) ranges in the "Mountains of Mexico from Southern Chihuahua and Hidalgo south to Oaxaca" (Miller et al., 1957). Of the two described races, *E. r. melanauris* breeds in the high Sierra Madre Occidental biotic province (Goldman and Moore, 1945) of Chihuahua and Durango, but may winter at lower elevations. Moore, who described this race, considered it migratory on the basis of specimens taken at 5,600 feet near Batel, Sinaloa in October, 1958.

Between May 1963 and July 1965, I spent 550 hours studying the nominate race in Desierto de los Leones and Miguel Hidalgo National Parks near Mexico City. *E. r. ruber* occurs sparsely at the upper limit of conifers (12,000 feet) and increases in numbers throughout the fir belt (11,500 to 9,500 feet), decreasing again in abundance at the ecotone of pine woodland and non-forested land at the base of the mountains. Perhaps in response to milder climatic conditions in the Transverse Volcanic and Sierra Madre del Sur biotic provinces, the nominate form manifests little seasonal movement. I noted a few family groups moving into the foothill fir-pine ecotone in late summer, while young birds infrequently strayed into the lower pine-oak woodland (ca. 8,000 feet) in August, and a few adults descended into open pine woodland scrub (ca. 7,000 feet) during harsh weather in winter. Annual fluctuation in wintering parulid populations in Mexico is suggested by Smith's (1909) comment that Red Warblers were ". . . few when compared with the Red-bellied Redstart or Red-faced Warbler." This is exactly opposite to my findings in the same area fifty years later.

The Red Warbler breeds in the mature conifer forest where sunlight penetrates freely to the forest floor, such as the brushy edges of trails, watercourses, and windfalls. Since logging favors this species by increasing open areas, the population density in such severely logged locations as my study plots may exceed that found in undisturbed forests. Below the forest canopy, heavily shaded areas support small ferns and mosses whereas sunnier areas are thickly carpeted with the brushy legume, *Acacena elongita.* Small conifer stands isolated from the main forest are generally avoided, even when they appear to meet all the postulated requirements of a typical breeding area. Unpublished notes of Chester Lamb, Paynter (1952), and Zimmerman and Harry (1951) show that while the Red Warbler is basically a bird of the coniferous forest it can be expected in deciduous growth, but unlike its congener, the Pink-headed Warbler (*E. versicolor*), it has not yet been found breeding in such vegetation.

The Red Warbler frequents the "substory" and "middle level" foraging zones of Miller (1963) and is more common in the latter. The species thus avoids direct competition with the Crescent-chested Warbler (*Vermivora superciliosa*) and the *Atlapetes* finches of the low-level shrubbery, and the wintering *Dendrocia* forms foraging in the tree crowns. Singing Red Warblers are often driven from the centers of their territories by wandering Audubon's Warblers (*D. auduboni*).

Mated pairs usually remain close together except during the post-breeding molt period or during severe winter weather. It is unusual to see more than two adults together but rarely two individual pairs may forage amicably together in mid-winter. Association with winter mixed-species flocks appears casual and is relatively infrequent. At such times, when disturbed by larger birds, Red Warblers do not normally exhibit displacement hostility toward smaller species such as kinglets (*Regulus*) or bushtits (*Psaltriparus*). On 17 March, 1965, a pair each of Slate-throated Redstarts (*Myioborus miniatus*) and Red Warblers foraged side by side in the same tree for an hour. Such tolerance between birds with apparently similar feeding methods and prey requirements seems remarkable, especially at the onset of their mutual breeding seasons.

The daily foraging area is quite small, often only a dozen meters square. The birds feed with quick repeated jabs into bark cracks and needle clusters, or glean the trunk crevices while hanging head down like a nuthatch. They may hover with the tail rapidly pumping up and down, probing like a hummingbird among the conifer needle fascicles. When feeding within deciduous growth, they do notably more fly-catching than bark-foraging. Foraging declines in the late forenoon. Many individuals then enter some shady spot where their brilliant color seems to disappear in the shadows. Here they rest from 30 seconds to several minutes, slumped down upon a branch, with closed eyes, often with the bill buried beneath the bend of a wing.

When the birds are awake and active, all movements are exceedingly quick with short pauses of spasmodic head-cocking punctuated by abrupt turns as the tail jerks nervously to-and-fro. The birds preen incessantly and without discernable pattern since the same plumage area is often redone during a single session. Males often preen vigorously after a conflict with another bird, and females may do so when disturbed while approaching the nest.

In March, 1965, an unusual example of crepuscular feeding was noted ten minutes before sunset when several pairs of Red Warblers appeared over a clearing to feed voraciously on a dense swarm of neuroptera flying over the open area. This continued well into dusk.

The normal flight is a few quick strokes, interrupted by a brief undulating glide. After crossing a clearing, the warbler glides on set wings the last few feet on into the foliage rather than halt at the outer extremities of the tree.

VOICE

Call notes are heard in diverse situations throughout the year, although with considerable reduction in rate during the molt. The Red Warbler's typical note is quite distinct from that of other sympatric parulids. Lowery and Dalquest (1951) suggested some resemblance to the note of the Golden-crowned Kinglet (*Regulus satrapa*). I would describe the call note as a sibilant *chi-ip* or *shee-ip*, with the terminal syllable "fussy" and rising in inflection, apparently caused by an increase in volume. Usually only one brid of a pair calls at a time, repeating the note every two to four seconds. Females utter a unique double note, a sharp *chip-chip* and may increase their call-rate to a trill when males prolong the interval between rounds of singing. Females also give an insect-like *buzzz* while driving other birds from the nest area. One mated female not yet building a nest gave a soft reedy trill followed by the double chip note. On 25 April 1965, a Sharp-shinned Hawk (*Accipiter striatus*) perched nearby caused a male warbler to utter a series of high-pitched *z-e-e-e-t* notes while holding its body motionless and bobbing its head. Another male, driving a wren (*Troglodytes*) from the nest, produced a raucous *sheeerrr-cheeeerrr* note. No obvious difference in notes or call rate was noted between breeding and non-breeding birds.

The male's song is complex, generally composed of three distinct note combinations. Usually, three forceful, clear notes are followed by a complex jumble of burrs, trills, and chips of lesser volume. One phonetic version from my notes was: *cheevy-cheevy-cheevy . . petle-petle-petle, chur chur*; Lea and Edwards (1950) noted one version as "*chivy, chivy chivvy, hu-r-r-r-r, chiv-chiv-chiv.*" Since there is much individual variation, up to six such series may be uttered, but three is about the average. A dry, reedy trill may terminate the series. Unmated birds incorporate a sharp clear *tchurr* never noted in songs of mated males. Gular movements continuing after cessation of audible song suggest other notes in a range beyond my hearing ability.

Courting males sing six to eight songs per minute, followed by silent periods of variable length. Mated birds move constantly, seldom giving two songs from the same perch and remain in sight of the female; unmated birds remain in one place comparatively longer, and infrequently sing in tree-tops.

On 14 March 1965, a bird sang a complete song while performing a display flight, while on 17 April a male known to be mated sang while making brief flights spanning three to four meter distances. Each landing terminated in an interesting redstart-like wing-and-tail fanning performance.

Most other species in this habitat increase their singing tempo as the afternoon skies darken during the summer rainy season, but the Red Warbler sings only in the bright morning hours. Even during the dry winter months, calling diminishes whenever clouds form.

TERRITORY AND COURTSHIP

By late February, most males are singing on well-defined territories. Concurrent with the increasing demands of bringing off the brood, the defended area is reduced in size and territorial behavior terminates in August when the young fledge and molt begins.

Prior to nesting, territory size varies depending on the number of males, vegetation density, and terrain configuration. Nine measured territories varied from 30 to 60 meters square, with an average size of 40 meters square. *Acacena elongita* provided most of the ground cover in these units and females always built their nests on the ground beneath this plant. Isolated sections of territories bisected by large clearings were ultimately left undefended.

Males challenge adjacent males by flying silently about three meters off the ground into the adjacent territory and immediately returning to the starting point. Series of such sorties may continue for 20 minutes, depending on the defender's response. Usually the reply is a lesser number of less extensive flights, but should a trespasser intrude too deeply into the territory or dare to alight, there invariably ensues a struggle in which both birds may fall to the earth silently locked in combat. The intruder is always ejected, and upon fleeing to its own territory, often breaks into song. Either bird may then preen, bill-wipe, or quickly rotate the rear quarters and rectrices as described by Hamilton (1959). While mated males sometimes expropriate parts of a single bird's territory, conflicts between adjacent conjugal males seldom result in any disruption of the previous boundaries. Two battling males once drifted into a third territory whose male attacked with one flight before adjourning to sing, and once five males (two of which were definitely new in the area) clashed in a spectacular encounter. I once saw a female attack a strange male. Another female repeatedly attacked her own mate after he had routed an intruder.

Courtship chasing begins in mid-March and varies from short darting flights by males toward females to extended pursuits through the understory. Following such flights, the birds sit inches apart and the male sings, often accompanied by soft calls from the female. Resumption of feeding and preening often follow several minutes of wing-flitting and fluffing of plumage. After a chase, the female often moves under the *Acacena* and creeps about pressing her breast into the ground as if seeking a nest site. Some males are so aroused by "site-seeking" that they fly down and strike their mates, especially if she pauses in an exposed situation. Such "pounces" are often of sufficient force as to knock the female off balance. One male made long flights across his territory while his mate went through these site-seeking motions, but usually a male will perch and often sing with a soft, lispy quality while watching the female intently, or he may wait until she resumes her place in the conifers before he sings. One female "pounced" on a male approaching a site she had just vacated. On one occasion I saw a male doing the searching and singing song fragments while the female played spectator.

"Pouncing" may not be restricted to nest-site searching; any time a female is near the ground, the male may utter a sharp *see-ipp* and pounce at her. Such behavior ceases with the advent of nest-building for some pairs, while other males persist in pouncing up to the time of hatching of the eggs.

One male singing about four meters from his mate responded to her single soft note by gliding to her side with an almost "floating" flight. Although he landed so that their wings touched, copulation did not occur. After a moment, he moved away and sang two short song fragments while the female preened intensively. On another occasion, a male displayed to his mate by gliding about 15 feet from limb to limb on set wings.

On 21 March 1964, a male accompanied by two presumed females attacked a flycatcher (*Empidonax*) which ventured between him and the more distant of the two females.

NEST-BUILDING

Nest construction was first noted on 14 March. The male neither assists the female in building the nest nor does he bring her food, but as an omnipresent observer, he watches her intently throughout the process and follows her during forays for food or material. If she momentarily leaves his view. he moves about the territory calling and singing song fragments. Should she pause while carrying material, he often "pounces" on her. She can be equally aggressive if he moves near the nest.

Nests are mostly composed of grass leaves and stems, but shreds of bark, fern-frond tips, conifer fascicles, and dead deciduous leaves may be included. The nests are woven about the stems of *Acacena* and are always well concealed by foliage. Exteriors bear varying amounts of fine moss and lichen, and all but one nest was lined with very fine shredded grass stems. The lining thickness varies considerably between nests. The unlined mid-June nest described by Elliott (1965) now appears to be exceptional, suggesting that late nests (re-nesting attempts?) may be atypical in construction. Two nests were cup-shaped and three oven-shaped, but no obvious correlation appeared between form and either plant cover type or density, or the time of completion during the breeding season. Skutch (1954) and Dawn (1963) found only oven-nests built by the Pink-faced Warbler in Guatemala. I noted that the Red Warbler builds the cup first and the dome later, while Skutch noted that this sequence is reversed by the Pink-faced Warbler. (For a photograph of a nest in Oaxaca, see Rowley, 1966:193.)

Rim-to-rim nest cup measurements ranged from 12.5 cm to 15 cm, with depths of 8.2 cm to 11.5 cm. The cup of open nests averaged 5 cm across and deep, while oven-nest interiors averaged 6.5 cm wide and 7.2 cm deep. Oven-nest entrances averaged 4.5 cm wide and 3.8 cm high.

Construction proceeds in a steady, unhurried manner. Early in the season, seven females averaged three to five trips every two minutes, but as the April rains began, the pace slowed to one trip per minute. Later in the day, pauses of 10 to 12 minutes duration were spent feeding and preening. Nest material is taken from on or very near the ground, and as many as six grass stalks may be carried at once. Items are retained in the bill while new ones are gathered and any material dropped is ignored. Certain females remain 20 to 30 seconds at the nest while others make repeated hurried trips with material followed by a prolonged period at the site. This suggests building when a suitable accumulation is acquired but I cannot confirm this. A bird is typically very cautious in approaching the site. Each female has a certain perch close to the nest where she sits with her beak full of material and peers about for some time. Dropping in a quick plummet into the *Acacena* about a meter from the nest, the female covers the remaining distance concealed under the foliage.

One first-year bird (brown-edged remiges) exhibited disorganization and uncertainty in her nest building, as she wandered about for extended periods, preened incessantly, and uttered a soft rapid trilling while attempting to build. She brought such unsuitable material as leaves thrice her own size and was once flipped end-over-end when she attempted to fly between two closely spaced upright stalks with a six-inch long twig held in her bill. She abandoned her efforts after nine days. All other nests I observed were completed in four to six days.

INCUBATION AND THE CLUTCH

Five of the nine nesting attempts that I observed reached the egg stage. Early in the breeding season, up to eleven days may elapse between nest completion and laying of the first egg; by May, laying follows immediately. Data from two nests indicate that eggs are laid on consecutive days, but when incubation actually begins is not yet known. On 14 June one nest had three recently hatched young and 3 other nests had 3 eggs each. Nest 65M1 had but two eggs when a predator reached it on 28 March, but the second egg had appeared only the previous morning suggesting that this clutch was not yet complete. One specimen label (Moore Collection no. 45819, 28 May 1946, Guerrero) bears the notation ". . . found nest with three eggs." Probably the average clutch is three eggs. After two young fledged from one nest on

12 June, two infertile eggs were found buried in the nest lining, suggesting a four egg clutch. All these data pertain to the nominate race. Nothing has been reported to date on breeding by *E. r. melanauris.*

The eggs exhibit a faint glossy white ground color which becomes duller as incubation proceeds. A wreath of densely concentrated, very small irregularly shaped cinnamon and russet spots rings the larger end of the egg. These spots decrease in quantity and size, and fade in color toward the egg's smaller end. Two eggs collected nine days after the start of incubation weighed 1.0 g each, the third 1.4 g. They measured 17 × 12.5, 17 × 13, and 16.5 × 13 mm. The two infertile eggs previously mentioned were only 15 × 12.5 mm each.

The male does not incubate nor does he approach the nest until the third or fourth day after the eggs hatch. During incubation, he remains at some distance from the nest and sings only "whisper-song" fragments. Despite his tendency to remain away from the nest during this period, he usually appears immediately at the female's side when she leaves the nest. "Pouncing" now disappears, but if his mate pauses while returning to the nest, the male becomes agitated and often moves toward the nest, calling rapidly. During the female's absence, the male reacts aggressively to any bird near the nest, but when the female returns, he generally ignores all other species, except wrens. These intruders elicit chases and a "threat-flight" in which the male warbler's wings produce a muffled, fluttering sound as the bird flies toward the wren.

Incubating females react to danger by sitting very tightly and may almost be stepped upon before the bird flushes. I often sat only a meter away from one relatively exposed nest and watched the female settle down and go to sleep. Although Dawn (1963) observed Pink-headed Warblers giving distraction displays, I did not see such behavior by the Red Warbler.

Events at nest 65M7 on 22 May suggest that the nest-site is as important as the nest itself. The female fluttered anxiously about while I photographed and then removed this nest which was in the incubation stage. After I departed she searched over an area of about 15 inch radius about the spot where the nest had been. I then placed the nest 70 cm from the original spot and again retired. The bird flew excitedly about, twice went to a twig 7 cm above the totally exposed nest, looked into it and then returned to the original spot, resuming her agitated search of this area for about four minutes. Finally, she mounted the twig over the nest, called once and dropped in, settling on the clutch. Minutes later, I approached to within a meter before she flushed. She could not be induced to re-enter the nest, although she did revisit the old site several times. The male appeared once briefly and departed without returning.

Females sit in oven-nests at a 45° angle to the long axis of the entrance, with their foreparts deep inside the bowl, tails protruding through the doorway. In cup nests, the female's eye is just level with the rim; thus, her brighter parts are covered and only the brown dorsum is exposed, rendering her quite inconspicuous.

Typical incubation rhythm is indicated by data from one female timed for 11 sessions on the clutch alternating with 12 recesses. The latter ranged from 3 to 19 minutes each, totaled 103 minutes and averaged 8.5 minutes. Sessions on the eggs ranged from 12 to 27 minutes, totaled 200 minutes and averaged 18.2 minutes. Twelve five-hour periods at two nests over a six day range indicate that the females were covering eggs about 66 per cent of the time.

My observations of incubation periods at five active nests parallel the findings of Skutch and Dawn for the Pink-faced Warbler. Dawn's (1963) April-nesting birds hatched in 16 days, two young fledging in 10 and 11 days respectively. Skutch's (1954) data, derived from three nests with five successful fledglings, are similar; his 11-day record referred to a "handled" bird and his 10-day bird was "frightened." The fledglings noted during my study left the nest after 10 and 11 days.

Austin (1961) gave typical data for warbler nestings as follows: Northern Egg Average 4–5 (6), Tropical Egg Average 2–3; Northern Incubation 11–14 days, Tropical Incubation 13–16 days; Northern Nestling 8–14 days, Tropical Nestling 12–14 days. The Red Warbler, which dwells in an essentially boreal environment, follows the trend of northern birds in its nestling period, but displays a tropical pattern in clutch size and incubation period.

THE NESTLINGS

Only the female broods, lingering on the nest until well after dawn and returning regularly throughout the morning until the young attain thermoregulation on about the fourth day. Brooding occurs thereafter only during the afternoon rains and overnight. Five brooding sessions, during the third day of nest life ranged from 3 to 19 minutes, but exceptionally, a session may run to 35 minutes.

Both parents are extremely cautious. They approach the nest by swiftly flying close to the ground and neither bird visits the site while something they consider disturbing is near. Though singing is now uncommon, males will sit concealed and motionless, calling softly for minutes on end. This seems not visibly to affect the female's activities. Nest defense is intensified and even large nightingale thrushes (*Catharus*) near the nest are attacked. One female "pounced" on a nearby group of three juncos, knocking two of them off balance. The male may dart out at nearby squirrels and his call-rate increases markedly. He may summon the female from the nest after she has brooded awhile, but until the third brood day the male will not approach the nest closely when she is absent. The adults often forage together near the nest, usually working on trees, while birds foraging far from the nest and individually do more fly-catching. This suggests the use of a less conspicuous feeding method while near the nest, but it may also involve the food requirements of the nestlings. By day three, most males assist the females in feeding the brood (male 64M1 was an exception, not approaching until the 7th day) and food items are still concealed in the mouth or throat. By day six the young can devour larger items and parts of caterpillars and small moths are often seen protruding from the adult's mandibles.

The nest cup is always scrupulously clean. The female devours the fecal sacs at the nest or carries them away. Only once did I see a male remove a fecal sac.

The youngest nestlings observed (two days old) weighed approximately 2.9 g. The posterior half of the crown exhibited minute traces of medium gray natal down about 2 mm long and a few isolated shorter tufts appeared on the humeral, marginal, and dorsal tracts. The eyes were closed. The mandibular tomium was bright yellow, the rest of the bill a shade darker. The tarsometatarsi and mouth-lining were soft pink. Only when the bill was tapped, could the young momentarily raise their heads with partially-opened gapes.

Three four-day old birds were found heaped in the bottom of the nest. Their eyes were not yet open and they did not raise their heads during handling. An unidentified mucous-like film covered the entire body of one bird and the head of another. The nestlings showed darker, thicker body down, but the forecrowns remained bare. Primary sheaths 2 mm long barely penetrated the skin. The marginal tract down had increased somewhat, but the femoral and ventral tracts remained bare. Body size had not increased appreciably (one bird weighed on a postage scale had only gained 0.5 g).

Seven-day old nestlings were found dozing with their faces toward the oven-nest entrance. They ranged in weight from 5 to 5.5 g. Plumage on the ventral wing and body surfaces was still lacking, but the primary sheaths were now 5 mm long and the young could momentarily sit erect. Although all were silent, their eyes were now open. They responded well to the slightest motion of a moth in the bill of a mock-up of an adult bird, and gaped when I touched the nest rim. Their tomia were a slightly duller yellow than on day three and the mouth/throat linings were bright blood red. Skutch (op. cit.) generalized that the mouth linings of nestling warblers are always yellow. However, he has since ascertained (pers. comm.) that this ". . . was based chiefly on my observations of members of the tropical genera *Basileuterus* and *Myioborus* whose mouths quite regularly seem to be yellow inside. . . . Recently I have discovered that in *Vermivora gutturalis* and *Geothlypis chiriquensis* the nestlings mouths are yellow on the marginal parts and red on the deeper parts. . . ." Skutch did not recall the mouth colors of the Pink-faced Warbler. A very young bob-tailed juvenile male taken by A. R. Phillips on 1 July 1964 (ARP no. 3496) weighed 8 g (the weight of some adults) and showed the "gape, pale yellowish buff, mouth, bright orange."

THE FLEDGLINGS

During the first few days out of the nest, juveniles frequent the low thickets, but when the remiges approach adult size (14–15 days after hatching), the fledglings move to the conifer mid-levels. They follow a parent bird, begging with a rapid *see-see-seep* call. As an adult approaches, the young tips-up the tail and spreads the half-opened, rapidly quivering wings on a horizontal plane. The begging call, interjected by squeaky notes, continues until food is placed in the gape. In addition to their own foraging efforts juveniles are fed by adults every one to three minutes. Older begging birds feed at about the same rate as their parents. Adults and young seek one another, but the vociferous young contrast with the silent adults. Young birds beg before redstarts and Wilson's Warblers (*Wilsonia pusilla*), but without response. One bob-tailed juvenile begged from a junco, but an adult Red Warbler swiftly placed itself between the two and displayed by extending its neck and rapidly fluttered its wings. The junco then flew off.

The remiges are fully grown when the dark tips of the juvenile plumage wear off changing the plumage color to buff. The fully grown youngster can now care for itself, as proven by its ability in fly-catching. Bob-tailed young attempting to feed in the latter manner are quite inept.

The adult males now become hostile toward their offspring and interfere with the females efforts to meet the youngs' demands. Three weeks after fledging, the females' attentions have similarly waned. Both adults attack the young, who often fight among themselves. Adults are now beginning the post-breeding molt and females particularly appear worn and ragged. Certain young birds still follow adults, but they no longer beg; they may even weakly return an older bird's attack. These independent young-of-the-year rarely call.

The mortality rate during nestings is very high. Of nine nesting attempts, five nests reached the completion stage and only two of these produced eggs which hatched. A four-egg nest fledged only two young, and three seasons of study disclosed only two out of thirteen pairs that attained the stage of feeding more than one young bird. Both these cases involved two young, and successful broods of three or more were never observed.

Double broods seem unlikely, and intraspecific nest helpers are no doubt rare considering the pronounced intraspecific hostility of this species.

SUMMARY

The Red Warbler, a Mexican endemic and, at least in the south, non-migratory, is common in coniferous forests, ranging from about 8,000 to 12,000 feet above sea level, being most abundant at the lower middle altitudes. It prefers the mid-level of conifers along edges and sunlit clearings, where it remains in pairs throughout the year. It does not readily associate with winter groups of other species.

Courtship consists of chasing, "pouncing," special display flights and singing. Song, given by the male only, is heard from February to June. The songs of mated and single males are different.

During three seasons of study, nine nesting attempts were observed, five of which passed to the incubation stage. The female alone prepares the nest, which is built on the ground and may be either cup or oven-shaped.

The normal clutch is three eggs, but one clutch of four was recorded. The male does not incubate, but shares in feeding the young, although he usually does not approach the nest until three days after the eggs hatch. Eggs pip in about 16 days and fledging occurs 10 to 11 days later.

Three weeks after fledging, the young are fully grown and, preceding the inception of the Fall molt, are driven away by their parents.

Nestling mortality is high and only two out of 13 nests fledged more than one bird. Success of three eggs was never recorded.

ACKNOWLEDGMENTS

Advice and assistance was provided by E. Wyllis Andrews, Richard Crocker, Gordon S. Orians, J. Stuart Rowley, and Alexander F. Skutch. Specimen data were recorded at the San Diego Natural History Museum, the University of California at Los Angeles, the Western Foundation of Vertebrate Zoology, and the California Academy of Sciences. John William Hardy provided access to a superb *Ergaticus* series and the journals of the late Chester C. Lamb at the Moore Laboratory of Zoology at Occidental College, Los Angeles. Dr. Rodolfo Hernandez Corzo of the Mexican Departmento de Conservacion de la Fauna Silvestre courteously provided a collecting permit. Dale A. Zimmerman and John Davis kindly read and commented on earlier versions of the manuscript. Davis and Allan R. Phillips offered special encouragement during the field studies.

LITERATURE CITED

Austin, O. L., Jr. 1961. Birds of the world. Paul Lamlyn, Ltd., London.

Dawn, W. 1963. Nesting of the Pink-headed Warbler. Nat. Hist., 72:28–31.

Elliott, B. G. 1965. The nest of the Red Warbler. Condor, 67:540.

Goldman, E. A. and R. T. Moore. 1945. The biotic provinces of Mexico. J. Mammal., 26:353.

Hamilton, W. J. III. 1959. Aggressive behavior in migrant Pectoral Sandpipers. Condor, 61:161–179.

Lea, R. B. and E. P. Edwards. 1950. Birds from the Patzcuaro region. Condor, 52:269.

Lowery, G. H., Jr., and W. W. Dalquest. 1951. Birds from the state of Veracruz, México. Univ. Kansas Publ. Mus. Nat. Hist., 3:531–649

Miller, A. H. 1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. California Publ. Zool., 66:66–67.

Miller, A. H., H. Friedmann, L. Griscom, and R. T. Moore. 1957. Distributional check-list of the birds of Mexico. Pacific Coast Avifauna No. 33.

Paynter, R. A., Jr. 1952. Birds from Popocatéptl and Ixtaccíhuatl, Mexico. Auk, 69:300.

Rowley, J. S. 1966. Breeding records of birds of the Sierra Madre del Sur, Oaxaca, México. Proc. of the Western Foundation of Vert. Zool., 1:193.

Smith, A. P. 1909. Observations on some birds found in southern Mexico. Condor, 11:63.

Skutch, A. F. 1954. Life histories of Central American Birds. Pt. 1, Pacific Coast Avifauna 31.

Zimmerman, D. A. and G. B. Harry. 1951. Summer birds of Autlán, Jalisco. Wilson Bull., 63:311.

DEPARTMENT OF BIOLOGY, WESTERN NEW MEXICO UNIVERSITY, SILVER CITY, NEW MEXICO. (PRESENT ADDRESS: 1213 E. SPRING STREET, TUCSON, ARIZONA 85719) 3 JUNE 1968 (ORIGINALLY RECEIVED 7 JUNE 1967).

PUBLICATION NOTES AND NOTICES

Waterfowl Migration Corridors East of the Rocky Mountains in the United States. By Frank C. Bellrose. Biological Notes No. 61, Illinois Natural History Survey, Urbana, Illinois, 1968: 23 pp. 6 maps. (Single copies available at no charge from the publisher.)

From an analysis of band recoveries; visual sightings of ground observers and aircraft observers; radar surveillance; formal waterfowl censuses; and the annual winter waterfowl inventory the author has arrived at updated versions of the Lincoln waterfowl flyway maps published years ago. Besides the informative text, excellent maps showing both the directions and intensities of the various flights are given for the fall migrations of the dabbling ducks, the diving ducks, and Canada Geese, and for both spring and fall migrations of Blue and Snow Geese.—G.A.H.

Symposium: Introduction of Exotic Animals: Ecological and Socioeconomic Considerations. Sponsored by the Texas Chapter of The Wildlife Society at the 18th Annual Meeting of the American Institute of Biological Sciences. Published by the Caesar Kleberg Research Program in Wildlife Ecology, College of Agriculture, Texas A & M University, College Station. 1968. 25 pp. No price given.

A series of seven papers on this sometimes controversial subject, including two on quarantine and disease problems. All authors were more or less on the side favorable to introductions and the symposium would seem to have been rather one-sided.—G.A.H.

SEXUAL AND AGONISTIC BEHAVIOR OF THE COMMON RHEA

Robert J. Raikow

The behavior of a group of Common Rheas (*Rhea americana*) was studied during 1962 and 1963 in large outdoor enclosures at the Detroit Zoological Park and the San Diego Zoo. The maintenance behavior of this species was described in an earlier paper (Raikow, 1968) and the present paper deals with aggressive behavior, courtship, and nesting.

AGONISTIC BEHAVIOR

Individual Distance.—Except during agonistic or reproductive activities when contact is necessary, each rhea maintains a zone of a few inches around itself into which other rheas are not permited to come. This individual distance is maintained by one rhea moving slightly away from another when they are standing or moving about in a group. During periods of excitement, as when rheas are gathered together to be fed by zoo visitors, casual and momentary bodily contact may occur without any reaction. However, if one bird pushes against another it may elicit a Head-forward threat display.

Head-forward Display.—When a rhea sits down the individual distance may increase to enclose the animal in a circle with a radius of several feet. The size of this circle varies with factors which are not clearly understood, but seem to involve sex, reproductive state, and the kind of intruder. Males are more apt to be aroused than are females. At times a resting rhea is completely unresponsive to the approach of another, but often it reacts with a Head-forward threat display. As the intruder approaches to within 20 feet or so the resting bird becomes alert and carefully watches the other. If the intruder comes no closer the rhea relaxes and resumes its rest. However if the other approaches to within 10 or 15 feet the rhea opens its bill and gapes, drawing its head back slightly and turning it so as to face the moving rhea continually. Again, if the intruder comes no closer, the rhea resumes its rest. More commonly, however, the resting bird will thrust its head toward the intruder with bill agape, often hissing loudly, then quickly draw its neck back into an S-curve. This may be repeated several times. (Fig. 1)

The response of other animals to this display is extremely mild. A rhea or llama which is wandering past only occasionally glances at the displaying bird, and usually ignores it completely.

If the intruder remains nearby for more than a minute or two the rhea may rise to the crouching position or even stand up. Having gotten to its feet it seems to lose its belligerency and may preen for a moment before wandering off with no further interest in the other individual.

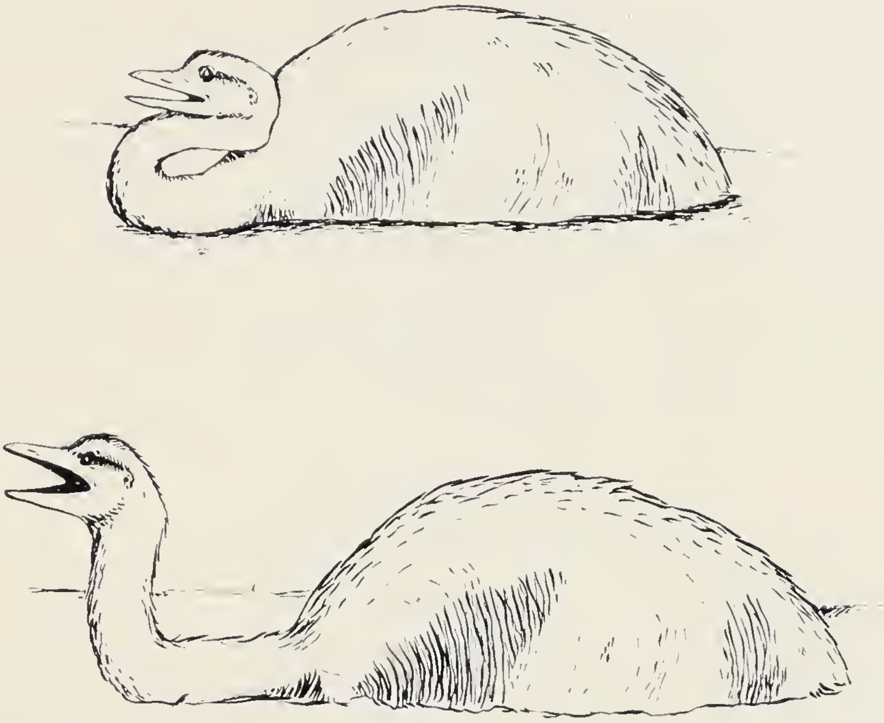


FIG. 1. The Head-forward Threat Display of the male rhea.

Discussion.—The Head-forward movement appears to be a ritualized act of biting, and includes various more-or-less modified components of the act. These are as follows:

a. Gaping and thrusting the head forward are intention movements of biting.
b. Hissing is presumably useful in intimidation, but its origin is not clear. Possibly it is derived from normal breathing activity, i.e., an exaggerated expiration sound (See Spurway and Haldane, 1953).
c. Beak-snapping occurs during threat displays in some birds, e.g., the Chaffinch (Marler, 1956), and is an intention movement of biting. It occasionally occurs in the rhea at the end of the forward neck thrust.
d. Wing-spreading occasionally occurs during the Head-forward display of a rhea on the ground. It may have some intimidation value by increasing the rhea's apparent size, or because of the sudden movement. This movement is common in nest defense where the spread wings cover the eggs or chicks, and sometimes occurs in a display by a male which is lying down but is not on a nest. Perhaps this inappropriate movement occurs because of the postural similarity of the two situations.

The various components of the display occur at different levels of motivation, resulting in a regular sequence of movements. The level of motivation increases as the external stimulation continues, and under low motivation the display is performed more slowly and may not be completed. Gaping is the first of the components to occur, and is thus the movement which is initiated at the lowest level of motivation. Under low motivation the subsequent movements of withdrawal and thrusting the head forward occur slowly, but under higher motivation the pauses between components disappear, and the entire act is performed in one quick, coordinated movement.

The cause of this reaction is uncertain. A rhea which is on the ground is more vulnerable to attack than when on its feet, so an increased alertness is probably of adaptive value. The greater sensitivity of males is possibly related to a state of broodiness, for a male on the ground during the breeding season may be sensitive to situations which might endanger the nest, if it had one.

Reproductive Behavior

The most conspicuous aspect of the reproductive behavior of the rhea is the dominant part played by the male. He performs courtship displays, builds the nest, incubates the eggs, and cares for the chicks. The female's role is limited to copulation and egg-laying. The rhea is both polygynous and polyandrous and apparently no pair-bonds are formed beyond the momentary association of copulation. Females lay eggs in the nests of various males, and if no male is ready with a nest the egg is simply dropped somewhere. The young are precocious and able to feed themselves almost from hatching, but must be protected by the male against predation.

Sexual Rivalry Between Males.—The breeding season is marked by an intense sexual rivalry between males. Hudson (1920) has noted that in the wild the younger males may be "attacked and driven off" by older males, and has described the combat which occurs between older males, in which they twist their necks together and bite viciously while running together in a circle. Such fighting was not observed in this study, possibly because one male established dominance over the others. There were four full-grown males in the group, but only two attempted to establish nests, and only one was seen attempting copulation or guarding eggs.

Chasing of other males was common. First the male stands in a characteristic threat posture with the front of the body lowered, the neck held in a low U-loop, and the eyes fixed on the other rhea. (Fig. 2) Then he extends his head forward and takes a few slow steps toward the other before breaking into a run. Often a less intense display is seen, in which the lowering of the body consists of a single, rapid bobbing motion, and the Head-forward Display merges quickly into a run without the initial walking steps.

As the pursuer runs he holds his wings raised above his back and his neck in an S-curve, thrusting it forward to bite when he gets close enough. Often he aims at the other's head, hitting it or missing by a few inches. The pursued rhea runs off in a characteristic defense posture with his neck drawn back

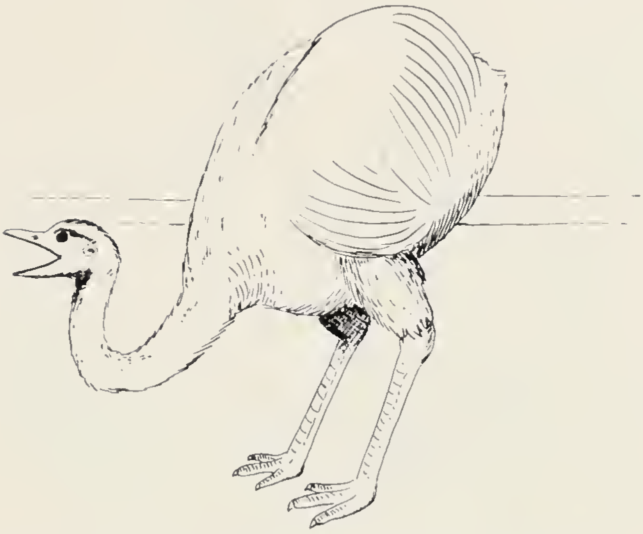


FIG. 2. The threat posture of the male rhea.

in an S-curve and his wings held high above his back, or sometimes spread laterally, and often flicked up and down rapidly and sporadically. He makes frequent sharp changes in direction, resulting in a zig-zag path of escape. This differs somewhat from the defense posture described by Portielje (1925) in which the wings are not fluttered and the neck is held upright rather than drawn back. This occurs when the rhea is not too excited. Wing flipping begins when the attacker draws near, and perhaps helps the pursued male to avoid being bitten. A chase seldom exceeds thirty or forty feet in length.

Courtship Display.—The Call Display involves three consecutive activities: (a) assumption of a call posture, (b) the call itself, and (c) a running display. The first indication of rising sexual drive in the male is a ruffling of the plumage of the head and upper neck. This may occur at almost any time, e.g., during feeding. It may be followed by later stages of the display, or may gradually disappear. The male may show the same ruffling prior to the wing display, described below, or before chasing another male.

As the level of motivation rises the ruffling of plumage extends to other areas, including the base and middle of the neck, the breast, the tibiae, the back, and the rump. The wings are then extended dorso-laterally. The rhea may remain at this stage for several seconds and then relax his plumage, or the next stage of the display may follow.

The actual display begins with a characteristic posture. (Fig. 3) The anterior end of the body is raised upward. The neck is held stiffly upward and forward, with the plumage ruffled to a maximum degree. The wings may be raised higher than before, and the base of the neck is expanded. The call is then given, sometimes immediately and sometimes after a pause of several seconds. The call is deep-toned, with two notes, and lasts about

FIG. 3. The Call Display of the male rhea.

one second. The first note is the deeper of the two, and falls in pitch, while the second note rises slightly higher than the first. It has been described as a deep-toned hissing (Darwin, 1955), the last tone of a siren (Portielje, 1925), and a deep booming (Wetmore, 1926). After calling once or twice the rhea may relax, or it may break into a run of several hundred feet, sometimes flipping the wings up and down alternately. One wing may be held higher than the other, and the rhea may change directions suddenly. This running is similar in appearance to the defense run described above. The male runs toward the female from behind or to one side, at which the female runs off with the male following. Portielje (1925) described the female as running *toward* the male, but this was not observed here. Her bearing is so like the defense posture that the performance has more the appearance of an aggressive chase than a courtship ritual, and perhaps the female so regards it when her reproductive drive is low.

Sometimes a male performs an incomplete, or even a complete call display when no female is nearby. Possibly this is a vacuum activity, but since there are always females around, though perhaps no nearer than several hundred feet, it may be that the male is responding to a visual stimulus. In any event it is clear that this display may be performed with only a very minimal ex-

Fig. 4. (a and b). The Wing Display of the rhea. The bird with its wings spread laterally is the male, the other a female.

ternal stimulus. In contrast, the other courtship displays occur only when another rhea is nearby.

Presumably the function of the call is to attract the attention of the female. It is apparently the only vocalization in this species other than the peeping of the chicks, hissing during threat, and some grunts used by the male to warn the chicks of danger. Why does it occur in this generally silent animal? Perhaps because these birds, living in groups in open country are in full view of each other much of the time, and are so accustomed to seeing other rheas that some unusual and highly specific signal is needed to overcome this familiarity so that the female's attention will be actively drawn to the display.

The male makes no attempt to copulate after running, but generally shows no further interest in the female. Possibly the major function of the display is the long-term stimulation of the female's reproductive drive.

In the Wing Display the male slowly approaches the female, lowers his neck in a low loop, and walks beside her, sometimes bobbing his head slightly. The plumage of his head and upper neck is ruffled. This may continue for several minutes while both birds peck and nibble at objects on the ground. Finally the male spreads his wings and walks beside or ahead of the female in the full display (Fig. 4) with the anterior end of the body lowered slightly and the neck in a low U-curve. The wings are extended laterally and slightly forward, at about right angles to the longitudinal axis of the body. The humerus extends out from the body and droops slightly, the radio-ulna is directed vertically downward, and the manus is extended outward and down at about a forty-five degree angle. Often the wings are held so low that the plumes drag on the ground. The plumage of the head and neck is generally heavily ruffled, while that of the back, flanks, rump, and tibiae are sometimes more lightly ruffled.

The male walks slowly beside the female, sometimes turning to give her a front view of his wings. The female may be unresponsive, though if the male persists she may walk quickly away. The display usually lasts ten to fifteen seconds, but sometimes persists for as long as two minutes. Longer displays reflect stronger motivation, for the posture is more stiffly maintained, the ruffling of feathers is at a maximum, and the male may perform a few head-bobbing movements as he walks. Most displays end when the female walks away, at which the male often engages in wing-preening. Occasionally the male may attempt to begin copulation, but the female generally evades him. He does so by grasping her at the base of the neck with his bill. Almost always she pulls away and runs off. As a result it is common to see females during this time with the base of their neck plucked free of feathers.

This display probably arose through the ritualization of displacement activities arising from approach-avoidance conflict. The most conspicuous component of the display is wing-spreading. The only non-display activity of this species which results in a similar wing posture is wing-preening. It would appear that the Wing Display is a ritualized wing-preening movement in which wing-spreading has been emphasized while the preening movements with the bill have been inhibited. These may occur, however, if the female responds negatively and the male is unable to attempt copulation. Early in the course of evolution of this display other displacement activities could have occurred during approach-avoidance conflict. The Wing Display, however, was presumably selected for because it was most effective as a social signal, probably because it is more distinct and unique than other movements, i.e., it results in the greatest change in the appearance of the male.

This kind of sexual display may have lead to the retention of the wings in this species during the course of evolution, despite the fact that they no longer served in locomotion. In such ratites as the emu, in which the wings are reduced to small vestiges, no such selection pressure apparently existed.

Regarding the other components of the Wing Display, the ruffling of the plumage is probably a ritualized expression of the autonomic pilomotor response to excitement (Morris, 1956), while Head-bobbing may represent either intention movements of the inhibited preening activity, or an intention movement of grasping the female. The pecking at the ground which sometimes occurs early in the display is presumably a displacement feeding activity.

The Head-bobbing Display of the male is apparently performed under sexual motivation, since it is usually directed toward a female. The male stands with the neck in a low loop. The head and neck are bobbed vigorously up and down through a path of about a foot in the sagittal plane, and sometimes simultaneously swung from side to side through a U-shaped arc in the transverse plane. This Head-bobbing is like that sometimes seen in the Wing Display, but greatly exaggerated.

The display is directed only toward a rhea which is sitting down, usually a female. She immediately becomes alert, rises to her heels, and a moment later to her feet. She may preen a bit after arising, and sometimes also bobs her head slightly. After arising she usually walks away. Often the male follows and performs a Wing Display, or intention movements of one. Once a male grasped a female at the base of the neck in an attempt to initiate copulation, but the female pulled free. Sometimes instead of arising slowly the female will leap suddenly to her feet and run away rapidly in the defense posture.

The most likely explanation for this behavior seems to be that it is a precopulatory display stimulated by the sight of a female on the ground, the position which she maintains during copulation. The Head-bobbing may be a ritualized intention movement of grasping, which initiates copulation.

Copulation.—Successful copulation was not observed during this study. Portielje (1925) gives the following description (translated):

> "During the quite extended copulation the hen lay on the ground with her neck stretched forward. The cock did not mount her, but sat behind her, propped up on his heels while holding the feathers of her lower neck with his beak, and from time to time making violently thrusting motions."

Brito (1949) notes that the act averages two minutes in duration.

Nest Construction.—The nest is roughly circular, about three feet across, and about one foot deep. In nature it is often placed in some shaded area or in tall grass (Wetmore, 1926). In the zoo, nests were constructed in both sunny and shaded areas, but eggs were laid only in the latter.

In constructing his nest, the male digs by kicking backward with his feet. either while standing or crouching in the nest. Movements of the body while crouched undoubtedly aid in shaping the nest. A low rim of loose material is raised slightly above the surrounding soil, and is often arranged with twigs or leaves. Some dirt may also be removed with the bill.

Nest Ceremony and Egg-Laying.—According to Sick (1964) and Steinbacher (1951) the male leads the female to the nest for egg-laying. This was also observed once during the present study, but in several other instances the female approached the male as he sat on the nest. The male responds to this approach by watching her closely, often rising to his heels. She approaches the edge of the nest and slowly walks around it, sometimes pausing to stand perfectly still for several minutes at a time. The male may rise to his feet, but usually remains sitting or crouching, twisting his neck grotesquely in his attempts to keep the female in view. He may even extend his neck straight out over his back, peering directly behind himself with his head upside-down. Usually during the first several minutes of this confrontation the male makes threat movements, crouching low and spreading his wings to cover the nest while giving Head-forward displays and snapping at the female. She does not return the attack but remains outwardly calm, often immobile. After several minutes the character of the male's activity changes. The aggressive movements are replaced by a more ritualized display with vigorous Head-bobbing and neck swinging movements. The female may respond with a very faint Head-bobbing, and the male still twists his neck around to follow her movement around the nest.

Finally the female crouches on her heels beside the male and deposits the egg on the rim of the nest. Her cloaca is held a few inches above the ground and the egg is deposited gently. Portielje (1925) describes an act in which the male extends one wing beneath the female's cloaca, catching the egg as it is dropped so as to cushion its fall. Such behavior was not observed in this study. Immediately after laying the egg the female rises and walks or runs away. The male then draws the egg beneath himself with his bill. As the male broods he alternately sleeps and is alert, holding his head high and looking about. Sometimes he sleeps deeply for half an hour or more with his neck folded in an S-curve, but mostly he holds his neck vertically and naps only for a few seconds, or one or two minutes at most.

In both sexes agonistic as well as reproductive motivation is present, and the aggressive drives must be reduced before reproductive behavior can occur. At first the male is agonistically motivated, and shows conflicting tendencies to attack (shown by the Head-forward Display) and to remain on the nest (shown by the crouching and wing-spreading). This is because the female presents both aggressive and reproductive stimuli. In order to reduce the male's aggressive reactions she must provide additional reproductive stimulation, in the form of some type of submissive behavior (Tinbergen, 1952). She does this by failing to respond to the male's threat display with a normal defense reaction. Instead she becomes almost immoble, and stands quietly or moves only slowly for several minutes, until the male begins to relax. As his aggressiveness wanes, the Head-forward threat movements are replaced by Head-bobbing and neck swinging which are probably ritualized Head-forward Displays. This apparently acts as a releaser, permitting the female to cease her submissive behavior and to continue on to the act of egg-laying. Once she has laid the egg, the female is no longer reproductively motivated, and she leaves.

Sometimes a female will approach a male on the nest, the ritual will occur, and then she will walk away without having crouched or laid an egg. Here

FIG. 5. The nest-defense posture of the male rhea.

her reproductive drive may be insufficient to overcome her reaction to the male's aggressiveness so that crouching beside him, which involves the suppression of her normal tendency to maintain an individual distance, cannot take place.

Nest Defense.—A characteristic threat display is given by an incubating male if he is aroused by the approach of another rhea. Crouching low on the nest, he spreads his wings laterally, holding them closely appressed to the ground, and covering the eggs, while at the same time giving a Head-forward threat display (Fig. 5). This is very similar to the purely aggressive threat display described above, with the addition of the nest-covering wing movement. It is also similar to the early part of the male's reaction to a female who approaches for the purpose of egg-laying, and undoubtedly that response is a little-modified Nest-defense Display. However in true nest defense the male is much fiercer in appearance, his posture is more stiffly maintained, and his movements are jerkier, indicating a greater intensity of aggressiveness.

SUMMARY

A group of Common Rheas was studied in a large outdoor enclosure at the Detroit zoo. A small individual distance is maintained, but the major defensive display is a head-forward movement derived by ritualization of biting movements. In Nest-defense this includes a nest-covering movement of the wings.

The male performs three types of displays. A Call Display begins with a booming call given in an upraised posture with the wings raised and the base of the neck swollen. The rhea then runs across the enclosure in a zig-zag course. He may chase a female, who then runs away in a similar manner, or may perform the display alone. It seems likely that the running phase is derived from an aggressive chase, and probably the female regards it as such. The function of this display is uncertain, perhaps it acts in long-term stimulation of the female.

The Wing Display is always directed toward a female, and may lead to copulation. The male walks beside the female with his neck in a low U-loop and his wings spread laterally. Then he may grasp the female at the base of her neck in an attempt to begin copulation, but the female usually runs away. The origin of this display may be the wing-preening posture of the male, which arises as a displacement activity resulting from approach-avoidance conflict prior to copulation.

A Head-bobbing Display of the male is directed toward a seated female. It may be a precopulatory display, but its origin is uncertain.

When the female is ready to lay an egg she comes to the nest and the male at first reacts aggressively, but gradually his defensive movements assume the appearance of a formalized display, permitting the female to approach closely. She crouches beside the male and lays the egg, then walks away, taking no further part in reproduction.

The nest is a shallow hole in the ground three or four feet wide and sometimes lined with a bit of loose vegetation. The male spends some time in it, resting or "defending" it against other rheas, even though it may contain no eggs.

In some ratites the wings are reduced to functionless vestiges, but in the rhea they are utilized in sexual displays and have apparently been retained by selection because of their value as a secondary sexual characteristic, rather than in their original function as locomotory structures.

ACKNOWLEDGMENTS

This study was done under the direction of Dr. William L. Thompson of the Department of Biology, Wayne State University, whose guidance and encouragement are gratefully acknowledged. Thanks are also due to Keith Kreag and James Drake of the Detroit Zoological Park, and to Kenton C. Lint of the San Diego Zoo.

LITERATURE CITED

Brito, P. 1949. Observacoes Sobre O Comportomento E A Reproducao Da Ema, *Rhea americana americana* (L.) Em Cateiverio. Bol. Mus. Nacion. Rio de Janeiro. Zool. Ser., 89:1–6.

Darwin, C. 1955. The voyage of the Beagle. Bantam Books edition, New York.

Hudson, W. H. 1920. Birds of La Plata, vol. 2:230–236. J. M. Dent and Sons Ltd. London.

Marler, P. 1956. Behaviour of the Chaffinch, *Fringilla coelebs*. Behaviour Suppl. V., E. J. Brill, Leiden.

Morris, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour, 9:75–113.

Portielje, A. F. J. 1925. Zur Ethologie bsw. Psychologie der *Rhea americana* L. Ardea, 14:1–14.

Raikow, R. 1968. The maintenance behavior of the Common Rhea. Wilson Bull. 80: 312–319.

Sick, H. 1964. "Rhea" in Thompson, A. L. (ed.) New dictionary of birds. McGraw-Hill, New York.

Spurway, H. and J. B. S. Haldane. 1953. The comparative ethology of vertebrate breathing. Behaviour, 6:1–34.

Steinbacher, G. 1951. Zur Brutbiologie des Nandus, *Rhea americana* L. Zool. Garten. N.F. 18:127–131.

Tinbergen, N. 1952. A note on the origin and evolution of threat display. Ibis, 94: 160–162.

Wetmore, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. U.S. Nat. Mus. Bull., 133:23–27.

DEPARTMENT OF BIOLOGY, WAYNE STATE UNIVERSITY, DETROIT, MICH. (PRESENT ADDRESS: MUSEUM OF VERTEBRATE ZOOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY.) 9 JANUARY 1967.

GENERAL NOTES

Juvenal plumage of the Spotted Rail *(Rallus maculatus.)*—The juvenal plumage of the Spotted Rail (*Rallus* (*Pardirallus*) *maculatus maculatus*) was described by Friedmann (Bull. U.S. Natl. Mus. 50, 1941) as ". . . similar to the adult but has all the chaetura black on the underparts replaced by dark hair brown and the white on the upper parts slightly washed with ashy buff and has the feathers of the top of the head, hind neck, and anterior interscapulars narrowly edged with mummy brown." (p. 104). This description was probably based on a juvenile from Argentina in the collection of the American Museum of Natural History (No. 471,936) which was apparently the only specimen in full juvenal plumage in collections in the United States at that time. This specimen is the central bird in Figures 1 and 2.

On 18 November 1963 the authors stopped briefly at a large cattail marsh near the sugar refinery of San Cristobal, 37 kilometers by road south southwest of Tlacotalpan, Veracruz, to check on the water level and hopefully to collect *Laterallus ruber.* On hearing a call much like that of a King Rail, we stopped and "squeaked" until finally within a few yards of us Dickerman saw a rail briefly and collected it. The bird was immediately

Fig. 1. Dorsal view of juvenal plumage Spotted Rails. *Rallus maculatus insolitus* (left, from Mexico), and *R. m. maculatus* (center and right from Argentina and Trinidad).

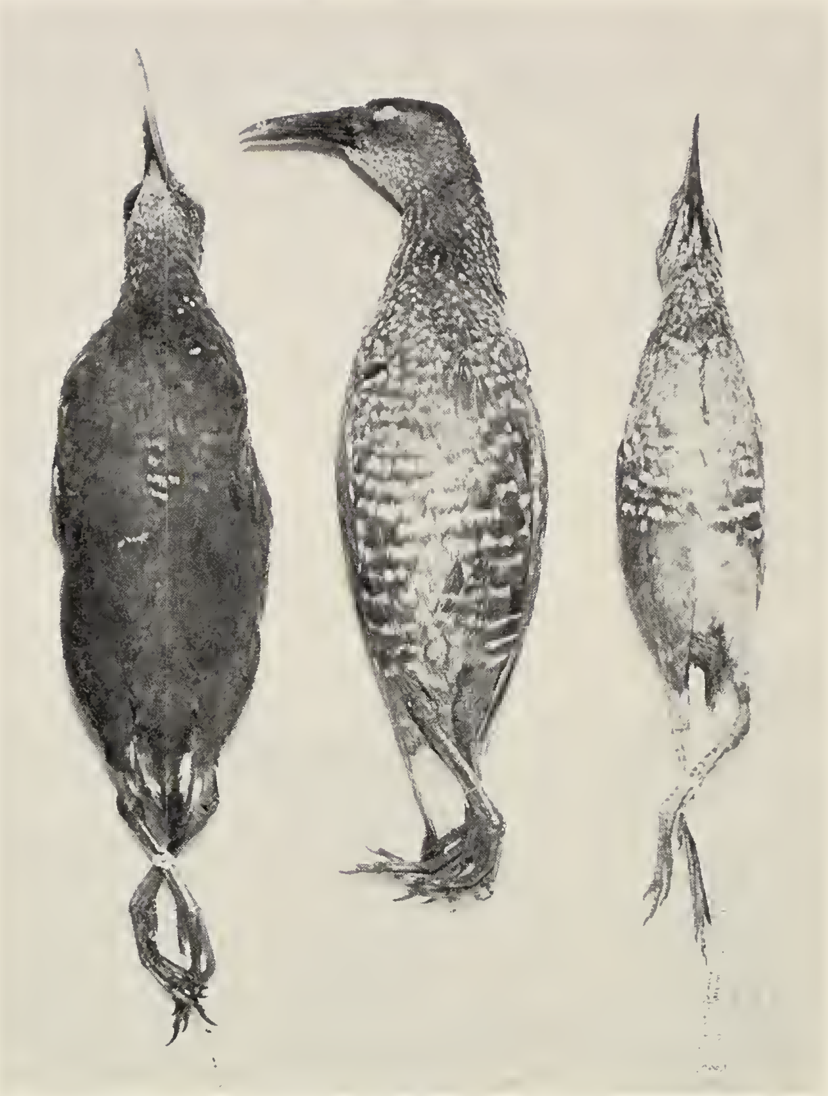


FIG. 2. Ventral view of juvenal plumaged Spotted Rails in Figure 1.

identified as a juvenile Spotted Rail, based largely on the presence of a few black feathers spotted or barred with white, which contrasted with the sooty gray feathers of the juvenal plumage (left specimen in Fig. 1 & 2). In checking our specimen with Friedmann's description of the juvenal plumage of the species, it would have been difficult to believe we had collected the same species, were it not for the few incoming feathers of the first basic plumage!

A survey of museum collections revealed two unreported juveniles of the nominate form; one from the Caroni Swamp, Trinidad (Peabody Museum No. 25,668), and the other from Paraguay (Field Museum Natural History, Conover Collection No. 11,009). In 1965 and 1966 a special effort was made to obtain additional juveniles from Mexico to determine if the first specimen was melanistic, or was characteristic of the northern population *Rallus maculatus insolitus* (*cf.* Dickerman and Warner, Wilson Bull., 73:336, 1961, and Watson, Wilson Bull., 74:349, 1962). Two were collected. The juvenal plumage of *R. m. insolitus* does appear indeed to be quite distinct from that of *R. m. maculatus* and perhaps offers the most diagnostic character of *insolitus* (*cf.* Phillips and Dickerman, Wilson Bull., 77:298, 1966 for discussion of the use of juvenal plumage as a subspecific character).

As will be noted in Figure 2, in the juvenal plumage of the Mexican populations, the ventral barring so pronounced in the *R. m. maculatus* juveniles is obsolete or lacking. The underparts of Mexican juveniles appear uniform sooty to dark grayish olive, with obscure darker bars. Dorsally the *insolitus* juveniles are darker, more uniform and have little or no white spotting. The other two Mexican specimens have a little more dorsal spotting than the specimen illustrated. The younger specimen of *maculatus* from Trinidad is largely downy on the back with its juvenile feathers still sheathed. The edges of the back feathers of the juvenal plumage of *insolitus* are a darker brown than are those of *maculatus.* This had also been the principal character used to separate adults of the two subspecies, until Watson (op. cit.) called attention to the reduced white spotting of *insolitus* but deprecated the value of dorsal color. On the basis of examination of a larger series than was available to Watson, we note that, contrary to his findings, the edgings of *fresh* dorsal feathers of *insolitus* are indeed darker brown, but *not* significantly narrower, than those of *maculatus.*

The specimen from Paraguay, although in a more advanced stage of molt, was apparently similar to the other juvenile *maculatus,* indicated by its flanks, which are pale gray strongly barred with sooty. In the mid-ventral area it is less barred than the Argentina specimen, and more comparable to the Trinidad specimen. The undertail coverts of the juvenile specimens of *maculatus* from Argentina and Paraguay are dusky gray or white, broadly tipped with buff, whereas in the 3 juvenile *insolitus,* these feathers virtually lack any suggestion of buff; the white undertail coverts are tipped with sooty gray.

The Spotted Rail has usually been segregated in a monotypic genus *Pardirallus* Bonaparte (=*Limnopardalis* Cabanis in some reference works). We prefer to follow those authors (such as de Schauensee, The species of birds of South America, 1966: 77) who merge this genus with *Rallus.* The outline of feathering at the base of the bill used by Friedmann (ibid) to separate *Rallus* from *Pardirallus* and *Ortygonax* does not seem to us to be very important, and, in any case, most authors now merge *Ortygonax* in *Rallus.* If this is done, and in view of the diversity already included in *Rallus,* we do not see how *Pardirallus* can be maintained.

The 1963 specimen of *insolitus* will be deposited in the Minnesota Museum of Natural History, University of Minnesota and the 1965 and 1966 specimens will be deposited in the collections of Cornell University and the Carnegie Museum.

ACKNOWLEDGMENTS

Juvenile specimens of *R. m. maculatus* were obtained on loan from the Field Museum of Natural History, Chicago, and the Peabody Museum of Natural History, Yale University. Dr. Dean Amadon kindly provided us with access to the collections of the American Museum of Natural History. Scientific collecting permits were provided by the Departmento de Conservacion de Fauna Silvestre of the Republic of Mexico.—Robert W. Dickerman, *Department of Microbiology, Cornell University Medical College, New York, New York* and Kenneth C. Parkes, *Carnegie Museum, Pittsburgh, Pennsylvania. 12 April 1968.*

Porcupine quills found in foot of Sharp-shinned Hawk.—During the spring of 1968 the Ontario Bird-Banding Association sponsored a project of banding Sharp-shinned Hawks (*Accipiter striatus*) at Whitefish Point, Chippewa County, Michigan. The species is often numerous during spring migration on this peninsula which lies at the eastern end of Lake Superior and extends northeast toward the mainland of Ontario. We were present from 4–11 May and found hawks migrating during the entire period (especially numerous on 8 May) although there were very few passerine birds present at any time to serve as prey species. On 11 May a female Sharp-shinned Hawk captured in a mist net was found to have three broken porcupine quills from one-half to one inch long in its left foot. These extended completely through the toes and had to be removed with tweezers. The bird had no food in its crop; in fact, of more than 60 hawks examined in the week, only four had full crops, attesting to a meager food supply. Although there are examples in the literature of Sharp-shinned Hawks attacking larger birds (Black-crowned Night Heron, Wood Duck, Common Crow, and domestic chickens), nothing was found regarding attacks on porcupines, dead or alive. The bird seemed to be in good condition, none the worse for its encounter, and flew away spiritedly when released. —ALICE KELLEY AND NEIL KELLEY, *3681 Forest Hill Drive, Bloomfield Hills, Michigan, 31 May 1968.*

The migration of the American Golden Plover through Surinam.—The American Golden Plover (*Pluvialis dominica*) has the fame of making a long transoceanic flight in autumn from Nova Scotia to northern South America and after a short stop proceeding to its winter quarters in Argentina. In spring the birds are said to return in a long overland flight more to the west of the southbound route over the Amazonian rain forest, then via central North America to the arctic breeding grounds so that the entire route is in the form of a giant ellipse. The map illustrating this supposed route dates from Cooke (U.S. Dept. Agr. Bull., 185:12, 1915) and still is one of the show pieces of bird migration which appears in even the latest handbook on migration by Dorst (The migrations of birds, 1962, p. 100) and even on the dustcover of Griffin (Bird migration, 1964). Lately Johnston and McFarlane (Condor, 69:165, 166, 1967) stated, in my opinion quite rightly, that some of these ideas perhaps deserve corrections and are at least unproven. As to the long oversea flight in autumn I might remark that recent field observations prove that there is quite a lot of island-hopping in the Caribbean. To mention only three authors: Pinchon (Faune des Antilles Françaises. Les Oiseaux, 1963, p. 37) states that in the French Antilles (perhaps pertaining to the main island Martinique though this is not specially mentioned) these birds are regular guests from the beginning of August till the end of November. The gunners of the island kill large numbers ("ils en font une hécatombe") a practice which is, according to the author, "justified, it must be admitted, by the quality of the bird." Mees (Junge and Mees, Zool. Verhandl. 37:27, 1958) saw a flock on 22 September 1953 on Trinidad which were still present when he left the island in December and ffrench (Herklots, The birds of Trinidad and Tobago, 1961, p. 80) remarks that large flocks annually visit the golf course at Pointe à Pierre during September and October.

The handbooks further state—once more copying Cooke—that after a short stop on the north coast of South America the plovers resume their travel overland to the pampas of Argentina. One gets the impression that the birds are in a desperate hurry to reach their winter quarters. This too needs some correction as we now know—apart from the presence of Golden Plovers on some islands in the Caribbean during two to four autumn months—that the plovers remain in the northern part of continental South America for two or more months. Foster Smith (Friedmann and Smith, Proc. U.S. Natl. Mus. 100:458, 1950 and Proc. U.S. Natl. Mus. 104:490, 1955) says that the Golden Plover is quite common on savanna ponds in Venezuela during October and November and lists as extreme dates 18 September and 5 December. He also drew attention to the interesting habit of these birds feeding at night on the well-watered lawns in oil company camps. A similar situation exists in Surinam where the Golden Plover is a regular if not very numerous migrant in open places with a very short vegetation and especially on recently harvested and burned over sugar cane fields where small flocks of up to 40 Golden Plovers occur, often in company with Upland Plovers (*Bartramia longicauda*). Mr. Th. Renssen who lives at the sugar estate Marienburg in the Commewijne District sees Golden Plovers regularly in this type of habitat and has collected a series of specimens for me.

The first date of occurrence in Surinam is 1 September (1 September 1963 1 & 5 birds at Maasstroom (sight), 1 September 1966 Marienburg (specimen), 1 September 1967 Marienburg (sight)). All birds up to the middle of October were in full or in nearly full breeding plumage so it is apparent that adults arrive first. In recent years I observed about a dozen birds staying for some time on a football field of the Police Training Center at the outskirts of Paramaribo. In 1957 they were rather late: from 11 October until 8 November, in 1966 from 9 until 23 September and in 1967 from 11–14 September. My latest dates in autumn are 7 November 1965 Maasstroom (specimen) and 8 November 1957 Paramaribo (sight). In contrast to the Upland Plover (Haverschmidt, Wilson Bull., 78:319–320, 1966) Golden Plovers do not remain during the northern winter in Surinam. However, from these records it is clear that the birds are in no hurry to travel southwards and stay in Surinam for at least two months.

In Surinam Golden Plovers occur rarely in spring. Mr. Renssen saw a flock of 4 in breeding plumage on a meadow at Moengo on the Cottica River on 2 February 1962, which seems very early. In this connection I may refer to the capture of a banded bird at Demerara River in Guyana on 30 January 1949 which is in my opinion an early spring migrant and not a wintering bird. Mr. Renssen further saw a bird in breeding plumage at Peperpot plantation on 20 March 1964 and a few in the same locality on 24 March 1964. The latest date in spring is of a bird in nearly full breeding plumage which was shot at Marienburg on 13 May 1967.

The birds which arrive in September appear to be healthy and the weights of my series of 14 specimens are: 1 September 1965, ♀ 122 g; 7 September 1963, 3 ♀♀ 109, 114, and 130 g; 26 September 1963, ♂ 147 g, ♀ 139 g and ? 111 g; 26 September 1964, ♀ 135 g; 1 October 1964, ♂ 155 g; 22 October 1964, ♀ 160 g; 29 October 1964, 2 ♀♀ 132 and 144 g; 7 November 1965, ♀ 122 g; 13 May 1967, ♂ 146 g. The contents of the gizzards of these birds were identified by Dr. D. C. Geyskes and contained insects: Coleoptera (Chrysomelidae, Curculionidae) and larvae of Lepidoptera.—F. HAVERSCHMIDT, *Wolfskuilstraat 16, Ommen, Holland, 5 March 1968.*

Mew Gulls in Ontario.—On the morning of 24 October 1967, Daniel Salisbury observed a Mew Gull (*Larus canus*) at St. Catharines (Port Weller) in the Welland Canal near its entrance at Lake Ontario. This bird was with a small flock of Ring-billed and a few Herring Gulls. It remained in this vicinity through the afternoon, either flying above the water or alighting on the surface or the concrete wall bordering the canal. In late afternoon, with the assistance of Salisbury and Arthur Clark, we collected this bird south of canal lock no. 1 in the same locality. It is an adult male (BSNS no. 5102) in winter plumage (dark flecking on head, neck and breast), was moderately fat and weighed 422.55 g; its testes measured (mm): left 9 × 3, right 5 × 2. We determined this individual to be of the race *L. c. brachyrhynchus*, a diagnosis verified by Dr. Richard C. Banks at the U. S. National Museum. This is the first record for Mew Gull in the Niagara Frontier Region and the Province of Ontario, and is apparently the first specimen of this subspecies taken in eastern North America.

On 28 November 1967, Salisbury found another Mew Gull in the Welland Canal just north of lock no. 4 at St. Catharines, about 10 km south of Port Weller. Apparently the same individual was seen by John Black the following day. It fed actively among Ring-billed, Herring and several Bonaparte's Gulls when water was released from the lock, and at times it rested on the water or the canal wall. We secured this bird on 30 November, assisted by Clark, Black, Salisbury and Adrian Dorst. It is a female (BSNS no. 5103) in first-year plumage, possessing heavy fat and with gonad measuring 9 × 2.5 mm. Its weight was 454.6 g and the plumage is slightly worn. We also assigned this individual to the race *brachyrhynchus* as did Dr. Banks. It constitutes the second record for the above mentioned three areas. Both specimens are in the Buffalo Museum of Science. External measurements (mm) are given in Table 1.

TABLE 1

	male (BSNS no. 5102)	female (BSNS no. 5103)
Wing	molting	332.5
Tail	142	121
Tarsus	48	46
Exposed culmen	33.5	31.5
Height of bill at base	11.5	10
Height of bill at gonys	10	9.5

The two Mew Gulls collected in Massachusetts, respectively, at Chatham on 8 February 1908, by N. A. Eldredge (second-year plumage) and at Newburyport on 3 March 1951, by A. H. Morgan (adult plumage), although initially identified as *L. c. brachyrhynchus*, were subsequently referred to the nominate race by Dr. Alexander Wetmore (Griscom and Snyder, The birds of Massachusetts, 1955:125). These two specimens plus a third taken on 19 April 1956, at Locks Cove, Newfoundland, and identified as *L. c. canus* (Godfrey, The birds of Canada, 1966:182), are, so far as we know, the only examples of Mew Gull other than the present two that have been secured in eastern North America. The specimen reported by Bent (U. S. Natl. Museum Bull., 113:145, 1921) as being taken at Quebec City has apparently been discounted and was omitted from the 5th edition (1957) of the A.O.U. Check-list. According to Godfrey (pers. comm.), the authority given by Bent for the record, Dionne, did not include it in his book on the birds of the Province of Quebec.

There have been several published sight records of the species for Massachusetts and New Jersey (see Griscom and Snyder, op. cit.; Bull, Birds of the New York area, 1964: 479; and Audubon Field Notes, 11:248, 1957 and 19:8, 360, 1965). An immature Mew Gull was reported by Salisbury and others as being observed at intervals from late January 1968 into early March on the lower Niagara River.

It is only possible to speculate on the routes that these three Mew Gulls followed in traveling to Ontario, and how long they were in transit and in the region before discovery. Mew Gulls' nearest breeding areas are about 2500 km to the northwest of the Niagara Frontier Region, and from midsummer on, individuals from these populations probably wander in various directions for comparatively short distances before eventually moving westward and southward toward their Pacific coastal wintering grounds.

Weather maps for about a week prior to the sighting of each of the first two Mew Gulls show that low pressure systems moving rapidly eastward in southern Canada were followed eventually by strong westerly and northwesterly winds as polar air masses passed across Canada and the Great Lakes into eastern United States. These Mew Gulls may have been influenced by this sequence of pronounced meterological events in their passage to Ontario. However, since similar weather patterns with systems of varying intensity occur over Canada and northern United States more or less frequently in autumn, it is conceivable that, if affected by them, these gulls wandered toward Ontario in shorter stages over more lengthy periods of time. We thank J. L. Baillie, Jr., R. C. Banks, J. C. Barlow, W. E. Godfrey, A. H. Morgan and R. A. Paynter, Jr. for their information and assistance.—Robert F. Andrle and Harold H. Axtell, *Buffalo Museum of Science, Buffalo, New York, 22 March 1968.*

Color aberrations in some alcids on St. Lawrence Island, Alaska.—While engaged in a study of the comparative breeding biology of plankton-feeding alcids on St. Lawrence Island, Alaska, in 1966 and 1967, I had opportunity to make observations on albinism and melanism in several alcid species.

Gross (Bird-Banding, 36:67–71, 1965) compiled a list including 54 bird families in which albinism has been reported; the family Alcidae is represented by seven species and 27 individuals. A. O. Gross (pers. comm., 1968) listed the alcids in which albinism has been recorded (number of individuals in parentheses): *Alca torda* (1), *Uria aalge* (2), *U. lomvia* (4), *Plautus alle* (2), *Cepphus grylle* (7), *C. columba* (1), and *Fratercula arctica* (10). Storer (Univ. California Publ. Zool., 52:121–222, 1952) and Tuck (The murres, 1961) mentioned additional records of *Uria* spp.; Storer also mentioned one albinistic *Plautus*. The present note records albinism in four individuals of three additional alcid species. The degree of albinism is categorized following Gross (op. cit.) and the terminology for color follows Palmer and Reilly (A concise color standard, 1956).

On 17 August 1967 an imperfect albino Parakeet Auklet (*Cyclorrhynchus psittacula*) was collected near its nest-site on Sevuokuk Mountain. The specimen (U.B.C. Mus. Zool. no. 13361), an adult female, weighed 289.5 g, was moderately fat and showed extensive abrasion of the remiges and retrices. Postnuptial molt had not commenced. The plumage on the dorsal surface, wings, tail, and chin showed albinistic characteristics; this plumage was a "washed-out" buffy brown rather than the normal black. This bird's mate was normally pigmented and their single chick, estimated to be about 24 days old on the basis of its 38.2 mm outer primary (Sealy, A comparative study of breeding ecology and timing in plankton-feeding alcids (*Cyclorrhynchus* and *Aethia* spp.) on St. Lawrence Island, Alaska, unpubl. M.Sc. Thesis, Univ. of British Columbia, 1968), was normally pigmented. The chick fledged at 35 days of age.

On 27 June 1967 a partial albino, adult Crested Auklet (*Aethia cristatella*) was observed flying and walking on boulders on Sevuokuk Mountain. Its wings and breast were white; the remainder of its plumage was apparently normally pigmented.

A Least Auklet (*A. pusilla*) with white rectrices was collected on Sevuokuk Mountain on 30 June 1967. This specimen (U.B.C. Mus. Zool. No. 13389), a subadult male, weighed 81.7 g and was moderately fat.

On 20 August 1967 a young, total albino, Least Auklet was found in a nest on Sevuokuk Mountain. It retained the normal plumage pattern, but the dark color of the upperparts was replaced by buffy tan (Fig. 1); a similar condition has been described for *U. lomvia* and *P. alle* (Storer, op. cit.). The auklet (U.B.C. Mus. Zool. No. 13359) had pink irises, legs and feet, and was about 24 days old on the basis of the 41.2 mm outer primary (Sealy, op. cit.). Its parents were not observed.

FIG. 1. Total albino Least Auklet chick, 20 August 1967, St. Lawrence Island, Alaska.

Sage (Brit. Birds, 55:201, 1962; Brit. Birds, 56:409, 1963) discussed melanism and its occurrence in British birds but did not record it in the Alcidae. Storer (op. cit.) mentioned three examples of melanism in *U. aalge* and Winge (Grønlands Fugle, 1898) and Tuck (op. cit.) reported several melanistic individuals of *U. lomvia.*

On 11 June 1967 I saw one apparently total melanistic *U. lomvia* flying in a flock of about 20 at sea near the Northwest Cape of the island.

This work was supported by a National Research Council of Canada grant to M. D. F. Udvardy.—SPENCER G. SEALY, *Department of Zoology, University of British Columbia, Vancouver 8, British Columbia. (Present address: Department of Zoology, University of Michigan, Ann Arbor, Michigan 48104). 3 March 1968.*

Flicker incubates pink plastic balls, on a lawn, for five weeks.—The following incident, brought to my attention by Mrs. Howard Vivyan of the Kirkland Bird Club in Clinton, New York, is an interesting addition to our knowledge of the sometimes unusual breeding behavior of the Yellow-shafted Flicker (*Colaptes auratus*). The bizarre courtship antics of the species are well-known to all observers. In the literature one may find examples of the odd places this species has been known to nest—haystacks, rotten stumps, old barrels and very occasionally on the ground. And the flicker is known to be an indeterminate layer and will continue to lay eggs if they are removed as soon as laid (Welty, The life of birds, W. B. Saunders Co., 1962, p. 295).

On 11 June 1967, Mrs. F. C. Lloyd, who lives three miles northeast of Clinton, near a wooded pond and open fields, found an egg on her front lawn lying next to a pale pink plastic ball, of the type that has a small protruding knob to snap into another ball, with a circumference of about four inches. On the 12th, another egg was laid and on the 13th a female flicker was discovered sitting on the eggs and pink ball. In all four eggs were laid; two were broken and then the remaining two were removed to the house (where an unsuccessful attempt was made in the next two weeks to hatch them in an improvised incubator). A second plastic ball was placed by the Lloyds on the lawn beside the first. At intervals, on the 16th–18th, the flicker was seen on the balls, so on the 20th Mrs. Lloyd put a small box on the ground nearby, hoping the bird would nest in that. When it was ignored, she fashioned a simple "grass nest" and placed the plastic balls in it. On the 22nd, she found the flicker sitting on the balls, outside the grass nest. Several more attempts were made to induce the bird to use the grass nest, but it always removed the balls to the ground nearby and when the balls were next placed in a small hole dug in the ground, they were also removed from it. On the 25th it was noted that the male was taking his turn at incubating. He at first seemed content to sit on the hole containing the balls, but in a little while, "kicked" them out, and sat on them on the bare ground. From 26 June through 5 July both birds took turns sitting. When not disturbed, the incubating birds remained one-half to three-quarters of an hour on the eggs, and there was always a bird on the nest as dusk fell. The male returned to the nest more rapidly than the female after being driven off. The last date the bird incubated was 11 July.

The "nest" was located on the ground near a tree which was situated halfway between the house and the road, or 18 feet from each. Actual distance of the nest from the tree varied from two feet to about 15 feet, as the balls were moved around and pushed closer to the road. Attempts to move the balls closer to the house, away from the road, only resulted in the birds' moving them back by pushing with the beak.—Sally Hoyt Spofford, *Laboratory of Ornithology, Cornell University, Ithaca, New York 14850, 22 March 1968.*

Hooded Warbler in Trinidad, West Indies.—On 17 December 1967, I saw a male Hooded Warbler (*Wilsonia citrina*) at Waller Field on the island of Trinidad, West Indies. The bird was in brilliant adult plumage, a phenomenon that is apparently normal for this species during the nonbreeding months of the year according to Dwight in Bent (U.S. Natl. Mus. Bull., 203:618–619, 1953)

I studied the Trinidad bird at the closest focal range of 7 × 50 binoculars for fifteen minutes. It was undoubtedly an adult male, for yellow edgings of black portions of the plumage were absent. The bird was in a moist thicket in company with another North American migrant, a Northern Waterthrush (*Seiurus noveboracensis*) as well as a female Black-and-white Manakin (*Manacus manacus*). Although I returned to the same thicket periodically through the remainder of December and in January, I did not see the Hooded Warbler again.

Bond (Birds of the West Indies, 1960) calls the Hooded Warbler a rare transient in the West Indies, where it has been recorded as far south in the Lesser Antilles as Martinique. The American Ornithologists' Union Check-List of North American Birds (1957) gives its winter range as "rarely to Central Panamá (Canal Zone)." Apparently the species has never been recorded on the continent of South America.

The present record therefore represents a considerable extension of the Hooded Warbler's range and is tantamount to a South American occurrence since Trinidad is within sight of Venezuela. On the other hand the advent of this bird on the island must be considered unusual, rather than the late recognition of a previously overlooked but regular migrant, for a species as unmistakable as this one would not have escaped the notice of a succession of ornithologists who have been collecting and observing birds in Trinidad for over a century. Several unmistakable species known to winter in Venezuela (e.g., Black-and-white Warbler (*Mniotilta varia*) may have eluded detection in Trinidad by bird watchers, but the Hooded Warbler is probably not one of these since its usual winter range lies considerably to the north and west.—C. Brooke Worth, *R. D. Delmont, N.J. 08314, 25 March 1968.*

Record of female Cardinals sharing nest.—The Cardinal (*Richmondena cardinalis*) has long been known for its aggressive territorial behavior, both the male and female taking part in defense of territory. It appears of value, therefore, to record observations of nest sharing by two female Cardinals in Topeka, Kansas during the summer of 1967.

On 29 June 1967 I was told that a female albinic Cardinal (known to have been in the same neighborhood for about four years) was sharing a nest with another female Cardinal. I visited the site immediately and as I approached, both females flew from the nest, which contained five eggs. Two additional eggs had fallen to the ground.

On 4 July I returned to set up a photographic blind near the nest, and again both females flew from the nest as I entered the yard. No additional eggs had been added to the clutch. While I watched from my blind, the male and normal female returned to a garage roof near the nest after a brief time and hopped about nervously peering down at the nest. The albinic female flew across the yard three or four times without alighting and on two of her flights was aggressively pursued by the normal female into another yard some distance from the nest. The normal female finally returned to the nest and resumed incubation.

As I approached the site at noon on 5 July both females flew from the nest, this time revealing four newly-hatched young and one egg. On this occasion all three adult birds returned at once and began feeding the young, the normal female later settling down to brood. Almost immediately the albinic female brought food and passed it to the brooding female who in turn stood up and fed the young. During this period in the blind I observed no aggressive behavior by any of the birds.

By noon on 8 July when I visited the nest for the last time, the fifth egg had hatched and all three adults were engaged in feeding the young. No brooding, food passing or aggressive behavior was observed during a 45 minute period.

Shared nesting is comparatively uncommon among the birds and for a normally monogamous, strongly territorial species like the Cardinal, this behavior must be rare indeed. Though not conclusive, the clutch size suggests that eggs were laid by both females and that all were fertilized by the one male seen in the neighborhood. Cardinal nesting records in Kansas indicate an average clutch size of 3.31 with extremes ranging from 3 to 5 eggs based on a sampling of 25 nests (Johnson, Directory to the bird-life of Kansas, Publication No. 23, University of Kansas Museum of Natural History, 1960). —Orville O. Rice, *1663 West 28th Terrace, Topeka, Kansas, 27 February 1968.*

Relationships among some South American seedeaters (*Sporophila*), with a record of *S. hypochroma* for Argentina.—In an estero (sawgrass area with standing water) 21 km east-southeast of Itá-Ibaté, northern Corrientes, Argentina, on 28 October 1967, my companion Richard S. Crossin collected what appeared to be a bright male of *Sporophila minuta.* The specimen weighed 9.4 g, and had enlarged testes (6 × 5 mm), dark brown irides, brownish legs, and a black bill lightly tinged with olive.

While attempting to identify this specimen, I was able to examine and compare specimens of various South Amercian species of *Sporophila* (listed below), and especially specimens of both sexes of *Sporophila minuta minuta* (for the purposes of this discussion *S. m. parva* is included with this form) and *S. m. hypoxantha.* These two forms are widely allopatric; *S. m. minuta* occurs in southern Central America and northern South America north of Amazonia, while *S. m. hypoxantha* occurs in southern Brazil, Paraguay, eastern Bolivia and northern Argentina. I believe that these forms are separate species, and that they are not as closely related as their superficial similarity suggests. Mensural data (Table 1; de Schauensee, Proc. Acad. Nat. Sciences of Philadelphia, 104:191, 1952)

TABLE 1
SOME MEASUREMENTS OF MALES OF SEVERAL FORMS OF *SPOROPHILA**

Sample (N)	Wing length	Tail length	Bill length	Tarsal length	Bill width
S. ruficollis (13)	52.8–55.3	38.9–42.5	5.6–6.2	13.2–14.2	4.7–5.4
S. hypoxantha (10)	52.6–55.6	41.5–42.8	5.6–6.5	13.2–14.2	4.4–5.1
specimen	53.6	41.3	5.3	13.4	4.6
S. hypochroma (7)	50.9–53.9	39.1–42.0	5.7–6.2	13.2–14.2	4.5–5.1
S. minuta (10)	49.7–52.4	40.4–42.4	5.7–6.4	13.6–14.9	5.3–6.0

* Comparably plumaged fully adult males, except *S. hypochroma* (males from various times of the year). Specimens of *ruficollis* and *hypoxantha* are from Corrientes, Argentina. Measurements are in millimeters, wing length = chord, bill length is from the nostril, and bill width was measured across the nostrils.

suggest that *S. m. minuta* has shorter wings, a shorter tail, longer legs, and, especially, a bill similar in length to that of *hypoxantha*, but wider, and thus more massive. From the examination of museum skins of both sexes of these forms, it is apparent that *hypoxantha* is larger in size. Males of *minuta* differ from *hypoxantha* in their browner (even slightly green-brown), less gray coloration, as pointed out by de Schauensee (op. cit., p. 192). They are also darker below on the average than are males of *S. m. hypoxantha.* The presence of a cheek patch in males of *minuta* also distinguishes that form from *hypoxantha.* The latter is, in this respect and in other features of pattern, similar to *Sporophila hypochroma, S. ruficollis* and *S. cinnamomea.* Females of *S. m. minuta* and *S. m. hypoxantha* are quite different; indeed, the females of a number of species of *Sporophila* are considerably less different. Females of *minuta* are yellower brown above, and duller brown below than are females of *hypoxantha.* The latter are more richly colored below, invariably showing some of the buffy or even rufous coloration of that area in males of this form. Most important, females of *hypoxantha* have a large white speculum in their primaries and a large white patch at the base of the secondaries and inner primaries; the speculum is lacking in females of *minuta*, which have only a small, indistinct area of white on their inner wing feathers. I believe that these differences are of sufficient magnitude to warrant species status for *Sporophila hypoxantha.*

Comparison of the questionable specimen from Corrientes with other specimens of *Sporophila* available in the American Museum of Natural History disclosed that its underparts (including its throat, ear coverts, breast, abdomen, sides and flanks) and rump exceeded in darkness the range of variation found in *S. hypoxantha.* These regions are deep rufous-chestnut in our specimen, which was found to match exactly adult male specimens of the central Bolivian *Sporophila hypochroma hypochroma.* I was able to examine seven of the latter (including the type); these included available American Museum of Natural History specimens, and, thanks to K. C. Parkes of Carnegie Museum, E. R. Blake of the Field Museum of Natural History in Chicago, and R. M. de Schauensee of the Academy of Natural Sciences of Philadelphia, specimens from these institutions. Also available for comparison were adult males of *Sporophila hypoxantha* (N = 25), *S. minuta* (18), *S. ruficollis* (30), *S. hypochroma hypochroma* (7,) *S. castaneiventris* (53), a hybrid of *S. h. hypochroma* × *S. castaneiventris* (Academy of Nat. Sciences of Philadelphia no. 10742, discussed by de Schauensee, loc cit., pp. 194–195) and *S. cinnamomea* (3). Critical comparison with *S. hypoxantha* and *S. ruficollis* was greatly facilitated by the recently-taken Corrientes material of both forms obtained by W. H. Partridge, and now in the American Museum of Natural History.

There is great similarity in mensural characters (Table 1) displayed by the above-mentioned forms. The females of some of them appear to be indistinguishable. These species differ mainly in the pattern of chestnut or rufous and gray of the males. Considering these patterns and mensural characters, the bird in question, although matching *S. h. hypochroma* is very similar to *S. hypoxantha.* As indicated in Table 1, these forms are virtually alike in measurements, with *hypochroma* perhaps tending to have slightly shorter wings and a shorter tail. Males of the two are alike except for the much darker underparts and rump of *S. hypochroma.* The Corrientes specimen is mensurally within the range of variation of both forms in all characters, except for its inordinately short bill. Since it has the underparts and rump of *hypochroma,* and exceeds the known variation of *hypoxantha* in this regard, it appears to represent *S. h. hypochroma.* The condition of its gonads suggests that it would have bred, thus indicating sympatry of *S. hypochroma* and *S. hypoxantha.* However, there exists the possibility that the specimen represents an aberrant individual of *S. hypoxantha.* The conspecificity of *hypochroma* and *hypoxantha,* suggested by their allopatry (except for the Corrientes specimen) and their close similarity in pattern and measurements, would render such an aberrant individual more likely. However, study of the possible area of contact between these two forms in Bolivia, or of further individuals of *hypochroma* breeding sympatrically with *hypoxantha,* is necessary to clarify this question. For the present, the conservative course is to consider the Corrientes specimen to be an example of *S. hypochroma,* thus regarding the two forms as sympatric and separate species. This represents a considerable extension of the range of *hypochroma* from Bolivia (see de Schauensee, loc. cit.,) but it is possible that this form breeds sporadically between there and Corrientes in the intervening region of eastern Bolivia and Paraguay.

I cannot accept the determination of Singh's (article in the newspaper The Daily Argosy, Georgetown, Guyana, of 25 October 1960, p. 6) *Sporophila hypochroma rothi* as a race of *S. hypochroma* on the basis of but one specimen. The tremendous distance between the range of *S. hypochroma hypochroma* in Bolivia (and Corrientes, Argentina) and Guyana, and the coloration of "*rothi*" beg another explanation. I feel that *S. hypochroma rothi* actually represents a hybrid between *S. castaneiventris* and *S. minuta,* two species which are common to abundant in the Abary region of Guyana (Snyder, D. E., The birds of Guyana, 1966:277–278) where *rothi* was obtained. Indeed, the description of the specimen, and even its picture, suggest that it is such a hybrid. The following comments (Singh, loc. cit.) from the description of *rothi* are noteworthy: "gray of the upperparts slightly darker than in *hypochroma*—about as in *castaneiventris*; secondaries broadly edged with gray, not ashy white as in *hypochroma*; white speculum at base of inner primaries much restricted . . . ; malar region chestnut as in *hypochroma* (and *castaneiventris*), but auriculars, sides of head and sides of neck gray as in *castaneiventris.*" By substituting *minuta* for "*hyprochroma*" in this description, these features are clearly intermediate between that form and *castaneiventris.* Nothing else in Singh's description precludes the possibility of his specimen being such a hybrid, which I consider much more likely than its representing a very disjunct, distinct, and rare form of *S. hypochroma.* The latter therefore reverts to a monotopic species. Regarding Singh's discussion of the relationship of *castaneiventris* and *hypochroma* (which have hybridized; see above list of specimens examined), taken from de Schauensee (loc. cit.), I consider these species related, but not conspecific. Indeed, *S. hypochroma* is probably more closely allied with *S. hypoxantha,* and possibly *S. ruficollis* and *S. cinnamomea,* than with *castaneiventris* (the latter is small, like *minuta*; and both sexes lack a speculum).

Finally I suggest the possibility that *Sporophila ruficollis* is a color phase of *S.*

hypoxantha. These "species" are identical in coloration and measurements (Table 1), except for the black throat of males of *ruficollis*. The ranges of *ruficollis* and *hypoxantha* almost exactly coincide (de Schauensee, loc. cit.). Both dark and light throated forms are found side by side in the same wet pampas of Corrientes, and probably elsewhere. Specimens exist with an array of throat colors from black through mixed brown (tan) and black to the pale rufous of *hypoxantha*. Studies are needed to establish whether or not this represents a case of polymorphism.

I am grateful for the support of my field work in Argentina by the National Science Foundation (grant G.B.—5891). I also thank Richard S. Crossin for assistance in the field, and Sheila C. Short for aid in measuring specimens.—Lester L. Short, Jr., *The American Museum of Natural History, New York, 16 March 1968.*

Status of the Lincoln's Sparrow in Jamaica, West Indies.—The Lincoln's Sparrow (*Melospiza lincolnii*) has been reported only a few times from the island of Jamaica, and it is worthwhile to add three new observations which may clarify the status of this species as a wintering bird in Jamaica and the Greater Antilles.

The first Jamaican record of this species was a specimen taken by James Bond in dense forest below Whitfield Hall, St. Thomas, at about 1,350 meters in the Blue Mountains, on 14 December 1934 (Bond, pers. comm.). This specimen, originally No. 108263 in the Academy of Natural Sciences of Philadelphia was presented by Bond to the Institute of Jamaica where it is now No. 241 in the bird series. The second Jamaican record was a sight observation by Geoffrey Carleton near Torre Garda, St. Thomas parish, in a brushy meadow at about 1,150 meters on 14 February 1952 (Linnaean Soc. of New York, News-Letter. No. 4, 1953). The third record was a bird which struck a window at Haberton, Content Gap, St. Andrews, at 1,030 meters, on 20 April 1959. This specimen, identified by C. Bernard Lewis of the Institute of Jamaica, is preserved in alcohol as No. 260 in the bird series at the institute. Another sight record is reported for Green Hills near Hardwar Gap, St. Andrews, at 1,290 meters (Gosse Club, Broad-Sheet, No. 1, August, 1963).

On 27 December 1964, the author observed a Lincoln's Sparrow in a small brushy ravine on a steep slope on the edge of tropical rain forest, near Hardwar Gap. The location, on the border of Portland and St. Andrew parishes, is at 1,320 meters. The bird was observed for several minutes as it fed in the undergrowth and then perched in an open bush. On 27 January 1965, within 100 meters of the above observation, I observed at least three Lincoln's Sparrows which were flushed from a tangle of a creeping fern (*Gleichenium* sp.) at the edge of the rain forest. It is possible that one of the three was the same individual seen a month earlier. On 10 January 1965, I observed a Lincoln's Sparrow among bushes in a steeply sloping pasture about 1.2 kilometers east of Whitfield Hall, St. Thomas, at an elevation of 1,430 meters.

To the above records one can add two Greater Antillean reports, both at low elevations. The first West Indian record was a sight observation by Danforth, near La Plata, Puerto Rico, on 14 December 1923. Another bird was recorded on the outskirts of Havana, Cuba, 8 January 1964 (Bond, pers. comm.).

In Jamaica, at least, the bird appears to be restricted to the mountains. Despite the handful of observations, this may be significant, because the island is frequently visited by North American bird watchers and ornithologists, and although the bird is generally secretive it seems unlikely that it would be completely overlooked in the lowlands. The author spent approximately seven times as many hours afield in the lowlands as in the mountains.

Although Bond (Birds of the West Indies, Houghton Mifflin, Co., 1961) lists the species as a vagrant to the West Indies, he notes that the list includes species which may be very rare winter residents or transients. In view of the increasing number of observations of Lincoln's Sparrows in the West Indies it seems not unlikely that the species winters regularly in small numbers in the highlands of Jamaica.

I wish to thank James Bond for criticizing the manuscript, and C. Bernard Lewis and Geoffrey Carleton as well as Bond for providing me with the details on their observations or specimens.—Michael Gochfeld, *RFD 1 Lexington Avenue, Mohegan Lake, New York 10547, 2 December 1967.*

Appendicular myology of passerine birds.—In recent years a notable renewed interest in the anatomy and taxonomy of passerine birds has occurred. However, the literature contains no concise statement of our present knowledge of the presence or absence of appendicular muscles among the many families of the Passeriformes (e.g., George and Berger, 1966, did not include such a summary). This summary of our current knowledge of the differences found among representatives of passerine families is presented in order to facilitate the work of students and in order to emphasize how little still is known about the appendicular myology of passerine birds.

The wing muscles:

The distal head of M. extensor indicis longus, the biceps slip, and Mm. latissimus dorsi pars metapatagialis, anconaeus coracoideus, entepicondyloulnaris, extensor pollicis brevis, and flexor pollicis are absent in all passerine birds thus far examined.

M. latissimus dorsi pars posterior is absent in *Fregilupus varius* (Sturnidae?), *Artamella viridis* (Vangidae), *Agelaius phoeniceus* (Icteridae), *Dendroica kirtlandii* (Parulidae), and in all members of the Ploceidae and Fringillidae thus far investigated (George and Berger, 1966:293). By contrast, pars posterior has been found in *Procnias nudicollis* (Cotingidae), *Paradisaea rubra* (Paradisaeidae), in *Sturnus* and *Aplonis* (Sturnidae), and in all genera of the Corvidae studied (Berger, 1956*a*, *b*, 1957; Hudson and Lanzillotti, 1955). A fully-developed M. latissimus dorsi pars metapatagialis has not been reported in any genus of passerine bird.

M. coracobrachialis anterior definitely is absent in *Agelaius phoeniceus* and in *Dendroica kirtlandii.* The muscle apparently is present, although weakly developed, in all other passerine birds studied. Histological examination may be necessary to determine the presence or absence of this muscle in small passerine birds.

M. abductor indicis is absent in *Dendroica kirtlandii, Agelaius phoeniceus, Spizella arborea*, and, according to Swinebroad (1954), in *Passer domesticus, Richmondena cardinalis, Zonotrichia albicollis*, and *Melospiza melodia.* The muscle is present but vestigial in development in other passerine birds (George and Berger, 1966:376).

M. ulnimetacarpalis dorsalis (flexor metacarpi posterior) is absent in *Dendroica kirtlandii, Agelaius phoeniceus*, and *Spizella arborea.* The muscle is weakly developed in other passerine birds.

M. pectoralis propatagialis brevis apparently is represented by an aponeurosis or tendinous band in all passerine birds studied. M. pectoralis propatagialis longus consists of a fleshy belly in *Sturnus, Aplonis, Fregilupus*, and *Dendroica* (in *Dendroica*, however, the belly is vestigial and inconstant in occurrence); so far as we know, the muscle is represented by a tendon or aponeurosis in other passerine birds.

M. tensor patagii brevis is much larger than M. tensor patagii longus in passerine birds. In most of these the two muscles are independent throughout their course, but the two muscles share at least part of a common origin in certain genera: e.g., Corvidae, *Fregilupus*, *Sturnus*, *Aplonis*, *Artamella*, and *Agelaius*. The statement in George and Berger (1966:318) that the two tensor patagii muscles are represented by a single belly in *Spizella arborea* should be verified.

A tendinous scapular anchor extends between the posterior margin of the posterior head of M. deltoideus major and the blade of the scapula in *Procnias*, the Corvidae, *Sturnus*, *Aplonis*, *Artamella*, and *Dendroica*. The scapular anchor apparently is absent in other passerine species studied, although an investigator unaware of this structure might easily remove it inadvertently in the course of dissection.

M. deltoideus minor consists of a single belly (pars dorsalis) in most birds, but there are two bellies in *Agelaius phoeniceus* (George and Berger, 1966:325). This appears to be the only passerine species thus far investigated in which two bellies have been reported.

It seems likely that a common pattern of insertion of M. biceps brachii exists in most, if not all, passerine birds: that is, the common tendon of the muscle bifurcates, with the bulk of the tendon inserting on the ulna but with a small tendon inserting on the radius.

Dendroica kirtlandii and *Agelaius phoeniceus* appear to differ from other passerine species studied in detail in possessing a double origin of M. pronator profundus: that is, a typical tendinous origin from the distal end of the humerus and, in addition, an unusual fleshy head from the humeroulnar pulley. Swinebroad's description of the origin of this muscle in *Passer domesticus* and several fringillid genera, however, suggests that a similar pattern of origin may be found in these birds.

Dendroica kirtlandii appears to differ from other passerine species studied in that M. ulnimetacarpalis ventralis has both a proximal and a distal head (not merely a V-shaped origin as in *Agelaius phoeniceus*, George and Berger, 1966:356).

In most species of passerine birds studied, M. extensor pollicis longus has a single head arising from the ulna only. In *Paradisaea rubra*, however, the single head arises only from the radius (Berger, 1956*b*). Two heads and two independent tendons of insertion are found in *Artamella viridis*; the two heads arise, respectively, from the radius and the ulna (Berger, 1957).

The hind limb muscles:

The leg-muscle formula for all passerine birds thus far studied is ACEFXY (George and Berger, 1966:236). The following formulae muscles, therefore, are absent in all passerine birds studied: piriformis pars iliofemoralis (B), gluteus medius et minimus (D), popliteus (G), ambiens (Am), and also the vinculum (V) between the tendons of insertion of Mm. flexor perforatus digiti III and flexor perforans et perforatus digiti III.

M. sartorius has two heads of origin in *Fregilupus varius* and in *Paradisaea rubra*. The muscle arises by a single head in all other passerine species thus far studied.

The postacetabular portion of M. iliotibialis is absent in the Tyrannidae and the Hirundinidae (Hudson, 1937). In all other passerine birds studied, M. iliotibialis consists of preacetabular, acetabular, and postacetabular portions.

An investigation is needed on the presence or absence of a deep distal head of M. femorotibialis externus among passerine birds. The deep distal head has been described for *Sturnus*, *Aplonis*, *Fregilupus*, *Artamella*, *Agelaius*, and *Dendroica* (Berger, 1957; George and Berger, 1966:394–395). A distal head was not described in the passerine species studied by Hudson (1937) or Stallcup (1954).

M. femorotibialis internus consists of two independent bellies and tendons of insertion in *Dendroica kirtlandii*, *Agelaius phoeniceus*, and *Fregilupus varius*. *Paradisaea* *rubra* has a single belly but two tendons of insertion. *Artamella viridis, Sturnus vulgaris,* and *Aplonis tabuensis* have a single belly and tendon of insertion. Hudson (1937) and Stallcup (1954) refer to slight divisions (into two parts) of the belly of M. femorotibialis internus in *Corvus*, *Pipilo*, and certain other passerine genera.

M. obturator externus consists of two independent bellies in *Procnias*, *Paradisaea*, *Artamella*, *Fregilupus*, *Sturnus*, *Aplonis*, *Vireo*, *Seiurus*, *Dendroica*, *Icterus*, *Agelaius*, *Molothrus*, *Piranga*, and several genera of fringillids studied by Stallcup (1954). Hudson (1937:27–28) also refers to two heads, "which unite before inserting," in *Tyrannus* and *Corvus*. Stallcup pointed out that M. obturator externus consists of a single head in *Passer*, *Estrilda*, *Poephila*, *Hesperiphona*, *Carpodacus*, *Pinicola*, *Leucosticte*, *Spinus*, and *Loxia* (that is, in ploceids and cardueline finches).

Additional comparative studies on the structure of M. gastrocnemius pars interna among passerine birds are needed. Stallcup referred to an "undivided" pars interna in ploceids and cardueline finches and to a "bipartite" structure in the other species he dissected. Whether or not an origin from the patellar ligament represents Stallcup's "bipartite" condition I do not know.

The tendon of M. extensor digitorum longus apparently passes under a bony bridge (supratendinal bridge or intermalleolar loop) near the distal end of the tibiotarsus in all passerine birds. The tendon also passes through a bony canal on the proximal end of the tarsometatarsus in *Procnias*, *Tyrannus*, *Corvus*, *Paradisaea*, *Artamella*, *Dendroica*, *Agelaius*, and apparently in all species studied by Stallcup (1954). The tendon of M. extensor digitorum longus is held in place by a ligament (rather than a bony canal) on the proximal end of the tarsometatarsus in *Fregilupus*, *Sturnus*, and *Aplonis* (Berger, 1957). Whether the bony canal or the ligament on the tarsometatarsus are constant characters for each species or whether they are, in part, a function of age is not known.

Hudson (1937:43) reported that M. flexor perforatus digiti IV arises by two heads (a typical head from the intercondyloid region of the femur, plus a lateral head) in *Tyrannus*. So far as can be determined from the literature, this muscle has a single origin from only the intercondyloid region in all other passerine birds.

There appears to be considerable interspecific variation (of unknown taxonomic significance) in the precise relationships between the origin of M. flexor perforatus digiti II and other toe muscles (see Hudson, 1937; Stallcup, 1954; George and Berger, 1966:440).

The tendon of insertion of M. flexor perforatus digiti II is *not* perforated by the tendons of M. flexor perforans et perforatus digiti II or M. flexor digitorum longus in *Paradisaea rubra*, *Fregilupus varius*, *Sturnus vulgaris*, *Aplonis tabuensis*, *Artamella viridis*, *Dendroica kirtlandii*, and *Agelaius phoeniceus*. The tendon of M. flexor perforatus digiti II presumably is perforated by both of the two deeper tendons in the species studied by Hudson and Stallcup.

George and Berger (1966:444) pointed out that *Vireo olivaceus* is the only passerine species known to have a M. flexor hallucis longus arising by a single head (from the intercondyloid area of the femur). *Dendroica kirtlandii* and *Agelaius phoeniceus* are the only known passerine species in which the muscle arises by three distinct heads. The muscle has two heads in all other species studied.

M. flexor digitorum longus arises from the femur and the tibiotarsus in *Tyrannus*, *Corvus*, and *Paradisaea*. A femoral origin has not been described in other passerine birds.

M. flexor hallucis brevis is absent in *Fregilupus*, *Sturnus*, *Aplonis*, and *Dendroica*. M. flexor hallucis brevis is present in the Corvidae, *Tyrannus*, *Paradisaea*, *Artamella*, *Agelaius*, and, presumably, in all of the genera studied by Stallcup (1954).

M. extensor brevis digiti IV apparently has been described for only one species of passerine bird, *Procnias nudicollis* (Cotingidae; George and Berger, 1966:462).

The remaining short toe muscles are so tiny in most passerine birds that a thorough study involving histological techniques is needed. Not enough detailed and accurate information is in the literature to justify a tabulation of the occurrence of the muscles. Hudson (1937:75) considered M. abductor digiti IV to be rudimentary in *Tyrannus* and *Corvus*, as did Berger (1957) for *Fregilupus.* Stallcup (1954:174) commented that the muscle was "extremely small, delicate and difficult to demonstrate." Stallcup also described M. lumbricalis as being "semitendinous throughout its length." No other author has identified M. lumbricalis in passerine birds.

LITERATURE CITED

Berger, A. J. 1956*a*. The expansor secundariorum muscle, with special reference to passerine birds. J. Morphol. 99:137–168.

Berger, A. J. 1956*b*. On the anatomy of the Red Bird of Paradise, with comparative remarks on the Corvidae. Auk, 73:427–446.

Berger, A. J. 1957. On the anatomy and relationships of *Fregilupus varius*, an extinct starling from the Mascarene Islands. Bull. Amer. Mus. Nat. Hist., 113:225–272.

George, J. C., and A. J. Berger. 1966. Avian myology. Academic Press, New York.

Hudson, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. Amer. Midl. Naturalist 18:1–108.

Hudson, G. E., and P. J. Lanzillotti. 1955. Gross anatomy of the wing muscles in the family Corvidae. Amer. Midl. Naturalist 53:1–44.

Stallcup, W. B. 1954. Myology and serology of the avian family Fringillidae, a taxonomic study. Univ. Kansas Publ., 8:157–211.

Swinebroad, J. 1954. A comparative study of the wing myology of certain passerines. Amer. Midl. Naturalist, 51:488–514.

Andrew J. Berger, *Department of Zoology, University of Hawaii, Honolulu, Hawaii.*
23 February 1968.

ORNITHOLOGICAL NEWS

The 1969 Annual Meeting

The 50th Annual Meeting held at Williamsburg, Virginia, 1–4 May 1969 is now history, and those who attended will testify that it was a very successful one in every way. The Local Committee is to be congratulated on the manner in which all arrangements were made. The full Proceedings will be published in the September issue of *The Bulletin.*

The meeting closed with the election of a new slate of officers whose names appear on the inside front cover of this issue.

The 51st Annual meeting will be held at Colorado State University, Fort Collins, Colorado in the later half of June 1970. The exact dates have not been fixed as yet. This will be a joint meeting with the Cooper Ornithological Society. Besides the paper sessions, which will probably be enlarged to cover three days, the meeting should offer many ornithological attractions, as Fort Collins is located on the High Plains, with the Colorado Front Range of the Rocky Mountains close at hand.

William W. H. Gunn has retired from the Editorial Board. Dr. Gunn has been a valuable member of the Board since 1959 and the Editor wishes to express his thanks to Dr. Gunn for his many services, and to wish him well as he assumes the Presidency of the Society.

At the recent meeting of the Executive Council special notice was taken of the devoted service to the Society of Mrs. Hazel Bradley Lory, who is retiring as Chairlady of the Membership Committee after ten years in that position.

The Subcommittee on Collections, of the Committee on Research of the American Ornithologists' Union, is conducting a survey of collections of birds in the United States and Canada. In the past, many studies utilizing museum materials have been handicapped by ignorance of the existence of potentially important specimens. We hope, by means of this survey, to enable future workers to take full advantage of all available material.

Survey forms have been sent to institutions and individuals known to have, or suspected of having, an ornithological collection. We request your assistance so that our survey will be as complete as possible.

If you have received a survey form, please complete it and return it promptly. If you have a collection and have not received a form, or if you know of other persons or institutions who have collections but who have not received a form, please notify Richard C. Banks, Bird and Mammal Laboratories, U. S. National Museum, Washington, D. C. 20560.

People who maintain a series of ten or more nesting boxes for Eastern Bluebirds have been sending nesting information to Dr. Douglas James, Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701. The data are used to evaluate the annual population fluctuations of bluebirds. Persons who qualify but are not now participating in the program should write Dr. James for the project report form.

ORNITHOLOGICAL LITERATURE

Review: Three papers on variation in flickers (*Colaptes*) by Lester L. Short, Jr. 1965*a*. Hybridization in the Flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist., 129:307–428. 1965*b*. Variation in West Indian Flickers (Aves, *Colaptes*). Bull. Florida State Mus., 10:1–42. 1967. Variation in Central American Flickers. Wilson Bull., 79:5–21.

These three papers represent the fruition of Short's extensive research on flickers begun in 1955 at Cornell University under the supervision of Charles G. Sibley. The main analysis is of 6,000 specimens which resulted from field work by Short and many others in critical areas of contact between phenotypically well-differentiated forms in the Great Plains and in Arizona. The studies of West Indian and Central American birds were based entirely on museum specimens and pertinent literature; the need for field work on the ecology and behavior of the flickers of these areas is stressed.

In the major paper, the genus *Colaptes* is broadened to include as subgenera the currently recognized genera *Chrysoptilus* (three species in South America) and *Nesoceleus* (one species in Cuba), as well as *Colaptes* (North and Central American flickers) and *Soroplex* (three species in South America), the latter two subgenera having comprised the genus *Colaptes* in the sense of Peters (Birds of the world, 1948, vol. 6).

Short derives "the ancestral North American flicker" from South America via Nicaragua and Central America, a notion supported by the fundamental diversity of the enlarged genus *Colaptes* in South America, where also the genus *Piculus* (said by Short to be closely related to *Colaptes*) has radiated. Short feels that all North American flickers belong to one species, *Colaptes auratus*, divided into five subspecies groups: the *mexicanoides* group, including two subspecies in Central America; the *cafer* group, including five subspecies in Mexico and western North America; the *chrysoides* group, including four subspecies in the southwestern United States and northwestern Mexico; the *auratus* group, including two subspecies in eastern and northern North America; and the *chrysocaulosus* group, including a subspecies in Cuba and a subspecies on Grand Cayman Island. The subspecies *borealis* of Ridgway, *canescens* of Brodkorb, *chihuahuae* of Brodkorb, *martirensis* of Grinnell, and *sedentarius* of van Rossem are not recognized in the major paper. Later (1967) Short provides evidence for the submergence of one of the subspecies of the *mexicanoides* group, *pinicolus* of Dickey and van Rossem. Although Short does not explicitly make this point, it is convenient to view the five subspecies groups as falling into three categories:

I. The *mexicanoides* group plus the *cafer* group (= "Red-shafted Flickers")
II. The *chrysoides* group (= "Gilded Flickers")
III. The *auratus* group plus the *chrysocaulosus* group (= "Yellow-shafted Flickers")

Indeed, these categories probably represent separate evolutionary trends from the original stock that invaded North America, and they are the "species" of much modern literature, including the A. O. U. Check-list of North American birds, 1957.

In a convincing interpretation, *chrysoides* is said to have evolved from either a pre-*cafer* (p. 404) or an early *cafer* (p. 412) population in Baja California. *Chrysoides* later spread north, east, and then southward along the coastal plains of northwestern Mexico. In the opinion of the reviewer, the ability of *cafer* stock to give rise to *chrysoides* has great significance, to be discussed further below. The possibility that *auratus* stock evolved from *cafer* or pre-*cafer* populations after spreading from the west in North America seems entirely logical on zoogeographic grounds. Short did not discuss this point but indicates that he plans to do so in the future (1967:19).

Cuban *chrysocaulosus* is derived from *auratus* by invasion from Florida, perhaps in the early Pleistocene. Evidently later, in the mid- to late Pleistocene, *chrysocaulosus* stock reached Grand Cayman Island from Cuba and evolved into *Colaptes auratus gundlachi. Chrysocaulosus* probably arrived in Cuba after *Colaptes fernandinae*, which had already pre-empted the ground-foraging niche and thereby "forced" *chrysocaulosus* into a more arboreal role, a situation worthy of close examination by both the ecologist and anatomist. Short's notion of a similar, though earlier, northern origin for the peculiar *fernandinae* is less appealing. By his own admission, *fernandinae* "resembles South American flickers of the subgenera *Soroplex* and *Chrysoptilus* more closely than it does *Colaptes auratus*." Rather, evidence suggests a South American origin for *fernandinae* from old *Colaptes* stock not necessarily involved in the ancestry of the subgenus to which *auratus* belongs.

The most penetrating treatment is afforded the populations from the long zone of contact between *cafer* and *auratus*, from British Columbia to Texas, where interbreeding is apparently free. In a narrow zone where only hybrids are present there were no signs of behavioral isolating mechanisms. However, because "pure" forms of *cafer* and *auratus* are not in contact, their possibly divergent behavior in pairing could not be seen in the hybrid zone, especially if hybrids are at an advantage there over pure parental types. The analysis of the several contacts in the plains is carefully documented; especially well studied were the series of samples taken at intervals along a transect following the Platte River Valley in Nebraska and Colorado. Short acknowledges his considerable debt to Dr. Frederick Test who permitted his use of much unpublished material in the form of specimens and notes from Test's extensive work with flickers years ago at the Museum of Vertebrate Zoology and in the field in Montana. Special analysis properly given to 15 mated pairs obtained in Montana by Test and his associates revealed no clear indication of mating preference. Even the hardiest splitter should now be convinced of the conspecificity of the two forms. Particularly commendable in the section on hybridization in the plains is the format of presentation of detailed data, often from single specimens, which affords the reader a level of examination not often permitted when diverse samples are pooled improperly. Flickers representing *cafer* and *chrysoides* were also studied in the field in Arizona, where the situation is much different from that in the plains. *Cafer* is basically an upland bird; *chrysoides* reaches its greatest density in the lowland and foothill saguaros, but occurs also in cottonwoods in canyons at the bases of mountains. Pure populations of *cafer* and *chrysoides* are not in contact except through one intervening hybrid population along the Agua Fria River and its tributaries. The "barrier is the grassland and open oak-juniper woodland generally found between lowland cactus desert and upland pine-oak woodland," where neither flicker can breed because of the lack of nesting sites. In the virtual absence of contact of the two forms I find weak Short's hypothesis (p. 377) that the geographic range of *chrysoides* is being limited by *cafer*. Strong differences in temperature and humidity tolerances, among other habitat requirements, are more probable reasons for the essential allopatry of their ranges.

Five other small and widely scattered hybrid populations were studied in addition to that along the Agua Fria River. Each is isolated from other hybrid populations and from parental stock. No two hybrid "swarms" are alike; they vary in degree of intermediacy toward one or the other parental type in expression of the various characters, evidently thereby reflecting response to local selective forces. Short's detailed discussion of habitats and possible avenues of gene flow in regions where *cafer* and *chrysoides* occur in close proximity is particularly excellent. The small samples of specimens from the limited areas of hybridization were thoroughly analyzed, with statistical treatment where possible. However, the lack of similar statistical treatment of data on size variation for comparative samples of *cafer* and *chrysoides* (Table 34) away from the hybrid areas renders difficult their interpretation.

Evidently contact between *cafer* and *chrysoides* was more extensive in the past when riparian vegetation was more continuous because of higher water tables and less habitat destruction. Very little gene flow occurs at present between *cafer* and *chrysoides*; all but one of the variously intermediate populations are apparently stabilized and isolated. In view of this virtual lack of gene exchange and because of the strong discontinuities in size, color, habitat preference, and, undoubtedly, climatic tolerance between the huge populations of "pure" *cafer* and *chrysoides*, I am inclined to minimize the importance of their limited hybridization. Therefore, despite the great idealistic appeal of including all North American flickers in one species, I do not follow Short in grouping *chrysoides* with *cafer*, but instead favor the retention of the Gilded Flicker as a separate species. It is all too easy to judge the extremely limited *chrysoides-cafer* contact as being equivalent to that of *cafer* and *auratus* in the Great Plains and, with that situation of massive interbreeding in mind, improperly include *chrysoides* with *cafer*.

However, this point of difference in taxonomic philosophy should not obscure the fact of Short's excellent treatment of this problem in the gathering and analysis of specimen data and in the interpretation of possible contact zones, often through his own field exploration.

To analyze hybrids between the *cafer* group and the *auratus* group, Short uses a series of scores representing gradations for each of the following six color characters for males (five characters for females, which lack a strikingly colored malar mark): Crown color, color of ear coverts, throat color, nuchal patch, shaft color, and malar color. The graduations for throat color, for example, are "0," vinaceus tan, as in *auratus*; "1," gray traces, usually on lower throat; "2," mixed gray and tan; "3," tan traces, usually near chin; and "4," gray, as in *cafer*. The individual scores for each character are then summed, which results in a total score between "0" for a "pure" *auratus* to "24" for a "pure" *cafer*. In females the range is from 0 to 20. Similar sorts of indices have been used in other studies of avian hybridization.

The philosophy underlying Short's entire discussion is that traces in one population (population B, for example) of characters expressed routinely in another population (A), and presumably evolved when A and B were not in contact, means that genes from population A are infiltrating population B because of secondary contact. Thus, traces of a red nuchal mark in 25 per cent of Californian Red-shafted Flickers are interpreted as being a result of introgressant "red nuchal genes" from Yellow-shafted Flickers in the eastern or northern part of the continent. Also according to this philosophy traces of "*auratus*" characters (except shaft color) in *chrysoides* of southwestern North America are a result of introgression of genes for that character, originally from *auratus*, genes that passed through *cafer* to finally reside in *chrysoides*. The expression of the various phenotypes, thus concludes Short, "attests to the ability of populations of the three forms to partake of one another's genetic variability" (p. 406).

However appealing this explanation may be for certain situations of hybridization in birds, for the North American flickers I feel that Short's interpretation is incorrect, and that introgression is only reasonably invoked as the explanation for the variability close to the hybrid zones in the plains and in Arizona. Thus, it is misleading to term the red nuchal mark an "*auratus* character;" rather it should be called a *flicker* character, lost in 75 per cent of *cafer* and in ? per cent of *chrysoides*, and present in 99+ per cent of *auratus*. Can we ignore the fact that a red nuchal mark occurs widely not only in most members of the genus *Colaptes*, but also in most members of the closely related genus *Piculus*, and indeed in a wide variety of other picids? Actually, the red nuchal mark is almost best termed a *picid* character in view of its wide expression in the family. The likely explanation for *most* of the occurrence of red nuchal traces, then, in *most* of the populations of *cafer* in western North America away from the hybrid zones, is that these traces have their genetic basis deep in the stock that gave rise to all flickers and their relatives, and that in certain forms (as in the *cafer* and *chrysoides* groups) the trait has been largely lost although it occurs even in these populations as an expression of *normal variation*, often in 25 per cent of the individuals (*cafer* and *mexicanoides* groups).

Short is aware of this problem when he writes (1965*a*:319): "Since it is impossible to separate effects due to introgression from those due to the genetic potential of *cafer* itself, a degree of error is incorporated in the use of this character [the nuchal mark] in the color analysis of hybrids. The magnitude of the error can be seen by an examination of the occurrence of nuchal traces in those forms geographically isolated from populations of the *cafer* group. These include the subspecies *rufipileus* of the *cafer* group, and *mexicanoides* and *pinicolus* [synonymized in the 1967 paper] of the *mexicanoides* group. The *chrysoides* group, as is shown below, is in genetic contact with the *cafer* group. There is introgression of genes determining the presence of the nuchal patch from the *auratus* group into the *cafer* group, and thence into the populations of *chrysoides*."

To continue Short's own line of reasoning, I believe that not only is the range of variation in extent of nuchal mark in the isolated *mexicanoides* a valuable yardstick by which to measure the extent of normal variability in *cafer*, but I would extend this to include the variation in the other five color characters in his hybrid index. Similarly, the normal variability in character expression in the isolated *chrysocaulosus* can be used as the standard against which can be measured the additional variability supposedly resulting from hybridization and introgression in the main groups of continental *auratus* (see below).

Short's own argument against use of this character is equally applicable to all of the other five color characters he used in his hybrid index. Like the traces of nuchal marks in far western *cafer*, traces of "*auratus*" ear covert color (in 23 of 74 specimens) and traces of "*auratus*" throat color (in 24 of 74 specimens) in populations of California and Oregon may have nothing to do with past hybridization; these traces can be interpreted as normal variability inherited from the ancestral gene pool. Furthermore, (1) the ability of *cafer* or pre-*cafer* stock to produce *chrysoides* with its yellow shaft color, and (2) the ability of *cafer* to produce *rufipileus*, independently, with its *chrysoides*-like crown color, and (3) in view of the simple genetic and dietary basis for the difference between red and yellow shaft colors in all flickers, and (4) the presence of red and black together in malar marks of *mexicanoides* are all additional points of evidence which demonstrate the degree of variability in North American flickers and provide arguments against any meaningful use of these characters as evidence for past hybridization and introgression *at any distance away from the hybrid zone.*

I believe that there is justification for re-interpretation of Short's hybrid index system as follows: Within a single character in the system (see 1965*a*:318, table 2) scores of 0 and at least some of the birds categorized as 1 are typical *auratus*, 2 is intermediate, and at least some of the birds in 3 and all of those in 4 are typical *cafer.* Because the scores of 1 and 3 in each character very likely include variation normally within *auratus* and *cafer*, respectively, let's permit each "pure" type (0 for *auratus*, 24 for *cafer*) to possess traces of at least three of the six color characters Short attributes as having resulted from hybridization with the other form. This is quite conservative; variation may actually permit traces of all six characters in either normal *auratus* or *cafer.* Under this reasonable re-assessment of the index, then, when the scores are summed for totals, males indexed at 0 to 3 are *auratus* showing normal variation, birds indexed at 4 or 5 may be either normally variable *auratus* or they may be hybrids, birds indexed at 6 to 18 are definite hybrids, birds indexed at 19 or 20 either may be hybrids or they may be normally variable *cafer*, and birds indexed at 21 to 24 are *cafer* showing normal variation. According to this analysis the zone of hybridization in the Great Plains becomes narrowed to that region where the specimens show variability beyond the range normally expected, variation that can be interpreted justifiably as that resulting from hybridization and introgression. Thus in Figure 3 on p. 327, most of the individuals from Schuyler, to and including Sutherland, are probably normal *auratus* with some hybrids (one definite hybrid from Sutherland). Samples from Big Springs are hybrids toward *auratus.* Birds from Crook are hybrids. Birds from Fort Morgan and Greeley are hybrids toward *cafer.* Samples from western Colorado are mostly *cafer* with some hybrids. Importantly, data on size variation demonstrate clearly that the influence of true introgression occurs over a zone much narrower than Short proposes on the basis of color characters. In wing length, for example, only the sample from Crook is definitely intermediate between *cafer* and *auratus* (Table 5, p. 332), although the two samples geographically adjacent to the Crook sample would almost certainly show the influence of hybridization more clearly if more specimens were available.

As support for this interpretation I should like to cite Short's own valuable data on "character indexes" for *mexicanoides* (1967:17) and *chrysocaulosus* (1965*b*:21–22). In *mexicanoides*, character index values ranged from 19–23 in 87 males (mean ± 2 S.E. = 21.46 ± 0.20). In *chrysocaulosus*, character index values in 35 males ranged from 0 to 3 (mean = 1.90 ± 0.22). In *auratus* of Florida, character index values of 37 males ranged from 0 to 3.5 (mean = 1.35 ± 0.36). My estimates above, based on the assumption that birds indexing at "21" to "24" are probably normal *cafer*, and that birds indexing at "0" to "3" are probably normal *auratus*, are thoroughly substantiated by the normal ranges of variation in these isolated populations.

One of the most striking revelations that came to me upon examining Short's generalized maps of the geographic distribution of flickers in North America is the great coincidence of phenotypic change in the various forms with major climatic boundaries on the continent. With this in mind one wonders to what extent the phenotypes reflect underlying genetic-physiologic adaptation to the general temperature and humidity regimes in the regions where they occur. The intermediate position of the hybrid zones in relation to the general climatic preferenda of parental populations, in both the plains and in Arizona, suggests that there may indeed be positive selection maintaining hybrids in regions where neither parental stock is at maximal selective advantage. I find no discussion of physiologic adaptation in Short's papers and would merely stress here the need for experimental work along these lines.

Short mentions that a study of flicker behavior (in preparation) and a review of the literature "have failed to produce any evidence for the occurrence of major differences in behavior among the forms of flicker that hybridize." Hopefully the paper in progress will include the careful observations of close range interactions both between territorial males and between mates needed to further elucidate the functions of the nuchal and malar marks in flickers. However similar the gross behavior of flickers may be, it seems unlikely that color differences in malar marks and presence or absence of nuchal marks in *cafer* and *auratus* are not accompanied by significant differences in behavior (head movements in appeasement situations, for example), regardless of whether these marks have anything to do with reproductive isolating mechanisms. One wonders, for example, if selection for the loss of the red nuchal mark in *cafer* was accompanied by simultaneous selection for the appearance of redness in the malar stripe. Admittedly, speculation about the evolution of these marks will be relevant only after meaningful data on their function are at hand, data which reveal the selection pressures operating to direct their evolution.

In summary, Short's meticulous analysis of phenotypic variation in the flickers of the North American hybrid zones and in the West Indies provides the evolutionist with a vast source of dependable material for interpretation. That there exist other plausible explanations for some of his findings should come as no surprise considering the complexity of the situation. His carefully gathered data set the stage for investigation of the numerous unsolved problems in the group. In addition to the need for further refined examination of phenotypic variation of populations in areas not well represented now by specimens (western United States, Mexico, and Central America), the most profitable lines of research on these readily available birds would seem to be in behavior (function of head marks, for example) and in comparative physiology (temperature and humidity tolerances and preferenda of birds representing the various phenotypes).—NED K. JOHNSON.

WATERFOWL IN AUSTRALIA. By H. J. Frith. East-West Center Press, Honolulu. 1967: 6 × 9 in., 328 pp., 5 col. pls. many bl. and wh. illus., 19 distribution maps. $10.00.

Our dearth of knowledge concerning Australian waterfowl has, until recently at least, been so severe as to once stimulate Ernst Mayr to write a paper (Emu, 45:229–232, 1946) reminding Australians how little was then known about their native waterfowl. The situation was especially serious in view of the fact that no fewer than six of Australia's 19 species of indigenous waterfowl represent monotypic genera that are largely or entirely restricted to that continent. Furthermore, these include such phylogenetically significant and taxonomically controversial genera as *Anseranas*, *Cereopsis*, *Malacorhynchus*, and *Stictonetta*, the last two of which have never been available for behavioral study outside Australia. In view of this, any amount of new information on Australian waterfowl must be enthusiastically welcomed; an entire book on the subject can only be regarded as a godsend.

H. J. Frith's studies on Australian waterfowl go back to the mid-1950s, when he discovered the interesting fact that several duck species of interior Australia have their breeding seasons timed by local water conditions rather than by photoperiod changes or other proximate factors. More recently he was placed in charge of the Division of Wildlife Research of the C.S.I.R.O., the governmental agency charged with conducting and integrating scientific research in Australia. This has placed him in the enviable position of organizing federally-supported research efforts related to waterfowl, and one of the fruits of this situation is the present book.

Unlike the recent monograph by Delacour, Frith has not resorted to the simple expedient of publishing extensive quotations of possible historical interest but dubious current value. Instead, each species is dealt with intensively, and the information on distribution and movements, habitats, and breeding biology are of particular value.

Some of these data are from still unpublished C.S.I.R.O. studies that would otherwise be totally unavailable to most biologists. Numerous photographs of both wild and captive waterfowl add interest, and those illustrating underwater swimming postures of various diving species are especially instructive. Particularly useful features of the book are the detailed distribution maps, the abundant mensural data, the sonograms of representative vocalizations, and the comprehensive colored paintings of Australian waterfowl. These illustrations are mostly based on live specimens and as a result the soft-part colors and postures are generally well done. That of the Freckled Duck is notable for its accurate shaping of the head and bill, although the body is too short and rotund. However, the Musk Duck suffers by comparison with Peter Scott's feather-perfect rendition of the species in Delacour's monograph. The plate of downy young was evidently not done from live specimens, since many of them are too fat, drawn off-balance, or are otherwise misleading. The Australian White-eye ("Hardhead") should not have a definite eye-stripe, the downy Magpie Goose should have a more yellow-orange bill and whitish underparts, and the *Dendrocygna* ducklings not only lack complete nape-stripes but the diagnostic markings of the two species have unfortunately been reversed. The most valuable feature of the plate is that it includes the first published color reproduction of a downy Freckled Duck.

Although it is not surprising that Frith should have concentrated on citing primarily Australian authors and regional literature, this reviewer found it a sobering experience, after having published a book and ten additional papers dealing partially or entirely with Australian Anatidae, to be grudgingly included in an otherwise gratefully anonymous category of "authors with no new information." This provincial outlook might account for Frith's numerous erroneous statements, including the idea that the Ringed Teal is a blue-winged duck, that ritualized feeding of shovelers "is usually performed face to face and is stationary," that copulation in Pink-eared Ducks has not been observed, that the courtship display of pochards is "not unlike that of the river ducks," or that the eclipse plumage of Blue-billed Ducks was previously unreported. Frith's "new" anserine tribe Stictonettini was in fact first suggested by the reviewer in 1960. Most remarkably, Frith reports that Musk Ducks "have two molts per year and both involve the wings and tail," which, if true, would be unique in the family and notable among birds as a whole. Frith confirms that the musky odor of male Musk Ducks is derived, as had been suspected, from the "uropygian" gland. There are a number of other minor spelling errors involving such names as J. C. Phillips, *Thalassornis*, and *Cairina moschata.* These weaknesses should not overly detract from the many good features which the book exhibits. Together with P. A. Clancey's recently published "Gamebirds of South Africa," it provides an invaluable source of material on plumages, measurements, and nesting biology data for a wide variety of southern hemisphere waterfowl. These books are bound to stimulate more research on species that have previously received little if any attention, and additionally provide a highly instructive counterpoint to the numerous volumes that have been published on northern hemisphere waterfowl.—PAUL A. JOHNSGARD.

THE BIRDS OF SOUTHEASTERN VICTORIA ISLAND AND ADJACENT SMALL ISLANDS. By David F. Parmelee, H. A. Stephens, and Richard H. Schmidt. National Museum of Canada Bulletin 222, Ottawa, 1967. x + 229 pp., 10 bl. & wh. pls., 4 figs. including 2 maps. $2.00 (Canadian).

Field students working in Arctic areas have two advantages over investigators in temperate or tropical regions: the total number of species in a restricted area is not large; and the long daylight period provides working time for a variety of detailed observations. The present report reflects these advantages, as well as the diligence of the authors and their field companion, George M. Sutton. Thus the report is much more than the routine faunal listing implied by the title.

In two summers' work on Victoria Island the authors managed not only to observe what birds were present, but also to make detailed observations on the courtship behavior; to find and carefully watch a great many nests; to collect critical specimens, particularly of the little known juvenal stages; and to band a sizable number of birds. Each of these topics is thoroughly discussed for the common species, and a final summarizing discussion of "The Annual Breeding Cycle" is also given. For most species spring arrival and fall departure dates are given and other observations of interest in particular cases are reported.

The result is a notable contribution to the breeding biology of the 67 species found on the island. Twenty-four of these species are from the order Charadriiformes, and the detailed observations on the courtship and nesting of several of the small sandpipers, the jaegers, and gulls will be of great value to students of these groups. Only seven passeriform species were listed other than as stragglers.

The ecology of the breeding species is barely touched upon, and then only in such vague terms as "marsh" or "dry tundra." One very interesting ecological discussion is the analysis of the vegetation that develops on the "mounds" used as lookout posts by Snowy Owls as a result of the nitrogen enrichment of the soil. Notes are included on the prey species of the predatory birds: hawks, falcons, jaegers, and owls.

A number of interesting and suggestive recoveries are reported for some of the banded birds.

A few notes of the mammals observed are included, and an appendix lists 39 species that were observed on Jenny Lind Island in the season of 1966.—George A. Hall.

PUBLICATION NOTES AND NOTICES

Attracting Birds: From the Prairies to the Atlantic. By Verne E. Davison. Thomas Y. Crowell Company, New York, 1967: 6⅛ × 9¼ in., xviii + 252 pp., 13 figs., 19 tables. $6.95.

This new addition to the steadily growing list of books on attracting birds runs the usual gamut of desirable information on the construction (with drawings) and placement of feeding stations and birdhouses. Where it deviates from most of, if not all, the other books is in the convenient organization and the detailed extent of the information (two-thirds of the book) on attracting particular birds and the plants that are especially useful. The book has one set of alphabetical entries for more than 400 species of birds that live in eastern North America and another set for more than 700 plants and foods that are important to them. As the publisher explains on the book's jacket:

"Each entry on a bird species contains information about its distribution and numbers, about the kind of nest it prefers and where it builds its nest. If the bird can be coaxed to close range from its natural habitat, the entry describes the type of man-made house it will occupy, lists the foods that are especially effective lures, and tells what type of feeder has been used most successfully. Every plant is briefly identified, and its usefulness as a nest or shelter noted. For each plant and nonplant food there is a list of birds in whose diet the item figures significantly."—O.S.P.

This issue of *The Wilson Bulletin* was published on 16 June 1969.

Editor of The Wilson Bulletin

GEORGE A. HALL
Department of Chemistry
West Virginia University
Morgantown, West Virginia 26506

Ornithological Literature Editor

Olin Sewall Pettingill, Jr.
Laboratory of Ornithology, Cornell University, Ithaca, N.Y. 14851

Suggestions to Authors

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subsequently identified. Summaries of major papers should be brief but quotable. Where fewer than five 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 "Style Manual for Biological Journals" (1964. AIBS). Photographs for illustrations should be sharp, 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. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A Word to Members

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

PAST PRESIDENTS OF THE WILSON ORNITHOLOGICAL SOCIETY

J. B. Richards, 1888–1889
Lynds Jones, 1890–1893
Willard N. Clute, 1894
R. M. Strong, 1894–1901
Lynds Jones, 1902–1908
F. L. Burns, 1909–1911
W. E. Saunders, 1912–1913
T. C. Stephens, 1914–1916
W. F. Henninger, 1917
Myron H. Swenk, 1918–1919
R. M. Strong, 1920–1921
Thos. L. Hankinson, 1922–1923
Albert F. Ganier, 1924–1926
Lynds Jones, 1927–1929
J. W. Stack, 1930–1931
J. M. Shaver, 1932–1934
Josselyn Van Tyne, 1935–1937
Margaret Morse Nice, 1938–1939
Lawrence E. Hicks, 1940–1941
George Miksch Sutton, 1942–1943
S. Charles Kendeigh, 1943–1945
George Miksch Sutton, 1946–1947
Olin Sewall Pettingill, Jr., 1948–1950
Maurice Brooks, 1950–1952
W. J. Breckenridge, 1952–1954
Burt L. Monroe, 1954–1956
John T. Emlen, Jr., 1956–1958
Lawrence H. Walkinshaw, 1958–1960
Harold F. Mayfield, 1960–1962
Phillips B. Street, 1962–1964
Roger Tory Peterson, 1964–1966
Aaron M. Bagg, 1966–1968
H. Lewis Batts, Jr., 1968–1969

PAST EDITORS OF THE WILSON BULLETIN

Lynds Jones, 1892–1900
Frank L. Burns, 1901
Lynds Jones, 1902–1924
T. C. Stephens, 1925–1938
Josselyn Van Tyne, 1939–1948
David E. Davis, 1949
George Miksch Sutton, 1950–1951
Harrison B. Tordoff, 1952–1954
Keith L. Dixon, 1955–1958
H. Lewis Batts, Jr., 1959–1963

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY
WEST VIRGINIA U. • MORGANTOWN, W. VA.

VOL. 81, NO. 3 SEPTEMBER 1969 PAGES 233–360

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—William W. H. Gunn, Apt. 1605, 155 Balliol Street, Toronto, Ontario.

First Vice-President—Pershing B. Hofslund, Dept. of Biology, University of Minnesota Duluth, Duluth, Minnesota 55812.

Second Vice-President—Kenneth C. Parkes, Carnegie Museum, Pittsburgh, Pennsylvania 15213.

Secretary—Jeff Swinebroad, 8728 Oxwell Lane, Laurel, Maryland 20810.

Treasurer—William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107.

Elected Council Members—Andrew J. Berger (term expires 1970); C. Chandler Ross (term expires 1971); Ernest P. Edwards (term expires 1972).

Membership dues per calendar year are: Sustaining, $10.00; Active, $5.00.
Life memberships, $150 (payable in four installments).
THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 104 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to "The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan." Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically.

THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December, at Morgantown, West Virginia. The subscription price, both in the United States and elsewhere, is $6.00 per year. Single copies, $1.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $1.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan.

Second class postage at Lawrence, Kansas, U.S.A. 66044

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by The Wilson Ornithological Society

VOL. 81, NO. 3 SEPTEMBER 1969 PAGES 233–360

CONTENTS

SPRING MIGRATION AND WEATHER AT MADISON, WISCONSIN *Steven G. Curtis* 235
PRE-NESTING AND NESTING BEHAVIOR OF THE SWAINSON'S WARBLER *Brooke Meanley* 246
TOWER-KILLED SPECIMENS AND OBSERVATIONS OF MIGRANT BIRDS FROM GRAND BAHAMA ISLAND *Herbert W. Kale II, Margaret H. Hundley, and James A. Tucker* 258
OBSERVATIONS OF BIRDS EXPLOITING A CENTRAL AMERICAN FRUIT TREE *Charles F. Leck* 264
ORAL FLANGES OF JUVENILE BIRDS *George A. Clark, Jr.* 270
VARIATION IN MAJOR BODY COMPONENTS OF THE TREE SPARROW (*SPIZELLA ARBOREA*) SAMPLED WITHIN THE WINTER RANGE *Carl W. Helms and Robert B. Smythe* 280
TERRITORIAL BEHAVIOR AND POPULATION REGULATION IN BIRDS A Review and Re-evaluation *Jerram L. Brown* 293

GENERAL NOTES

AN APPARENT AGONISTIC DISPLAY OF THE WHISTLING HERON (*SYRIGMA SIBILATRIX*) *Lester L. Short, Jr.* 330
USE OF MAN-MADE ISLANDS AS NESTING SITES OF THE COMMON LOON *John E. Mathisen* 331
EGG TRANSPORTATION BY A FEMALE MALLARD *Alphonse Avitabile* 331
A RECORD OF THE TUFTED DUCK FOR CONNECTICUT *George T. Austin* 332
GREAT HORNED OWL NESTING IN A POPULATED AREA *Edwin C. Franks and John E. Warnock* 332
THE NEST, EGGS, AND YOUNG OF THE ELEPAIO *Andrew J. Berger* 333
AN UNUSUAL NEST SITE OF THE STARLING *Luis F. Baptista* 335
FALL AND WINTER FOOD HABITS OF RED-WINGED BLACKBIRDS AND BROWN-HEADED COWBIRDS IN WESTERN OKLAHOMA *Stephen V. Goddard* 336
SHARP-TAILED SANDPIPER AND PALM WARBLER IN ALASKA *Joseph W. Taylor* 337
RESPONSES OF THREE AVIAN SPECIES TO BURNING *William R. Edwards and Jack A. Ellis* 338
FUNCTIONAL GONADS IN PEREGRINES *Clayton M. White* 339
INSECTICIDE RESIDUES IN LEAST BITTERN EGGS *M. Keith Causey and Jerry B. Graves* 340

ON ABNORMALLY CROSSED MANDIBLES IN BIRDS .... *Kenneth C. Parkes* 342
ORNITHOLOGICAL NEWS 343
ORNITHOLOGICAL LITERATURE 344
Eric Eastwood, *Radar Ornithology*, reviewed by Jeff Swinebroad; Boonsong Lekagul, *Bird Guide of Thailand*, reviewed by Eugene Eisenmann; Austin L. Rand, *Ornithology: An Introduction*, reviewed by D. A. Lancaster; C. Brooke Worth, *A Naturalist in Trinidad*, reviewed by Margaret H. Hundley; Paul L. Errington, *Of Predation and Life*, reviewed by Tom J. Cade; James Fisher (Ed.), *Thorburn's Birds*, reviewed by Don R. Eckelberry.
PUBLICATION NOTES AND NOTICES 342, 352
PROCEEDINGS OF THE FIFTIETH ANNUAL MEETING
Jeff Swinebroad, Secretary 353

SPRING MIGRATION AND WEATHER AT MADISON, WISCONSIN[1]

STEVEN G. CURTIS

ONLY a small portion of the literature on the influences of weather on bird migration considers the recording of migration on the basis of quantitative day-to-day changes in the numbers of transient migrants at a given location. Ground counts if taken daily can be useful in providing information on the arrival and the departure of migrants, and on the attending weather conditions. Radar and moon watching techniques provide the best known approaches for obtaining quantitative data on migration in progress but often reveal little of the species involved and little of the points of inception and termination of migration waves.

During the springs of 1963, 1964, and 1966 daily counts of the grounded (or stopover) transient populations of night migrating passerines were conducted at Madison, Wisconsin. The influxes and departures revealed by these counts are examined in relation to general weather conditions and specific weather components.

METHODS

The data were obtained at a twenty-acre study area at Picnic Point on the University of Wisconsin campus on 45 days from 15 April to 29 May in 1963 and on 42 days from 15 April to 27 May in 1964. Also in 1964 migration data were collected on 37 days from 15 April to 21 May at a 4.5-acre study area in the Stevens Pond region of the University of Wisconsin Arboretum several miles south of Picnic Point. These data were pooled with the 1964 Picnic Point data. In 1966 data were gathered on 29 days from 15 April to 21 May at a 6.5-acre woodlot located about 5 miles southwest of Madison. All three study areas were dominated by deciduous trees and attracted roughly the same bird species. Because counts could not always be made every day and because day-to-day changes in numbers of observed migrants are used as a measure of migration, the number of units of usable data is reduced to 44 for 1963, 40 for 1964, and 20 for 1966 (total = 104).

All passerines that were identified by sight or call were recorded. Birds flying over were not included in the analysis. Counts were conducted in the morning hours, with a few exceptions. The study areas were covered systematically and intensively by slowly traversing the irregular network of trails. This method has been used effectively in similar studies by Bennett (1952), Dennis (1954), and others. The area and distance traversed were held essentially constant, although the time spent afield varied with bird densities. The figures obtained are regarded as fair approximations of the actual numbers of birds present in the areas.

None of the species studied occurred in large enough numbers for a sufficient period of time to allow a meaningful analysis of their individual migratory responses

---

[1] Journal Paper No. 77, University of Wisconsin Arboretum, Madison.

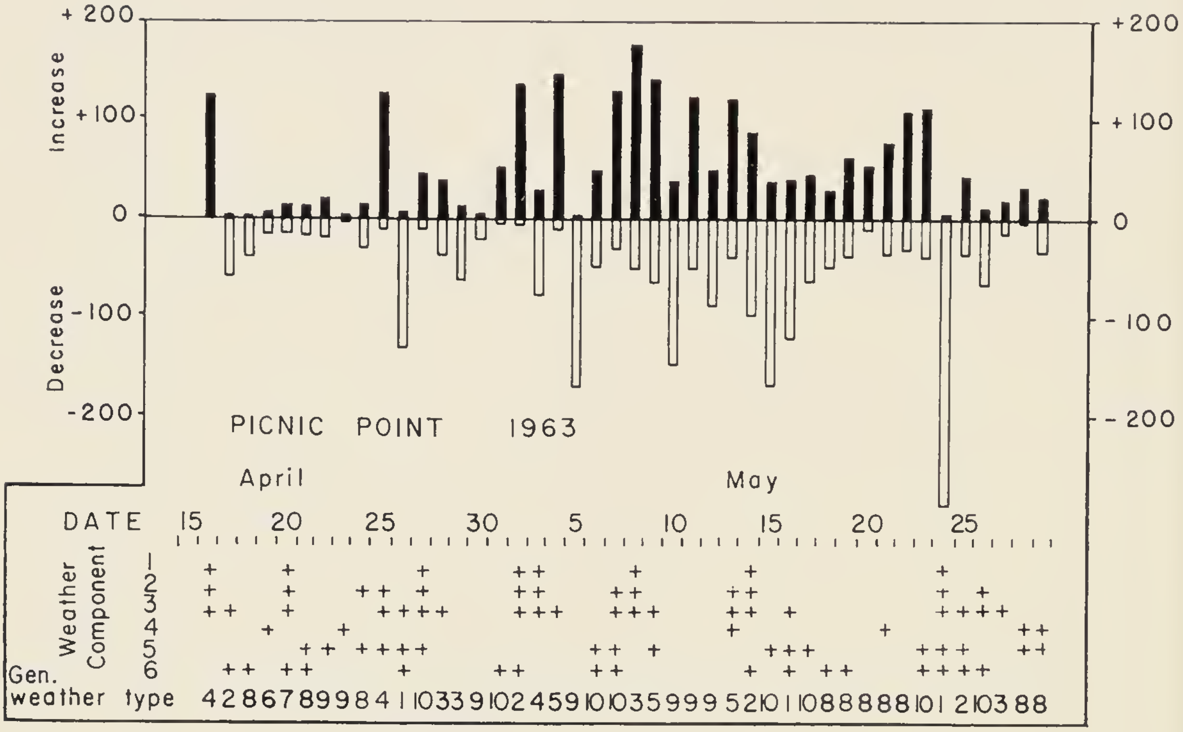


FIG. 1. Increases and decreases in numbers of migrants from previous day, 15 April to 29 May, 1963. Plus signs indicate presence of specific weather components: 1. temperature increase 10° F from previous evening; 2. temperature increase 5° F from previous evening; 3. calm or southerly winds (ESE-WSW); 4. rain in the evening; 5. winds less than 7 knots; 6. 30% cloud cover or less. The general weather situation for each night is given at bottom.

to weather. Therefore the daily counts for each of the species were pooled and only the total day-to-day changes considered. The day-to-day changes in numbers of migrants were found by summing the increases of all species that increased in numbers from the previous day and, independently, summing the decreases of all species that decreased from the previous day. For example, if 20 Myrtle Warblers (*Dendroica coronata*), 10 Palm Warblers (*Dendroica palmarum*) and 50 White-throated Sparrows (*Zonotrichia albicollis*) were observed on the first day, and 30 *D. coronata*, 40 *D. palmarum* and 15 *Z. albicollis* seen on the second day there would be an increase of 40 (10 for *D. coronata* plus 30 for *D. palmarum*) and a decrease of 35 (from 50 to 15 *Z. albicollis*). For every day there was thus both an increase and a decrease from the previous day, the increase being a measure of arrival and the decrease a measure of departure from the Madison area (Fig. 1, 2, and 3). (These changes inevitably include those resulting from counting errors, and local movements, as well as from actual migration. However, I feel migration was responsible for most of the large changes observed.) The day-to-day changes were calculated for each study area. In 1964 the Stevens Pond and Picnic Point data were lumped after total daily changes had been calculated for each. To obtain comparable figures based on daily change per twenty acres the daily change totals were multiplied by factors of 0.82 for 1964 and 3.0 for 1966.

The observed fluctuation in the numbers of grounded migrants was examined in relation to temperature, wind direction, wind strength, sky cover, precipitation, and

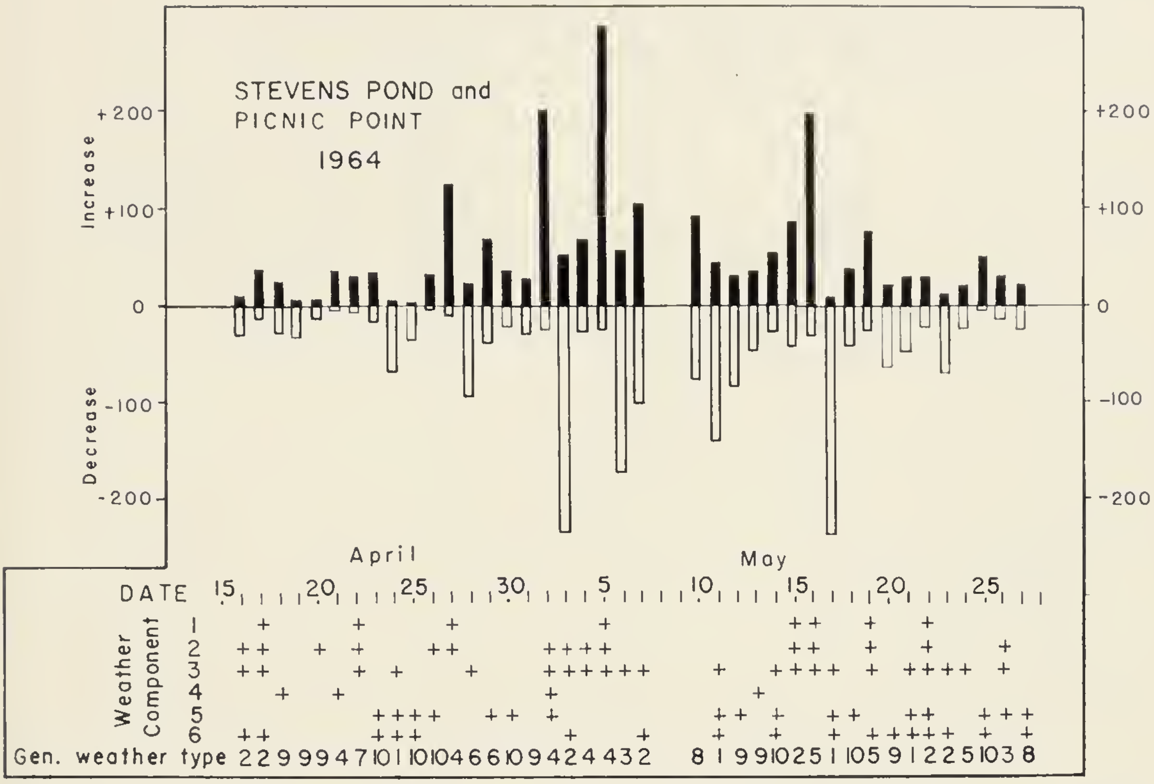


FIG. 2. Increases and decreases in numbers of migrants from previous day, 15 April to 27 May, 1964. Plus signs indicate presence of specific weather components: 1. temperature increase 10° F from previous evening; 2. temperature increase 5° from previous evening; 3. calm or southerly winds (ESE-WSW); 4. rain in the evening; 5. winds less than 7 knots; 6. 30% cloud cover or less. The general weather situation for each night is given at bottom.

general weather conditions. Meteorological information was obtained from the official U.S. Weather Bureau reports for Truax Field at Madison and the U.S. Weather Bureau's Daily Surface Maps. The method of correlating specific weather components with observed decreases in numbers of migrants follows that of Brooks (1965). All nights on which a given weather component to be tested for correlation occurred were considered plus nights for that component. All nights on which this condition did not exist were considered minus nights. For departures the average population decrease for plus nights was then compared with the average population decrease for minus nights by means of the Chi-square test. The same procedure was used for arrival data; however, the emphasis in this paper is placed on the relation of weather components to departures from the Madison area.

For this study, the hours near dusk (18:00 to 23:00 C.S.T.) were considered most critical for emigration. Observed decreases in migrant numbers were tested for correlation with the specific weather components which prevailed during this time period. The weather components which existed for each evening are shown in Figures 1, 2, and 3. For arrivals the time period from 22:00 to dawn is probably most important. Observed increases were tested for correlation with weather components occurring during the night. With the exception of night rainfall the occurrence of the weather components was the same as for departures (Fig. 1, 2, and 3).

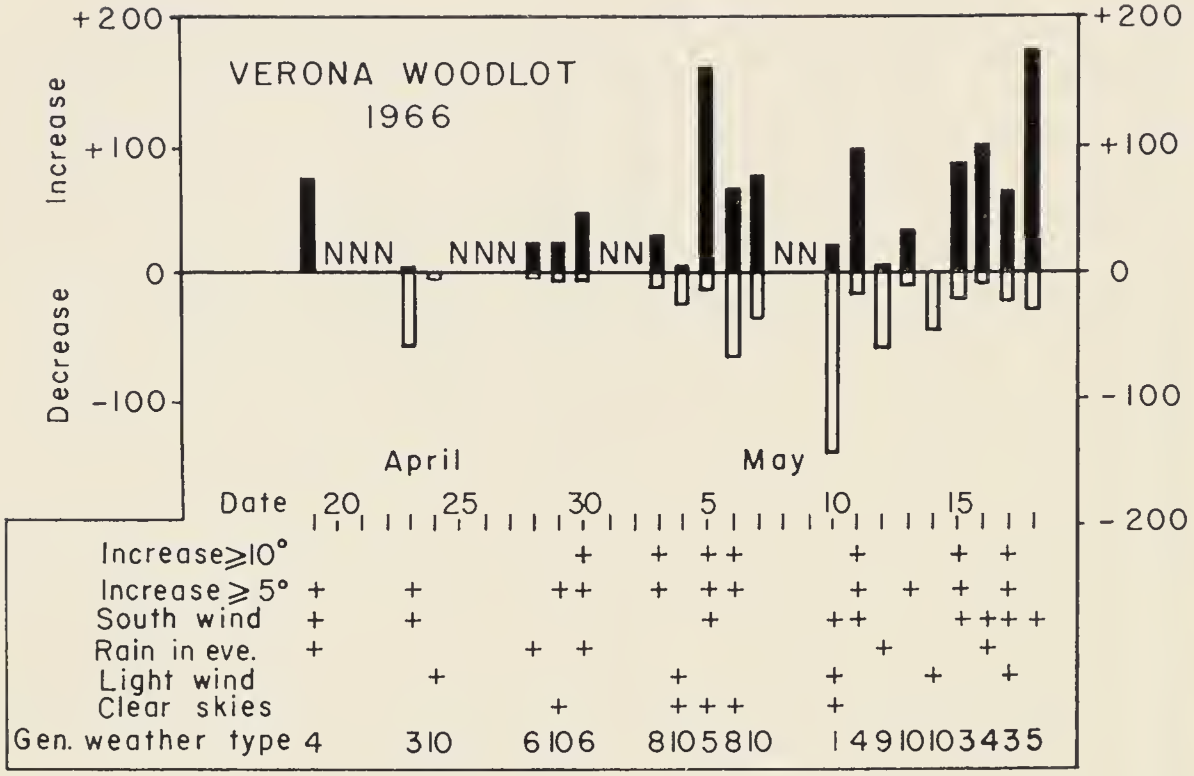


FIG. 3. Increases and decreases in numbers of migrants from previous day, 15 April to 21 May, 1966. The plus signs indicate presence of specific weather components. The general weather situation for each night is given at bottom.

SPECIFIC WEATHER COMPONENTS

Many studies have examined the relation of migration to the various weather components, and some controversy has arisen over the relative importance of each of a rather wide variety of weather components. Thus, Lack (1960*b*) regarded temperature as the single most important meterological factor in the inception of migration in spring, while wind direction (following wind) rather than temperature was considered important in summer and fall (Lack, 1963).

At Madison temperature increases of 10° F or more from the previous evening showed no correlation with observed decreases in numbers of birds (Table 1). Drury and Keith (1962) have suggested that in late spring temperature rises of 5° F were adequate stimuli. However, I found no correlation with temperature increases of 5° (Table 1). Arrivals at Madison were significantly correlated with both temperature increases of 5° F or more and temperature increases of 10° F or more (Table 2).

Devlin (1954) thought that south wind or calm at the critical time (hour just before nightfall) was most important in inducing migratory flight in spring, while Williams (1950) felt that wind direction was unimportant.

TABLE 1

CORRELATION OF DEPARTURES WITH SPECIFIC WEATHER COMPONENTS

Weather Components	Average Decrease Plus Nights	Average Decrease Minus Nights	Chi-square	Degree of Correlation
Temperature increase 10°F	–37.6	–50.0		no
from previous evening	n=23	n=81	2.2	correlation
Temperature increase 5°F	–31.8	–53.1		no
from previous evening	n=39	n=65	2.8	correlation
Southerly winds (ESE to WSW)	–56.9	–38.0		Positive correlation
or calm	n=51	n=53	3.8	$P \leq 0.05$
Rain in evening	–19.8	–52.2		Negative correlation
	n=15	n=89	15.9	$P \leq 0.01$
Light winds (less than 7 knots)	–55.9	–42.1		no
	n=39	n=65	2.2	correlation
Clear skies (30 per cent cloud	–63.1	–37.0		Positive correlation
cover or less)	n=39	n=65	7.5	$P \leq 0.01$

At Madison, there was a positive correlation with southerly winds (Table 1). Arrivals were strongly correlated to southerly winds (Table 2).

Lack (1960*b*) concluded that very little emigration occurred with rain or mist. Rainfall during the hours around dusk seemed to inhibit emigration from Madison (Table 1). Arrivals were correlated with night rainfall (Table 2).

Most researchers agree that strong winds, regardless of direction, inhibit migration and that migration is correlated with light winds. Lack (1960*a*) showed that radar studies of the spring emigration in Norfolk established statistically that more emigration occurred with light than strong winds. The data from the Madison study showed greater average decrease for evenings with winds less than 7 knots than for evenings with stronger winds, but the difference is not significant (Table 1).

Most researchers have concurred that migration is favored by clear to partly cloudy skies. Some migration also occurs on nights of complete overcast (Hassler et al., 1963; Drury and Nisbet, 1964; and others). More birds departed from the Madison area when there was less than 30 per cent cloud cover (Table 1). Arrivals showed no correlation with light winds or clear skies (Table 2).

GENERAL WEATHER PATTERNS

Lack (1960*b*) concluded that the volume of emigration is determined by particular weather factors and not by general weather situations. Later (1962), however, Lack found that the general weather situation significantly

TABLE 2

CORRELATION OF ARRIVALS WITH SPECIFIC WEATHER COMPONENTS

Weather Components	Average Increase Plus Nights	Average Increase Minus Nights	Chi-square	Degree of Correlation
Temperature increase 10°F	+88.6	+45.4		Positive correlation
from previous night	n=23	n=81	22.3	$P \leq 0.01$
Temperature increase 5°F	+76.2	+42.1		Positive correlation
from previous night	n=39	n=65	11.2	$P \leq 0.01$
Southerly winds (ESE to	+72.4	+38.1		Positive correlation
WSW) or calm	n=51	n=53	10.7	$P \leq 0.01$
Rain during night	+73.3	+46.4		Positive correlation
	n=33	n=71	7.5	$P \leq 0.01$
Light wind (less than 7 knots)	+44.2	+61.4		no
	n=39	n=65	2.8	correlation
Clear skies (30 per cent cloud	+43.9	+61.6		no
cover or less)	n=39	n=65	3.0	correlation

influenced migration. In any event, the reactions of birds to general weather situations can profitably be examined synoptically.

In temperate North America weather patterns drift eastward in a constant progression of high and low pressure systems each characterized by associated predictable patterns of wind, sky cover, and temperature variations. Thus, over the course of a spring season, various generalized synoptic patterns are repeated over southern Wisconsin in cycles. For purposes of analysis in this study ten stages of a typical weather cycle were recognized as depicted diagrammatically in Figure 4. All of the midnight weather patterns (as depicted on the Daily Weather Maps) for the migration seasons of 1963, 1964, and 1966 were classified and assigned to one of the ten possible stages (Figs. 1, 2, and 3). Because a few of the situations represented intermediates between two stages a subjective decision had to be made as to their assignment. All the population data for each of the days were then grouped with their respective weather types and the average population changes determined for each of the ten stages (Fig. 5).

Weather features and population changes during each of the ten selected stages of a weather cycle are as follows:

1. Conditions during stage one are characterized by calm to light southerly winds, and clear skies. Large decreases in numbers of birds were observed under these conditions (implying emigration). This type of weather occurred a total of eight times during the course of the three spring seasons, and on each occasion the decrease in number of birds far exceeded the increase (Fig. 5).

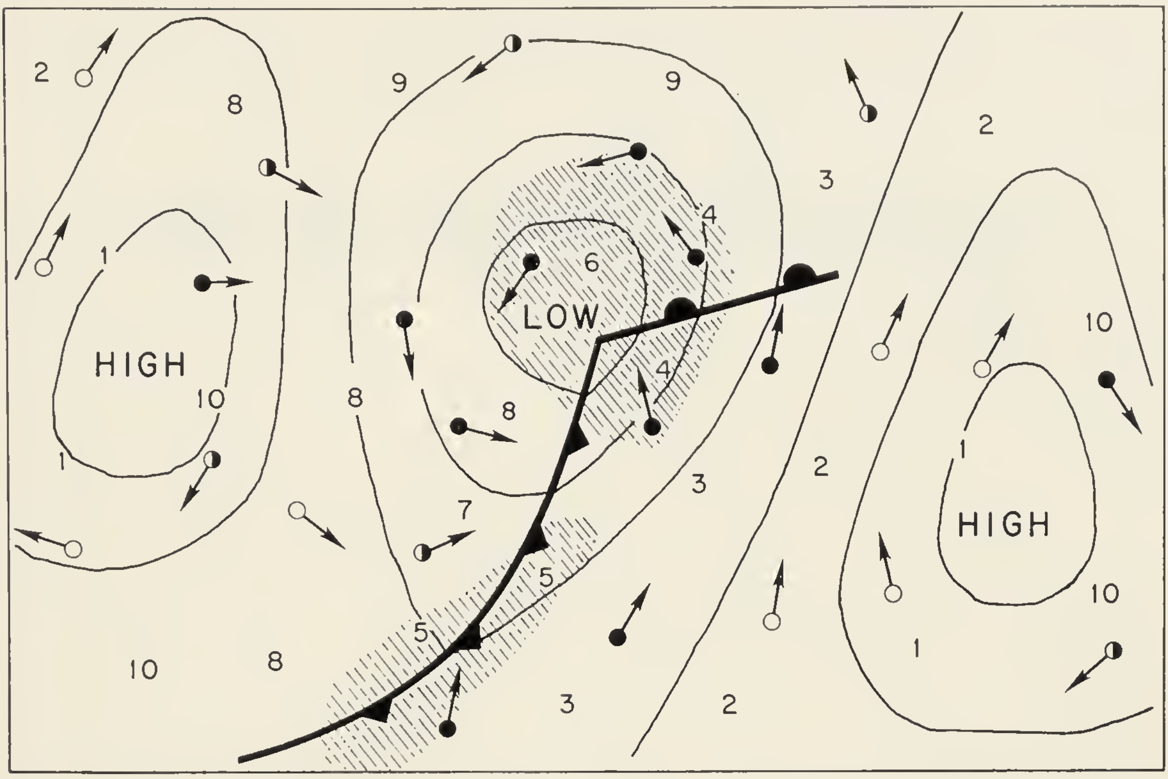


FIG. 4. Hypothetical map of a typical spring weather cycle with a high pressure system to the east (with clockwise winds) followed by a low pressure system (with counterclockwise winds and associated fronts and rain activity), followed by another high pressure system. These patterns drift eastward across North America. The numbers denote the ten zones or stages of a typical spring weather cycle as used in this study for correlation with migration. High levels of migration occurred in the region of northward airflow (stages 1–5); low levels in zones 6–10. Greatest departures occurred in stages 1 and 2, while greatest arrivals occurred in stages 4 and 5. ▲▲ Cold front; ◠◠ Warm front; Shaded area—Rain activity. Arrows indicate wind direction with circles on arrows indicating sky conditions.

2. Substantial decreases occurred under the conditions of clear skies and well developed northward air flow (parallel north-south trending isobars) characteristic of weather stage two where the center of a high has moved farther to the east than in stage one. Some increases were also noted for type 2 weather (Fig. 5).

3. Stage 3 has conditions similar to those of stage two except the skies are mostly overcast. Somewhat larger average increase was noted than for stage two (Fig. 5). It seems probable that overcast grounded some of these arriving migrants. Mueller and Berger (1966) reported that the mean weight of migrant Swainson's thrushes was lowest after clear nights (15 per cent cloud cover or less) and highest after overcast nights (85 per cent cloud cover) indicating that the latter were probably grounded sometime early in the night by heavy overcast before a long flight had depleted their fat reserves.

4. As the high pressure center moves farther east and a low pressure system approaches from the west stage four is characterized by southerly winds with rain occurring over southern Wisconsin during the night.

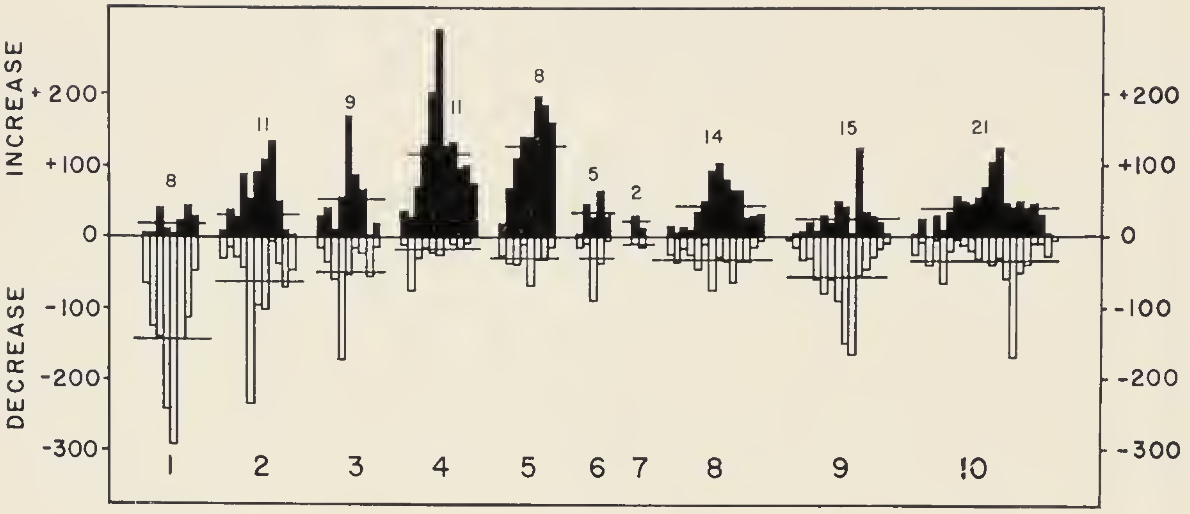


FIG. 5. Increases (shaded) and decreases (unshaded) in migrant numbers occurring under each of ten weather categories as shown in Figure 4. Each of the 104 nights is presented with average change for each weather category indicated by horizontal line. See text for description of ten weather categories.

5. Stage five shows essentially the same situation as that represented in stage four except that the rain is associated directly with a cold or stationary front, with characteristic drop in temperature and often a wind shift. Substantial increases were noted for both stage four and stage five weather conditions. Presumably this reflected large scale groundings of passing or "onrushing" migrants as they encountered moderate to heavy rains, thunderstorms, vertical and horizontal air turbulence, or shifts in wind direction. Bagg et al. (1950) referred to these massive groundings as "arrested waves." Lack (1960*b*), Dennis (1954), and others reported similar groundings associated with rain and fronts.

Significant decreases sometimes took place on the night following a night of frontal or precipitation grounding. These decreases can be explained by local dispersal during the day following such a grounding, as suggested by Mueller and Berger (1966). Alternatively, these decreases could have been due largely to emigration. This assumes the physiological "drive" to continue migration remained high following nights of interrupted flight, especially if these interruptions occurred early in the night before fat reserves were substantially reduced.

The first five weather stages fairly well represent the overall pattern typical of the zone of southerly winds occurring on the west side of a high pressure cell and in the warm sector of a low pressure system (Fig. 4). As Bagg et al. (1950) have suggested, it is in these zones of northward airflow that the majority of the birds migrate in the spring. At Madison the greatest daily turnover of migrants occurred under the conditions applying in stages one to five (Fig. 5).

6. The weather pattern associated with the center of a low (as represented by stage six) occurred on only five evenings. Little migration would be expected under such disturbed conditions. Nisbet (1957) has remarked: "The principal feature of the reactions of the birds to weather changes is a strong discrimination against migrating in active cyclonic weather." The changes in numbers noted at Madison with stage six weather were small (Fig. 5).

7. Stage seven shows the strong southwesterly winds that sometimes occur after the passage of a cold front. The key feature is the cooler southwesterly winds, with air of continental polar or arctic origin. Small numerical changes occurred with this weather situation, which occurred on only two nights. Usually westerly to northeasterly winds occur after the passage of a cold front.

8, 9. Stages eight and nine are characterized by northwesterly and northeasterly winds associated with the cold sector of a low and the eastern portion of a high.

10. Stage ten represents the situation on the east side of a high pressure cell characterized by light variable winds (usually northerly) and quite often, cloudy skies. Average increases were generally light (with a few exceptions) and were approximately balanced by decreases for eight, nine, and also for ten (Fig. 5).

In summary, the average turnover for weather patterns represented by stages six–ten was relatively low as compared with that for stages one–five (Fig. 5).

DISCUSSION AND CONCLUSION

The observations obtained in this study support those of other students of bird migration that the major portion of the spring migrants proceed northward in the flow of southerly winds that occurs in the region to the west of a high pressure system, and in the warm sector of a low pressure system. The weather conditions that apply at such times provide assistance to northward progress in the form of tail winds. While Lowery and Newman (1955) have clearly shown that the flight directions very often do not correspond exactly to the prevailing wind direction, flying into headwinds is not a common feature of long distance nocturnal migration. Mueller and Berger (1966) have presented further data in support of this and note that it would be inefficient for a bird to continue migration into an appreciable head wind.

The analyses made in this study show that a large portion of migrants seem to receive their cues for departure from the Madison area just before the development of north-south trending isobars and northward airflow. It is as though the rather neutral conditions of a high pressure center carry information on the sustained period of northward airflow that will generally follow. This is not to imply that the birds anticipate favorable migrating conditions (sustained following winds) before they occur but that natural selection has favored responses to weather cues which generally precede northward airflow. It seems unlikely that birds are able to respond to general weather as such, but quite probably they do respond to combinations of specific weather components that are characteristic of a general weather situation. For example, perhaps the birds are able to respond to the passage of a high pressure ridge by one or more of the following characteristic features: clear skies or winds shifting to southerly or calm. Devlin (1954) found that calm conditions were favorable for migration and that on each of nine calm spring nights "there was a 'breeze' from the south 100 feet above the ground." Decrease in the observed numbers of migrants at Madison showed positive correlation with clear skies, calm or southerly winds or winds shifting to southerly, weather components characteristic of the passage of a high pressure ridge.

There have been many diverse opinions on which individual weather components are important to migration. Analyzing migrational activity with specific weather components alone, generally fails to produce a clear pattern of overall migrant response to weather. The various weather components are not independent variables but are related to one another and to the general weather situation. The effects of specific weather components on migration should be examined in relation to the general weather situations rather than independently.

SUMMARY

1. During the springs of 1963, 1964, and 1966 the day-to-day changes in numbers of "stopover" migrants at several study areas near Madison, Wisconsin, were used as an index to the arrival and departure of spring migrants in south-central Wisconsin.

2. The daily changes in numbers of stopover migrants were statistically correlated with weather components by means of the Chi-square test. Decreases in numbers of migrants at Madison were found to be positively correlated with clear skies and calm or southerly winds. Temperature changes showed no correlation and rain was found to be unfavorable for the initiation of migratory flight. Arrivals were correlated with southerly winds, night rainfall and temperature increases of 10° F or more or 5° F or more from the previous evening.

3. Ten weather patterns representing successive stages of a typical spring weather cycle were chosen and each of the nights of the three spring migration seasons assigned to one of these stages. The average increase and decrease in number of migrants per night were then calculated for each stage. Significant migration occurred in the weather zone stages between a high pressure system on the east and a low pressure system on the west. Largest decreases were observed when the center of a high pressure system was located just east of Wisconsin. As a low pressure system approached and moved through Wisconsin from the west, large numbers of migrating birds were grounded by shower activity and frontal passage. Little evidence of migration was noted in the weather zones to the west or north of a low pressure center or in the east sector of a high pressure system.

ACKNOWLEDGMENTS

The study was carried out under the supervision of Dr. J. T. Emlen to whom I am most grateful for guidance, encouragement, and for critical reading of the manuscript. I am especially indebted to P. Krombholz, who shared in the collection of the field data in 1963 and 1964, and to S. Martin who gathered the Stevens Pond data. I also wish to acknowledge H. C. Mueller for helpful discussion, as well as for critical reading of the manuscript.

LITERATURE CITED

BAGG, A. M., W. W. H. GUNN, D. S. MILLER, J. T. NICHOLS, W. SMITH, AND F. P. WOLFARTH. 1950. Barometric pressure-patterns and spring bird migration. Wilson Bull., 62:5–19.

BENNETT, H. R. 1952. Fall migration of birds at Chicago. Wilson Bull., 64:197–220.

BROOKS, W. S. 1965. Effects of weather on autumn shorebird migration in east-central Illinois. Wilson Bull., 77:45–54.

DENNIS, J. V. 1954. Meteorological analysis of occurrence of grounded migrants at Smith Point, Texas, April 17, May 17, 1951. Wilson Bull., 66:102–111.

DEVLIN, J. M. 1954. Effects of weather on nocturnal migration as seen from one observation point at Philadelphia. Wilson Bull., 66:93–101.

DRURY, W. H., AND J. A. KEITH. 1962. Radar studies of songbird migration in coastal New England. Ibis, 104:449-489.

DRURY, W. H., JR., AND I. C. T. NISBET. 1964. Radar studies of orientation of songbird migrants in southern New England. Bird-Banding, 35:69–119.

HASSLER, S. S., R. R. GRABER, AND F. C. BELLROSE. 1963. Fall migration and weather, a radar study. Wilson Bull., 75:56–77.

LACK, D. 1960*a*. Migration across the North Sea studied by radar. Pt. 2. The spring departure, 1956–1959. Ibis, 102:26–57.

LACK, D. 1960*b*. The influence of weather on passerine migration. A review. Auk, 77:171–209.

LACK, D. 1962. Migration across the southern North Sea studied by radar. Pt. 3. Movement in June and July. Ibis, 104:74–85.

LACK, D. 1963. Migration across the southern North Sea studied by radar. Pt. 5. Movements in August, winter and spring, and conclusion. Ibis, 105:461–492.

LOWERY, G. H., JR., AND R. J. NEWMAN. 1955. Direct studies of nocturnal bird migration. *In* A. Wolfson (Ed.) Recent studies in avian biology. University of Illinois, Urbana.

MUELLER, H. C., AND D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. Bird-Banding, 37:83–112.

NISBET, I. C. T. 1957. Passerine migration in south Scandinavia in the autumn of 1954. Ibis, 99:228–268.

WILLIAMS, G. G. 1950. Weather and spring migration. Auk, 67:52–65.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF WISCONSIN, MADISON, WISCONSIN, (PRESENT ADDRESS: JAMES FORD BELL MUSEUM OF NATURAL HISTORY, UNIVERSITY OF MINNESOTA, MINNEAPOLIS, MINNESOTA 55455) 2 OCTOBER 1967.

PRE-NESTING AND NESTING BEHAVIOR OF THE SWAINSON'S WARBLER

BROOKE MEANLEY

THE Swainson's Warbler (*Limnothlypis swainsonii*) is one of the least known of southern birds. Although fairly common in some parts of its range, observations of its breeding biology have been made by few persons. Substantial observations have been made by J. Fred Denton at Augusta, Georgia (Griscom and Sprunt, 1957:50–53), and by Eleanor Sims at Charleston, West Virginia (Sims and DeGarmo, 1948:1–8).

I made observations on breeding behavior, mainly during the years 1963–1967, in Canebrakes (*Arundinaria gigantea*) along the Ocmulgee River about 5 miles south of Macon, Bibb County, Georgia; in canebrakes along the Arkansas River about 5 miles north of Pendleton Ferry, Arkansas County, Arkansas; and in deciduous thickets composed mainly of sweet pepperbush (*Clethra alnifolia*) and greenbrier (*Smilax rotundifolia*) in the Dismal Swamp, Nansemond County, Virginia. A few observations were made near Macon during the mid-1940's, and at Alexandria, Rapides Parish, Louisiana, during the mid-1950's. For a description of Swainson's Warbler habitat at these stations see Meanley (1966).

METHODS

All observations were made with binoculars. The size of a territory was determined by repeatedly locating the male on either side of lines 50 feet apart.

Several females were color-marked after they were captured by flushing them from their nests into mist nets. Males were captured for color-marking by mist netting in their territories.

ARRIVAL ON BREEDING GROUNDS AND PAIRING OF BIRDS

In central Georgia, central Louisiana, and east-central Arkansas, Swainson's Warblers arrive on their breeding grounds chiefly during the first two weeks of April. They are one of the last of the southern breeding warblers to arrive, but they are earlier than the northern transient warblers.

A local male population arrives at its breeding ground during a period of about one week. At Macon in 1966, the season being late, the first males (four) arrived in my study area (100 acres) on 12 April; by the next morning there were eight males; nine on the 14th; and 10 on the 15th. the date I departed from the area. When I returned on 28 April, there were 19 males in the area.

Sprunt and Denton (Griscom and Sprunt, 1957:51) stated that females arrive about 10 days later than males. Further evidence that males migrate ahead of females is provided by seven birds that struck a television tower

TABLE 1

SIZES OF SWAINSON'S WARBLER TERRITORIES

Locality	Size (acres)	Reference
Ocmulgee Riverbottom, Bibb Co., Ga.	0.3	author
Monkey John Swamp, Jasper Co., S. C.	0.6	author
Savannah Riverbottom, Richmond Co., Ga.	0.72	Griscom and Sprunt (1957)
Savannah Riverbottom, Richmond Co., Ga.	0.79	Griscom and Sprunt (1957)
Ocmulgee Riverbottom, Bibb Co., Ga.	0.83	Griscom and Sprunt (1957)
Little River Swamp, Tift Co., Ga.	0.91	Griscom and Sprunt (1957)
Dismal Swamp, Nansemond Co., Va.	1.7	author
Dismal Swamp, Nansemond Co., Va.	3.9	author
Dismal Swamp, Nansemond Co., Va.	4.8	author

north of Tallahassee, Florida, in 1966. The birds were picked up at the base of the tower by H. L. Stoddard, Sr., as follows: 4 April, two males; 15 April, one male and three females; and 19 April, one female.

When I visited my study area at Macon on 4 April 1967, Swainson's Warblers had not yet returned. Nine days later (on the 13th), I revisited the area and found 12 males on their breeding territories. Of these one male was paired. I could tell from the frequency of the singing of males that most of the birds were not yet paired. Seven paired males that I have observed during pre-nesting in various localities sang less often than at other times during the breeding season. At Alexandria, Louisiana, a color-marked male that arrived on 3 April was paired by 17 April.

TERRITORY

Size of territories.—During the breeding season Swainson's Warblers were found in groups or "colonies," like Kirtland's Warblers (*Dendroica kirtlandii*) (Mayfield, 1960:2); as isolated pairs; or as unmated males. isolated, or in "colonies." The sizes of territories where birds occur in groups usually are smaller than where isolated birds are found (Table 1). For example, the territory of one isolated pair in the Dismal Swamp covered nearly five acres, the territory of another pair nearly four acres. However, in an area in the Ocmulgee River floodplain forest there were four territories on seven acres, and some of the seven acres was unoccupied.

The smallest Swainson's Warbler territory that I measured contained only 0.3 acres. It was located in a block of woodland approximately two acres in size, and it was separated from the main forest by a cleared power-line right-of-way 50 yards wide. An unmated male occupied this territory during most of the breeding season.

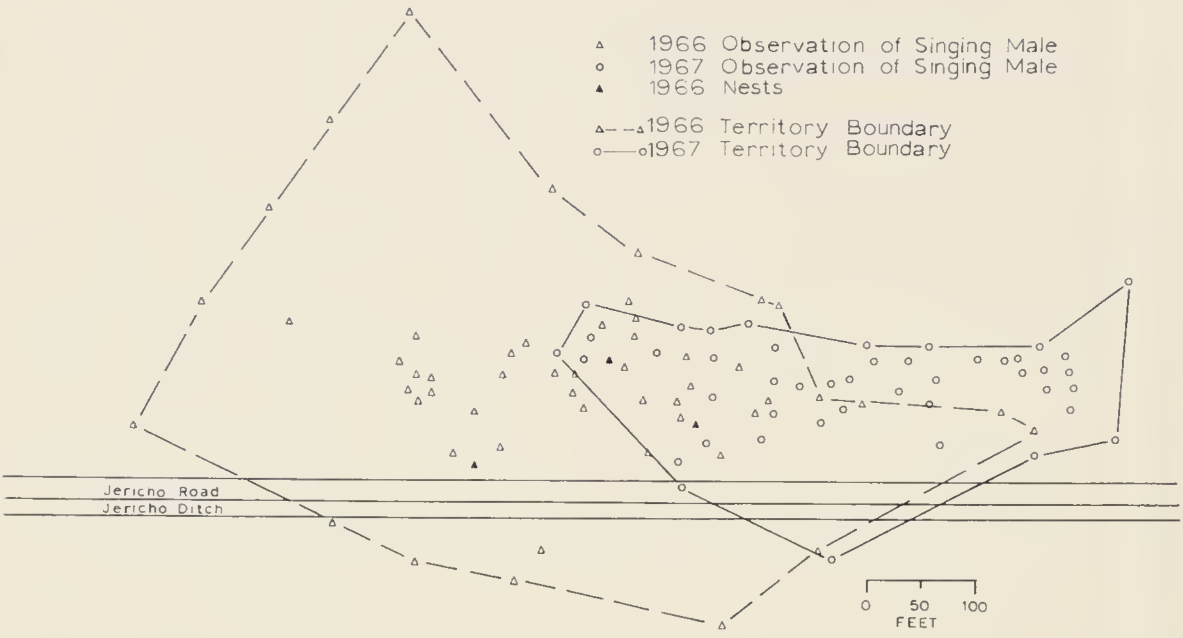


Fig. 1. Territories of a male Swainson's Warbler during the middle of June in consecutive years (1966 and 1967) in the Dismal Swamp, Virginia.

Sometimes in such non-continuous habitat males occupy split territories or territories composed of separate segments. One territory in Monkey John Swamp near Savannah, Georgia, had three segments. Two of the segments were on opposite sides of a cypress (*Taxodium distichum*) pond; the third was across a road from the pond. The occupied segments totaled 0.6 acres.

In an isolated territory of a pair of Swainson's Warblers in the Dismal Swamp, the section with the least understory (3.5 acres) was occupied only 30 per cent of the time; while the part of the territory with the most understory (1.3 acres) was occupied 70 per cent of the time. The female's three unsuccessful nests were located in the 1.3-acre section.

Apparently there is variation in the sizes of the territories of some passerines during the breeding season, but I have been unable to map territories of the Swainson's Warbler throughout the breeding season to show this. Stenger and Falls (1959:136) found that the area utilized by male Ovenbirds (*Seiurus aurocapillus*) was larger during the premating, mating, incubation, and nestling periods than during nest-building and egg-laying. I have observed that some male Swainson's Warblers occupy larger areas during the first day or two following their arrival on the breeding grounds.

It is well known that individuals of many species may return to the same general area in successive years. During my study, a marked male Swainson's Warbler occupied a territory in the Dismal Swamp in 1967 which was adjacent to and partially overlapping his 1966 territory (Fig. 1).

Territorial Behavior.—Males establish territories almost immediately after their arrival on the breeding grounds. One color-marked Arkansas male occupied the same territory for at least four months (15 April–15 August). Its mate disappeared after one unsuccessful nesting attempt.

Territories are defended through use of song, chasing, and combat (Meanley, 1968). Hostile encounters between Swainson's Warblers usually take place along the boundary of adjacent territories. Observations of such encounters were based mainly on the activities of paired versus unpaired males. The four paired males were more aggressive than the five unpaired males and usually initiated the border encounters. A territorial male with an incubating mate at Pendleton Ferry, Arkansas, apparently had more time for hostile activity and thus was involved more often than a paired male at Macon, that was travelling with its mate during pre-incubation. Six hostile encounters between the same neighboring paired and unpaired males at Macon took place at a single point along the boundary.

The Arkansas male would fly from any point in its territory to start a fight at the mutual boundary. It would start *chipping* excitedly as it moved toward the boundary. Both males *chipped* constantly during border clashes. In addition to chasing, the birds fluttered about on the ground after making contact, and sometimes flew together a few feet up from the ground grasping at each other's bills. At Macon, as the males chased each other along the boundary, the paired female was close by but remained 10 to 15 feet within her territory, *chipping* excitedly.

Toward the end of an encounter the Arkansas male usually performed a display near the boundary, in which the wing and tail feathers were spread and the tail vibrated. Sometimes he would side-step back and forth along a branch emitting loud and soft *chips.* I have observed this display given by several males. Ficken and Ficken (1962:110) observed a somewhat similar display in the Redstart (*Setophaga ruticilla*) after prolonged encounters.

Following boundary encounters males drifted back onto their territories and usually sang unbroken courses of songs for several minutes. Sometimes males started singing close to the boundary in which case the songs were incomplete, consisting only of the first two or three notes. Then as they moved farther into their respective territories they sang complete songs. Sometimes following a border encounter, each time one of the males sang, the other would utter a *zeep* note.

There was usually little antagonism toward other species and vice versa.

PRE-NESTING ACTIVITY OF PAIRS

Most of my information on activities of paired birds before nest building is based on observations made 13 and 14 April 1967 of a pair on their territory in a canebrake near Macon. The pair was under observation approximately 75 per cent of the daylight time during the two-day period. Observations could be made throughout most of the day, because of the frequent chipping of the female. I believe that my observations were made during the early stages of pairing because of the date and because the six closest territorial males were unmated.

All paired males that I have observed during pre-nesting sang less often than at other times during the breeding season. Some such males sang only in early morning; others sang in early morning and a half dozen times or less in the remainder of the day. During the early morning song period the Macon male sang both complete and incomplete songs, but I heard him sing no muted (whisper) songs during the two-day observation period.

The Macon pair ranged over a territory of about 1.5 acres. One side of the territory bordered the Ocmulgee River, which at that point was approximately 75 yards wide. Another side was contiguous to a territory occupied by an unpaired male. One side of the neighboring bird's territory also bordered the river. An unpaired male held a territory immediately across the river. The river appeared to be an effective barrier as none of the four birds studied was seen to cross it during the two days of observations.

Hostile encounters between the neighboring paired and unpaired males occurred twice one day and four times in the other day of observations. During these encounters the female of the paired bird remained close to her mate, but within her territory.

The pair spent the day mostly on the ground within 20 feet of each other, often foraging 3 to 4 feet apart. Courtship feeding was not observed. The foraging pair was presumably aided in keeping close together by the frequent *chipping* of the female.

On one occasion a third bird, presumably a female, joined the pair in feeding on the ground for about three minutes. The visiting female was not chased, but the paired female *chipped* constantly until the visitor left the area.

What may have been a form of courtship display, in which the male flew down to the female and either pecked her rump feathers or pounced on her, occurred about three times each hour throughout the day.

After observing this behavior a few times, I could always anticipate when it was going to happen. The male, feeding on the ground usually within 10 feet of his mate, would discontinue feeding and mount a branch or fallen cane pole, usually from 6 to 12 inches above the ground. Then he remained virtually motionless in a crouched position for 1 to 5 minutes facing and presumably watching the female feeding on the ground. In this position the body feathers of the male were fluffed out, particularly on the sides, and his head was drawn in close to his body. Occasionally he would slowly move his head slightly to one side. If the female moved too far out of range the male would shift to a closer perch and continue his crouched stance. The male's performance reminded me of a cat (*Felis*) getting ready to pounce on its prey. The male would then fly to the female and either peck at her as they moved along the ground for a distance of 2 or 3 feet; or he would pounce upon her and they would tussle or flutter together on the ground like two birds in combat. These encounters normally lasted less than 10 seconds. During the chase the female responded with a faint *tweet-tweet-tweet.* The female made no attempt to leave the ground in the course of this action or immediately following it. The pair then started feeding quietly within a few feet of each other.

Nice (1943:174–175) reported pouncing in the Song Sparrow (*Melospiza melodia*) as a form of courtship display, " . . . confined typically to the early stages of the nesting cycle . . . " The male " . . . suddenly flies down to his mate, collides with her, and immediately flies away with a loud song. At times he hits her severely . . . " And Howard (1929:22) observed that following the sexual chase, recently paired Yellow Buntings (*Emberiza citrinella*) flutter together on or near the ground, or peck each other as they rise in perpendicular flights, like males when fighting.

Howard (1929) believes that the sexual chase and pouncing shows that the male is ready to copulate (although the female is not yet ready to receive him). Based on Song Sparrow observations Nice (1943:174–175) states that pouncing by the Song Sparrow early in the season " . . . has no immediate connection with copulation . . . Pouncing on the mate occurs during the long period while song is inhibited and also during [nest] building. It may be a technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt."

NEST BUILDING

Nest building at Macon, Georgia, and Pendleton Ferry, Arkansas, started about three or four weeks after the first males arrived on the breeding grounds. A completed nest ready for eggs was found at Macon on 27 April 1946, and nests with full clutches were found by 3–4 May 1945. A nest containing one Swainson's egg and three Brown-headed Cowbird (*Molothrus ater*) eggs was found at Pendleton Ferry, 1 May 1967. The nest was probably constructed during the third week in April.

Based on observations on the Allegheny Plateau near Charleston, West Virginia, Sims and DeGarmo (1948:4) stated that nest building begins about two weeks after arrival on the breeding grounds. They found a completed nest as early as 1 May.

The earliest nesting is reported by Wayne (1910:150) who collected eggs containing small embryos on 28 April at Charleston, South Carolina. Perhaps the latest date is a nest with slightly incubated eggs found on 13 July 1886 at Savannah, Georgia (Perry, 1886:188).

In canebrakes the nest is rarely located in the densest part of the stand but nearer the edges where the stands are thinner and the cane poles are smaller. Only one of 12 nests that I observed was in a dense stand. Nests found by Howell (1928:284) in Alabama were similarly located. In a mature mountain cove hardwood forest at Charleston, West Virginia, Sims and DeGarmo (1948:4) found that in selecting a site, " . . . the bird avoids placing the nest in dense cover, yet in all instances, a patch of some type of such cover is within a distance of twenty-five to fifty feet. In many cases, this thicket is a growth of greenbrier but may be grape, honeysuckle, blackberry or bittersweet. There appears to be a definite effort to locate the nest in such a manner that it is in close proximity to a screen of protective cover."

All nests that I found in territories in which I determined the boundaries through systematic measurement were inside of the territory. However, often they were near the edge, or the male spent most of his time in an area to one side of the nest. Sprunt and Denton (Griscom and Sprunt, 1957:51) had this to say relative to the location of the nest in the defended territory: "The territory defended by the male is used primarily for mating and feeding and not for nesting. The nest itself is usually located along the margin of the territory but may be entirely outside of it, . . . "

The Swainson's Warbler builds a large and rather bulky nest, apparently larger than that of most warblers that nest above the ground. The nest, usually placed at a height of 2–6 feet from the ground, is built by the female from materials gathered close to the nest site. During a sustained working period, one bird averaged about one trip per minute. Nests that I have seen under construction from the beginning took parts of two or three days to complete. The birds worked at nest building mostly in the forenoon.

Nests are constructed of a rather wide assortment of materials, but there is selection of certain plant parts. The number of species of plants represented in a nest somewhat depends on the composition of the forest in which the nest is located. There seldom were more than a dozen species of plants represented in the nests I examined. The number of pieces of plant parts in a Pendleton Ferry, Arkansas, nest totaled 418; the number in a Dismal Swamp, Virginia, nest was 323. Most pieces were in the lining of the cup. Sticks are seldom used in nests, and the few that occur in some almost seem incidental. But the first of three nests built by the same female in a single season in the Dismal Swamp, Virginia, contained a great many sticks, which is the reason that it weighed more than the second or third nests.

In canebrakes the foundation of a nest is often a bunch of dead leaves that have lodged in the axils of a cane stalk. The Dismal Swamp female referred to above used the relatively large leaves of swamp magnolia (*Magnolia virginiana*) as a platform for each of her three nests. The nests were located at sites where several greenbrier (*Smilax* sp.) vines crossed a horizontal limb of a shrub so that the half dozen magnolia leaves formed a rather level base. Deposited upon these magnolia leaves were the dried leaves, sticks, vines, and tendrils that formed the rather loose outer layer of the nest. Most of the leaves were swamp magnolia, red maple (*Acer rubrum*), red bay (*Persea borbonia*), and greenbrier. Most of the sticks were greenbrier.

The next layer was more compactly structured, consisting almost entirely of decomposed or skeletonized leaves of the swamp magnolia. This layer formed the outer shell of a cup composed of finer materials in which the eggs were deposited. In positioning these leaf skeletons, the tips of the leaves were placed near what became the bottom of the cup (bowl), and they were then drawn toward the rim at a gradually sloping angle to the curve of the cup. All of these leaves were placed in a regular pattern, being drawn clockwise from near the base on one side of the cup to emerge and protrude from the rim at almost the opposite side. All of the protruding petioles were then pointing away from the circle of the rim at a narrow angle clockwise. This layer was constructed similarly in all three nests. Swamp magnolia leaves being elongated in shape, are well suited for this part of the nest structure. Next to this layer of magnolia leaves was a layer of cypress twigs with needles.

The inside of the cup was lined with rootlets (unidentified) and petioles of red maple flowers. All three of the Dismal Swamp nests were lined with these petioles. Apparently they are a preferred item for the lining as I have also found them in nests at Macon, Georgia. Chapman (1907:53) reports that J. N. Clark found them in linings of nests of the Worm-eating Warbler (*Helmitheros vermivorus*) in New Jersey.

The Dismal Swamp female that built three nests in one season used fewer materials in constructing each succeeding nest; thus the nests were progressively lighter. The dry weights of each was 47.7, 39.8, and 26.3 grams. A Pendleton Ferry, Arkansas, nest weighed 24.3 grams.

Dimensions of the Arkansas nest were as follows: greatest outside diameter 15.0 cm; inside diameter of cup 4.0 × 5.0 cm; outside depth 7.8 cm; inside depth of cup 4.2 cm.

EGG LAYING, CLUTCH SIZE, AND INCUBATION PERIOD

At two Louisiana nests, there was a lapse of two days between the completion of the nests and the laying of the first egg. Eggs were laid daily until the clutches were complete. Incubation began with the laying of the last egg in the clutch.

Clutch size in six Georgia nests was as follows: 4 of 3 eggs and 2 of 4 eggs. The somewhat globular eggs are white; slightly spotted eggs are rarely found (Wayne, 1910:149).

By marking eggs, the incubation period of nests at Augusta, Georgia was determined to be 14–15 days (J. Fred Denton, pers. comm.).

COWBIRD PARASITISM

In some parts of its breeding range, the Swainson's Warbler may be rather heavily parasitized by the Brown-headed Cowbird. During the first week in May 1967, at Pendleton Ferry, Arkansas, I located three Swainson's Warbler nests, all of which were parasitized. At one of the nests the warbler was incubating three Cowbird eggs and one of its own. Three days later it was still incubating, but one of the Cowbird eggs and its own egg were missing.

Kirn (1918:97–98) reported several parasitized nests in Copan County, Oklahoma; Sims and DeGarmo (1948:5), in the course of three years, found three of 18 nests parasitized at Charleston, West Virginia.

BEHAVIOR DURING INCUBATION PERIOD

I obtained most of my information on behavior during the incubation period from a nesting pair in the first week of May at Pendleton Ferry, Arkansas. The pair was the one mentioned above whose nest contained three Cowbird eggs and one warbler egg. This nest was located about two feet above the ground between two cane poles. Incubation was performed by the female.

During incubation the Pendleton Ferry female spent about 78 per cent of her daylight time on the nest. The average time on the nest was 70 minutes; the average time off was 19 minutes. The longest period recorded on the nest was 110 minutes, the shortest, 30 minutes. The longest period off the nest was 25 minutes, the shortest, 15 minutes. At Tifton, Georgia, Norris and Hopkins (1947:8) observed a female that remained on her nest continuously for nearly four hours. Lawrence (1953:138), summarizing studies of six wood warblers, found that attentiveness ranged from 67 to 83 per cent.

The Pendleton Ferry female, unlike others that I have seen, always sat in the same position when incubating. She left the nest in the same direction but did not always feed in the same area. She fed as far as 75 yards from the nest but usually about 30. She fed both alone and with her mate. On one occasion the male which had not sung for more than an hour flew to within 50 feet of the nest and sang two songs. The female *chipped,* left the nest, and the two flew off together to feed. Sometimes on leaving the nest the female flew out to about 30 yards from the nest where she *chipped* several times presumably to attract the male. Upon returning to the vicinity of the nest the female invariably *chipped* two or three times just before settling down on the nest.

A female in the Dismal Swamp was often fed by her mate when she left her nest during the incubation period. She would follow the male on the ground like a fledgling following its parent. The male, moving about with cocked tail, would gather food and present it to her.

During the several days of my observations, the Pendleton Ferry male never visited the nest. He did not come closer than 40 feet, and usually stayed more than 100 feet distant. However, Norris and Hopkins (1947:8) and Sims and DeGarmo (1948:5) reported males visiting incubating females at the nest. At dusk the male was usually seen closer to the nest (40–50 feet) than during the lighter part of the day. He fed and sang in all areas surrounding the nest. He did not sing as much as an unmated male in an adjacent territory.

CARE OF YOUNG

My information on the care and feeding of nestlings is based on observations made during a 7-hour period in the Dismal Swamp on 7 July 1967.

Between 09:45 and 16:45 the 3-day old nestlings were fed 14 times, eight by the male and six by the female. The intervals between feedings ranged from 9 to 59 minutes.

The female was at the nest 53 per cent of the time brooding the young and sometimes standing on the rim. If she was brooding when the male came to the nest she would move to the rim while he fed the young. Of this pair only the male removed fecal sacs from the nest; however, at a Macon, Georgia, nest, the female also removed fecal sacs, sometimes by swallowing them.

The male always approached from the same direction and worked his way slowly through the undergrowth until he was 2–3 feet beneath the nest, then he hopped up to the rim. The female approached from various directions, and flew directly to the rim of the nest from 20–30 feet out. On three occasions the male and female departed from the nest at the same time. Each time they flew in different directions.

Sims and DeGarmo (1948:5) found that at several West Virginia nests, young left after 10 days. At Augusta, Georgia, the young remained 12 or more days (Griscom and Sprunt 1957:53). Young that I observed at Macon, Georgia, fledged at 10 days.

Fledglings of another Dismal Swamp brood, just two days out of the nest, were fed only by the female during my two days of observation. The male was usually within 100 feet of the young, and sang much of the time.

On three occasions, just as the female was about to feed one of the fledglings, the male pounced on her.

DISCUSSION

Nesting success for this species appears to be low. Of 15 nests for which I have complete records, only 5 were successful. Sims and DeGarmo (1948:5) reported only 6 of 18 nests as successful.

Of the several factors working against nesting success, three appear to be most important. One is the vulnerability of the Swainson's Warbler's poorly concealed nest, which is placed close to the ground and contains white eggs. Other breeding parulids that nest in similar habitats, the Black and White Warbler (*Mniotilta varia*), Worm-eating Warbler, Ovenbird, Louisiana Waterthrush (*Seiurus motacilla*), Kentucky Warbler (*Oporornis formosus*), and Hooded Warbler (*Wilsonia citrina*) have speckled eggs and usually conceal their nests better.

The large bulky nest of the Swainson's Warbler, constructed mostly of leaves, apparently is quite suitable as a home for the wood mouse (*Peromyscus* sp.). I have known of several new Swainson's Warbler nests taken over by mice during the egg-laying stage. However, I do not know whether the birds deserted their nests prior to or because of the presence of mice. Legg (1946:25) also noted evidence (scats) of mouse use of a deserted Swainson's Warbler nest.

In another paper (Meanley, 1966:164) I mentioned the effects of flooding on Swainson's Warbler productivity during the nesting season in floodplain forests of the Atlantic Coastal Plain.

And the Swainson's Warbler may have an even greater time maintaining its numbers as the Cowbird continues to extend its breeding range farther into that of the Swainson's Warbler (Webb and Wetherbee, 1960).

SUMMARY

The Swainson's Warbler is one of the least known of southern birds. Although fairly common in some parts of its summer range, observations of its breeding biology have been made by very few persons. The present study was conducted mostly at Macon, Georgia; Pendleton Ferry, Arkansas; and Dismal Swamp, Virginia.

In central Georgia and east-central Arkansas, Swainson's Warblers usually arrive on their territories during the first two weeks in April. Territories in several localities ranged in size from 0.3 to 4.8 acres. A color-marked Arkansas male occupied the same territory for at least four months. Hostile encounters between territorial male Swainson's Warblers usually take place along the boundary of adjacent territories. Paired males were more aggressive than unpaired males. Toward the end of an encounter one of the two males would usually perform a display in which the wing and tail feathers were spread and the tail vibrated. Following boundary encounters males drifted back onto their territories and usually sang unbroken courses of songs for several minutes.

During pre-nesting at Macon, a mated pair spent the day mostly on the ground within 20 feet of each other, often foraging 3 to 4 feet apart. What may have been a form of courtship display, in which the male flew from a perch down to the female and either pecked her rump or pounced on her, occurred about three times each hour throughout the day. During this period the male sang less than at other times during the breeding season.

First nests are usually built by the first week in May. Although other investigators reported finding nests of this species outside of the defended territory, all nests that I have found were within the territory. The large, bulky nest of this species usually is placed 2–6 feet above the ground. It is built by the female from materials gathered close to the nest site; and takes two or three days to complete.

Three and occasionally four white eggs are laid. The female incubates for 14–15 days. The Cowbird parasitizes nests in some parts of the breeding range of the Swainson's Warbler.

During incubation the female spends about 78 per cent of daylight time on the nest. Both sexes feed young and clean nest. Young remain in nest from 10–12 days.

ACKNOWLEDGMENTS

I am grateful to Dr. Paul A. Stewart of the Agricultural Research Service, U.S. Department of Agriculture, for reviewing the manuscript; and to Mrs. Nancy Coon of the Patuxent Wildlife Research Center for the diagram of the territories.

LITERATURE CITED

Chapman, F. M. 1907. The warblers of North America. D. Appleton Company, New York.

Ficken, M. S. and R. W. Ficken. 1962. The comparative ethology of the wood warblers: a review. Living Birds, 1:103–122.

Griscom, L. and A. Sprunt, Jr., 1957. The warblers of America. Devin-Adair Company, New York.

Howard, H. E. 1929. An introduction to the study of bird behavior. Cambridge University Press, London.

Howell, A. H. 1928. Birds of Alabama. Dept. of Game and Fisheries of Alabama, Montgomery.

Kirn, A. J. 1918. Observations of Swainson's Warbler. Oologist, 35:97–98.

Lawrence, L. DeK. 1953. Notes on the nesting behavior of the Blackburnian Warbler. Wilson Bull., 65:135–144.

Legg, W. C. 1946. Swainson's Warblers' nests in Nicholas County. Redstart, 13:24–25.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Inst. of Science, Bloomfield Hills, Michigan.

Meanley, B. 1966. Some observations on habitats of the Swainson's Warbler. Living Bird, 5:151–165.

Meanley, B. 1968. Singing behavior of the Swainson's Warbler. Wilson Bull., 80:72–77.

Nice, M. M. 1943. Studies in the life history of the Song Sparrow, II. Trans. Linnaean Soc. of New York, 6:1–328.

Norris, R. A. and M. Hopkins, Jr. 1947. The breeding of Swainson's Warbler near Tifton, Georgia. Oriole, 12:7–9.

Perry, T. D. 1886. Nesting of Swainson's Warbler. Ornithol and Ool., 11:188.

Sims, E. and W. R. DeGarmo. 1948. A study of Swainson's Warbler in West Virginia. Redstart, 16:1–8.

Stenger, J. and J. B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull., 71:125–140.

Wayne, A. T. 1910. Birds of South Carolina. Contrib. Charleston (South Carolina) Mus. I.

Webb, J. S. and D. K. Wetherbee. 1960. Southeastern breeding range of the Brown-headed Cowbird. Bird-Banding, 31:83–87.

U.S. DEPARTMENT OF THE INTERIOR, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND. 19 AUGUST 1967.

TOWER-KILLED SPECIMENS AND OBSERVATIONS OF MIGRANT BIRDS FROM GRAND BAHAMA ISLAND

Herbert W. Kale, II, Margaret H. Hundley, and James A. Tucker

From 20 to 24 October 1966 the Florida Audubon Society held its annual leaders' conference near West End, Grand Bahama Island, located approximately 55 miles due east of West Palm Beach, Florida. During this period 137 species of birds were observed, several of which represent new records for the Bahamas and West Indies. On the night of 21–22 October weather conditions caused mortality of migrating birds at the 200-foot TV reception tower on the grounds of the Grand Bahamas Hotel and at the 400-foot U. S. Air Force Missile Tracking System towers located approximately three miles east of West End. The number of species seen in the area and found dead under the towers warrants a brief résumé of the weather patterns and some of our observations.

During 17–20 October a cold front extending from Cape Hatteras across Florida to the Yucatan peninsula gradually moved southeasterly. Prior to its arrival, winds had been light from the east and northeast while prefrontal winds accompanied by showers and thunderstorms ranged from SSE and SW at 10–20 knots. The front passed Grand Bahama at 07:00 on 20 October and was followed by clearing skies and winds from the NW and N at 15–20 knots extending from Hatteras to the Bahamas. Heavy rains fell on south Florida during passage of the front. By midnight on 20 October the front was stationary over Cuba. From midnight on the 20th through late afternoon on the 21st strong northeasterly winds at 15–20 knots blew from Hatteras to the Bahamas. Shortly after noon on 21 October the front began moving slowly northward accompanied by heavy rains. Winds north of the front continued from the northeast at 10–20 knots and gradually shifted westerly by midnight. Heavy rains began falling on Grand Bahama around 19:00 and continued throughout the night, ending shortly before dawn on 22 October. After northward passage of the front, winds were southerly, 5–10 knots, and remained so for the next few days, even though the front again moved southward over the Bahamas on 23 October.

During 20 and 21 October, many birds were observed on the hotel grounds and golf course. The most numerous species by far was the Palm Warbler (*Dendroica palmarum*). A Pigeon Hawk (*Falco columbarius*) was observed to capture and kill several without stopping to eat them. Cape May Warblers (*Dendroica tigrina*), American Redstarts (*Setophaga ruticilla*), and Mourning Doves (*Zenaidura macroura*) were also present in large numbers. While viewing one flock of doves we watched an immature Red-tailed Hawk (*Buteo jamaicensis*) capture one and fly to a utility pole where it plucked and ate it.

TABLE 1

BIRDS FOUND BENEATH TOWERS ON GRAND BAHAMA ISLAND, 22 OCTOBER 1966. (See A.O.U. Check-list, 5th ed., 1957 for scientific names.)

Species	Numbers	
	TV Tower[1]	Tracking Tower[2]
Yellow-billed Cuckoo	1	1
Yellow-bellied Sapsucker	0	1
Eastern Wood Pewee[3]	1	0
Acadian Flycatcher[3]	1	0
Gray-cheeked Thrush[4]	12	27
Red-eyed Vireo	2	2
Black-and-White Warbler	1	4
Parula Warbler	7	7
Magnolia Warbler	0	1
Cape May Warbler	2	9
Black-throated Blue Warbler	1	6
Bay-breasted Warbler	1	0
Blackpoll Warbler[4]	3	18
Palm Warbler	0	1
Ovenbird	1	9
Northern Waterthrush	0	1
Common Yellowthroat	1	4
American Redstart	0	5
Scarlet Tanager[4]	0	1
Bobolink	0	1
Rose-breasted Grosbeak	1	0
Grasshopper Sparrow	0	1
Totals: Number	37	99
Totals: Species	14 spp.	18 spp.

[1] 200-foot TV reception tower on grounds of Grand Bahama Hotel, West End.
[2] 400-foot USAF Missile Tracking System reflecting tower, 3 miles east of West End.
[3] Specimen deposited in American Museum of Natural History.
[4] One specimen kept by H. W. Kale.

During passage of the front on the night of 21–22 October numerous birds were heard calling in the vicinity of the hotel beginning around 22:00, and several warblers were seen fluttering in the glare of the street lamps. The three species of warblers mentioned above were identified visually in the darkness. Numerous birds were calling in the air above the nearby TV tower. Nonflashing red lights were located at the top and at the midway point of this tower. By midnight Kale picked up several exhausted and injured birds —Gray-cheeked Thrush (*Hylocichla minima*), Ovenbird (*Seiurus aurocapillus*), Black-and-White Warbler (*Mniotilta varia*) and Cape May Warbler.

The next morning I. Fritz, Tucker, and Kale searched in the undergrowth surrounding the tower and picked up the birds listed in column 1 of Table 1. Most of these fell on the southwest side of the tower where an extremely dense patch of vegetation probably prevented our finding all the casualties.

Even in the driving rain fire ants quickly found the birds that fell to the ground. By the next morning all dead birds were being eaten by ants and some were partially buried under sand as a result of this activity.

Permission was obtained from Mr. Richard Baden, director of the USAF Missile Tracking Station near West End, to search the grounds beneath the reflecting tower in the afternoon of 22 October. The 400-foot transmitting tower, located about 0.5 mile distant was not checked. The terrain under the reflecting tower is flat and well-mowed, hence dead or injured birds were readily seen. Many of these had already been fed upon by predatory birds. Only heads, wings, tails and legs remained of some birds. Mr. Baden stated that he often saw birds of prey feeding on the grounds after tower kills. Fire ants were numerous and active. Column 2 of Table 1 lists the 99 birds of 18 species we picked up, most of which were found southwest of the tower. Mr. Baden reported that he had seen much larger kills where the grounds were littered with hundreds of dead and injured birds. Predators and ants rapidly removed most of them. Although our search was by no means exhaustive, we found little evidence of any previous kills in the fall of 1966. One Mockingbird (*Mimus polyglottos*) skeleton and fragments of wingbones of two other unidentified passerines were found.

The most numerous species killed at the towers were the Gray-cheeked Thrush and the Blackpoll Warbler (*Dendroica striata*). During this same period Gray-cheeked Thrushes were observed migrating on the Florida mainland, but the Blackpoll which is a rare fall migrant in Florida was not reported anywhere along the southeastern coast from North Carolina to Florida (Audubon Field Notes, 21:19–25, 1967). The land departure point in the migration route of the Blackpoll Warbler has been the subject of some controversy (see Murray, 1966, Dennis, 1965, Baird and Wingate, 1965). Weather maps for 20 October show the cold front extending from the Canadian maritime provinces to Cuba on a line west of Bermuda, thus migrating birds might have left the mid-Atlantic Coast, or the New England Coast, on a flight that would carry them east of the Bahamas, and then been wind-drifted SW as the wind shifted NE during the night. By utilizing the strong tail winds they might still reach Grand Bahama without catabolizing much fat. Although no weights were taken, all of the tower-killed birds were in excellent condition with fat classes (according to the McCabe index, 0–5) estimated to range from 3 to 5. Most of the Blackpolls were in the upper ranges (classes 4 and 5) and were picked up on the southwest quarter of the tower suggesting arrival from a northeast direction. Nevertheless, this does not rule out the possibility, as suggested by Murray, that these birds may have departed from the southeastern coast of the U. S.

On the morning of the 22nd, the grounding effect of the previous night's weather was evident by the large number of migrants observed feeding in the area. Numerous Eastern Wood Pewees (*Contopus virens*) and Catbirds (*Dumetella carolinensis*) had arrived the night before as none had been seen before this time. Several exhausted and weakened birds were found on the hotel grounds during the day—Gray-cheeked Thrush, Blackpoll Warbler, Ovenbird, Palm Warbler. Some of these expired and some were able to recover sufficiently to fly off.

The number of distinctly western species observed during this period (see annotated list below) suggests to us that these birds perhaps arrived on the night of 19–20 October with the front, or on NW winds on the 20th. By 23 and 24 October no new migrants were observed and many of the birds that had been present disappeared. This was made particularly noticeable with the disappearance of most of the Palm Warblers. Throughout the remainder of the week, according to L. S. Hubbard, who remained on Grand Bahama, few migratory birds were seen.

Missile Tracking System towers are located on all of the larger islands of the Bahamas downrange from Cape Kennedy. Undoubtedly nocturnal mortality occurs from time to time at all of them. They offer unique and so far untapped opportunities for studies on birds migrating over these islands.

NEW AND ADDITIONAL RECORDS FOR THE WEST INDIES

White-winged Dove (*Zenaida asiatica*). This species occurs in the southernmost Bahamas and southward according to Bond (1961, 1959–1966), thus a single individual observed feeding in a flock of Mourning Doves on 22 October 1966 is noteworthy. The only other record from Grand Bahama was an observation by Hundley on 14 November 1964.

Rufous Hummingbird (*Selasphorus rufus*). This species has not been recorded anywhere in the West Indies, even though it is of irregular occurrence in Florida as a rare migrant and/or winter visitor. An immature male with rufous color on sides, flanks and back was first sighted by Tucker near the TV tower shortly after dawn on 22 October. This same bird was observed for ten minutes by Kale while it was feeding on flowers in the same area around 08:00. It approached the observer within three or four feet while feeding. An hour later it was watched while feeding by Hundley. We realize that it is possible to confuse the immature of this species with the immature of Allen's Hummingbird (*S. sasin*), but the likelihood of this far western species being present, rather than *S. rufus* is so remote that we feel correct in listing the latter species as a first record for the West Indies.

Sprague's Pipit (*Anthus spragueii*). This species was observed at close range on the golf course by Tucker late in the afternoon of 20 October, and was sighted again the next afternoon in the same area by Kale. Photographs taken by Myron Elliot were examined by James Bond. This is the first record for the species in the West Indies.

Wilson's Warbler (*Wilsonia pusilla*). An adult female or immature bird was observed for several minutes by Kale as it fed in Australian pines (*Casuarina* spp.) near the TV tower on 22 October. It was seen later in the morning in the same area by Kale, Tucker and Mrs. Doris Mager. Bond (op. cit.) lists four records (all in autumn) for the species, three in western Cuba, and one from New Providence.

Scarlet Tanager (*Piranga olivacea*). Bond (op. cit.) considers this species to be a rare transient in the West Indies. One immature male was picked up under the USAF Missile Tracking System tower near West End on 22 October 1966. It had been partially eaten by an avian predator, but the head, wings, tail, and ventral plumage were preserved by Kale. It represents the first record for Grand Bahama Is.

Brown-headed Cowbird (*Molothrus ater*). A single male feeding in a horse paddock was observed by Kale on 21 October 1966. One of the attendants reported that it had been present for several days and often entered the horse stalls. It was seen again on 22 October by Kale, Tucker, and W. Biggs in the same place. Bond (op. cit.) gives records from Cuba and one for New Providence. The present observation is the first record for Grand Bahama Is.

Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). An immature male was seen feeding in a flock of Mourning Doves on the golf course by many observers on 22 October 1966. A photograph taken by L. S. Hubbard was examined by Bond. Bond (op. cit.) lists three autumn records for the species from Cuba and Barbados. A previous record for the Bahamas was a bird seen on Grand Bahama on 16 October 1965 by Hundley and other observers.

Clay-colored Sparrow (*Spizella pallida*). One individual was observed feeding on the lawn of the Grand Bahama Hotel in company with several Palm and Cape May warblers for over 20 minutes on 20 October 1966 by Tucker, Hundley, Kale and others. Bond (op. cit.) lists three specimen records for the West Indies, two from Cuba (26 January, 5 December 1960), and one from New Providence (11 December 1959).

Lincoln's Sparrow (*Melospiza lincolnii*). Three individuals of this species were seen near the TV tower on 22 October 1966, first by Tucker and later by Hundley and Kale. Bond (op. cit.) gives several records for Jamaica, Puerto Rico and Cuba. Other Bahamas records are from Eleuthera by Hundley on 26 November 1964, Harbor Island in late November 1966 and 1967, and on Great Abaco in November 1967 (C. R. Mason, pers. comm.).

SUMMARY

The species composition of birds killed on the night of 21–22 October at towers on Grand Bahama Island is presented with a description of the weather patterns preceding and following frontal passage. Gray-cheeked Thrushes and Blackpoll Warblers comprised almost half of all the birds killed. During this period a large number of migrants passed through the Bahamas, including several western vagrants. An annotated list of new and additional records for the West Indies represented by tower-killed birds or observations made during 20–24 October 1966 is included.

ACKNOWLEDGMENTS

We are grateful to numerous individuals for assistance, especially Mr. Richard Baden, Director of the USAF Missile Tracking System Station, West End, Grand Bahama, for permission to search for birds; Mr. Wesley Biggs for help in collecting dead birds;

Dr. Wesley Lanyon, and Mrs. Roxie Laybourne, for specimen determinations; Mr. Edward Manak, Hurricane Forecast Center ESSA, U. S. Dept. of Commerce, Miami, Florida, for assistance in obtaining weather data; and Mr. James Bond, Dr. William B. Robertson and Dr. Glen E. Woolfenden for comments and suggestions during preparation of the manuscript. This research was supported in part by the Florida Audubon Society and NIH Grant AI-06587 to the Florida State Board of Health.

LITERATURE CITED

BAIRD, J., AND D. B. WINGATE. 1965. Blackpoll Warbler banded in Bermuda recovered in North Carolina. Bird-Banding, 36:192.

BOND, J. 1959[66]. Fourth [to Eleventh] supplement to the Check-list of Birds of the West Indies. 1956. Acad. Nat. Sci., Philadelphia.

BOND, J. 1961. Birds of the West Indies. Houghton Mifflin Co., Boston.

DENNIS, J. V. 1965. The Blackpoll Warbler in fall on Nantucket. EBBA News, 28: 175–178.

MURRAY, B. G., JR. 1965. On the autumn migration of the Blackpoll Warbler. Wilson Bull., 77:122–133.

ENTOMOLOGICAL RESEARCH CENTER, VERO BEACH, FLORIDA 32960; P. O. BOX 158, STONINGTON, MAINE 04681; AND 2912 WEST AVENUE, AUSTIN, TEXAS 78705. 15 FEBRUARY 1968.

ANNOUNCEMENT

The Manomet Bird Observatory, situated on a Massachusetts sea cliff overlooking Cape Cod Bay, began fulltime operation in August, 1969 as the first permanent observatory on the Atlantic Coast of North America. The observatory will offer facilities where scientists and amateur naturalists can investigate environmental biological problems with emphasis upon banding and ornithological studies.

In addition to the research program, the MBO will serve as a training center for banders and will provide opportunities for young people to observe and participate in ornithological research.

The Manomet Bird Observatory begins operation with a valuable backlog of records on both passerines and migrant seafowl. Operating as an "Operation Recovery" station for the past three autumns, approximately 7800 birds of 101 species have already been netted and banded. All birds are weighed and measured in accordance with Operation Recovery procedures and ectoparasites are routinely collected. A regular "Seawatch" from Manomet Point has produced worthwhile information on autumnal seafowl flights and will be continued.

Facilities and living quarters at the observatory will be available to qualified researchers and volunteer helpers, upon prior arrangement with the Director. Those seeking more information about the program and about membership in the Manomet Bird Observatory should write to the Director, Manomet Bird Observatory, Manomet, Massachusetts 02345.

OBSERVATIONS OF BIRDS EXPLOITING A CENTRAL AMERICAN FRUIT TREE

Charles F. Leck

Skutch (1954, 1960) provides some general information about the diets of various common Central American birds, but except for brief observational notes (Diamond and Terborgh, 1967, Land, 1963, Leck and Hilty, 1968, and Willis, 1966), comparatively little is known about the avian utilization of particular species of native trees. This study was undertaken to outline the exploitation of a single fruit tree in Costa Rica.

METHODS

This study was carried out in a disturbed river bottom forest along the Rio Higueron on the Finca Jimenez, near Cañas, Guanacaste Province, N. W. Costa Rica. This is a region of savanna and dry forest. An individual tree was studied from 11–15 July 1967, for a total of 16 hours between 06:00 and 11:00. Data gathered included the methods of feeding, daily arrival times, aggressive behavior (intra- and interspecific), and frequency of exploitation.

The tree selected was *Trichilia cuneata* (Family Meliaceae), a typical tropical fruit tree with conspicuous bird-attracting fruits. This species is found in thickets and forests from Guatemala to Panama (Standley, 1937:583). Its dehiscent fruits are about one centimeter in diameter, and each contains several soft green seeds. The pericarp is orange and cartilaginous, while the endocarp, which is exposed in the ripe fruit, is bright orange-red. The study tree (approximately 10 m tall with an ovoid crown) was suitable because its small size permitted me to record the total number of birds feeding in it.

RESULTS AND DISCUSSION

Frequency of visitations.—The number of individual visits for each species recorded in the 16 hours of observation is given below. Actual feeding on the fruit was observed for all species except those marked by an "O". The two most common species (marked with an asterisk) were present throughout most of the observation periods, and were not seen to make distinct trips to and from the tree. (The names are those used by Eisenmann, 1955).

Citreoline Trogon (*Trogon citreolus*)—15
Golden-fronted Woodpecker (*Centurus aurifrons*)—*
O Streak-headed Woodcreeper (*Lepidocolaptes souleyetii*)—1
Masked Tityra (*Tityra semifasciata*)—21
Long-tailed Manakin (*Chiroxiphia linearis*)—35
O Piratic Flycatcher (*Legatus leucophaius*)—1.
Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*)—5
Streaked Flycatcher (*Myiodynastes maculatus*)—13
Boat-billed Flycatcher (*Megarhynchus pitangua*)—7
Social Flycatcher (*Myiozetetes similis*)—3

O Greenish Elaenia (*Myiopagis viridicata*)—5
Magpie Jay (*Calocitta formosa*)—6
O Rufous-and-White Wren (*Thryothorus rufalbus*)—2
O Clay-colored Robin (*Turdus grayi*)—3
Yellow-green Vireo (*Vireo flavoviridis*)—*
Red-legged Honeycreeper (*Cyanerpes cyaneus*)—24

It is important in such studies to indicate (as was done by Land, 1963) the species actually seen feeding on fruits, for one cannot assume that all the visiting birds are eating the fruit. Some species may come to feed on the insects associated with the fruits (e.g. *Drosophila*), rather than the fruit itself. Other species may simply be attracted to the assemblages, and yet not actually be involved in feeding at the tree. Some observations I made on an *Apeiba tibourbou* (tree) which was *not* in fruit are relevant here. In five mornings of observation, I recorded 95 visits by 17 species of birds representing 10 families (S.W. Costa Rica, 7–11 August 1967). If the same species make similar visits to the tree while it is in fruit, assumptions concerning the use of the tree as a food resource could be erroneous. Thus, the interesting study by Diamond and Terborgh (1967), which lists species "assembled for the purpose of feeding" in two fruiting trees, would have been more valuable if they had indicated which species were actually seen feeding on the fruits.

It should be noted that a woodpecker, *Centurus aurifrons*, was one of the two most frequent visitors to the tree. Land (1963) found that another species of woodpecker, *Centurus pucherani*, was the most common visitor to a *Miconia* tree in Guatemala, and he was able to observe it eating fruits. In addition, Otvos (1967) has reported varying amounts of fruit eating in the several species of *Centurus* he studied in Costa Rica. The quantities of fruit in the diets of such woodpeckers, as well as many flycatchers, suggest that birds may have rather flexible feeding habits in the tropics (Diamond and Terborgh, 1967), and this should have interesting ecological implications, particularly with regard to niche sizes.

Among the nineteen other species which Land (1963) saw feeding on *Miconia* fruit, there are eight additional genera which I observed in this study: *Trogon, Tityra, Myiodynastes, Megarhynchus, Pitangus, Turdus, Tangara*, and *Thraupis*. The last three genera were also recorded by Willis (1966), while *Trogon* and *Tityra* were listed by Diamond and Terborgh (1967) in fruiting trees whose identity was not reported. It would be of interest to determine seasonal and geographical variations in the extent of fruit eating in such genera. For example, I have found that *Myiodynastes, Megarhynchus*, and *Myiozetetes* (all tyrannids) take significantly more berries in the dry season than during the latter part of the wet season, at

Barro Colorado Island, Canal Zone. This change is apparently correlated with the increased fruit abundance in the dry season.

Methods of feeding.—Two general types of feeding behavior were distinguished: (For species which use both methods, an asterisk indicates which method was used most frequently.) (1.) Species which capture fruit in a "flycatcher" fashion. The bird flies from a perch, takes the berry while in flight, and returns to the perch. Yellow-green Vireo, Citreoline Trogon, Boat-billed Flycatcher, Masked Tityra, Social Flycatcher, Sulphur-bellied Flycatcher, Streaked Flycatcher*, and Long-tailed Manakin*. (2.) Species which perched near the fruit and removed the berry from the pericarp while perched. Yellow-green Vireo*, Masked Tityra*, Golden-fronted Woodpecker, Red-legged Honeycreeper, Magpie Jay, Streaked Flycatcher, and Long-tailed Manakin.

The Boat-billed Flycatcher and the Magpie Jay both showed variations from these general methods of obtaining the berries. The flycatcher would occasionally take entire fruits and remove the pericarp by beating the fruit against the perch. Skutch (1960:353) recorded a similar behavior for this species when it feeds on cicadas. However this species most frequently obtained fruits in a typical flycatching fashion. The one Magpie Jay held a fruit against a branch with its foot, and pecked at the pericarp until the berry was removed. Parrots and toucans will also use their feet in fruit manipulation while feeding.

Numbers of birds.—Only seven of the sixteen species were ever observed to be represented by more than one individual at a given time. My observations agree with those of Diamond and Terborgh (1967) who state that "birds arrived at and left . . . fruiting trees as individuals or else as groups of several individuals belonging to one species." The pattern of visitation of the seven species represented by more than one individual was as follows:

Citreoline Trogon—at the tree daily; two birds present together on two mornings, single individuals on the other mornings.

Golden-fronted Woodpecker—daily; usually several (1 male, 1 female, and an immature) visited the tree simultaneously.

Masked Tityra—daily; often two birds, although individual visits were also common.

Long-tailed Manakin—daily; generally a male and female together, sometimes a second male also present.

Magpie Jay—present only on 12 July, when a group of six invaded the tree for a short period.

Yellow-green Vireo—daily; usually several present, although single birds sometimes noted.

Red-legged Honeycreeper—daily; most frequently a male-female pair; on one morning a second male was also present.

TABLE 1

TOTAL NUMBERS OF SPECIES AND INDIVIDUALS VISITING THE TREE

	11 July	12 July	13 July	14 July	15 July
Number of species each morning	9	12	11	10	11
Number of individuals each morning	17	26	18	17	20

The total numbers of species and individuals utilizing the tree were quite similar on each of the five mornings of observation (Table 1). This might indicate that a given fruit tree is usually a food source for "local" birds only. Exceptions would include flocking species which tend to wander over large areas, such as the Magpie Jay, or solitary species which are highly mobile, such as the Mountain Elaenia (*Elaenia frantzii*) (Leck and Hilty, 1968). Thus, while the problem of competitive exclusion, as considered by Willis (1966), was not resolved, it seems that the fruit tree has specific limitations on the numbers of species and individuals using it imposed by spatial factors, in addition to factors inherent in the tree itself.

Aggressive behavior.—Table 2 summarizes the encounters observed. There were more cases of intraspecific (10) than interspecific (7) aggression. Since the encounters seldom caused the supplanted individual to leave the tree or to stop feeding, they apparently do not effectively reduce the competition which might exist, unless they significantly reduce the feeding *rates*. The intraspecific aggression may be based on individual territoriality, but further study is needed to clarify the basis of this behavior. Moynihan

TABLE 2

AGGRESSIVE ENCOUNTERS RECORDED AT THE TREE

Aggressor	Supplanted Species	No. of Records
Golden-fronted Woodpecker	Streaked Flycatcher	3
Golden-fronted Woodpecker	Yellow-green Vireo	1
Golden-fronted Woodpecker	Rufous-and-White Wren	1
Golden-fronted Woodpecker	Red-legged Honeycreeper	1
Golden-fronted Woodpecker	Sulphur-bellied Flycatcher	1
Golden-fronted Woodpecker	Golden-fronted Woodpecker	1
Yellow-green Vireo	Yellow-green Vireo	5
Streaked Flycatcher	Streaked Flycatcher	2
Citreoline Trogon	Citreoline Trogon	2

(1962) has provided some discussion on the role of supplanting attacks in the social behavior of coerebids and tanagers, from studies in Panama.

Daily arrival times.—Most species arrived shortly after sunrise. Ten species made their first arrival at the tree between 06:00 and 07:00, three species between 07:00 and 08:00, and three species after 08:00 (these late species were the Rufous-and-White Wren, Clay-colored Robin, and Streak-headed Woodcreeper). Activity was relatively constant each morning until about 09:00, when a rapid decline in the number of species at the tree was noted, and after 09:30 there was very little activity.

The pattern of early feeding may simply reflect a physiological need to eat as soon as activities are undertaken in the morning, and a general avoidance of activity during the warmer hours of the day. The fact that the various species feed more or less simultaneously may also indicate that there is a lack of competition for the fruits. My more recent studies in Panama have indicated that fruits are in fact often superabundant, with productivity far greater than utilization. If however the fruits are sometimes a limited resource, best available (i.e. in quantity and quality) in the early morning, then competition could also produce the observed early morning exploitation pattern. When such competition occurs, there is usually little or no "fruit fall" on the ground, and the fruits are eaten before they are ripe.

Additional notes.—In the same tree I studied, Dr. Arnold Small observed 12 species, including a Plain Xenops (*Xenops minutus*) and a Scrub Euphonia (*Tanagra affinis*). On another *Trichilia cuneata* in the same area, Dr. Small saw several Collared Araçari (*Pteroglossus torquatus*) eating, and I recorded feeding by a Kiskadee Flycatcher (*Pitangus sulphuratus*).

SUMMARY

A tropical fruit tree in the family Meliaceae was observed to be visited by 16 species of birds, representing 11 families. Of these, 11 species were actually observed feeding on the fruit; and two general methods of feeding were noted. A variety of intra- and interspecific aggressive interactions were recorded. Most species arrived before 07:00. The species exploiting the tree most frequently included a woodpecker, a manakin, and a vireo.

ACKNOWLEDGMENTS

This study was conducted while I was a participant in a tropical biology course with the Organization for Tropical Studies, which is supported in part by the National Science Foundation.

The Botany Department of the University of Costa Rica kindly verified the identification of the fruit tree. Dr. Arnold Small offered helpful suggestions during the field work, and Dr. Larry Wolf aided me in distinguishing the rather similar *Myiodynastes luteiventris* and *M. maculatus.* Drs. Stephen T. Emlen, Richard B. Root, Daniel H. Janzen, and Harrison B. Tordoff each provided constructive criticism during the various stages of preparation of this article.

LITERATURE CITED

DIAMOND, J. M. AND J. W. TERBORGH. 1967. Observations on bird distribution and feeding assemblages along the Rio Callaria, Department of Loreto, Peru. Wilson Bull., 79:273-282.

EISENMANN, E. 1955. The species of Middle American birds. Trans. Linnaean Soc., New York :7.

LAND, H. C. 1963. A tropical feeding tree. Wilson Bull., 75:199–200.

LECK, C. F. AND S. HILTY. 1968. A feeding congregation of local and migratory birds in the mountains of Panamá. Bird-Banding, 34:318.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll.:143.

OTVOS, I. S. 1967. Observations on the feeding habits of some woodpeckers and woodcreepers in Costa Rica. Condor, 69:522–525.

SKUTCH, A. F. 1954. Life histories of Central American birds. Pacific Coast Avifauna:31.

SKUTCH, A. F. 1960. Life histories of Central American birds (II). Pacific Coast Avifauna:34.

STANDLEY, P. C. 1937. The flora of Costa Rica (Part II). Field Mus. Nat. Hist., Chicago, Botanical Series:18.

WILLIS, E. O. 1966. Competitive exclusion and birds at fruiting trees in western Colombia. Auk, 83:479–480.

NEUROBIOLOGY & BEHAVIOR, LANGMUIR LABORATORY, CORNELL UNIVERSITY RESEARCH PARK, ITHACA, NEW YORK, 15 NOVEMBER 1967.

ANNOUNCEMENT

A study is being conducted to determine the migration routes of Bald Eagles breeding in Minnesota and Bald Eagles wintering in South Dakota. Both immature and mature birds have been color-marked yellow, green, turquoise, or in combination. Information desired: color and portion of wing or tail that is marked, date of sighting, location, and activity of the bird. Exact time of sighting and name of person making the observation is also necessary. Send information to: Thomas C. Dunstan, Dept. of Biology, Univ. of South Dakota, Vermillion, South Dakota 57069.

ORAL FLANGES OF JUVENILE BIRDS

George A. Clark, Jr.

In the pre- and posthatching development of birds a number of structural features are present for only a relatively short time. Such traits, particularly prominent externally, may have significance in aging birds, as taxonomic characters, and as subjects for the study of adaptation. Examples of transitory structures which have recently been studied are natal plumages (cf. Clark, 1964) and egg teeth (Parkes and Clark, 1964).

In this paper I review the occurrence, variations, and possible taxonomic significance of the transitory enlarged flanges of the bill bordering the mouth in juveniles of nidicolous birds. This inquiry was undertaken to determine whether or not the marked differences in form of flanges might be of taxonomic significance. A summary of this topic is believed of potential value, particularly to call attention to the many major gaps in available information.

A problem in studying transitory characteristics is obtaining a suitable series of developmental stages of living juveniles or preserved specimens. Many of the available records for flanges are based unfortunately on study of only one or a few stages, not necessarily those most informative. Interpretations based on samples covering only a limited range of ages should be made cautiously as illustrated below in the discussion of flanges in the Mockingbird (*Mimus polyglottos*).

SOURCES OF DATA

Selected specimens were examined in the collections of the United States National Museum (Washington, D. C.), the American Museum of Natural History (New York), and the University of Connecticut (Storrs). In addition, a number of live juveniles have been observed, and a few of these photographed. Furthermore, numerous books and journal articles were checked for information on flanges. No attempt has been made, however, to cite all references mentioning or figuring flanges.

GENERAL COMMENTS

At least two rather distinct kinds of enlarged flanges are known to occur in juveniles. In the form found in woodpeckers and wrynecks, the major enlargement of the flanges is primarily on the lower jaw instead of being distributed around the corner of the gape as in passerines (see Fig. 1). In both woodpeckers and passerines, the flange is probably detectable before hatching, reaches its maximal relative development during early posthatching growth, and then regresses during the latter part of the nestling period. Presence of a flange is thus generally indicative of a young bird, although adult birds of a relatively few species have various kinds

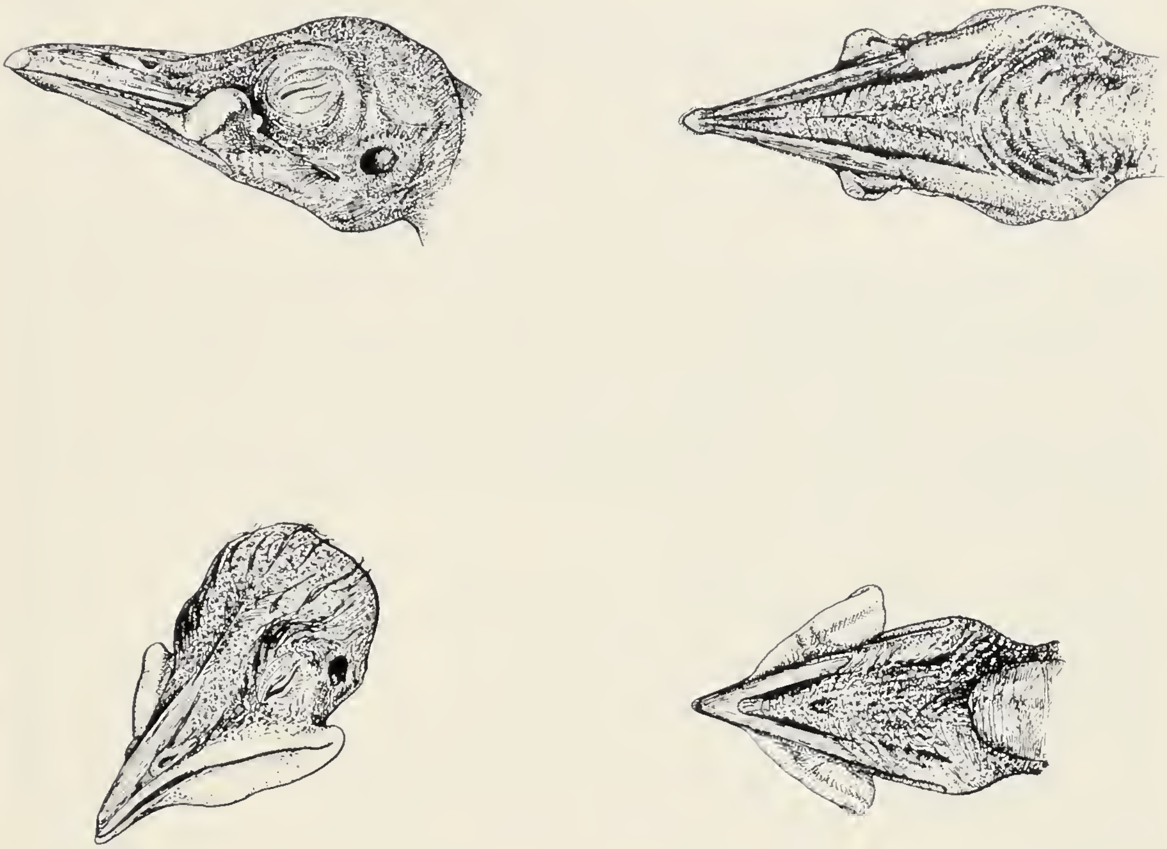


FIG. 1. Juvenile oral flanges of a flicker (*Colaptes* sp.; top) and a Starling (*Sturnus vulgaris;* bottom.)

of flaps along the gape (see Wackernagel, 1954, for some examples, and also the discussion below under Callaeidae).

The structural difference between the passerine and woodpecker flanges is perhaps correlated with a functional difference. Blume (1961) has noted for the Black Woodpecker (*Dryocopus martius*) that the stimulus for the young juvenile to accept regurgitated food is the parental touching of the bill pad or flange. Kilham (1962:131) mentioned for young Downy Woodpeckers (*Dendrocopos pubescens*) that "one method of feeding these nestlings was to approach from the side, brushing the fleshy knob at the base of the bill with a bit of food impaled on a toothpick. The young would open their bills and swallow the food readily." However, as pointed out by Schifter (1967), Hoyt (1944) observed that begging occurs in very young Pileated Woodpeckers (*Dryocopus pileatus*) without tactile stimulation. Possibly these apparently contradictory findings can be resolved by considering tactile stimulation as only one of the means by which young woodpeckers may be induced to open their bills. It is possible that the flanges of woodpeckers do have greater tactile sensitivity than those of passerines, for Dewar (1908) found that touching the flanges of a six-day old Sky

Lark (*Alauda arvensis*) elicited no response. Similarly I noted that rubbing the flanges with a plant stem failed to produce gaping in two Traill's Flycatchers (*Empidonax traillii*) held in my hand on their second or third day after hatching.

Wackernagel (1954) studied the histology of both woodpecker and passerine flanges and found, in general, a relatively low concentration of sensory Herbst corpuscles. He suggested that any differences in sensitivities should be based on differences in the finer nerve endings which have not yet been critically studied. As Wackernagel pointed out, definitive conclusions on the function of flanges must await experimental evidence. Statements attributing great tactile sensitivity to passerine flanges (cf. Welty, 1962: captions of Figs. 17.9 and 17.21) are at best questionable in the absence of experimental evidence.

In another kind of functional interpretation Dewar (1908) proposed that the passerine flanges help to keep food from slipping outside the nestling's mouth during feeding by an adult.

More common has been the suggestion that the lightly colored flanges serve as outlines of the opened juvenile mouth to guide the adult in feeding young (Butler, 1916; Swynnerton, 1916; Wackernagel, 1954; Armstrong, 1965). This idea is supported by the tendency for hole-nesting species to develop relatively larger flanges, as Ingram (1907) and Wackernagel (1954) have found for European passerines and as is apparently also the case for North American species (see below). To the human observer looking into a darkened nest hole, such as that of the Tree Swallow (*Iridoprocne bicolor*), the juvenile flanges may appear as one of the most conspicuous objects. By analogy, an adult bird moving rapidly from the bright exterior into the darkened nest chamber without time for dark adaptation might be significantly aided in feeding the young by the bright outline of flanges.

The greatly enlarged flanges of the kind found in hole-nesting passerines can probably be considered as another example in the list of special adaptations often associated with hole-nesting in birds (von Haartman, 1957). It appears probable that there has been much convergent evolution in the development of flanges, but present information is too limited to determine which similarities of different taxa are due to convergence.

SYSTEMATIC ACCOUNT

The ordinal and familial classification followed here is that of Wetmore (1960). There are apparently no records of conspicuously developed oral flanges in orders Sphenisciformes through Psittaciformes of Wetmore's checklist; however, juveniles of a number of species included within these orders do show a fold of skin at the corner of the mouth, perhaps homologous to the oral flanges of passerines. I have observed such folds on juveniles of the genera *Ciconia, Buteo, Circus, Falco, Actitis,* and *Rynchops* (see also Wackernagel, 1954, on *Vanellus*).

Detailed data on nestlings are needed especially for Psittacidae, Trochilidae, Trogonidae, Momotidae, Bucerotidae, Galbulidae, Bucconidae, Capitonidae, and Ramphastidae.

Cuculidae.—Murphy and Amadon (1953: Fig. 41) published a photograph which may be interpreted as showing a slight degree of flange enlargement in juvenile *Coccyzus americanus.* The presence of passerine-like flanges in *Cuculus micropterus* is indicated by the lower photograph in Plate 1 of Neufeldt (1966).

Strigidae.—On a downy *Otus asio,* I noted a weakly developed fold about the base of the mouth opening. There is no evidence known to me for special enlargement of flanges in this family.

Steatornithidae.—Ingram (1958) reported no conspicuous enlargement of the gape in *Steatornis* nestlings.

Apodidae.—I have seen moderately developed flanges on a study skin of juvenile *Apus apus.* Moreau (1942) and Wetherbee (1961*a*) have noted the absence of such flanges at hatching in *Micropus* (*Apus*) *caffer* and *Chaetura pelagica* respectively. Flanges probably occur on older specimens, for these appear to be shown in a photograph of juvenile *Chaetura pelagica* published by Fischer (1958: Fig. 19).

Coliidae.—Schifter (1967) has studied in detail the external development of three species of this family. In *Colius macrourus* and *C. indicus* he found flanges which at least superficially resemble those of woodpeckers; however, the enlargements on the lower mandible are, as he noted, longer and less spherical in outline in the colies. It is curious that such enlargements of the lower mandible do not occur in *C. striatus* (Schifter, 1967).

Todidae.—No flanges were detected by me on three young specimens of *Todus subulatus.* This family needs additional study.

Meropidae.—Witherby et al. (1938:265) have reported that the flanges of juvenile *Merops apiaster* are very small and inconspicuous.

Coraciidae.—Wackernagel (1954) has reported that flanges generally resembling those of passerines occur in *Coracius garrulus* and this interpretation is well supported by photographs published by von Frisch (1966:46).

Upupidae.—Witherby et al. (1938:268) stated for juvenile *Upupa epops* that the flanges are large, thick, and conspicuous. Wackernagel (1954) has noted in addition that these flanges are structurally like those of passerines.

Indicatoridae.—There is little available information on the status of flanges in honeyguides. I noted a weakly developed fold on very young *Indicator indicator.* Friedmann (1955:209–210) cited Ranger to the effect that in *I. minor* there is some enlargement of the colored corners of the gape from the 26th to the 35th days posthatching and that this enlargement is absent at hatching.

Schifter (1967) has apparently interpreted the photographs in Friedmann (1955) as showing that honeyguides have woodpecker-like flanges; however, in these published photographs I have been unable to convince myself that Schifter's interpretation is necessarily correct.

Picidae.—This family, containing the woodpeckers and wrynecks, is the only one placed by Wetmore (1960) in his suborder Pici. As already noted, the woodpeckers

TABLE 1

SOME RECORDS OF ORAL FLANGES OF PICIDAE

Species	Sources of record
Jynx torquilla	Barruel, 1954:133 (photographs).
Colaptes auratus	Brewster, 1893; Burns cited by Bent, 1939:276; Wetherbee and Wetherbee, 1961.
Chrysoptilus melanochloros	This study.
Picus viridis	Witherby et al., 1938:280, after Gurney; Blume, 1961.
Picus canus	Wackernagel, 1954.
Dryocopus martius	Blume, 1961.
Dryocopus pileatus	Hoyt, 1944:377, 380.
Centurus carolinus	Kilham, 1961.
Dendrocopos major	Blume, 1961.
Dendrocopos villosus	Bendire cited by Bent, 1939:16.
Dendrocopos pubescens	Kilham, 1962.
Picoides tridactylus	This study.
Picoides arcticus	Bates cited by Forbush, 1927:272.

and wrynecks have an unusual form of mouth flange thus far unreported for any other group except possibly the colies. It would be of great interest to know definitely whether this kind of bill "knob" occurs in any additional groups outside the suborder Pici.

Figure 1 illustrates the condition of this flange in *Colaptes* sp. Table 1 presents a list of woodpecker species for which a similar flange has been reported or illustrated. In general, it appears that the flange of woodpeckers is much reduced by the time the young leave the nest as observed by me for *Colaptes auratus* and reported in the literature for *Picoides arcticus* (Forbush, 1927:272, after Bates) and *Dryocopus pileatus* (Hoyt, 1944).

Wetherbee and Wetherbee (1961:148) observed the form of the bill flange in *Colaptes auratus* and suggested that the presence of maximal enlargement of the flange on the lower jaw might be developmentally associated with the prognathus condition of the lower jaw. However, protruding lower mandibles have also been reported for newly hatched young of a number of other avian families (kingfishers, jacamars, toucans, barbets, hoopoes; cf. Skutch, 1944*a*, *b*; Skead, 1950) for which there is no report of a woodpecker-like flange. Indeed, Hoopoes (*Upupa*) are reported to have a passerine-like flange (Wackernagel, 1954).

Passeriformes.—Table 2 lists those passerine species for which I have seen flanges. These represent 17 of the 70 passerine families listed by Wetmore (1960). In addition, there are numerous literature reports and illustrations indicating the presence of these flanges in other species and families (cf. Swynnerton, 1916; Wackernagel, 1954). It appears likely that flanges occur throughout the passerines; any exception to this generalization would be quite unexpected.

Ficken (1965) surveyed the color of the mouth linings and found inter-

Table 2

Passerine Species for which the Author has seen Flanges on Living (*) or Preserved Specimens

- Tyrannidae
  - *Muscivora forficata*
  - *Sayornis phoebe* *
  - *Empidonax traillii* *
- Hirundinidae
  - *Iridoprocne bicolor* *
  - *Riparia riparia*
  - *Stelgidopteryx ruficollis*
  - *Progne subis*
- Corvidae
  - *Cyanocitta cristata* *
  - *Corvus corax*
  - *Corvus brachyrhynchos*
  - *Corvus ossifragus*
- Grallinidae
  - *Corcorax melanorhamphus* *
- Paridae
  - *Parus atricristatus*
- Cinclidae
  - *Cinclus mexicanus*
- Troglodytidae
  - *Troglodytes aedon* *
  - *Telmatodytes palustris*
- Mimidae
  - *Dumetella carolinensis*
  - *Toxostoma rufum*
- Turdidae
  - *Turdus migratorius* *
  - *Hylocichla mustelina*
  - *Sialia sialis*
- Muscicapidae
  - *Colluricincla harmonica*
  - *Myiagra freycineti*
  - *Panurus biarmicus*
- Bombycillidae
  - *Bombycilla cedrorum*
- Sturnidae
  - *Sturnus vulgaris* *
- Vireonidae
  - *Vireo olivaceus*
  - *Vireo gilvus*
- Parulidae
  - *Limnothlypis swainsonii*
  - *Vermivora* sp.
  - *Dendroica petechia*
  - *Seiurus motacilla*
  - *Wilsonia canadensis*
- Ploceidae
  - *Passer domesticus*
- Icteridae
  - *Sturnella neglecta*
  - *Agelaius phoeniceus* *
  - *Icterus galbula*
- Fringillidae
  - *Pheucticus ludovicianus*
  - *Pipilo erythrophthalmus*
  - *Spizella passerina* *

esting correlations with commonly recognized taxonomic groupings in the passerines. It is perhaps significant that, according to Ficken's data, yellow mouth linings occur in those families which are commonly hole or cavity nesters, e.g., Hirundinidae, Paridae, Certhiidae, Cinclidae, Troglodytidae, and Sturnidae. Presumably a yellow mouth lining would appear brighter than a red one in a darkened cavity. In addition, it may be noted that at least two species of hole-nesting Sittidae, not listed by Ficken, also have yellow mouth linings (Norris, 1958:227).

Variations in the color of the passerine flanges are not reviewed in detail here, but, in general, the flanges have a light color, often yellow, white, or cream-colored. However, in *Prunella modularis* the flanges are pink (Romanoff, 1960). In those groups having young with red mouth linings, there is apparently typically a marked contrast between the lighter flange color and the interior of the mouth as seen, for example, in nestling Red-winged Blackbirds (*Agelaius phoeniceus*).

In many passerines the degree of maximal development of the flanges appears to be, at least qualitatively, related more to nest site than to taxonomic position. On the basis of present information it appears that degree of temporary enlargement of flanges will not be especially useful in the classification of passerine families.

The following comments are restricted to those families containing species with especially marked development of the flanges or for which unusually detailed observations have been reported in the literature.

Corvidae.—Ingram (1920:864 and Fig. 10) reported that *Corvus monedula*, the only British corvid which nests in holes, has flanges which are relatively larger than those of other British corvids.

Paridae.—Wackernagel (1954) has presented measurements for the growth and regression of the flanges in nestling *Parus major.*

Sittidae.—Norris (1958:226–227, 230, 291) reported that nestlings of *Sitta pygmaea* have broader and more conspicuous flanges than do the young of the similar species *S. pusilla.* This difference was presumed to be adaptive in association with the deeper and darker nest cavities of *S. pygmaea.* This case, like that reported by Schifter (1967) for colies, is particularly interesting in illustrating a substantial divergence in the early phases of ontogeny of species which are rather similar as adults.

Mimidae.—Wetherbee (1961*b*) observed that the newly hatched Mockingbird (*Mimus polyglottos*) has flanges as large as those of the newly hatched Starling (*Sturnus vulgaris*). Partly on this basis he argued against the generalization that hole-nesting birds tend to have relatively larger flanges. However, relative size of flanges at hatching apparently does not indicate the maximal degree of development, for the illustrations of Horwich (1966) indicate that maximal relative size of flanges in Mockingbirds is far less than that in the Starling (see below).

Turdidae.—Wackernagel (1954) published measurements covering flange development in *Turdus merula.*

Sylviidae.—Wackernagel (1954) has also reported measurements for young *Acrocephalus scirpaceus* in which the flanges attain maximal relative development about six days after hatching.

Callaeidae.—Falla (in Thomson, 1964:877) reported that wattles of adults of species in this family develop from a fold of skin at the base of the nestling's gape.

Sturnidae.—Figure 1 shows a very extensive development of flanges reached in the juvenile Starling (*Sturnus vulgaris*). Wackernagel (1954) and Hudec and Folk (1961) have given details on the flanges of this species. Maximal development occurs about eight days posthatching according to Wackernagel. By the 20th day posthatching regression of the flange is virtually complete. Hudec and Folk have noted the possible functional correlations between the opening of the eyes at 7–8 days after hatching and the beginning of regression in size of the flanges at the ninth day after hatching.

Although the flange of the lower mandible in *Sturnus* is somewhat broader than the upper, as noted by Wackernagel, the appearance is not at all like that of woodpeckers.

Ploceidae.—This rather heterogeneous family contains the estrildines and viduines, members of which are unique among known birds in having transitory globules with light-reflecting properties at the corners of the nestling gape (Friedmann, 1960). The viduines are brood-parasitic on the estrildines, and there has been controversy over the extent to which similarities, including those of the reflective globules, between viduines and certain estrildines are the result of evolutionary affinity as opposed to convergent evolution (cf. Delacour, 1943; Steiner, 1960; Friedmann, 1960, 1962; Nicolai, 1964). Nicolai (p. 134) reported considerable intraspecific variation in timing of final loss of the gape and mouth markings in Estrildinae and Viduinae. If this situation occurs in other passerine families, the value of flanges as precise aging characters will be minimal.

SUMMARY

The occurrence and variations of the oral flanges in nestlings of nidicolous birds are reviewed. The taxonomic significance of these flanges remains generally unknown for apodiform, coliiform, trogoniform, coraciiform, and piciform birds. As hole-nesting passerines tend to have relatively larger flanges at maximal development than do open-nesters, the degree of enlargement of the flanges in juvenile passerines generally appears to be correlated more closely with nest site than with taxonomic position.

ACKNOWLEDGMENTS

I am grateful to the staffs of the United States National Museum and the American Museum of Natural History for providing access to specimens. Useful information was provided by L. J. Gorski, while helpful comments on an earlier draft of the manuscript were given by A. H. Brush. Mrs. Stephani Schaefer prepared Figure 1. Financial support was received from the University of Connecticut Research Foundation.

LITERATURE CITED

Armstrong, E. A. 1965. Bird display and behavior. 2nd ed. Dover, New York.

Barruel, P. 1954. Birds of the world. Their life and habits. Oxford Univ. Press, New York.

Bent, A. C. 1939. Life histories of North American woodpeckers. U.S. Natl. Mus. Bull., 174.

Blume, D. 1961. Über die Lebensweise einiger Spechtarten (*Dendrocopos major, Picus viridis, Dryocopus martius*). J. Ornithol., 102, Sonderheft: 1–115.

Brewster, W. 1893. A brood of young flickers (*Colaptes auratus*) and how they were fed. Auk, 10:231–236.

Butler, A. G. 1916. Directive-marks in nestling birds. Ibis, 1916:521.

Clark, G. A., Jr. 1964. Ontogeny and evolution in the megapodes (Aves: Galliformes). Postilla, 78:1-37.

Delacour, J. 1943. A revision of the subfamily Estrildinae of the family Ploceidae. Zoologica, 28:69–86.

Dewar, J. H. 1908. The flanges and mouth-spots of nestlings. Brit. Birds, 1:258–259.

Ficken, M. S. 1965. Mouth color of nestling passerines and its use in taxonomy. Wilson Bull., 77:71–75.

Fischer, R. B. 1958. The breeding biology of the Chimney Swift *Chaetura pelagica* (Linnaeus). New York State Mus. and Sci. Serv. Bull., 368:1–141.

Forbush, E. H. 1927. Birds of Massachusetts and other New England states. Vol. II. Commonwealth of Massachusetts.

Friedmann, H. 1955. The honey-guides. U.S. Natl. Mus. Bull., 208.

Friedmann, H. 1960. The parasitic weaverbirds. U.S. Natl. Mus. Bull., 223.

Friedmann, H. 1962. The problem of the viduinae in the light of recent publications. Smithsonian Misc. Coll., 145:1–10.

Frisch, O. Von. 1966. Beitrag Zur Ethologie der Blaurache (*Coracias garrulus*). Z. Tierpsychol., 23:44–51.

Haartman, L. Von. 1957. Adaptation in hole-nesting birds. Evolution, 11:339–347.

Horwich, R. H. 1966. Feather development as a means of aging young mockingbirds (*Mimus polyglottos*). Bird-Banding, 37:257–267.

Hoyt, S. Y. 1944. Preliminary notes on the development of nestling Pileated Woodpeckers. Auk, 61:376–384.

Hudec, K., and C. Folk. 1961. Postnatal development in the Starling (*Sturnus vulgaris* L.) under natural conditions. Zool. Listy, 10:305–330.

Ingram, C. 1907. On tongue-marks in young birds. Ibis, 1907:574–578.

Ingram, C. 1920. A contribution to the study of nestling birds. Ibis, 1920:856–880.

Ingram, C. 1958. Notes on the habits and structure of the Guacharo *Steatornis caripensis*. Ibis, 100:113–119.

Kilham, L. 1961. Reproductive behavior of Red-bellied Woodpeckers. Wilson Bull., 73:237–254.

Kilham, L. 1962. Reproductive behavior of Downy Woodpeckers. Condor, 64:126–133.

Moreau, R. E. 1942. The breeding biology of *Micropus caffer streubelii* Hartlaub, the White-rumped Swift. Ibis, 1942:27–49.

Murphy, R. C., and D. Amadon. 1953. Land birds of America. McGraw-Hill, New York.

Neufeldt, I. 1966. Life history of the Indian cuckoo, *Cuculus micropterus micropterus* Gould, in the Soviet Union. J. Bombay Natl. Hist. Soc., 63:399–419.

Nicolai, J. 1964. Brutparasitismus der Viduinae als ethologisches Problem. Z. Tierpsychol., 21:129–204.

Norris, R. A. 1958. Comparative biosystematics and life histories of the nuthatches *Sitta pygmaea* and *Sitta pusilla*. Univ. California Publ. Zool., 56:119–300.

Parkes, K. C., and G. A. Clark, Jr. 1964. Additional records of avian egg teeth. Wilson Bull., 76:147–154.

Romanoff, A. L. 1960. The avian embryo. Macmillan, New York.

Schifter, H. 1967. Beiträge zum Fortpflanzungsverhalten und zur Jugendentwicklung der Mausvögel (Coliidae). Zool. Jahrb., Syst. Bd., 94:68–161.

Skead, C. J. 1950. A study of the African Hoopoe. Ibis, 92:434–463.

Skutch, A. F. 1944*a*. The life history of the Prong-billed Barbet. Auk, 61:61–88.

Skutch, A. F. 1944*b*. Life history of the Blue-throated Toucanet. Wilson Bull., 56:133–151.

Steiner, H. 1960. Klassifikation der Prachtfinken, Spermestidae, auf Grund der Rachenzeichnungen ihrer Nestlinge. J. Ornithol., 101:92–112.

Swynnerton, C. F. M. 1916. On the colouration of the mouths and eggs of birds. I. The mouths of birds. Ibis, 1916:264–294.

Thomson, A. L. (ed.). 1964. A new dictionary of birds. McGraw-Hill, New York.

Wackernagel, H. 1954. Der Schnabelwulst des Stars (*Sturnus vulgaris* L.). Rev. suisse Zool., 61:9–82.

Welty, J. C. 1962. The life of birds. Saunders, Philadelphia.

Wetherbee, D. K. 1961*a*. Neonates and incubation period of Chimney Swift. Wilson Bull., 73:86–87.

Wetherbee, D. K. 1961*b*. Observations on the developmental condition of neonatal birds. Amer. Midl. Nat., 65:413–435.

Wetherbee, D. K., and N. S. Wetherbee. 1961. Artificial incubation of eggs of various bird species and some attributes of neonates. Bird-Banding, 32:141–159.

Wetmore, A. 1960. A classification for the birds of the world. Smithsonian Misc. Coll., 139:1–37.

Witherby, H. F., F. C. Jourdain, N. F. Ticehurst, and B. W. Tucker. 1938. Handbook of British birds. Vol. 2. Witherby, London.

BIOLOGICAL SCIENCES GROUP, UNIVERSITY OF CONNECTICUT, STORRS, CONNECTICUT 06268, 27 SEPTEMBER 1967.

NEW LIFE MEMBER

Dr. Larry T. Schwab has recently become a Life Member of The Wilson Society. He holds a bachelor's and an MD degree from West Virginia University, and is currently resident physician in ophthalmology at the West Virginia University Medical Center. His interests in ornithology are centered around the study of migration and bird photography, and he has published several notes on his observations. He is a member of the A.O.U. and the Southern Appalachian Botanical Society as well as several conservation organizations.

VARIATION IN MAJOR BODY COMPONENTS OF THE TREE SPARROW (*SPIZELLA ARBOREA*) SAMPLED WITHIN THE WINTER RANGE

Carl W. Helms and Robert B. Smythe

Odum et al. (1961) divided migratory populations of small birds into three groups based upon patterns of fat deposition and migration: "1) short-range migrants that become moderately obese but begin migration before peak deposition, 2) short-range migrants that attain moderate obesity but begin migration after peak deposition levels have been reached, 3) long-range migrants that become extremely obese just prior to long flights" (Odum loc. cit., p. 516). We have been interested in the seasonal bioenergetics, particularly during migration, of populations assigned to the first of these categories because their initial depot fat reserves are unspectacular, yet, must provide energy for at least the first migratory flight.

This paper 1) extends the earlier work of Helms and Drury (1960) on the Tree Sparrow (*Spizella arborea*) a cold-temperate to sub-arctic migrant with no detectible premigratory obesity in free-living representatives of the species, and 2) leads to reformulation of the migrant categories given above.

METHODS

Collection.—During the winter of 1962–1963, 60 Tree Sparrows were collected in the vicinity of Lewisburg, Pennsylvania (see Table 1).

Individuals were weighed after collection (± 0.1 g); fat class was determined (Helms and Drury, 1960); wing length was measured to the tip of the longest primary with the wing flattened and straightened; sex was estimated by cloacal examination; and birds were killed by cardiac pressure if collected by net or trap and sealed in an individual plastic bag. Within two hours, each specimen was weighed (± 0.2 mg), re-sealed in a plastic bag, and frozen at –29°C. Birds were held at this temperature two to six months before extraction.

Extraction.—Specimens were thawed within their plastic bags to prevent moisture condensation and weighed (± 0.2 mg) to determine weight loss during storage (less than 0.1 g in all cases and usually less than 0.02 g).

a. "*Short*" *Method.*—Half of the sample was extracted using the following method adapted from Odum (1960).

Thawed birds were aged and sexed by dissection and refrozen. They were sliced in a freezer and transferred to a weighed (± 0.2 mg) pan. After thawing in a closed desiccator (without desiccant), the pan and bird were weighed to determine grinding loss (under 1 g in all cases). The pan and bird were placed in a vacuum oven at 40°C for 72 hours, cooled in a desiccator for 20 minutes, and weighed. Tissues were quantitatively transferred to a pint jar using a 5:1 petroleum ether-chloroform mixture and covered with solvent. The jar was sealed, placed on a shaker for 24–48 hours, opened, and the solvent mixture heated to boiling for 5–10 minutes. Solvent was decanted from the specimen into a filter flask under vacuum through a Büchner funnel containing a dry weighed disc of number 1 filter paper. The specimen was covered with the original

TABLE 1

TREE SPARROW SAMPLES, LEWISBURG, PENNSYLVANIA

		Sample Sizes:					How Collected:		When Collected:		How Extracted:	
Period:	Dates:	Total	♂♂	♀♀	Adults	Immatures	Net	Trap	Morning	Afternoon	Short Method	Soxhlet Method
Fall Migration	13–30 November 1962	12	5	7	2	10	12	0	0	12	6	6
Early Winter	8–12 December 1962	12	8	4	7	5	0	12	4	8	6	6
Mid-Winter	1–7 February 1963	12	4	8	12	0	0	12	2	10	6	6
Late Winter	4–7 March 1963	9	3	6	9	0	0	9	3	6	6	3
Spring Migration	17–27 March 1963	15	8	7	15	0	15	0	6	9	6	9
Total Period:	13 November 1962 — 27 March 1963	60	28	32	45	15	27	33	15	45	30	30

amount of solvent and boiled for 10–20 minutes. This solvent and the extracted tissues were decanted onto the filter paper used previously and the jar and tissues rinsed with petroleum ether. The filter paper and extracted tissues were dried under vacuum for 6 hours at room temperature and weighed.

Suggested modifications of the procedure include 1) razor blade slicing of thawed carcasses, 2) a change of solvent after 12–24 hours, and 3) use of a top-loading pan balance (± 0.02 g). The first modification would eliminate condensation upon cold tissues during handling. The second would be particularly desirable for very fat birds. The third would involve no loss in precision due to the large errors inherent in handling exposed hygroscopic tissues and might improve reliability by speeding all steps of the process.

b. *Soxhlet Method for Sectional Extraction.*—The second half of the sample was extracted by the following method adapted from Odum and Perkinson (1951).

Thawed specimens were rapidly dissected, noting age and sex, into the following body regions: a) skin and feathers with subcutaneous fat, b) ventral abdominal wall (abdomen) with peritoneal fat, c) viscera (proventriculus through large intestine) with visceral fat, d) liver with hepatic fat, e) posterior (back), f) thorax and heart, and g) head and neck (see Odum and Perkinson, 1951—sections were identical except that the heart and thorax were not extracted separately). Except for perforation of the skull and four incisions through the pectoralis masses, sections were not further macerated.

These body sections were placed in separate weighed (± 0.2 mg) glass extraction thimbles of appropriate size, and weighed. Tissues were dried as above, transferred to a desiccator for 20 minutes, and weighed. Each section was extracted for a minimum of 18 hours in a Soxhlet extractor using a 5:1 mixture of reagent grade petroleum ether (30–60°C) and reagent grade chloroform. Tissues were dried under vacuum at room temperature for six hours and weighed. Solvent and fat were transferred quantitatively to weighed beakers with petroleum ether, and dried with heat to tackiness and under vacuum to constant weight.

e. *Methodological Differences.*—The birds used in the short and Soxhlet methods did not differ significantly in weight weight ($\bar{d} = 0.17 \pm 0.33$ g, $P > 0.5$) although they may have been heterogeneous with respect to this variable ($F = 1.86$, $df = 29, 29$, $P \cong 0.05$). They did not differ significantly in wing length ($\bar{d} = -0.1 \pm 0.4$ mm, $P > 0.5$) nor were wing lengths heterogeneous ($F = 1.03$, $df = 29, 29$, $P > 0.1$). Total water ($\bar{d} = 0.14 \pm 0.18$ g, $0.5 > P > 0.4$) and total fat ($\bar{d} = -0.04 \pm 0.16$ g, $P > 0.5$) did not differ significantly but dry fat-free weight did ($\bar{d} = -0.28 \pm 0.13$ g, $0.5 > P > 0.2$). However, this difference was not highly significant and was less than 5 per cent of the mean dry fat-free weight. Moreover, variances were not significantly heterogeneous ($F = 1.19$, $df = 29, 29$, $P > 0.1$). We concluded that differences due to extraction method were negligible and pooled all birds in subsequent analyses.

Calculations.—Weight at capture was designated Wet Weight. The difference between weights before and after grinding or dissecting was used to calculate a correction factor for losses which were assumed to be evenly distributed among all body components. These losses were under 5 per cent of wet weight in all cases and were under 1 per cent in most. [(Weight before drying minus weight after drying) multiplied by (the correction factor)] plus (the difference between wet weight and weight before grinding or dissection) equalled Total Water. (Weight before extraction minus weight after extraction) multiplied by the correction factor equaled Total Fat. Wet weight minus total fat equaled Wet Fat-free Weight and this value minus total water equaled Dry Fat-free Weight which was equal to the tissue weight after extraction and drying times the correction factor. Water and fat as percentages of wet weight and Water and Fat Indices (Total Water/Dry Fat-free Weight and Total Fat/Dry Fat-free Weight, respectively) were also calculated. Total Lipid equaled the net weight of ether: chloroform soluble material from all sections extracted by refluxing multiplied by the correction factor. This value did not differ significantly from calculated total fat for these birds and will not be reported because it was not determined from the total sample. Results from the individual sections extracted by the Soxhlet method will be reported separately.

Statistical Notations.—Various symbols are used throughout this paper. For the sake of brevity, they will be listed here (see Steel and Torrie, 1960).

a. *Averages.* Sample mean $= \bar{x}$; sample median $= \hat{x}$; sample standard deviation $= s$; and sample standard error $= s_{\bar{x}}$.

b. *Differences.* Difference between sample means $= \bar{d}$; standard error of the difference $= s_{\bar{d}}$; $t = \bar{d}/s_{\bar{d}}$; variance ratio $= F$; degrees of freedom $= df$; probability $= P$; $* = 0.05 > P > 0.01$; and $** = 0.01 > P$. The term "significant" is reserved for tested observations attributable to chance no oftener than once in twenty occurrences, *i.e.*, $0.05 > P$.

RESULTS

Age and Sex.—Adults were significantly heavier (wet weight and fat-free weights) and larger (wing length) than immatures, but within the fall and early winter periods (the only subsamples containing known immatures), adults differed significantly from immatures only in wet weight ($\bar{d} = 1.24 \pm 0.60$ g, $P \cong 0.05$). The only significant heterogeneity between adults and immatures within the fall and early winter periods was also in wet weight ($F = 4.31$, $df = 3, 14$, $0.025 > P > 0.01$). In spite of these differences, the data will be pooled with respect to age in the subsequent sections of this paper because birds of the year could not be separated from older birds in the February and later subsamples. See Heydweiller (1935).

Males were heavier (wet weight $\bar{d} = 0.88 \pm 0.44$ g, $P \cong 0.05$; total water $\bar{d} = 0.55 \pm 0.17$ g, $0.005 > P > 0.001$; dry fat-free weight $\bar{d} = 0.25 \pm 0.12$ g, $P \cong 0.05$) and larger (wing length $\bar{d} = 2.6 \pm 0.5$ mm, $0.001 > P$) than females, but did not differ significantly from them in any fat variables or in water index or per cent. These differences appear to be compatible with the wet weight difference between sexes of 0.85 g (adults only) reported by Heydweiller (1935).

In the Tree Sparrow, the differences between sexes in variables that could be determined in intact individuals were not large enough to be reliable aids in determining sex. Using the shape of the cloacal protuberance (rounded abdominal junction and conical structure in females; angular abdominal junction and cylindrical structure in males), 67 per cent of the birds taken in this study were correctly sexed in the field. This is close to the reliability obtained by Heydweiller (1936) who sexed this species using plumage characteristics. It is doubtful that more reliable sexing is possible without laparotomy or autopsy.

The only significant heterogeneity between sexes was in dry fat-free weight ($F = 2.53$, $df = 31, 27$, $0.025 > P > 0.01$). Data were separated by sex in the subsequent treatments in this paper but no major differences appeared and results will be reported from the pooled sample for the sake of simplicity even though this entails a certain loss of efficiency in statistical testing.

Time of Day.—More birds were collected in the afternoon than in the morning during this study. However, morning collections were made in all subsample periods except the first (see Table 1) and there was no significant diel heterogeneity so that temporal bias does not seem to be a major concern. The most conspicuous trend during the day was an expected increase in body fat (total fat $\bar{d} = 0.50 \pm 0.21$ g, $0.05 > P > 0.025$). Helms and Drury (1960) discuss diel variations in wet weight and visible fat in this species. Due to the small number of morning collections, their distribu-

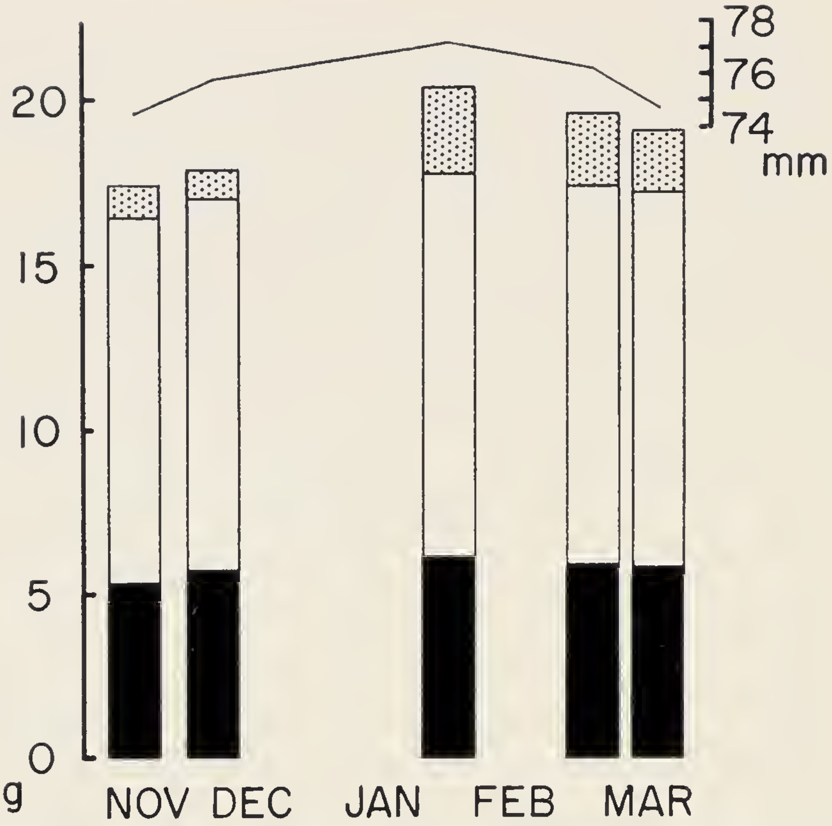


FIG. 1. Seasonal Changes in Body Composition and Wing Length. Black rectangles represent dry fat-free weight, white rectangles represent total water and the two together represent wet fat-free weight. Stippled rectangles represent total fat. All components in each sample equal wet weight. Wing length is indicated by the upper line. Fat-free weights (dry and wet), water, and wing length did not differ significantly between samples. Wet weight and total fat were significantly higher in early February than in early December. They were also higher in spring than in fall. (See Tables 2 and 3).

tion throughout the subsamples, and the general lack of significant differences between morning and afternoon collections, diel differences will be neglected in the remainder of this study.

Season.—Data from each subsample are given in Tables 2 and 4. Sample differences are given in Tables 3 and 4. Some of these data are plotted in Figures 1 and 2.

Seasonal trends are apparent and agree closely with those found by Helms and Drury (1960). Weight and fat were highest in mid-winter and lower in spring and fall. Fall to winter comparisons reveal significant differences in wet weight and fat, but not in fat-free weights or total water (when only adults are compared). However, winter to spring comparisons indicate no significant differences in any of the components analyzed. There was no period of vernal premigratory or migratory fattening in the Tree Sparrow sampled on its wintering ground.

The data in Table 2 and Figure 1 suggest that size (wing length) and mass

TABLE 2

MEAN FIELD AND EXTRACTION DATA[1]

Period:	Wing Length (mm)	Visible Fat (fc)	Wet Weight (g)	Wet Fat-Free Weight (g)	Total Water (g)	Total Fat (g)	Dry Fat-Free Weight (g)
A. Fall Migration	74.5 ± 0.7	2.9	17.44 ± 0.26	16.37 ± 0.24	11.06 ± 0.16	1.07 ± 0.05	5.31 ± 0.10
B. Early Winter	76.2 ± 0.8	2.7	17.94 ± 0.48	16.98 ± 0.38	11.28 ± 0.31	0.97 ± 0.12	5.70 ± 0.15
C. Mid-Winter	77.3 ± 0.7	2.9	20.40 ± 0.43	17.81 ± 0.22	11.75 ± 0.14	2.59 ± 0.26	6.06 ± 0.12
D. Late Winter	76.3 ± 0.6	3.2	19.55 ± 0.48	17.45 ± 0.41	11.52 ± 0.25	2.10 ± 0.16	5.93 ± 0.18
E. Spring Migration	75.6 ± 0.5	2.8	19.15 ± 0.46	17.17 ± 0.29	11.39 ± 0.19	1.98 ± 0.21	5.78 ± 0.11
All Data	76.0 ± 0.3,	2.9	18.88 ± 0.23,	17.14 ± 0.15,	11.39 ± 0.09,	1.74 ± 0.11,	5.75 ± 0.07,

[1] Values reported as $\bar{x} \pm S_{\bar{x}}$ except Visible Fat where x is tabulated.

TABLE 3

FIELD AND EXTRACTION DATA, DIFFERENCES.[1]

Period:	$\bar{d}$ Wing Length (mm)	Visible Fat (fc)	$\bar{d}$ Wet Weight (g)	$\bar{d}$ Wet Fat-Free Weight (g)	$\bar{d}$ Total Water (g)	$\bar{d}$ Total Fat (g)	$\bar{d}$ Dry Fat-Free Weight (g)
A—B Fall— Winter	+1.7 ± 1.0	–0.2	+0.51 ± 0.55	+0.61 ± 0.45	+0.22 ± 0.35	–0.10 ± 0.13	+0.39 ± 0.18*[2]
B—C Winter— Winter	+1.2 ± 1.0	+0.2	+2.45 ± 0.65**	+0.83 ± 0.44	+0.47 ± 0.34	+1.62 ± 0.28**	+0.36 ± 0.20
C—D Winter— Winter	–1.0 ± 1.0	+0.3	–0.85 ± 0.65	–0.35 ± 0.47	–0.22 ± 0.28	–0.50 ± 0.30	–0.13 ± 0.22
D—E Winter— Spring	–0.7 ± 0.8	–0.4	–0.40 ± 0.67	–0.29 ± 0.50	–0.13 ± 0.32	–0.11 ± 0.27	–0.16 ± 0.21
E—A Spring— Fall	–1.1 ± 0.9	+0.1	–1.71 ± 0.53**[2]	–1.02 ± 0.37*[2]	–0.46 ± 0.25	–0.91 ± 0.22**[3]	–0.46 ± 0.15**[2]

[1] Values reported as $\bar{d} \pm s_{\bar{d}}$ except for Visible Fat where $\hat{x}_2 - \bar{x}_1$ is given.

[2] Adults only, difference not significant ($P > 0.05$).

[3] Adults only, difference significant ($0.05 > P$).

TABLE 4

WATER AND LIPID PERCENTAGES AND INDICES, MEANS AND DIFFERENCES.[1]

Period:	Means: Water % Wet Weight	Fat % Wet Weight	Water Index	Fat Index	Differences: $\bar{d}$ Water % Wet Weight	$\bar{d}$ Fat % Wet Weight	$\bar{d}$ Water Index	$\bar{d}$ Fat Index
	per cent	per cent	(g/g)	(g/g)	per cent	per cent	(g/g)	(g/g)
A. Fall Migration	63.4 ± 0.4	6.1 ± 0.3	2.08 ± 0.03	0.202 ± 0.009				
B. Early Winter	62.9 ± 0.4	5.3 ± 0.6	1.98 ± 0.03	0.168 ± 0.019	-0.5 ± 0.6	-0.9 ± 0.6	-0.10 ± 0.04^{*2}	-0.034 ± 0.021
C. Mid-Winter	57.7 ± 0.8	12.5 ± 1.00	1.95 ± 0.04	0.425 ± 0.039	-5.2 ± 0.9**	+7.2 ± 1.1**	-0.03 ± 0.04	+0.257 ± 0.043**
D. Late Winter	59.0 ± 0.5	10.7 ± 0.7	1.95 ± 0.04	0.375 ± 0.037	+1.2 ± 1.0	-1.8 ± 1.2	0.00 ± 0.06	-0.050 ± 0.054
E. Spring Migration	59.7 ± 0.7	10.1 ± 0.9	1.98 ± 0.023	0.338 ± 0.033	+0.7 ± 0.8	-0.6 ± 1.1	+0.03 ± 0.05	-0.037 ± 0.050
All Data	60.6 ± 0.4	8.9 ± 0.5	1.99 ± 0.01	0.300 ± 0.018	+3.8 ± 0.8^{**3}	-3.9 ± 0.9^{**3}	+0.10 ± 0.04^{*2}	-0.136 ± 0.034^{**3}

[1] Means tabulated as $\bar{x} \pm s_{\bar{x}}$; differences tabulated as $\bar{d} \pm s_{\bar{d}}$.

[2] Adults only, difference not significant ($P > 0.05$).

[3] Adults only, difference significant ($0.05 > P$).

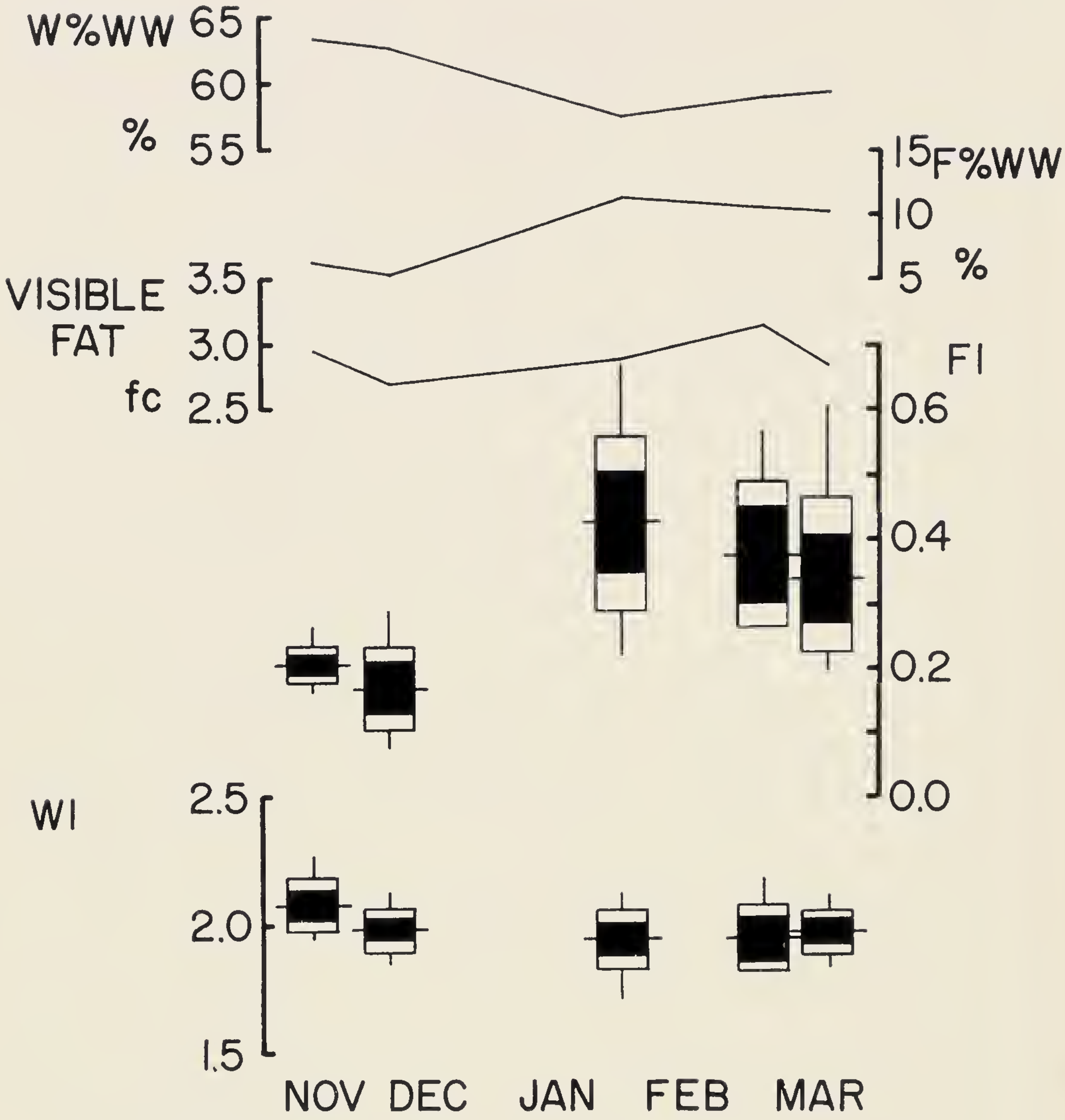


FIG. 2. Seasonal Changes in Relative Body Composition. Water as a per cent of wet weight (W%WW), fat as a per cent of wet weight (F%WW), visible fat, fat index (FI), and water index (WI) are plotted. For fat and water indices, range is given as a vertical line, mean as a horizontal line, two standard errors above and below the mean as a solid rectangle, and one standard deviation above and below the mean as an open rectangle. Non-overlap of black rectangles indicates that means probably differ significantly. (See Tables 2 and 4).

(fat-free weights) may tend to increase in mid-winter. Although these tendencies are insignificant, they are regular and parallel. If verified with larger samples, the latter trend might reflect the maturation of birds of the year (Heydweiller, 1936; Baumgartner, 1938), but further growth of primaries would not be expected during this period. While Helms and Drury (1960) emphasized the constancy of individuals within the winter population and the fidelity (*Ortstreue*) of returning adults, many Tree Sparrows were banded at all seasons and not seen again. It is possible that the winter population of this species undergoes a flux of individuals in a given area, particularly in the juvenile component (see Heydweiller, 1935). Whether this flux represents movement of individuals or mortality of smaller birds is uncertain. From the work of Helms and Drury (1960), it is evident that quasi-migratory or migratory movements may alter the population by late February. These possibilities need investigation.

DISCUSSION

Fat and Migration. In two independent field studies (Helms and Drury, 1960; this paper), the Tree Sparrow has been found not to increase in weight on its wintering grounds prior to migration. According to the migrant patterns proposed by Odum et al. (1961), the Tree Sparrow could be assigned only to the first category as a bird that does become moderately obese but attains this condition only after the initiation of migration.

Tree Sparrows collected in Pennsylvania (this study) had an average fat below 2.0 g and a fat index below 0.4 at the onset of migration (total fat ranged between 1.0 and 3.6 g, fat index between 0.2 and 0.4). In Massachusetts samples, there was no indication that heavy individuals were more likely to undertake flight than light ones (Helms and Drury, 1960). As the migratory season progressed, birds taken within the winter area tended to be both lighter and leaner (both studies). A sample of three Tree Sparrows collected by F. N. Cowell at Agava Bay, Ontario, between 23 and 26 April 1965, averaged 17.3 g. Thus, none of the available field data suggest that this species increases in weight as migration proceeds. Moreover, upon arrival at the breeding grounds, members of other species tend to be consistently lean (Oakeson, 1954; King et al., 1965).

The only data suggesting weight increases in Tree Sparrows during migration come from caged birds. Individuals kept by Weise (1956) and West (1960) in Illinois increased in weight between late March and the end of April; birds in our own laboratory behaved similarly, reaching a peak weight between 19 and 20 g by early May. These weights, however, only approximated normal field weights at the onset of migration. Winter Tree Sparrows held in cages appear to be in an unfavorable energy balance and their weights seem to be quite anomalous when compared with those of free-living birds in winter. We suggest that captive individuals of this species which are 1) exposed to low ambient temperatures with relatively high rates of air movement leading to wind-chill, 2) prevented from seeking protected habitat day and night, 3) excluded from direct solar radiation, or 4) fed an atypical diet (Martin, 1965) are in bioenergetic difficulty reflected in weight loss and, in very cold periods, by winter mortality. Therefore, patterns of weight variation seen in caged birds of this species cannot be valid reflections of normal processes in wild individuals and populations. Until evidence appears to the contrary, it is logical to assume that the Tree Sparrow does not increase its lipid reserve during the course of vernal migration. Moreover, increased reserves seem to be unnecessary. Total fat during the first half of March averaged 1.98 ± 0.21 g. Assuming that 0.22 g of this reserve was unavailable structural lipids (based upon unpublished regressions of sectional and total fat in this species), 1.76 g of fat would have been available for energetic utilization (16.7 kcal of reserve). Using the power comsumption estimate of Nisbet et al. (1963) of 0.076 kcal/g body weight- hr for migratory flight, an average Tree Sparrow, weighing 19.15 g, could have flown for over 11 hours on fat alone. At an average ground speed of 25 miles per hour (Drury and Keith, 1962), this would have taken an average individual about 290 miles. Assuming full replenishment of reserves between flights, fewer than eight flights of this distance would take a Tree Sparrow to the vicinity of Coppermine, N. W. T., Canada, in the most distant portion of the breeding range of the eastern population, while fewer than five flights would take him to Churchill, Manitoba, Canada. Upper James Bay (Lake River area), Ontario, Canada, could similarly have been reached in three flights. Assuming abundant food and a suitable thermal environment, flight losses could be replaced in a week or less (based upon data from caged birds), so that a migrant beginning flight in mid-March could reach the most distant part of the breeding range by early or mid-May and nearer areas by early April. Actual arrival is not before late May (Baumgartner, 1937; Snyder, 1957). Therefore, due to the early start on migration and the leisurely movements necessitated by the climatic situations encountered en route and in the breeding areas, there is no need to postulate an increased weight for this species as movement progresses. With the relatively long spring migratory period of this species, weights and fat reserves could decrease during the period of migration and, as suggested by the small Agava Bay sample, may actually do so.

The Tree Sparrow, therefore, does not fit the categorization of Odum et al. (1961) with respect to patterns of fat-deposition—it is also doubtful that potential migratory distances in excess of 2,000 miles are "short-range." The distance from central Pennsylvania to Coppermine is roughly equivalent to that from the former location to northern South America, although, with its limited energetic reserves, the Tree Sparrow would not be able to cross the Gulf of Mexico. In contrast, the trans-Gulf migrants studied by Caldwell, Odum, and Marshall (1964) and trans-oceanic migrants studied by Nisbet et al. (1964) add appreciable fat before making the required water crossing.

It is interesting to note that in this group of migrants, weight and fat reserves are not high during periods of intracontinental movement but become elevated when needed, prior to sustained over-water flight. *Extra* fuel exacts an energetic price and would be selected against in all cases. It appears, therefore, that the categorization of Odum et al. (1961) should be simplified to two categories as follows: 1) intracontinental migrants, and 2) intercontinental migrants. In the former category there would be a complete spectrum of migratory populations from those with low initial reserves performing a leisurely migration with essentially short flights in sequence to those with high initial reserves performing a more rapid migration with fewer but longer flights. In the latter category, intracontinental patterns of fat deposition would be expected until individuals approached the region of departure for extensive single over-water (or desert) flights at which point massive reserves, adapted to the distance to be flown, might be added. Although more data are needed, these patterns seem to be clear. Increasing attention should now be directed to functional differences in the patterns revealed and to the ecological and evolutionary implications of such differences.

SUMMARY

1. Sixty Tree Sparrows (*Spizella arborea*) were collected during the winter of 1962–1963 in central Pennsylvania. Birds were measured, weighed, and frozen. Subsequently, specimens were thawed, weighed, dried, and extracted (petroleum ether: chloroform, 5:1) to determine wet weight, total fat, total water, fat-free weights, and fat and water indices. Age and sex were noted.

2. Adults were heavier (wet and fat-free weights) and larger (wing length) than immatures, but age classes could not be separated throughout the study. Age groups were, therefore, pooled. Males were heavier (wet and fat-free weights) and larger (wing length) than females, but the sexes did not differ significantly in fat. The most conspicuous diurnal change in major body components was in fat.

3. Subsamples collected from mid-winter through spring migration contained birds that were significantly fatter than fall and early winter birds. Wet weight and fat did not increase prior to vernal migration. There were no significant seasonal changes in water, fat-free weights, or wing length.

4. There is no field evidence for vernal premigratory fattening or for increased reserves as migration proceeds in this species, nor do additional reserves appear to be necessary since the Tree Sparrow should have adequate lipid levels to reach any portion of the breeding range in the time at its disposal. Therefore, we suggest a modification of the migrant categories proposed by Odum et al. (1961) to a) intracontinental migrants showing varying but moderate migratory reserves adapted to the species flight patterns (frequency of flights, distance of flights, time available for migration), and b) intercontinental migrants with varying but more massive maximal migratory reserves adapted to the barriers that must be crossed in a single flight but whose reserves are usually deposited only prior to such single flights.

ACKNOWLEDGMENTS

We would like to thank Harvey Arnold, Michael Rosenzweig, and John McGinnis for statistical advice, William Aussiker for field assistance, F. N. Cowell for furnishing specimens taken during migration, Eugene Odum for methodological sugestions, and Jack Harclerode and Ernst Mayr for their critical evaluation of the manuscript in preliminary form. This work was supported by grant AM 06798 (USPHS).

LITERATURE CITED

Baumgartner, A. M. 1937. Food and feeding habits of the Tree Sparrow. Wilson Bull., 49:65–80.

Baumgartner, A. M. 1938. Seasonal variations in the Tree Sparrow. Auk, 55:603–613.

Caldwell, L. D., E. P. Odum, and S. G. Marshall. 1963. Comparison of fat levels in migratory birds killed at a central Michigan and a Florida Gulf Coast television tower. Wilson Bull., 75:428–434.

Drury, W. H., Jr., and J. A. Keith. 1962. Radar studies of songbird migration in eastern New England. Ibis, 105:234–237.

Helms, C. W., and W. H. Drury, Jr. 1960. Winter and migratory weight and fat: field studies in some North American buntings. Bird-Banding, 31:1–40.

Heydweiller, A. M. 1935. A comparison of winter and summer territories and seasonal variations of the Tree Sparrow (*Spizella arborea*). Bird-Banding, 6:1–11.

Heydweiller, A. M. 1936. Sex, age and individual variation of winter Tree Sparrows. Bird-Banding, 7:61–68.

King, J. R., D. S. Farner, and M. L. Morton. 1965. The lipid reserves of White-crowned Sparrows on the breeding ground in central Alaska. Auk, 83:236–252.

Martin, E. W. 1965. The influence of available protein on the energy balance of Tree Sparrows (*Spizella arborea*). Bull. Ecol. Soc. Amer., 46:115 (abstr.).

Nisbet, I. C. T., W. H. Drury, Jr., and J. Baird. 1963. Weight-loss during migration. Bird-Banding, 34:107–159.

Oakeson, B. B. 1954. The Gambel's Sparrow at Mountain Village, Alaska. Auk, 71: 351–365.

Odum, E. P. 1960. Lipid deposition in nocturnal migrant birds. Proc. XIIth Internatl. Ornithol. Congr., Helsinki 1958: 563–576.

Odum, E. P., and J. D. Perkinson, Jr. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., 24:216–230.

Odum, E. P., C. E. Connell, and H. L. Stoddard. 1961. Flight energy and estimated flight ranges of some migratory birds. Auk, 78:515–527.

Snyder, L. L. 1957. Arctic birds of Canada. Univ. Toronto Press, Toronto.

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

Weise, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, 37:274–287.

West, G. C. 1960. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. Auk, 77:306–329.

DEPARTMENT OF BIOLOGY, BUCKNELL UNIVERSITY, LEWISBURG, PENNSYLVANIA. PRESENT ADDRESSES: (C.W.H.) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF GEORGIA, ATHENS, GEORGIA 30601 AND (R.B.S.) DEPARTMENT OF ZOOLOGY, UNIVERSITY OF NORTH CAROLINA, CHAPEL HILL. 12 MAY 1967.

TERRITORIAL BEHAVIOR AND POPULATION REGULATION IN BIRDS

A Review and Re-evaluation

Jerram L. Brown

A close relationship between territorial behavior and population regulation in birds was claimed by Howard (1920) in his classic essay on territoriality and has been emphasized by both earlier and more recent authors (see Wynne-Edwards, 1962). At present, opinions on this matter vary considerably; but there seems to be widespread entertainment, and in some circles acceptance, of the idea that territorial behavior significantly limits many avian populations. Frequently appended is the theory that territoriality has evolved because of this effect through a process which has been called "group selection" but which might better be referred to as "interpopulation or interdemic selection" (Brown, 1966). These ideas apparently were first fully developed by Kalela (1954:2, 18, 41) and have recently been elaborated in the ecological literature by Wynne-Edwards (1962, 1963, and elsewhere) and in the popular press by Lorenz (1966:31). The role of territorial behavior in population regulation is now regularly covered in college textbooks of ecology and behavior (e. g. Andrewartha and Birch, 1954:490; Odum, 1959:222; Kendeigh, 1961:222; Macfadyen, 1963:264; Davis, 1966:68; Smith, 1966:372; MacArthur and Connell, 1966:139; Etkin, 1967:32), despite the claims of some ecologists (e. g. Lack, 1954, 1966) that it is of relatively little importance.

Surprisingly, the facts necessary for an evaluation of the role of territorial behavior in population regulation have received relatively little critical attention except in parts of works with a more general orientation. As a result the various ways in which territorial behavior may affect a population do not appear to have been as clearly distinguished and as thoroughly studied as their presumed importance might suggest. This review attempts to identify and evaluate the effects of territorial behavior on population density by examining the evidence from the best studied territorial species. The approach employed, which stresses comparative population dynamics, also enables new insight into the evolution of certain perplexing types of social organization and behavior in birds.

Consideration will be limited mainly to species in which the same territory is used for feeding, mating, and nesting, Nice's (1941, 1943) Type A territories, since these species offer the most persuasive evidence for the population limiting effects of territorial behavior.

EFFECTS ON REPRODUCTION

General.—Territorial individuals tend to occur in a *regular* dispersion pattern, which is more evenly dispersed than a *random* one; *clumping* of territorial individuals is rare. Operationally, territories are best defined in terms of areas "defended" over a period of time—that is, by collections of points in space and time which are characterized not only by the presence of the individual but also by the manifestation of a particular pattern of behavior, such as attack or threat toward intruders or proclamation of ownership (Noble, 1939; Emlen, 1957), the dissenting opinion of Pitelka (1959) notwithstanding. In many species the defended area is essentially equal to the "home range", "utilized area", or "activity space", although this may be true only in certain phases of the reproductive sequence in some species, such as the Black-capped Chickadee (*Parus atricapillus*) (Stefanski, 1967). In these species the analogy to a mosaic is especially clear; the defended areas abut extensively but do not overlap significantly (over a short period of time). The use of the word "territory" implies this mosaic effect at least to a certain extent. When activity spaces of different individuals overlap broadly and the areas defended, if any, are not clearly demarcated, then use of the term "territory" is not justified. One may then speak more simply of overlapping home ranges, with or without some degree of intolerance of other individuals. A regular or uniform pattern of dispersion may occur in the latter situation without recognizable territories. It is consequently not safe to infer the existence of territoriality from dispersion data alone.

Theoretically, if the territories were made small enough, all members of the population, regardless of its size, could fit into the available living space. But it is the special attribute of territoriality that at higher population densities some individuals may defend more than their proportional share of area in the more productive habitats. The ecological effects of this attribute are complex.

The critical density levels.—The principal ways by which territorial behavior might be hypothesized to influence reproductive rate at different population densities and in different habitats are summarized in Table 1. Three critical levels of population density may be recognized according to the presumed effects of territoriality on patterns of dispersion. At *Level 1* in the table territorial behavior assures a mosaic pattern of dispersion; the population is not sufficiently dense that any individual would be prevented from breeding in its preferred habitat by the territorial behavior of other individuals. At *Level 2* some individuals become dissuaded from breeding in the preferred habitat by the territorial behavior of the birds already established there; but these birds typically breed in other, less productive habitats. At *Level 3* all habitats where breeding could possibly occur are occupied by territorial individuals, and a *surplus* of potential breeders exists as non-breeding *floaters*, the *population reserve* of Meunier (1960) and others.

The classification of populations into levels according to the effects of territorial behavior on them is intended as a model to be tested and as an aid to conceptualization of the processes supposed to be involved rather than as an arbitrary means of pigeonholing populations. The three levels need not be mutually exclusive. Some species may remain at one level for many generations while other species may contain in various parts of their ranges populations at all levels. Similarly single populations may change levels in successive years. Consequently, in general an entire species cannot safely be assigned to one level; statements in this paper which do so usually refer to a specific population which was studied.

Table 1 also shows the algebraic relationships involved in comparing net reproduction in habitats of different quality under the three critical conditions of population density. For simplification only two qualities of habitat are considered, an assumption which, although unrealistic, should not alter fundamentally the relationships discussed. The expressions in Table 1 are derived from the fact that the net reproductive rate for the whole population, R_T, can be expressed as the total number of young produced to maturity in both habitats divided by the total number of mature adults there, including breeders and floaters.

$$R_T = \frac{R_p N_{Bp} + R_r N_{Br}}{N_{Bp} + N_{Br} + N_{Fp} + N_{Fr}} = \frac{\text{number of young produced to maturity in poor and rich habitats combined}}{\text{number of breeding and non-breeding adults in poor and rich habitats combined}}$$

TABLE 1

HYPOTHETICAL EFFECTS OF TERRITORIAL BEHAVIOR ON BREEDING DENSITY AND REPRODUCTION IN RICH AND POOR HABITATS AT THREE CRITICAL LEVELS OF TOTAL POPULATION DENSITY.

Critical Population Density Level	NUMBERS Rich Habitat	NUMBERS Poor Habitat	NET REPRODUCTION Rich Habitat Rate*	Rich Habitat Total	Poor Habitat Rate*	Poor Habitat Total	Total Population Rate*	Total Population Total
1	N_{Br} $N_{Fr} = 0$	$N_{Bp} = 0$ $N_{Fp} = 0$	R_r	$R_r N_{Br}$	—	0	R_r	$R_r N_{Br}$
2	N_{Br} $N_{Fr} = 0$	N_{Bp} $N_{Fp} = 0$	R_r	** $R_r N_{Br}$	R_p	$R_p N_{Bp}$	$\frac{R_r N_{Br} + R_p N_{Bp}}{N_{Br} + N_{Bp}}$	$R_r N_{Br} + R_p N_{Bp}$
3	$N_{Br} + N_{Fr}$	$N_{Bp} + N_{Fp}$	$R_r \frac{N_{Br}}{N_{Br} + N_{Fr}}$	** $R_r N_{Br}$	$R_p \frac{N_{Bp}}{N_{Bp} + N_{Fp}}$	** $R_p N_{Bp}$	$\frac{R_r N_{Br} + R_p N_{Bp}}{N_{Br} + N_{Fr} + N_{Bp} + N_{Fp}}$	** $R_r N_{Br} + R_p N_{Bp}$

N = number of individuals of breeding age
B = breeders
F = floaters; potential breeders
R = net reproductive rate per breeding individual

r = rich habitat
p = poor habitat
* Rate per individual in population (breeding and non-breeding)
** Total reproduction limited by number of territories

The various expressions in Table 1 represent restatements of this relationship as it is affected by the different patterns of dispersion at the three critical levels. Examples of natural populations at each of these three levels will now be examined.

Level 1: no limits.—At level 1 marginal habitats need not be occupied and there are no floaters. At this level preferred habitats should not be settled as densely as they would be in years when less desirable habitats are occupied. Since the concept of a Level 1 population requires that individuals not be forced out of optimal habitat into marginal habitat by aggressive competition for territories, the habitats actually occupied should not differ greatly in quality. Such appears to be the case in the Kirtland's Warbler (*Dendroica kirtlandii*), for which "there is plenty of habitat available to all without crowding" (Mayfield, 1960:51). Due in part to cowbird (*Molothrus ater*) parasitism the species is unable to populate all available seemingly optimal areas, so it has no need to occupy marginal ones.

A different situation was encountered in the Tree Sparrow (*Spizella arborea*) population studied by Weeden (1965) for three seasons in Alaska, in which "seemingly suitable habitat remained unused" (p. 205) and denser population levels were accommodated simply by reduction of territory size through elimination of the least used parts of the territories, no irreducible minimum being reached.

Some populations may reach Level 1 conditions only rarely. In Kluyver and Tinbergen's (1953) studies on Great (*Parus major*) and Blue (*Parus caeruleus*) Tits at Hulshorst, Holland there appeared to be overflow from the preferred habitat (mixed wood) into the marginal habitat (pine wood) in most years, but in a few years there seemed to be too few tits to fully occupy the area of preferred habitat. These would be years at Level 1.

Cyclic species, such as the ptarmigans (*Lagopus* spp.) probably return to Level 1 conditions periodically.

It seems likely that some species, especially those with relict or very small populations, such as those whose populations have been decimated by man through hunting (rather than habitat alteration) could be classified at Level 1, for example the Eskimo Curlew (*Numenius borealis*) and certain other shorebirds.

Regardless of the reasons why a population may have been kept to such a low density, the essential point is that since there is no ecologically significant competition for territories under such conditions, territorial behavior can have no significant limiting effect on the reproduction in the population. On the contrary, as most authors agree, territoriality under conditions of low density should aid in raising subsequent densities by helping to ensure for each family a near optimal area for nesting.

Level 2: buffer mechanisms.—When optimal habitats become so crowded that some individuals set up territories in habitats that are clearly poorer in the requisites for reproduction but are not crowded, Level 2 densities exist. Under these conditions the most attractive habitats (defined as those which have the highest population densities) tend to fill up first (i.e. Chaffinch (*Fringilla coelebs*), Glas, 1960). If the size of territories in the population were rigidly fixed and constant from year to year, this would result in a stable number of territories and a constant density of pairs in the preferred habitat, where all space would be occupied, and in a variable number of territories and density of pairs in the marginal habitats, so long as the latter had not reached their saturation limits.

Kluyver and Tinbergen (1953) in a classic study of population densities of three species of titmice in two adjacent habitats over a long period of years demonstrated that in the mixed wood habitat, where densities were high and food supply superior

(Kluijver, 1951:83, 1963), the year to year variation in density was relatively small and not proportional in magnitude to the variation in the total population in the study area. On the other hand, in the pine-wood part of the study area the food supply was poorer, densities were lower and more variable. These authors showed that the density in the preferred habitat, the mixed wood, was in effect buffered; while that in the pines was not. They referred to this phenomenon as the *buffer effect* and concluded that it was due primarily to a balance between habitat preference for the mixed wood and the repelling influence of individuals defending their territories there. In a study of the buffer effect in the Chaffinch, Glas (1960) provided similar data. Lack (1958, 1964, 1966) was unable to demonstrate the buffer effect in his British populations of Great and Blue Tits, the principal species studied by Kluyver and Tinbergen.

The buffer effect has not been clearly demonstrated in other species, but the explanation that it is due in part to territoriality has been widely accepted.

In a few species the existence of a buffer effect is suggested by observations that certain "poor" habitats of notably lower breeding density are not occupied at all in years when the density of the species in "better" habitats is lower. This was true for the Skylark (*Alauda arvensis*) population studied by Delius (1965). Similarly, the emigration of Song Sparrows (*Melospiza melodia*) in fall from a dense population to less dense ones (Tompa, 1962) suggests that a buffer effect might be present.

Lack's (1958, 1964) failure to find evidence of a buffer effect might be due to differences in the study areas used. A peculiarity of the region where Kluyver, Tinbergen, and Glas worked was that the habitat with a stable population (mixed wood) was *small* in area compared with the habitat with the more variable population (pine wood), which was typical of large areas adjacent to the studied population. Furthermore, in the Dutch work the two habitats studied were extensively *contiguous* on the study areas. Neither of these peculiarities was true for the populations reported on by Lack.

In order for the causative mechanism of the buffer effect to operate in the manner conceived by Kluyver and Tinbergen individual birds must be presented with a *choice* of habitats within the small region where the individual is likely to seek a territory. Since titmice, chaffinches, and other territorial species show a strong propensity to set up territories in the same places in successive years or in the local region where they were hatched, most individuals probably would not search over a wide area. If they did not encounter a choice between rich and poor habitats in the area of their search, they could not take part in the buffer effect. It would seem then that the amount of *contiguity* between rich and poor habitats might be critical for the buffer effect to operate. This is a point on which adequate field data are lacking.

The prediction that dense breeding populations of a territorial species should show less yearly variation than other less dense populations of the same species was tested by Brewer (1963) using data from yearly breeding bird censuses in five localities as reported in Audubon Field Notes. The predicted inverse relationship between mean density and variability was *not* obtained when species were considered singly. Brewer ascribed the failure of his data to show the predicted inverse relationship to the long distances separating most of the census areas, which ranged from Minnesota to Maryland, and stated that in two areas "only" 60 miles apart variability was, as postulated, negatively correlated with density in seven species and positively correlated in only two, all of which are territorial. In interpreting such data it must be realized that what constitutes optimal habitat in one geographical region may quite logically support a lower density than certain suboptimal habitats in another region simply because the former habitat is located near the periphery of the species range or in a region which is not well suited to the species for climatic reasons. Consequently, Brewer's test, although inconclusive when rigorously interpreted, does serve to point out complexities which must be taken into account in future studies of the buffer effect.

Still another factor must be considered when looking for the buffer effect. According to the model in Table 1 a buffer effect can be predicted for populations at Level 2, but its effect should be much less or absent at Levels 1 and 3. Before stating for any given population that a buffer effect might be expected, it must be shown that the birds are nesting in habitats differing sharply in density or productivity (and presumably attractiveness) (therefore not at Level 1) and that floaters are not prominent (therefore not at Level 3). Apparently because of the census methods employed (nest box occupancy, singing male) it was not possible to calculate the density of floaters in any of the populations which have been studied in respect to the buffer effect (or there were none).

Only further field studies will be able to show whether the buffer effect is widespread and has an important effect on dispersion among bird populations or is only the result of a certain set of conditions not yet empirically identifiable which were found locally in the study areas of Kluyver and Tinbergen (1953) and Glas (1960). In view of the small number of populations (6), species (4), study areas (2), and geographical regions (1) in which the buffer effect has been shown and of the conflicting evidence from studies of other populations including some of the same species (Lack, 1958; Brewer, 1963), I share Lack's (1964, 1966) reservations and believe that judgement on the significance of the buffer effect in bird populations ought to be suspended until more data on natural populations become available. Certainly, until such are available, there is no justification for pointing to the buffer effect as a widespread and important means by which territorial behavior limits breeding density. Its present status is that of an hypothesis accompanied by little and conflicting evidence.

Since it is known for a number of species (e.g. Great Tit, Kluijver, 1951:83, 1963; Lack, 1955, 1958, 1964; Pomarine Jaeger (*Stercorarius pomarinus*) and Snowy Owl (*Nyctea scandiaca*) Pitelka, Tomich, and Treichel, 1955; Buzzard (*Buteo buteo*) Mebs, 1964; Ovenbird (*Seiurus aurocapillus*) Stenger, 1958) and undoubtedly in others that density of territories is directly correlated with the richness of the food supply, it is reasonable to assume that avian productivity in the preferred areas (judged by density) would exceed that in the marginal areas if all other factors (including density) were equal. Data of Kluijver for the Great Tit indicate that the number of young fledged per breeding pair per season would be higher in the habitat of highest density than in the habitat with normally lower densities if the densities were equal in the two habitats (which they usually were not).

Territorial behavior at Level 2, according to the model in Table 1, should result in lower production per pair in the marginal habitats than in the rich ones. This would result in a *lower rate* of production for the population as a whole including rich and poor habitats but would *increase the total production of the population*, not decrease it as N. Tinbergen (1957:20–21) has claimed: in addition to the regular production from the rich habitats there would be an increment from marginal habitats that were not previously being utilized. (These relationships may be seen in Table 1 by comparing the rate and amount of reproduction for the whole population at Levels 1 and 2.) Consequently, competition for territories would be increased until all possible habitats were fully exploited, at which time the buffer mechanism in its simplest form would cease to operate. It is obvious that territorial behavior at Level 2 is not a mechanism of population control when the whole population is considered. It would be significant *only in preferred habitats* and primarily for the range of population sizes and densities in which preferred habitats were filled but possible marginal habitats were not. Its effect for the population as a whole should be viewed not simply as curtailing production and preventing overpopulation (Wynne-Edwards, 1962:149) but as insuring the maximum production from the available habitat. This in turn would tend toward greater competition for territories in favorable as well as unfavorable habitats.

In view of these logical considerations it is clear that some authors have oversimplified the situation. For instance, N. Tinbergen, (1957:20) who then apparently believed that the general "function" of territoriality was dispersion, has written, "The existence of a dispersion mechanism [territorial behavior] means that density is reduced in the most desirable habitats. If the less desirable habitats are occupied as a consequence of this, but offer less good chances of success (or, of course, if many birds are prevented from settling down and breeding at all) this would mean that the dispersion mechanism would reduce absolute numbers by reducing overall breeding success." Although a reduction is spoken of, such a reduction could never actually occur since it would be a reduction from a situation that does not exist. Tinbergen was, in my interpretation, comparing the situation as it is with the situation which might exist if the species were suddenly to become non-territorial and all floaters were allowed to breed in the most desirable habitats. As I have shown above, in going from Level 1 to Level 2 an increase in absolute numbers would occur in a real population, *not a reduction*, nor would there be a reduction in density. A further complication, which cannot be considered here, arises from depressions in productivity due to high densities. Because of this complication reproductive rate in a "poor" habitat sparsely populated might exceed that in a "rich" habitat densely populated (Perrins, 1963, 1965).

Some other population studies, although not concerned specifically with the buffer effect, yield some insight into how the movements of individuals are affected. The dynamics of European Blackbird (*Turdus merula*) populations have been studied in a number of areas (e.g. England, Snow, 1958; Poland, Graczyk, 1959; Germany, Erz, 1964; Czechoslovakia, Havlin, 1962, 1963; Switzerland, Ribaut, 1964). It has been found that in populations of high density many young individuals are unsuccessful in establishing territories apparently because of territorial behavior. Under these conditions some first-year birds remain as floaters in the dense populations and some probably seek territories elsewhere, where the density is lower. Since some populations seem to produce either more or less than is needed for simple replacement of losses, it can be inferred that there is probably movement from the more productive into the less productive populations. At Oxford (Snow, 1958) the high density populations produced more birds than could breed there, and probably supplied the low-density populations with some breeders. In contrast, on the continent some high-density populations which were studied produced less than enough to maintain their high density, hence must have depended on immigration from other populations, presumably of lower density. Thus the flow of individuals, although always going from the over-productive to the under-productive populations, need not always go from high-density to low-density populations, despite the known limiting actions of territoriality at high densities in the populations studied. This anomaly is due to reasons other than the limiting of breeding density by territoriality (see below), and is, therefore, not inconsistent with the model described in Table 1.

Level 3: floaters.—In theory, when the number of potential breeders is sufficiently great, a point is reached at which an upper limit is imposed on breeding density by means of territorial behavior; this condition is designated as Level 3 in Table 1. Individuals above this limit, by definition, would be prevented from breeding anywhere, except in completely unsuitable habitat, by the territorial behavior of the breeders. This level is distinguishable from Level 2 (in theory) by the absence of suitable unutilized habitat and by the presence of floaters in at least the rich habitat. The model described in Table 1 requires that total reproduction at Level 3 be limited in poor as well as in rich habitats.

It should be noted that in the model although the rate of reproduction for the population as a whole becomes lower as the proportion of floaters becomes greater, *total* production is, nevertheless, *greater* than at Level 2, no matter how low the *rate* may become. Reproduction, according to the model, is constant because the number, density, and rate of reproduction of actual breeders is constant (in an unchanging environment); the number of floaters and the reproductive rate for the population as a whole is irrelevant to total reproduction (in the model). In nature, reproductive rate of the breeders may be lowered at Level 3 for reasons other than the exclusion of surplus individuals from breeding. The model states only the predictions of reproduction according to the theory of population limitation by territorial behavior; it is not intended to predict the action of other density-dependent factors, some of which are discussed later.

Since it is Level 3 at which the classical limiting effects of territoriality should be best shown, it is desirable to examine the evidence for the existence and operation of Level 3 conditions. The foundation of the argument that territorial behavior limits breeding density consists of a *combination of behavioral and ecological observations.* The behavioral evidence involves observations of individuals being prevented from establishing new territories in areas already claimed by other individuals through aggressive behavior of the owners. The ecological evidence consists of data on the stability of breeding populations and on the existence of a fraction of the population which is capable of breeding but does not do so except when some or all of the breeding population is removed.

The behavioral evidence alone is insufficient to indicate whether or not territorial behavior is exerting any limiting effect on total reproduction. An individual prevented from establishing a territory in one place may be successful elsewhere or even at the same place at a later time. Many observations of both successes and failures of birds attempting to set up territories on already occupied areas have been published (e. g. Lack and Lack, 1933; Lack, 1954; Hinde, 1956).

The ecological evidence concerning stability of breeding density is also insufficient by itself to conclude anything about the effects of territorial behavior on a population. Lack (1966) has argued that territorial behavior, if it is significant, ought to impart greater stability to breeding density than might otherwise be the case. But under Level 1 conditions territorial behavior would not necessitate stability because the limit to breeding density would not have been reached. At Level 2 stability might be expected in the better habitats but not in the poorer ones; however, even in this case stability is a relative matter. At Level 3 one might predict a stable breeding density, but again there are exceptions and a rigid upper limit is not required for territoriality to be effective. Stability need not necessarily occur if there is variation in the environmental factors which set the behavioral limit. For example, in the Red Grouse (*Lagopus lagopus scoticus*) Jenkins (1963) felt that territorial behavior was preventing some individuals from breeding in all years, yet breeding density varied from 14 to 34 birds/40 ha in different years. This variability was attributed to environmental factors acting on the birds' behavior.

If stability does occur, it might be caused by other factors, such as stability in winter food supply, number of nest sites, winter survival, and need not be wholly attributed to territorial behavior. In general, one cannot safely conclude anything about the presence, absence, or importance of territorial behavior in population regulation from data on population stability alone; nor is conspicuous stability of breeding densities a necessary consequence of partial limitation of breeding densities by territorial behavior.

In polygamous species with Type A territories the numbers of females may constitute a unique "control" against which to compare those of the males. Brenner (1966) in a study of Red-winged Blackbirds (*Agelaius phoeniceus*) in a Pennsylvania cattail marsh found that although the density of females in the marsh varied considerably over five years (from 7 to 42) the number of males remained remarkably stable (17 to 21). This suggests that the marsh was always saturated (Level 2 or 3) in respect to males but not with respect to females. Large yearly changes in the numbers of females (and, presumably, the total population of males), which were directly correlated with rainfall, nesting cover, and insect biomass, were masked in the numbers of territorial males. If the number of females can be accepted as a reasonable index of the abundance of potential male territory holders (adult and yearling), then this population study would appear to constitute an unusually clear case of the buffering of breeding density among males through their territorial behavior.

The ecological evidence concerning the existence of a *surplus* of potential breeders during the breeding season is critical, since the theory that territorial behavior prevents some individuals from breeding by denying them territories requires that a surplus be present. If it can be shown for a territorial species that a surplus is present and that surplus individuals will establish territories and breed when the previous owners are removed, it would seem safe to conclude that the presence of the previous owners was somehow preventing the surplus from breeding, most likely by territorial defense. Consequently, *from the standpoint of the limitation of breeding density information on the existence and magnitude of breeding surpluses is crucial.*

The existence of a floating population of mature but non-territorial adults is not easily demonstrable, since the commonest census techniques, counting singing males or occupied nest boxes, tend to miss floaters or not to distinguish them from breeders. A method for identifying individuals, or at least preventing confusion between them, is required.

The most abundant type of information suggesting the existence of a surplus consists of observations of rapid replacement of lost mates. Many examples of this phenomenon were described by Darwin (1871:738–741) and many more since (references in Meunier, 1960; Wynne-Edwards, 1962). Although such cases are suggestive, they concern individuals rather than populations, and they give little information on the relative size of the surplus, its ecological distribution, or its existence from year to year. Furthermore, negative results such as failure of a female chickadee to replace her lost mate (Smith, 1967) usually are not reported, making it difficult to evaluate the positive ones. Consequently, none of these observations by themselves can be taken as conclusive evidence that a surplus of significant proportions is widespread and of regular yearly occurrence in the population concerned.

In a few studies breeding birds have been removed from their territories in larger numbers. Such studies have been widely accepted as providing dramatic proof of the limiting effects of territorial behavior on total reproduction, but there are reasons to doubt whether this conclusion is justified.

The experiments of Stewart and Aldrich (1951) and Hensley and Cope (1951), during an outbreak of the spruce budworm (*Choristoneura fumiferana*) in northern Maine, in which a large percentage of all individuals of all avian species was removed by shooting from a 40-acre tract of spruce-fir forest showed that a spectacular replacement of territorial males over a short period of time occurred. In 1949, only 148 territorial males were censused before collecting began; but collecting from June 15 to July 8, yielded 420 adults (original owners plus their replacements). In the following year the experiment was repeated; 154 pairs were censused, and 528 adults were subsequently collected. Although a rapid replacement of males was demonstrated in both 1949 and 1950, *none of the females of the 10 most abundant species removed was replaced* (Table 1 of Hensley and Cope). Consequently, there is no evidence 1) that a surplus of females existed, 2) that any females were denied opportunity to breed by territorial behavior, or 3) that reproduction in the population was being limited to the slightest degree by territorial behavior. The replacements in these species consisted entirely of males (and a very few individuals labelled "undetermined"). Moreover, even in the original populations which were first collected, males outnumbered females in the abundant warbler species by from 1.7 : 1 to 9 : 1, the excess of males being generally less conspicuous in the second summer. The reasons for this apparently uneven sex ratio in the adult population are not clear.

In the Pied Flycatcher (*Ficedula hypoleuca*), in which 30 per cent of males were unpaired in Curio's (1959) population, the greater mortality of females than males, claimed by Curio (but see Lack, 1966:112), was suggested by Meunier (1960) as the cause of the surplus and the limiting factor for the number of breeding pairs. For a number of European species other than strictly hole-nesters Meunier has pointed out that the non-breeding individuals in populations studied by various authors were almost all males.

A surplus of non-territorial males has been demonstrated by shooting of territorial males in August in Red Grouse (Jenkins, Watson, and Miller, 1964) and in mid-March in Rock Ptarmigan (*Lagopus mutus*; Watson, 1965*a*). In the removal experiments of Orians (1961) on Red-winged Blackbirds only males were shot, and these were repeatedly and rapidly replaced. Removal experiments with females were apparently not performed, but since this species is polygynous, the existence of a surplus population of females would not necessarily be expected (although female territoriality does occur in the species, Nero, 1956).

Holmes (1966) conducted removal experiments on Dunlins (*Erolia alpina*) in Alaska, where the species holds Type A territories through the incubation period. A total of 31 adults of both sexes in two years was collected during the period of arrival on the breeding grounds from a plot which normally supported 4 or 5 pairs. However, birds deserting their territories in late June or early July because of the nest predation by jaegers (*Stercorarius* spp.) were not replaced, despite the continuance of territorial activity through mid July.

Systematic experiments on the promiscuous Blue Grouse (*Dendragapus obscurus fuliginosus*) in British Columbia revealed no significant evidence of a surplus of adult males (Bendell and Elliott, 1967). Of the yearling males only about 11 per cent normally entered the territorial population, but on plots where all territorial birds were removed 64 per cent did so. This suggests that the establishment of breeding territories was being inhibited in about half of the yearlings by the normal breeding population.

There was no evidence of a surplus of hens. Similarly the removal of 10 territorial male Ruffed Grouse (*Bonasa umbellus*), also promiscuous, from a 360 acre area in spring resulted in replacement by only 2 birds, both yearlings (Dorney, 1960, cited by Bendell and Elliott).

In a few studies floaters have been detected by means of the individual recognition enabled by banding. Kendeigh (1941) and Kendeigh and Baldwin (1937) have analyzed data on non-breeders from a 19-year study of a dense breeding population of House Wrens (*Troglodytes aedon*). Kendeigh (1941:42) wrote: "The size of the house wren's territory is compressible with increasing number of birds present, at least down to a minimum. When the territories are reduced on an average to that minimum, resistance to invasion by more individuals becomes exceptionally increased . . . and the population tends to be thereby limited." This conforms well with Huxley's (1934) analogy to "elastic discs". Restricting the analysis to the 10-year period of most efficient trapping Kendeigh (1941) estimated that during the first period of breeding 15 per cent of the males and 13 per cent of the females "did not make serious attempts at nesting"; for the second period of breeding the figures were 20 and 25 per cent respectively. If males which held territories but failed to attract mates are included, the figures rise to 28 per cent for the first period and 35 per cent for the second. A closer analysis of the non-breeders showed that they varied considerably in their "reproductive vigor," from those who did not hold territories in either breeding period to those who did in both but lacked only a mate. The percentage of first-year males was higher among the unmated birds (80 per cent) than among the mated ones (57 per cent). The reasons for non-breeding in these individuals are not known and it cannot be simply assumed that the territorial behavior of their neighbors was responsible (see below).

In a five year study of a color-marked population of Skylarks Delius (1965) estimated the proportion of non-territorial floaters at 10 per cent in most years, with males predominating. Some of these individuals replaced breeding males which had disappeared, thus showing that they were not inherently unable to breed. Most seemed to be one-year-old birds. In one year when the density of breeders was 20 per cent lower than usual no non-breeders were seen.

In a population of the European Blackbird Ribaut (1964) found in two successive breeding seasons a non-breeding fraction constituting about 14 per cent of the total population (64 birds). Breeders which died were quickly replaced from the reserve population, which included females as well as males. Reserve males attempted to hold territories but were prevented from doing so by the established owners. It should be mentioned that this was an urban population and showed some of the characteristics of urban and suburban Blackbird populations in Europe (Erz, 1964; Graczyk, 1959; Havlin, 1962, 1963; Lack, 1966), rich winter food resources, high population density, and high survival rates. Despite the high survival rate and abundant food supplies of the urban populations studied by Erz and Ribaut, the population density could not apparently be maintained by reproduction of the populations studied but depended on immigration from other populations. In the case of Ribaut's population this failure of reproduction to keep pace even with a low mortality rate was due primarily to a high frequency of nest desertions, not to limitation of the numbers of breeders.

A surplus of non-territorial cock Ring-necked Pheasants (*Phasianus colchicus*) amounting to 11 per cent of the total male population was detected by Burger (1966) in the year of highest population density in a three-year study in Wisconsin. Few if any surplus birds were found in the other two years.

An unusually large surplus of individuals which were excluded from holding suitable territories existed in the population of Australian Magpies (*Gymnorhina tibicen*) studied by Carrick (1963). The numbers of non-breeders in the breeding season were not given in his preliminary report, but judging from the large surplus in Australian mid-winter, 60 per cent of the population, and the high survival rate, the breeding surplus must have been very large. Vacancies in the breeding population were quickly replaced from the non-breeders, indicating that some of the deprived individuals were physiologically capable of breeding and probably prevented from doing so by the unavailability of territories.

Although many authors have concluded that territorial behavior was limiting the breeding density of a population studied by them, the evidence on which their conclusions were based has sometimes been unsubstantial, such as the observation of an individual bird failing to establish a territory at a particular place at a particular time. I have tried to emphasize in this section what should be, but has not always been, self-evident, namely, that something more than the observation of a few individuals fighting and threatening is necessary to conclude anything about the effects of territorial behavior on population dynamics, specifically about the limiting effects of territorial behavior. A number of critical points must be confirmed on the population level before it can be concluded that breeding density is being limited by territorial behavior in the Level 3 manner and that recruitment is thereby curtailed.

First of all it must be established that some individuals are being deprived of a chance to breed. It must be shown that a surplus exists and that it constitutes a significant fraction of the population. A surplus can exist for reasons other than territoriality, for example, when the number of suitable holes for hole-nesters is limited (references cited by Meunier, 1960; Pfeifer, 1963) or when delayed reproduction is the rule, as in certain colonial seabirds. The second requirement, therefore, is the demonstration that it is the territorial behavior of the established birds that is preventing the floaters from breeding. This can be done by mass depopulation of a particular area, as was done in a number of studies described above, or better, by selective removal of territory owners, leaving the floaters intact. In only two cases known to me has the latter been done after the spring arrival period was over on a population basis with a positive result (Orians, 1961; Bendell and Elliott, 1967). However, some authors working with populations known to have a surplus have noted that accidental losses from the established breeding population were quickly replaced from the non-breeding fraction (e.g. Delius, 1965; Ribaut, 1964; Snow, 1958; Carrick, 1963; Rowan, 1966).

Furthermore, if the conclusions are to be extended to include limitation of total reproduction, a third requirement must be added. It must be shown that territoriality prevents some females from breeding. Most workers have concentrated on the males, probably because they are the more territorial sex and more conspicuous. Nevertheless, as we have seen, generalizations valid for males are not valid for females until proven so. The data of Delius (1965) on Skylarks, Ribaut (1964) on European Blackbirds, and Carrick (1963) on Australian Magpies show that some females are prevented from breeding in these species by territorial behavior, but in a number of other important studies data on females is lacking or suggest that females are not limited, as in polygynous species and the depopulation studies of Stewart and Aldrich (1951) and Hensley and Cope (1951).

Lastly, even when surpluses including females have been demonstrated as being caused by territoriality, interpretations about the importance of territoriality for the species as a whole and for other species require caution. It is natural that in attempting to demonstrate the existence of limiting effects of territorial behavior an investigator would choose the densest population available. But if this population is not representative of populations of the species in the same region existing under natural conditions, it would be incorrect to generalize. Unfortunately, many study areas owe their unusually high densities to artificial conditions created by man, such as public parks, botanical gardens, managed hunting grounds, and agricultural situations.

For example, as Lack (1966:125) has pointed out, the peak density of Blackbirds in the Oxford Botanic Gardens was about ten times that in Wytham Wood and much greater than in any other known population existing under approximately natural conditions.

For Australian Magpies (*Gymnorhina* spp.) Robinson (1956:274) has described the human influence as follows: "It appears that it is the dairying districts throughout Australia which are carrying the biggest populations at present. These are all in the higher rainfall belts which produce the maximum of cultivated green feed possible during the year. These are really artificial conditions humanly created, as the habitat has been considerably changed by man. In its natural state it was mostly heavy forest country with no pasture and Magpies were rarely seen. In the drier areas Magpies are not so plentiful, and are seldom seen in the dry interior where average rainfall drops below ten inches and droughts are common." He observed that the population increase on his study area over a ten year period was correlated with clearing and pasturing, as well as the provision of extra water (p. 266). It is not surprising that the simultaneous enrichment of the food supply and destruction of trees used for nesting would produce a surplus of birds which were unable to find nesting territories.

Other species in which surpluses including females have been associated with human manipulation of the environment are the House Wren, Red Grouse, and Partridge. The extent of the human influence in some of these cases is difficult to evaluate. Apparently the only population of a monogamous species with such a surplus in which human influence can be completely excluded is in the Rock Ptarmigan, and even in this species bigamy occasionally occurs (although many hens may remain unpaired; Watson, 1965*b*).

In my opinion, this amount of reliable information is hardly sufficient for sweeping generalizations concerning the limiting effects of territorial behavior on reproduction, which so frequently are seen in textbooks and journal articles.

Lack's views.—In his reviews of avian population studies Lack (1966, 1954, and earlier) has repeatedly de-emphasized the role of territorial behavior as a limiting factor for breeding densities. His principal recent criterion for judging the importance of territorial behavior was not the magnitude and persistence of a breeding surplus which is emphasized in this paper, but was the stability of breeding densities around an upper limit (e.g. 1966:78). For a number of cases cited by recent authors as examples of population regulation through territorial behavior (e.g., in the studies of European Blackbirds, Song Thrushes (*Turdus philomelos*), Song Sparrows, Great Tits, Red Grouse, and Rock Ptarmigan). Lack pointed to sharp differences in densities in different years and in different habitats as objections to this interpretation. He repeatedly took opposition to Huxley's (1934) "elastic disc" hypothesis on these grounds. On the other hand, again using density as a criterion, he accepted territorial behavior as a limiting factor for Tawny Owls (*Strix aluco*), despite a steady increase of nearly 90 per cent in number of breeding pairs in the study area.

In my opinion, stability of breeding density is not an adequate criterion for assessing the limiting effects of territorial behavior, for reasons already stated. It may provide hints, but it is not decisive.

Contrary to Lack, I find no reason why territoriality could not participate in limiting Red Grouse or other species at quite different densities in different years, the variation being attributable to variations in the history, age, or condition of the birds. Nor is it difficult to conceive of territorial behavior helping to limit Song Sparrow populations at different densities in British Columbia and Ohio. In both types of variation, yearly and regional, the limit is a function of the *interactions* between the quality of the environment, the condition and number of competing individuals, and the behavior of the species.

These interactions are strikingly shown in Tompa's (1962, 1964) study of the Song Sparrow on Mandarte Island, British Columbia. This population had been stable at a level about 10 times Nice's (1943) population in Ohio; and Tompa (1962) concluded because of the fully occupied habitat, the stability at high density, and the emigration which was temporally correlated with territorial behavior, that the population was limited by the behavior of the birds. Lack (1966) objected on the grounds that the 1963 population showed an increase of 50 per cent over the allegedly stable population of 1960–62. However, there were surplus, non-territorial males and territorially induced emigrations of males and females in all years of the study. This indicates Level 3 conditions for the males and Level 2 for the females. The increase in 1963, was apparently brought about by a quirk in the weather (Tompa, 1964:52) which by killing many adult territory holders made possible the establishment of an unusually high number of bachelor territories by first year birds in 1962. In 1963, most of these individuals retained their territories and obtained mates, thus accounting for the sudden rise in the breeding population. The important point to note is that the weather played

Table 2

Assignment of Selected Populations to the Critical Levels of Breeding Density described in the Text and in Table 1. Levels 2 and 3 Indicate Limitations of Breeding Density Mediated by Territorial Behavior During the Breeding Season; Level 1 Indicates Absence of Territorial Limitation at that Time. Surplus Individuals are Indicated as Percentages of the Total for the same Sex, Where Possible.

Species	Reference	Place	Habitat	Surplus Non-territorial Males	Females	Level	Comment
Blue Grouse	Bendell and Elliott 1967	B.C.	Conifer	0	0	1	Yearling males at Level 3
Kirtland's Warbler	Mayfield 1960	Michigan	Jack pine	0	0	1	
Tree Sparrow	Weeden 1965	Alaska	Tundra	0	0	1	
Long-billed Marsh Wren	Verner 1964	Washington	Marsh	0	0	1	Bachelor territories 19–36%
Great Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered

TABLE 2 cont.

				Surplus Non-territorial			
Species	Reference	Place	Habitat	Males	Females	Level	Comment
	Lack 1966	England	Broad-leaved woods	0	0	1	
Blue Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
	Lack 1966	England	Broad-leaved woods	0	0	1	
Coal Tit	Kluyver and Tinbergen 1953	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
	Gibb 1960	England	Pines	0	0	1	
Chaffinch	Glas 1960	Holland	Pine wood	0	0	1	
			Mixed wood	0	0	2	Density buffered
Many passerines	Hensley and Cope 1951	Maine	Spruce woods	Many	Few	Males 3 Females 1	
Song Sparrow	Tompa 1964	B.C.	Shrubbery	4–8%	0	Males 3 Females 2	
Skylark	Delius 1965	England	Dunes	— 10% —		3	Mostly males (?)
Blackbird	Snow 1958	England	Botanic Garden	+	+	3	
	Ribaut 1964	Switzerland	Park	19%	8%	3	
House Wren	Kendeigh and Baldwin 1937	Ohio	Garden Orchard	15%	13%	3	
Australian Magpie	Carrick 1963	Australia	Savannah, pasture, woods	>50%	>50%	3	
Red Grouse	Jenkins 1963	Scotland	Heather	— + —		3	
Rock Ptarmigan	Watson 1965	Scotland	Tundra	— + —		3	
Partridge	Jenkins 1961*a*, *b*	England	Fields	— + —		3	
Red-winged Blackbird	Orians 1961	California	Marsh	+	—	Males 3	Polygynous

a role in determining the limit which was mediated by the territorial behavior of the birds. The complexity of the interaction between environment, condition and number of competing individuals, and behavior is again shown, and the danger of using stability of breeding density as a criterion is illustrated.

Yearly and regional variations in the degree of crowding necessary to prevent some individuals from holding territories should be expected, and the concept of a rigid maximum breeding density which is independent of the environment should be rejected. The use of the surplus as an indication of a limiting effect of territoriality frees one from reliance on stability of breeding density.

The only population that Lack (1966) admitted was probably limited by territorial behavior was that of the Tawny Owl studied in a British broad-leaved woodland by Southern (1959). In contrast, it will be apparent from a reading of my discussions of Levels 2 and 3 and from Table 2 that, using different criteria, I have accepted many cases of partial limitation by territoriality which were rejected by Lack; my assignment of a population to Level 2 or 3 indicates my belief that territorial behavior was participating in the limiting of breeding density in that population, either by forcing some individuals into poorer habitats or by preventing them from breeding altogether.

The conclusions of Lack and others on the importance of mortality in non-breeding seasons and on the unimportance of territorial behavior in setting breeding densities of titmice have been challenged by Smith (1967) on the basis of her study of survival and dispersal of Black-capped Chickadees. She emphasized the importance of determining precisely the time at which the major losses from the population occur and whether or not they coincide with the resurgence of territorial behavior in the spring and the resultant dispersal of winter flocks. At least some of the disagreement on this matter appears to be semantic.

Other behavioral, density-dependent effects.—In addition to the effect of territoriality of excluding some individuals from breeding, there are other consequences of behavior at high population densities which depress reproduction. There is evidence that density-dependent depression of reproductive success can arise from an increased frequency of agonistic encounters resulting from the compression of territories or overlapping of activity spaces and the presence of floaters continually attempting to set up new territories in defended areas. Depression of reproductive success at high population densities in natural populations of mammals is now well known (Christian, 1963), but it is rarely reported for birds. It was first reliably reported by Kluijver (1951, Kluyver, 1963) for the Great and Blue Tits. Lack (1958, 1966) demonstrated a reduction in clutch size at higher breeding densities in the Great, Blue, and Coal Tits. Perrins (1965:621) found a similar relationship in the Great Tit. Kluijver demonstrated that clutch size and the percentage of females attempting second broods were lower in the years of higher densities in his study areas. The effect was shown in comparisons between habitats in the same years and between years in the same habitats. Kluijver was inclined to attribute the effect essentially to an increased frequency of agonistic encounters at high population densities, but the food supply was not measured or controlled.

In a summary paper on the Australian Magpie, Carrick (1963) reported evidence for an effect of agonistic encounters on ovarian function. In this species oocyte development could be "inhibited by emotional factors, such as intrusion of a strange magpie of either sex into the territory, an undue amount of boundary fighting, or domination by another female of the same group" (p. 749). Inhibition of nesting in resident females because of the presence of non-territorial individuals was directly observed and said to have been confirmed experimentally. In the male, Carrick found that certain physical environmental stimuli were necessary for maturation of the testes but that age and "social status" determined how far development would proceed. Further suggestive evidence of a depressive effect of agonistic stimuli on gonadal function was provided in a report by Ficken et al (1960) in the Budgerigar (*Melopsittacus undulatus*). They demonstrated that the presence of a mirror in the cage inhibited ovarian but not testicular development. A neurobehavioral demonstration of the inhibitory effects of agonistic behavior on ovarian development was given by Phillips (1964) in the Mallard (*Anas platyrhynchos*): lesions in the medial archistriatum produced both reduction in agonistic behavior and disinhibition of ovarian follicle development in the same individuals.

A different side effect of behavior at high populations densities was observed by Kendeigh (1941:28–29) in the House Wren. As males competed aggressively for nest boxes (which were in excess of requirements) they cleaned out eggs and young of former owners; of 331 matings recorded, eggs were destroyed in 13 cases and young in five, resulting in about a five per cent loss from this cause. Kendeigh wrote, "Although there is considerable variation in this aggressive behavior, it tends to be most intense during years when the total house wren population on the area is highest" (p. 117).

An effect of high population density on parental behavior may be indicated in certain upland game birds. Jenkins (1961*a*, 1961*b*) found an inverse correlation in the Partridge (*Perdix perdix*) between frequency of agonistic interaction and chick survival. In Red Grouse it was shown that chick survival was correlated with general physiological condition of the adults (as reflected in body weight, incidence and severity of parasitism, and summer survival), persistence of the parents with the nest and the brood, and frequency of distraction display (Jenkins, 1963; Jenkins et al, 1963). It seems possible that an unusually high frequency of agonistic encounters in the Partridge might have been detrimental to general health or hormone balance thus reducing the effectiveness of parental behavior. Density-dependent depressions of population density have been reported for several other species, but the mechanisms are unclear.

In any consideration of reproductive success as a function of agonistic behavior it is necessary to make sure that the food supply is controlled. Although compression of territories and creation of a surplus increases the frequency of agonistic encounters, it also reduces the share of the food supply available to each territory holder. Perrins (1963, 1965) in a study of the Great Tit demonstrated that weight of nestlings and survival for the first three months of life in an area where the density was 0.43 pairs per acre were higher than in nestlings from an area with a density of 1.3 pairs per acre. He considered it likely that this difference was due to the amount of food available during the development of the young; however, the less likely possibility of an effect of agonistic behavior on the frequency of feeding the young was not excluded by his data, and he has cautiously reserved judgement on the role of the food supply in this case.

The importance of isolation for the breeding of some species of birds in captivity is well known to aviculturists; crowding or the presence of other birds in these species somehow inhibits reproduction. Extreme crowding in poultry (*Gallus domesticus*) is thought to affect adrenal function (Siegel, 1959, 1960). Subordinate dominance status in a group of the same species, regardless of density, seems to depress testis function (Flickinger, 1966). Whether or not such endocrine effects are of widespread significance in mediating behavioral effects on reproduction or mortality in natural populations re-

TABLE 3
CRITICAL PERIODS FOR POST-BREEDING LOSSES IN EUROPEAN TIT POPULATIONS, WITH SPECIAL REFERENCE TO GIBB'S (1960, 1962*a*) STUDY OF COAL TITS

	Phase I	Phase II
Principal Characteristic	Dispersal	Death from food shortage
Season	Autumn (Spring)	Late winter
Agonistic Behavior	Territory defense	Rank-dominance
Food Supply	Not critical	Critical

mains to be determined. Only in the Australian Magpie (Carrick, 1963) is there evidence of the importance of endocrine effects in a natural population.

High densities do not necessarily cause low reproductive success in natural populations. For example, the dense population of Song Sparrows studied by Tompa (1962, 1964) and the dense population of European Blackbirds in the Oxford Botanic Garden studied by Snow (1958) both maintained high levels of production relative to other populations of the same species despite unusually high densities of breeders. On the other hand, a dense population of European Blackbirds studied by Ribaut (1964) had such poor reproductive success that the maintenance of the high population density probably depended on immigration from other areas.

Although the density-dependent behavioral effects on reproduction referred to above share in the regulation of population density, they have not been shown in any species to be the primary factors responsible for population declines from high levels (Lack, 1966).

EFFECTS ON MORTALITY

In certain populations of titmice (Kluijver, 1951; Lack, 1955, 1958, 1964, 1966; Gibb, 1960, 1962*a*; Perrins, 1963) and probably other species the principal fluctuations in breeding density are effected by mortality in the non-breeding seasons (but see Smith, 1967, for a contradictory interpretation). The possibility exists, consequently, that territoriality may have a greater effect on population fluctuations in some species through its effects on mortality in summer, autumn, and winter than through its effects on reproduction. The effects of territorial ownership may persist through the year in some resident species in the form of dominance in the home area even though boundaries may not be defended, as has been demonstrated in a number of species including the Great Tit (references in Brown, 1963*b*).

That survival is enhanced by territorial ownership in a number of resident species is suggested (but not proven) by the high rate of loss from populations of marked individuals lacking territories (e.g. Black-capped Chickadee, Smith, 1967). The food value of the territory is important to winter survival. In Kluijver's (1951) study, Great Tits holding breeding territories in the pine wood but wintering in the mixed wood, where the winter food supply was richer, suffered a higher mortality rate than individuals whose breeding territories coincided with their wintering areas in the same mixed wood. The higher rate of survival of the latter birds might be attributed to their probable dominance at food sources over the individuals from the pine wood.

It is convenient to consider post-breeding losses (after the post-juvenal molt) as occurring in two phases as summarized in Table 2. These may be demonstrated in the data from Gibb's (1960) study of a Coal Tit population. The first phase consists of *dispersal*; it occurs mainly in autumn (but also in spring) and may result in either a loss or a gain in particular local populations. The number in the whole population of the species is, however, unaffected by dispersal alone.

The bulk of dispersal takes place before competition for food has become critical (but not in Perrins' study). In the four years of Gibb's study the percentage of birds disappearing from the population varied only from 46 to 53 in this phase (July through September). It is noteworthy that the number of emigrants was not density-dependent (Gibb, 1960, 1962*a*).

The second phase occurs primarily during the late winter. It consists of the actual death of individuals due directly or indirectly to food shortage and accompanied by severe competition for food. The percentage of birds disappearing for Coal Tits during this phase, from October through March, varied greatly, from 34 to 77 per cent and was inversely correlated with the level of the food stock at the end of winter.

The role of territoriality differs in the two phases. In the first, territoriality reduces the population in one area by shunting the surplus into vacant territories and other areas but causes no loss to the species. This process sets the stage for the second phase. In the second phase, in which the behavioral effect is expressed as dominance resulting from territorial ownership rather than as strict territoriality, losses are due to death, and their magnitude is directly correlated with food scarcity. Because the second phase is irreversible and more sensitive to the degree of overpopulation, it is more efficient as a regulator. In fact, if the second phase were not to occur, the effect of the first phase might be largely nullified when the birds returned in the spring to breed in the vicinity where they were hatched.

The first phase probably enables a higher number of tits to survive the second phase, and it determines which individual tits will survive, namely those holding fall territories in favorable habitats and consequently remaining dominant there in contests for food during the winter when competition and individual selection are intense. Although we may conclude that the limiting effect of autumn territoriality exists for tit populations, fluctuations in the number of survivors of the winter are governed primarily by the food supply.

It is clear for these populations that territoriality affects but does not regulate the number of birds which survives the winter and sets up breeding territories the next spring. The primary effects of territoriality and dominance are first to disperse the population more equitably in relation to the food supply and second to ensure that the vigor of the survivors of the winter is not damaged by the competition for food during the winter.

In the Red Grouse population studied by Jenkins, Watson and Miller (1963; and Jenkins, 1963) the situation differs from that for the titmice in that the number that survived the winter generally exceeded the number of territories. Therefore, a fraction of the population of potential breeders was regularly deprived of the opportunity to breed through lack of territories. The number of breeding territories was established in the fall and varied yearly with the general vigor of the cocks (as indicated by their weight, incidence and severity of parasitism, and summer survival rate). In years when the physiological condition of the cocks was good more of them were able to meet the strain of holding territories than in years when it was bad. The condition of the birds appeared to be related to the quality and quantity of their food, heather, which was apparently determined by the weather. In Red Grouse the *general level* of the breeding population appears to be limited *jointly* by the *territorial behavior of the species and the food supply*, while the yearly *fluctuations* in breeding density appear to be caused by factors affecting the *food supply*.

CONTROL OF THE SURPLUS

The usual fate of potential breeders in excess of those which actually breed varies with the species. The alternatives for a non-territorial individual whether in spring or fall are to stay in an area known to be desirable but fully occupied, and perhaps eventually to fill a vacancy should it arise, or to emigrate and perhaps find a territory elsewhere. The strategies normally employed by surplus individuals facing this choice in different species determine the fates of the potential surpluses.

Especially among permanent residents which show autumn territoriality and some degree of place-dependent dominance in winter hierarchies, emigration of the non-territorial or low ranking individuals may become necessary for their survival long before the breeding season. These are typically species in which "irruptions" may sometimes occur and the amount of migration varies greatly from year to year.

The result of these migrations may be that a potential surplus of breeding birds is disposed of even before it has a chance to reach the breeding season; those individuals which might have become non-breeding floaters had they survived are eliminated through a combination of unfavorable environmental conditions and virtual exclusion from those environmental requisites which would have enabled their survival had they not been pre-empted by the territorial or dominant individuals.

For the Old World tit populations which have been studied, a breeding surplus seems not to be present mainly because it does not survive until the breeding season and because the territories of tits are compressible within the limits of the population densities which normally survive the winter. In the Red Grouse population of Jenkins (1963: 698–9) heavy mortality of surplus individuals occurred during and following times of dispersal. In spring and summer, surplus birds were seen in marginal areas and seemed to be more susceptible to infections by nematode worms, *Trichostrongylus tenuis* Eberth, than were territory owners. In this species the surplus appeared to have a significantly higher mortality than the breeders.

It is clear that single-factor explanations of such cases are inadmissible. It is primarily the *interaction* of aggressive behavior (manifested as territoriality, dominance, or both), food supply, and weather conditions which *limits* these populations. Furthermore, *fluctuations* in density seem to be attributable to the *interaction* between food supply and weather conditions, rather than to territorial behavior, which, if it varies at all, varies as a function of the first two variables and numbers.

In some other species the non-breeders survive well enough to constitute a fair proportion of the population during the breeding season. Such surplus individuals may either exist separately where survival is assured but successful nesting is nearly impossible, as in the Australian Magpie (Carrick, 1963), Great Reed Warbler (*Acrocephalus arundinaceus*) (Kluyver, 1955), and Red-winged Starling (*Onychognathus morio*) (Rowan, 1966) or they may mix with breeding individuals in weakly defended or neutral areas in or near occupied territories, as in the House Wren (Kendeigh, 1941), Skylark (Delius, 1965), and other passerines. Surpluses which exist separately from the breeding population seem on the basis of presently available data to be larger than those which mix with the breeding population. Perhaps this is because the surplus individuals in the former case need not compete directly with territory holders for the essentials of survival, whereas in the latter they must. This would enhance survival in both surplus and breeding birds.

If all utilizable habitats are just filled and the rates of recruitment and immigration exactly balance the rates of mortality and emigration, there will be no surplus. But if this balance is tipped slightly on the positive side a surplus will tend to accumulate. Although territoriality might in some species limit breeding density, it places no direct limitation on the density of floaters. Consequently, it cannot be said to "limit the population"—a frequent oversimplification in the literature.

The size of the surplus, or the density of floaters, N_F, is determined by the number added to the population each year in excess of the number needed to maintain the fixed upper limit of density of territory holders, a, and by the rate of survival of the surplus individuals, s. When the density of breeders, N_B, is taken as one, then for a given year the increment above replacement equals the reproductive rate per breeder (to maturity) minus the mortality rate, m, per breeder (exclusive of emigration and immigration),

$$a = rN_B - mN_B = r - m$$

Over n years N_F equals the excess from the preceding year, a, plus the survivors from the excesses produced in previous years.

$$N_F = a + as + as^2 + \dots + as^{n-1}$$

As a geometric progression this equation can be stated in the following form:

$$N_F = a\left(\frac{1-s^n}{1-s}\right)$$

Since s can only be a fraction between 0 and 1, s^n approaches zero as n approaches infinity. Consequently, in the limit $s^n = 0$,

$$N_F = \frac{a}{1-s}$$

Survival rate is here assumed for simplification to be relatively independent of age after maturity. That this is a reasonable general assumption for birds on the basis of the available evidence was tentatively supported by Lack (1954), Farner (1955), and Meunier (1960), who reviewed survival rates in birds. An exception to this generalization was shown by Berndt and Sternberg (1963) for the Pied Flycatcher but questioned by Lack (1966).

The relationship between survival rate of the surplus individuals and the size of the surplus is shown in Figure 1. It may be seen that the problem of control of a surplus should tend to be much more severe in longer-lived species than in those with a high mortality rate. For two hypothetical species each with an a of 10 per cent, average survival rates of 0.6 and 0.8 would yield surpluses of 25 and 50 per cent of the breeding populations respectively. Thus, a small difference in survival rate of the surplus individuals could make a large difference in the size of the surplus.

Since larger species tend to have longer life expectancies, we can predict that the problem of a surplus will be exaggerated in those species. The surprisingly large surplus of non-breeding "flock" birds in the Australian Magpie, up to 183 per cent of the breeding population (in winter) (Carrick, 1963), becomes somewhat more understandable in view of the (presumed) high survival rate of the species, and in particular of the non-breeding birds. On the other hand, the production of a considerable surplus by a small, short-lived passerine is likely to be due more to reproductive excess.

THE SURPLUS AS A SELECTIVE FORCE

When territorial behavior together with other factors results in the continual existence of a surplus population of one or both sexes over a long period of time, the surplus becomes a predictable feature of the environment of the population and the possibility of

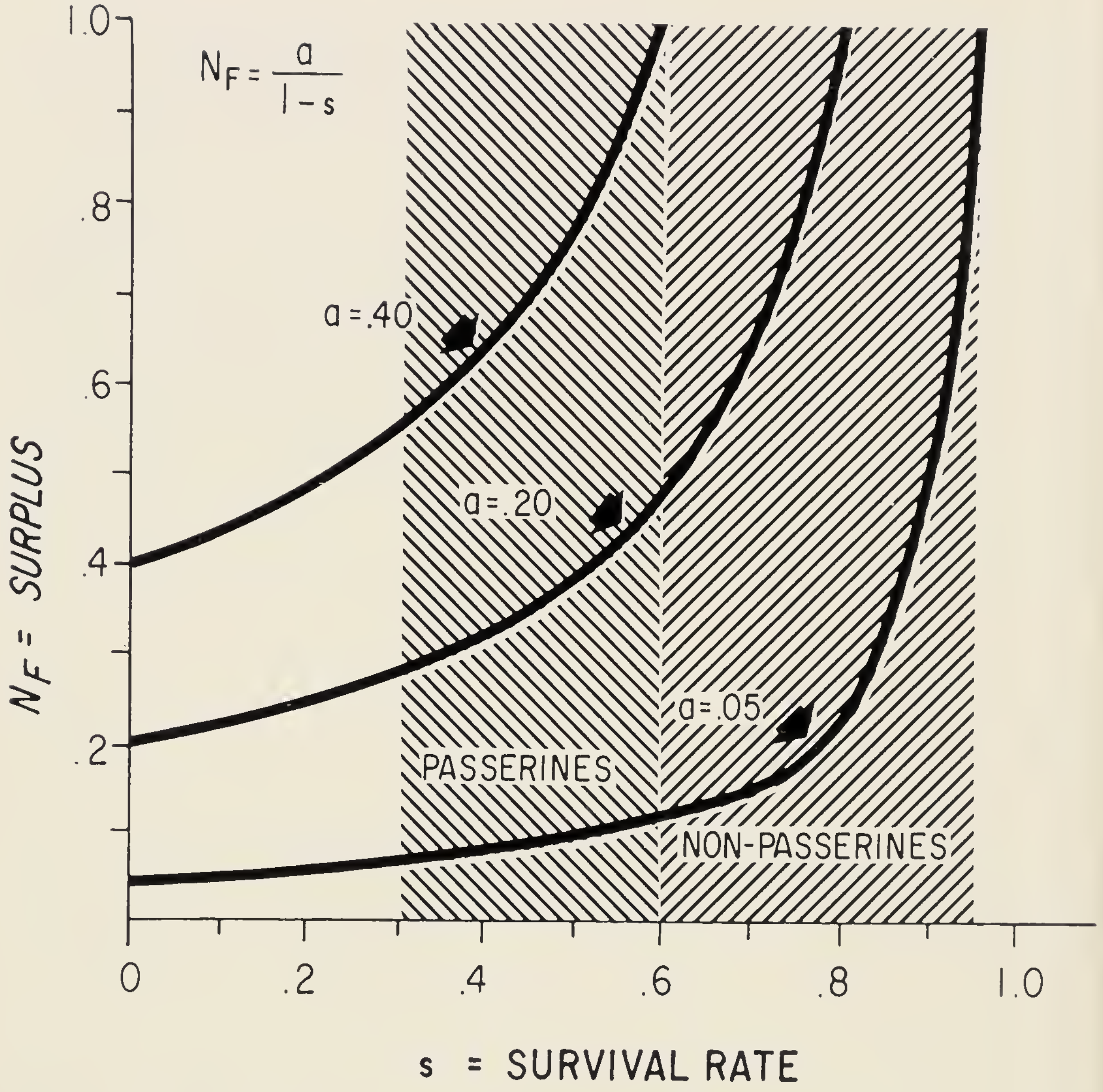


Fig. 1. Curves showing the size of the predicted surplus, N_F, in relation to mean survival rate, s, of the surplus for various amounts of excess of population gains over losses, a. Both N_F and a are expressed as proportions of mean breeding density, which is taken as 1.0. The approximate ranges for adult survival rates of temperate zone passerines and non-passerines are from Lack (1954:91–92), and are merely suggestive; game birds are excluded.

evolutionary adaptation to it emerges. Some of the phenomena which might be interpreted as adaptations to a persistent surplus will now be considered. Circumstances which cause some individuals to attempt breeding in habitats where success is unlikely should have similar evolutionary effects.

Adaptations which might have the secondary effect of reducing the surplus seem to belong to the "last resort" type. They are adaptations to an environment which is less favorable than the previous one in the sense that the chances of being prevented from breeding are higher. Individuals with the highest net reproductive rates will still be selected for, but the selected rates will be lower than before. Delayed maturation, emigrations, lower clutch sizes, group territoriality, year around territoriality, polygyny, smaller territories, and related phenomena may in some cases be so interpreted.

Polygyny.—When any tendency toward polygyny exists, its evolution should be favored by a surplus of potential breeders of both sexes. Consequently, polygyny in some species might be considered as an adaptation of females to the persistence of a surplus. As Verner (1964) and Verner and Willson (1966) have mentioned, in a species in which the female chooses her mate, when a female can leave more offspring by mating with an already mated male in a "good" territory than by mating with an unmated one in a "poor" territory or lacking one, this will favor genetic predisposition in the female toward polygyny. For example, in the Great Reed Warbler some males set up territories in areas where it is impossible for the female to build a proper nest, while other males in suitable habitat for nesting are polygynous (Kluyver, 1955); females who choose polygyny with a male in suitable habitat for nest building will leave more offspring than those choosing monogamy with a male in unsuitable habitat.

When polygynous males also leave more offspring than monogamous ones, then polygyny will be favored in both sexes. Under these conditions there is also selection on the females for their ability to choose males who attract the greatest number of successful females (Fisher, 1929).

The common factor in these situations seems to be that of exclusion of some males from breeding. As population density increases, more males are excluded from breeding, more females are available per territorial male, and the greater is the reward to a successful polygynous male. Shortage of nest space in a colony, or of good habitat for nest building (Great Reed Warbler), or heterogeneity in the distribution of food resources among territories of males may increase the differential between desirable and undesirable males to the females, thus in effect increasing the surplus and increasing the evolutionary advantages of polygyny for the successful breeders.

Delayed maturation.—Delayed maturation may in some cases also be interpreted as an evolutionary adaptation to a persistent surplus or to the conditions which cause it. As noted by Lack (1954), Orians (1961), and Selander (1965), the relationship between age of first breeding and body size is not consistent since large or moderate sized species of ducks and gallinaceous birds may breed in their first year while many smaller species do not breed until subsequent years. Orians (1961:308) has noted that slow maturation rates are characteristic of species in which breeding sites are limited and has written, "Probably these are all species which are ineffectively controlled between breeding seasons so that surpluses of breeding birds are regularly present." Following Selander's (1965) modification of Lack's (1954) explanation, one can interpret a large surplus as decreasing the probability that a first year male can mate and rear young successfully; consequently, it should be less advantageous for him to take the risks associated with the attempt. That first-year male American Redstarts (*Setophaga ruticilla*) are less successful than adults in mating and nesting was shown by Ficken and Ficken (1967).

In a population at equilibrium ($s + m = 1$) the number of young, N_Y, which must be fledged yearly to just replace annual losses to the breeding population, N_B, depends on the rate of survival after fledging, s, and the age at first breeding, b, in the following manner:

$$N_Y = \frac{(1 - s)\ N_B}{s^b}$$

With the use of this equation it can be seen that the loss in reproductive potential due to evolution of delayed maturity, although large in species with low survival rates, is much less severe in species with high survival rates. For example, if breeding were delayed from the first breeding season to the second in a species with a survival rate of $s = 0.2$, each pair in order to just replace annual losses to the breeding population would have to fledge five times as many young as it would if the pair bred in its first year; when $s = 0.5$, then twice as many; and when $s = 0.8$, only one third more. Adaptation to the existence of a surplus by means of delayed maturation is, consequently, more likely in a species having a high rate of survival.

Group territoriality.—In some permanent resident species, especially those that defend Type A territories all year, first year birds sometimes linger in the territories of their parents and help in nest building, nest defense against other species, and feeding the young (Skutch, 1935, 1961). Such species seem to be preadapted for the evolution of group territories. The additional selective force necessary for group territories to evolve from a simple family group (as opposed to evolving from a colony) might well be provided by a surplus in the following way. As the density of competitors for territories increases, the probability of an individual's being excluded from the breeding population rises. Consequently, for most males more energy must be expended in competition for territory at high breeding densities. This added cost might be offset by allowing subordinates, which would normally be excluded, to participate in territorial defense and other family affairs (except mating). In small family groups the presence of additional members probably would help in maintaining territories even though the principal burden would rest on the dominant male. Subordinate birds would aid in detecting intruders, and by sheer numbers and noise would contribute psychologically to driving them out. Dominance of large groups over smaller ones was noted by Robinson (1956) in *Gymnorhina dorsalis* and by Power (1966) in the defense of nest holes by parakeets. That large numbers of less aggressive individuals by simple persistence can successfully overcome the resistance of single aggressive males was observed by Orians and Collier (1963) when Tricolored Blackbirds (*Agelaius tricolor*) successfully founded a colony on the territories previously owned by Red-winged Blackbirds. Furthermore, the aid of earlier offspring in caring for later ones should lessen the cost of "aggressive neglect" (Hutchinson and MacArthur, 1959; Ripley, 1961) on the part of the dominant male. That intraspecific aggressive neglect can reduce reproductive efficiency was illustrated in the Red-winged Starling when young in the nest "starved to death" during a protracted territorial battle (Rowan, 1966: 400).

The probability of an individual's eventually gaining the opportunity of successful breeding, if the surplus is large and persistent enough, may be greater if it remains within the family group awaiting the demise of its elders (as do young males in the Superb Blue Wren (*Malurus cyaneus*) Rowley, 1965), than if it forsakes all claims to its old territory and attempts to establish a new one in the face of uniformly fierce defense (Selander, 1964). Under conditions where the chances of infiltrating another group or establishing a new territory in a suitable habitat are remote, an individual can still contribute to raising the frequency of its genes in the population even without actually breeding. Since its siblings are genetically more closely related to it than are the offspring of competing families it can help to increase the frequency of its genes in successive generations by aiding its parents even if it is denied the opportunity to breed itself (Hamilton, 1964). A demonstration of this in the Superb Blue Wren was given by Rowley; groups with helper males produced 1.9 fledglings per adult annually, while groups without helpers produced only 1.2.

Under such Level 3 conditions there is probably intense competition between groups, with each group tending to enlarge its territory at the expense of its neighbors. Those groups which maintain themselves in successive generations, expand, and take over the areas of other groups, either by fission and expansion of the successful groups or by infiltration of emigrants into other groups, are the most successful in terms of gene frequencies in the population. Consequently, the fate of the individual and of its genes in such cases depends on the fate of its group (especially its kin).

The evolution of behavioral and other traits involving conferral of benefits on close relatives has been called kin selection (Smith, 1964; Brown, 1966). A mathematical theory by which the evolution of such social traits can be described, along lines consistent with theories based on individual fitness, has been given by Hamilton (1964). Briefly, the hypothesis that I have developed is that in a species which is preadapted by the occasional participation of young birds in the care of subsequent broods, kin selection for this and related traits within the family becomes intensified through the persistent presence of a large surplus of potential breeders and the environmental conditions which lead to the surplus. This would act to increase the role of the young in the family, to lengthen their stay with the parents, and to increase the tolerance of the parents for such a relationship. The added birds would then participate not only in territorial defense, but also in foraging, predator detection, and, in some cases, care of the young. Social organizations with communal cooperation in nest building but retaining internal territories, such as certain "lodge builders" (Crook, 1965) require different explanations.

A number of species with group territories have been studied, the three species of Crotophaginae (Davis, 1942), two of the three species of Australian magpies (*Gymnorhina dorsalis*, Robinson, 1956; *G. tibicen*, Carrick, 1963), the Superb Blue Wren (Rowley, 1965), and one of the communal species of American jays (*Aphelocoma ultramarina*) (Brown, 1963*a*). A number of other species are known to have group territories, for example, the Jungle Babbler (*Turdoides striatus*) (Andrews and Naik, 1965), and certain Galapagos mockingbirds (*Nesomimus macdonaldi*) (Hatch, 1966); further references may be found in Wynne-Edwards (1962), Davis (1942), and Crook (1965). Of these only for *Gymnorhina tibicen* has it been established that an actual surplus exists for a long period of time. This point and the related phenomenon of delayed maturation require further attention.

Whether or not individuals in these groups tend to be close relatives, which is required by theory, is not known with certainty, except for *Malurus*; the long-term banding studies which would be necessary to settle the question have not been done. In some primate species with group territorial defense it is known from observation of marked individuals that members of troops defending a territory do tend to be closely related (Washburn, Jay, and Lancaster, 1965).

In the Australian magpies (*Gymnorhina* spp.) (Robinson, 1956; Carrick, 1963), the joining of a flock by an outsider is known, as is the staying of birds hatched by the group and their eventual reproduction within the group. Since the more successful groups should tend to produce more young than there will be places available, it is to be predicted that some birds would leave the more successful groups and perhaps eventually find their way into the less successful ones. Despite this predicted mixing, however, there should in this system be a greater amount of inbreeding than would occur in the more usual pair-territory system.

There has been no adequate evolutionary interpretation of group territories by earlier authors. Davis (1942) discussed the evolution of communal nesting in the Crotophaginae but did not stipulate the ecological conditions favoring group territorial defense per se. Crook (1965), in discussing certain cases of communal social organizations, stressed the assistance in finding food, which in his view might be critical at times of food scarcity. This is probably involved but it cannot be the critical factor. In *Gymnorhina dorsalis*, a prime example of a communal species, the males are conspicuously aggressive within the group and they rarely participate in nest building, incubation, or feeding of the nestlings (Robinson, 1956:289). Non-breeding immature birds do not seem to contribute significantly in feeding the young (op. cit.:295), although they occasionally help in certain regions. In *Malurus cyaneus* multi-male groups raised 42 per cent more independent young than did pairs, but the difference was due mainly to the incubation period rather than to the period when the young were being fed (Rowley, 1965). Consequently, communal food-finding does not seem likely to be serviceable as a general explanation for the evolution of group territoriality.

THE EVOLUTION OF TERRITORIAL BEHAVIOR

The prevention-of-overpopulation hypothesis.—Kalela (1954) and Wynne-Edwards (1959, 1962, 1963) have advanced the hypothesis that territorial behavior has evolved because of its limiting effects on population densities by preventing overpopulation and the resulting destruction of food populations. Howard (1920), Meise (1930), and earlier authors (cited by Wynne-Edwards, 1962) also considered control of population density to be an important property of territorial behavior. For a fair evaluation of this hypothesis it would be necessary to consider also various alternative hypotheses together with the evidence relevant to each. Space does not permit such a procedure, but it is desirable at this point at least to consider whether or not the available data on populations are consistent with the hypothesis. More recent hypotheses will then be considered.

The data seem sufficient to conclude that territorial behavior tends to spread a population relatively evenly over its available habitat at Levels 1 and 2, with higher densities in the richer habitats than the poorer ones. Local "overpopulation" due to chance and to unusual attractiveness of certain habitats would consequently be less than if there were no other means whereby the population could achieve the same dispersion pattern. However, other means are possible, judging from their existence in other species (Lack, 1954) ; and the hypothesis of Wynne-Edwards does not adequately explain why these other means did not evolve in the now territorial species.

The critical point for the overpopulation hypothesis is met with Level 3 populations, for it is at this level that individuals are prevented from breeding altogether. Surpluses of significant size involving females have only rarely been demonstrated; and in some of these cases there is doubt that the surplus was caused entirely by territoriality. The better demonstrations of surpluses mainly involve habitats altered by man. The prevention-of-overpopulation hypothesis for the evolution of territoriality is only weakly supported by this rather small amount of reliable evidence.

Other criticisms of Wynne-Edwards' theory regarding territoriality have been advanced (Smith, 1964; Brown, 1964; Crook, 1965; Williams, 1966; Lack, 1966; Wiens, 1966.) These arguments, in my opinion, quite convincingly eliminate the prevention-of-overpopulation hypothesis from serious consideration as the major force selecting for territorial behavior. They may be summarized as follows:

1. Community Complexity. Population regulation is never completely under the control of the species by itself but depends in a complex way on interactions between members of the ecological community. Evolutionary adaptations tending to favor one species at the expense of a predator-, prey-, or competitor-species can lead to a "counter-adaptation" in other species. Consequently, the evolution of population regula-

tory mechanisms cannot be conceived of as occurring wholly within the gene pool of the species concerned, for it must also involve evolution and zoogeographic change in other species. Community complexity is important for the stability of the populations of the member species (MacArthur, 1955, and others).

2. Avian Food Habits. Most bird species are not restricted to a single food species but can switch from one to another when one becomes scarce, thus tending to relieve heavily utilized species from further destruction when low densities are reached. Great diversity in diet has been revealed by food-habits studies in many birds. The concept of "specific search images" and the data which support it are consistent with this interpretation (L. Tinbergen, 1960; L. Tinbergen and Klomp, 1960; Mook, Mook, and Heikens, 1960; Gibb, 1962*b*). The sudden appearance and disappearance of some plant and invertebrate foods, such as weed seeds and insects, helps to protect them from overexploitation, for example, the periodic cicadas (Lloyd and Dybas, 1966). Some food species actually depend on being eaten for dispersal, the hard pits of certain fruits, for example. Birds *in the reproductive season* may actually harvest only a small proportion of the populations of many insect species. In the studies discussed by Lack (1966:288) bird predation typically took a relatively small percentage of the populations of insect food species which were the main ones fed to nestlings, and birds were not the principal predators on the insect species utilized by the birds as food.

3. Alternative Means of Population Regulation. The more conventional views of population regulation, which rely on density-dependent mortality often involving the food supply and predation, have been comprehensively reviewed by Lack (1954, 1966), but received little attention from Wynne-Edwards (1962). Although Lack might have erred in underestimating the role of behavior in population regulation, there seems to be no reason to completely replace the conventional interpretation with one based mainly on behavior.

4. Slowness of Interpopulation Selection. Interpopulation selection is too slow and inefficient to be effective when compared to "inter-individual" selection. Genetic change in the frequencies of types of populations requires either extinction of established populations or colonization, whereas genetic change in types of individuals requires only the conception or death of an individual (in birds).

Extinction of a bird population *through over-exploitation* of its food supply seems never to have been observed or recorded in nature, nor has the extinction of a regular food species through overexploitation by birds been observed to my knowledge. In the absence of proof that interpopulation selection for prevention of overpopulation actually occurs today, one would have to assume that such selection is no longer important and that the traits concerned evolved long ago—a convenient, if lame, excuse for lack of evidence.

5. Required Dispersion of Populations. Interpopulation selection requires a large series of almost completely isolated populations—a degree of isolation which is the exception rather than the rule on continents. Although the division of populations into demes is a concept which applies well to some bird species, the degree of isolation of these demes required for the successful operation of inter-demic selection for population regulation in opposition to strong individual selection would be rare except on oceanic islands. The degree of isolation necessary for effective interpopulation selection should be greater than that needed for genetic drift to be significant. In most continental species, despite the well known Ortstreue, there would seem to be enough interchange between local populations to allow superior genotypes to flow more rapidly through

a species than they could be defeated by interpopulation selection. For example, Berndt (1960) in a study of the Pied Flycatcher showed that 10 per cent of the recovered adult females which had been ringed as nestlings were found breeding 19 to 235 km from the hatching site.

6. Origin Unexplained. Interpopulation selection can theoretically explain the continuance of a character but cannot easily explain its origin within a population. For simple traits mutation or genetic drift might suffice, but for a highly complex trait such as territorial behavior, involving display, fighting, avoidance, releasers, and appropriate responses to key stimuli, a constructive evolutionary force such as is supplied by individual selection is required.

7. Resistance to Individual Selection Unexplained. Wynne-Edwards (1963) regarded population regulatory mechanisms such as territoriality as so deeply tied in with the biology of the species as to effectively resist the forces of change imposed by individual selection. A comparison was drawn to the mesoderm and coelom. Yet social organizations in birds are anything but conservative; great diversity is well known even in closely related groups, e.g. the genera *Agelaius* (Orians, 1961) and *Aphelocoma* (Brown, 1963*a*), families Icteridae, Ploceidae (Crook, 1964, 1965). The evident diversity in avian social organizations even in species of recent evolutionary origin is proof that the behavioral traits on which the various organizations are based are subject to relatively rapid evolutionary change. Neither can the various types of social organizations be considered homologous in different species as the mesoderm and coelom are.

8. Diversity of Territorial Systems Unexplained. Although many types of social organization are known in birds, the hypothesis of their evolution via interpopulation selection for prevention of overpopulation does not adequately explain why a particular kind of organization is found in a particular species. In contrast, this aspect is relatively easily explained through recourse to individual selection (Brown, 1964).

9. Adequacy of Individual Selection. It was reasoned by Wynne-Edwards (1962, 1963) that since territorial behavior was an adaptation for population control (in his view), it could not have evolved by individual selection. Most authors have based their theories on individual selection, and it is difficult to see why individual selection should now be thought of as working against the evolution of territorial behavior, without being given a more persuasive argument (see below).

A role for interpopulation selection in the evolution of social organizations cannot be completely ruled out by the above considerations. The balance of evidence suggests that individual selection is much more powerful and faster than interpopulation selection in the evolution of avian social organizations, but a minor, complementary role for the latter, especially at the species level, should not be excluded as a possibility. More quantitative approaches to the problem than are now available would seem to be necessary to substantiate even this hypothetical complementary role in nature. Lacking the necessary, sophisticated quantitative studies, the case for interpopulation selection in the evolution of avian social organizations is exceedingly weak at present.

Basic questions.—A part of the confusion in the literature on territorial behavior stems from confusion in statement of the basic questions. Rather than ask about the "functions" of territoriality (Hinde, 1956; Tinbergen, 1957; Lack, 1966), it would be more to the point to state directly that our primary interest is in the evolutionary origin, development, and maintenance of territoriality and that we approach this problem through a study of the effects of territorial behavior on gene frequencies. One of the dangers in speaking of the "functions" of territory is that the mechanisms of selection by which a particular function might act on the gene pool of the species are often left vague and unspecified. Thus, Tinbergen (1957) in an article on "The Functions of Territory" has stressed the role of territorial behavior in dispersion. Although dispersion is a population phenomenon and not easily explained on the basis of Darwinian natural selection except as a secondary consequence of some other primary benefit to an individual, no attempt was made by him to overcome this difficulty, probably because he had not addressed himself directly to the actual evolutionary mechanism involved, but rather to the vague concept of function.

Wynne-Edwards (1963) while supporting the role of territoriality in dispersion, took the logical next step in this line of reasoning and proposed a selective mechanism based on what he called intergroup selection, which might better have been termed "interpopulation selection" so as not to confuse it with kin selection (Brown, 1966). It is useless to ask whether territoriality is good for the species, good for the population, or good for the individual, and to reason from the answer how territoriality might have evolved. The answers to these questions might be yes or no in all three cases depending on one's personal inclination. More important is the question of relative fitness (in the sense of population genetics) of territorial and non-territorial individuals in specified environments. It is clear from the data on surpluses and from behavioral observations that a clear difference in fitness often exists, since non-territorial individuals simply cannot reproduce under Level 3 conditions and since those holding poor territories (Level 2) must also be a disadvantage. Behavior of this sort, which raises one individual's fitness at the expense of another, has been termed "selfish behavior" and can be treated theoretically in the context described by Hamilton (1964:15). In this sort of treatment the idea of "function" need not be considered at all.

The fitness differential between territorial and non-territorial individuals is so great and so widespread—in potentially every territorial species—that we are justified in seeking a general theory for the evolution of territorial behavior based on individual selection. Such a general theory has been proposed and examples of its power to explain diverse territorial systems have been given (Brown, 1964). Its essence is that for territorial behavior to evolve in respect to a given object, be it mating priority, living space, foraging area, or nesting site, 1) a situation must exist in which there can be aggressive competition for that object, 2) territorial individuals must be more successful than non-territorial individuals in acquiring that object, and 3) the successful acquisition of the object of territorial behavior must raise the overall fitness of successful individuals over that of unsuccessful ones. Competition for these objects is not merely "conventional" or "symbolic"; it is real.

The consequences to an individual bird of failure to obtain a territory, regardless of its type, are usually so obvious—failure to breed, or to live—that differences in fitness between individuals with and without territories are readily demonstrable or imaginable in virtually every territorial species. The selection pressures which might cause territorial behavior to evolve by acting on individual genotypes are thus both readily apparent and powerful.

Crook's hypotheses.—In a recent review of social organization in birds Crook (1965) mentioned some ideas relevant to the evolution of territorial behavior. In his view, ". . . the primary reason for territorialism remains the need for individual food exploitation." (p. 204). In territorial species, individuals who competed successfully for territories were supposed to raise more young than gregarious types 1) because their manner of feeding would be made more efficient by absence of interference from other conspecific individuals, 2) because over-exploitation of their private realm would be prevented, and 3) because their nests would be more protected from predators because of their uniform dispersion.

A number of objections may be raised. Crook wrote that success in foraging in one group of territorial species "depends on a combination of stealth (cryptic approach), speed and skill", and he went on to suppose that "the solitary nature of these species is an adaptation to their mode of food exploitation" (p. 195). It is not clear to me that hummingbirds, Ospreys, and kingfishers use much "stealth" in foraging, nor that they require solitude for effective finding of food. The advantage of solitude even to the most sensitive species would seem to be slight; even if intraspecific solitude were achieved, interspecific interruptions would remain. Given the same number of individuals and the same area of uniform habitat, it is difficult to understand why there would not be more interference with foraging under a territorial system than in a system of dispersion based simply on food abundance, perhaps with the addition of a slight tendency to avoid conspecifics. Such a small increase in foraging efficiency seems hardy worth the effort of territorial defense.

In my opinion, it is only when the demand for certain food resources exceeds the supply (Levels 2 and 3) that it becomes economical in terms of time and energy to fight and threaten for them, provided that they can be feasibly defended (Brown, 1964).

Crook was impressed by the correlation between the uniform dispersion of nests and their "crypticity"; consequently, he invoked predation as another factor favoring the evolution of territorial behavior, as has Lack (1966:279). But this correlation may have another explanation. If territoriality has already evolved because of selection pressures other than predation, then the nest may or may not be cryptic depending on the predation to which it is subsequently exposed. Lacking the protection offered by colonial nesting, it is logical that nests of territorial species would tend to be more protected or cryptic; similarly, colonial nests need not be so cryptic because of the protection afforded by the colony site and the behavior of the colonists.

Crook's approach seems to have been to consider groups of species with specified types of foraging habits and to speculate on how territorial behavior in the nesting season might be more beneficial to them than gregarious behavior. This method of approach is dangerous because it does not directly consider the problem of fitness differentials between individuals of different behaviors within one system; rather, it tends to compare whole systems, e.g. the territorial versus the gregarious. When the great difference in fitness between territorial and non-territorial individuals in an already territorial species is considered, it seems unnecessary to compare systems in seeking possible selection pressures leading to and reinforcing territorial behavior. It is desirable, however, to seek the ecological factors which make it profitable in terms of time and energy to defend territories with various qualities. Exemplary studies of this type have been carried out by Orians (1961), Verner (1964), and Willson (1966).

In a colonial species it is again instructive to consider the difference in fitness between territorial and non-territorial individuals. The territorial individual would gain nothing in most species through a greater isolation of its nest or defense of a feeding territory, for in most colonial species the food is distant from the nest site and is not economically defensible either because it is too mobile (swifts, swallows, seabirds) or so transient that its continual presence is unreliable and not worth the evolutionary gamble of territorial behavior (Orians, 1961; Brown, 1964; Crook, 1965).

Conclusion.—The consideration of the effects of territorial behavior on populations at different density levels, which has been attempted in this paper, reveals the importance of population density in relation to the selection pressures acting on territorial and non-territorial individuals. It is necessary to consider different types of social organization not only under ideal conditions, but also under conditions of severe competition. At Levels 2 and 3, where some individuals are led to choose inferior territories or not to attempt breeding at all, the relative fitness of territorial and non-territorial individuals is especially clear. Regardless of what the hypothetical properties of a superior territory in a particular species may be, they will have to be "worth fighting for" if they are to provide an adequate explanation for the evolution of territorial behavior.

SUMMARY

In examining the factual evidence on which the concept of population regulation through territorial behavior is based it was found desirable to differentiate between three critical population densities. The effect of territorial behavior on limitation of reproductive success should differ at each level. At the lowest density, Level 1, territory sizes should not be limited by competition for territories and no individuals should be prevented from nesting in good habitats. At middle densities, Level 2, some individuals should be excluded from the better habitats but should establish territories in poorer habitats. This may under certain conditions create the "buffer effect". At the highest densities, Level 3, some individuals should be prevented from breeding and would form a breeding surplus or reserve which might exist as a floating population in and around occupied territories or on separate ground.

The evidence supporting these hypothetical actions of territorial behavior on reproduction is found to be mostly behavioral and especially weak at the population level. The widespread importance of a buffer effect in population control has not been substantiated; the evidence is at present sparse and inconsistent. The prevention of *females* from breeding by territorial behavior has only very rarely been demonstrated in significant numbers. Surpluses involving primarily males are known in several species. In future population studies more attention should be paid to determining the magnitude and persistence of the surplus, especially in females. When a surplus exists, removal of the breeding population would be desirable to show that the surplus individuals would breed if allowed to establish themselves on territories. Although the hypothesis of population regulation through territorial behavior is a tempting one, too few critical studies on it have been done to conclude now that it is of widespread importance in limiting reproduction of avian populations; and, in any case, such a limit will be determined not by territorial behavior alone but by complex interactions between the environment, the number of birds competing for territories, and territorial behavior.

Territorial behavior probably also influences populations in some species by increasing the emigration and mortality rates of individuals unsuccessful in finding territories.

The size of the surplus depends on the excess of gains over losses and should be especially sensitive to variations in survival rates between species.

The surplus and the conditions which tend to create it are considered as a link in the control of population density both through behavioral effects influencing reproduction, mortality, and dispersal and through natural selection acting on individuals. The surplus and conditions which create it are conceived as selective forces. Some of the hypothesized evolutionary consequences are lowered reproductive rates, polygyny, delayed maturation, and group territoriality.

The hypothesis of the evolution of territoriality via individual selection resulting from

aggressive competition is reaffirmed, and the hypothesis based on interpopulation (group) selection for prevention of overpopulation is rejected.

ACKNOWLEDGMENTS

This work was supported in part by U.S. National Institutes of Health Research Grant MH-07700. I wish to thank Bailey LeF. Brown for refreshing my memory on the algebra of geometric progressions.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press.

Andrews, M. I., and R. M. Naik. 1965. Some observations on flocks of the Jungle Babbler, *Turdoides striatus* (Dumont) during winter. Pavo, 3:47–54.

Bendell, J. F., and P. W. Elliott. 1967. Behaviour and the regulation of numbers in Blue Grouse. Canadian Wildl. Serv. Rept. Ser. No. 4. Dept. Indian Affairs and Northern Development, Ottawa.

Berndt, R. 1960. Zur Dispersion der Weibchen von *Ficedula hypoleuca* im nordlichen Deutschland. Proc. XII Intern. Ornithol. Congr.: 85–96.

Berndt, R., and H. Sternberg. 1963. Ist die Mortalitätstrate adulter *Ficedula hypoleuca* wirklich unabhängig vom Lebensalter? Proc. XIII Intern. Ornithol. Congr.:675–684.

Brenner, F. J. 1966. The influence of drought on reproduction in a breeding population of Redwinged Blackbirds. Amer. Midl. Naturalist, 76:201–210.

Brewer, R. 1963. Stability in bird populations. Occ. Papers Adams Center Ecol. Studies, 7:1–12.

Brown, J. L. 1963*a*. Social organization and behavior of the Mexican Jay. Condor, 65:126–153.

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

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull., 6:160–169.

Brown, J. L. 1966. Types of group selection. Nature, 211:870.

Burger, G. V. 1966. Observations on aggressive behavior of male Ring-necked Pheasants in Wisconsin. J. Wildl. Mgmt., 30:57–61.

Carrick, R. 1963. Ecological significance of territory in the Australian Magpie, *Gymnorhina tibicen*. Proc. XIII Intern. Ornithol. Congr.:740–753.

Christian, J. J. 1963. Endocrine adaptive mechanisms and the physiologic regulation of population growth. Pp. 189–353 in Mayer, W. V., and R. G. van Gelder (Eds.) Physiological mammalogy, Vol. 1. Mammalian Populations. Academic Press, New York.

Crook, J. H. 1964. The evolution of social organization and visual communication in the weaver birds (Ploceinae). Behaviour, Suppl. 10:178.

Crook, J. H. 1965. The adaptive significance of avian social organizations. Symp. Zool. Soc. London, 14:181–218.

Curio, E. 1959. Beiträge zur Populationsökologie des Trauerschnäppers (*Ficedula h. hypoleuca* Pallas). Zool. Jahrb. Abt. Syst., 87:185–230.

Darwin, C. 1871. The descent of man. The Modern Library, Random House Inc., N.Y.

Davis, D. E. 1942. The phylogeny of social nesting habits in the Crotophaginae. Quart. Rev. Biol., 17:115–134.

Davis, D. E. 1966. Integral animal behavior. Macmillan, New York.

Delius, J. D. 1965. A population study of Skylarks. Ibis, 107:466–492.

Emlen, J. T., Jr. 1957. Defended area?—A critique of the territory concept and of conventional thinking. Ibis, 99:352.

Etkin, W. 1967. Social behavior from fish to man. Univ. Chicago Press.

Erz, W. 1964. Populationsökologische Untersuchungen an der Avifauna zweier nordwestdeutscher Grossstädte. Z. wiss. Zool., 170:1–111.

Farner, D. S. 1955. Birdbanding in the study of population dynamics. Pp. 397–449 *in* Recent studies in avian biology (A. Wolfson, ed.) Univ. Illinois Press, Urbana.

Ficken, M. S., and R. W. Ficken. 1967. Age-specific differences in the breeding behavior and ecology of the American Redstart. Wilson Bull., 79:188–199.

Ficken, R. W., A. Van Tienhoven, M. S. Ficken, and F. C. Sibley. 1960. Effect of visual and vocal stimuli on breeding in the Budgerigar (*Melopsittacus undulatus*). Anim. Behav., 8:104–106.

Fisher, R. A. 1929. The genetical theory of natural selection. Clarendon Press, Oxford.

Flickinger, G. L. 1966. Response of the testes to social interaction among grouped chickens. Gen. Comp. Endocrinol., 6:89–98.

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

Gibb, J. A. 1962*a*. The importance of territory and food supply in the natural control of a population of birds. Sci. Rev., Australia, 20:20–21.

Gibb, J. A. 1962*b*. L. Tinbergen's hypothesis of the role of specific search images. Ibis, 104:106–111.

Glas, P. 1960. Factors governing density in the Chaffinch (*Fringilla coelebs*) in different types of wood. Arch. Neerl. Zool., 13:466–472.

Graczyk, R. 1959. (Forschungen über das Auftreten und den quantitativen Stand der Amsel (*Turdus merula* L.) in Polen.) Ekol. Polska, Ser. A, 7:55–82.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I, II. J. Theoret. Biol., 7:1–52.

Hatch, J. J. 1966. Collective territories in Galapagos mockingbirds, with notes on other behavior. Wilson Bull., 78:198–207.

Havlin, J. 1962. (Age structure and mortality rate in Blackbird populations.) Zool. Listy, 11:279–285.

Havlin, J. 1963. (Breeding density in the Blackbird *Turdus merula* Linn.) Zool. Listy, 12:1–17.

Hensley, M. M., and J. B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk, 68:483–493.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis, 98: 340–369.

Holmes, R. T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor, 68:3–46.

Howard, H. E. 1920. Territory in bird life. Dutton and Co., New York.

Hutchinson, G. E., and R. H. MacArthur. 1959. Appendix: On the theoretical significance of aggressive neglect in interspecific competition. Amer. Naturalist, 93:133–134.

Huxley, J. 1934. A natural experiment on the territorial instinct. Brit. Birds, 27: 270–277.

JENKINS, D. 1961*a*. Social behaviour in the Partridge *Perdix perdix*. Ibis, 103*a*: 155–158.

JENKINS, D. 1961*b*. Population control in protected Partridges (*Perdix perdix*). J. Anim. Ecol., 30:235–258.

JENKINS, D. 1963. Population control in Red Grouse (*Lagopus lagopus scoticus*). Proc. XIII Intern. Ornithol. Congr.:690–700.

JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.) in northeast Scotland. J. Anim. Ecol., 32:317–376.

JENKINS, D., A. WATSON, AND G. R. MILLER. 1964. Current research on Red Grouse in Scotland. Scottish Birds, 3:3–13.

KALELA, O. 1954. Über den Revierbesitz bei Vögeln und Säugetieren als populationsökologischer Faktor. Ann. Zool. Soc. "Vanamo", 16:1–48.

KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. Illinois Biol. Monogr., 10:1–120.

KENDEIGH, S. C. 1961. Animal ecology. Prentice Hall, Inc., Englewood Cliffs, N.J.

KENDEIGH, S. C., AND S. P. BALDWIN. 1937. Factors affecting yearly abundance of passerine birds. Ecol. Monogr., 7:91–123.

KLUIJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea, 39:1–135.

KLUYVER, H. N. 1955. Das Verhalten des Drosselrohrsängers, *Acrocephalus arundinaceus* (L.), am Brutplaz, mit besonderer Berücksichtigung der Nestbautechnik und der Revierbehauptung. Ardea, 43:1–50.

KLUYVER, H. N. 1963. The determination of reproductive rates in Paridae. Proc. XIII Intern. Ornithol. Congr.:706–716.

KLUYVER, H. N., AND L. TINBERGEN. 1953. Territory and the regulation of density in titmice. Arch. Néerlandaises Zool., 10:265–287.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

LACK, D. 1955. British tits (*Parus* spp.) in nesting boxes. Ardea, 43:50–84.

LACK, D. 1958. A quantitative breeding study of British tits. Ardea, 46:92–124.

LACK, D. 1964. A long-term study of the Great Tit (*Parus major*). J. Anim. Ecol., 33 (Suppl.):159–173.

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

LACK, D., AND L. LACK. 1933. Territory reviewed. Brit. Birds, 27:179–199.

LLOYD, M., AND H. S. DYBAS. 1966. The periodical cicada problem. II. Evolution. Evolution, 20:466–505.

LORENZ, K. 1966. On aggression. Harcourt Brace and World, Inc., N.Y.

MACARTHUR, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology, 36:533–536.

MACARTHUR, R. H., AND J. H. CONNELL. 1966. The biology of populations. Wiley and Sons, Inc., New York.

MACFADYEN, A. 1963. Animal ecology, 2nd Ed. Pitman and Sons, Ltd., London.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

MEBS, T. 1964. Zur Biologie und Populationsdynamik des Mäusebussards (*Buteo buteo*). J. Ornithol., 105:247–306.

MEISE, W. 1930. Revierbesitz im Vogelleben. Mitt. Ver. sächs. Ornithol., Dresden, 3:49–68.

MEUNIER, K. 1960. Grundsätzliches zur Populationsdynamik der Vögel. Z. wiss. Zool., 163:397–445.

MOOK, J. H., L. J. MOOK, AND H. S. HEIKENS. 1960. Further evidence for the role of "searching images" in the hunting behavior of titmice. Arch. Néerlandaises Zool., 13:448–465.

NERO, R. W. 1956. A behavior study of the Red-winged Blackbird. Wilson Bull., 68: 5–37, 129–150.

NICE, M. M. 1941. The role of territory in bird life. Amer. Midl. Naturalist, 26: 441–487.

NICE, M. M. 1943. Studies in the life history of the Song Sparrow, I, II. Trans. Linnaean Soc. New York, 4:1–247, 6:1–328.

NOBLE, G. K. 1939. The role of dominance in the social life of birds. Auk, 56: 263–273.

ODUM, E. P. 1959. Fundamentals of ecology. 2nd Ed. W. B. Saunders Co., Philadelphia.

ORIANS, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr., 31:285–312.

ORIANS, G. H., AND G. COLLIER. 1963. Competition and blackbird social systems. Evolution, 17:449–459.

PERRINS, C. 1963. Survival in the Great Tit, *Parus major*. Proc. XIII Intern. Ornithol. Congr.:717–728.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol., 34:601–647.

PFEIFER, S. 1963. Dichte und Dynamik von Brutpopulationen zweier deutscher Waldgebiete 1949–61. Proc. XIII Intern. Ornithol. Congr.:754–765.

PHILLIPS, R. E. 1964. "Wildness" in the mallard duck: effects of brain lesions and stimulation on "escape behavior" and reproduction. J. Comp. Neurol., 122:139–155.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor, 61:233–264.

PITELKA, F. A., P. Q. TOMICH, AND G. W. TREICHEL. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecol. Monogr., 25: 85–117.

POWER, D. M. 1966. Agonistic behavior and vocalizations of Orange-chinned Parakeets in captivity. Condor, 68:562–581.

RIBAUT, J. 1964. Dynamique d'une population de Merles noirs *Turdus merula* L. Revue Suisse Zool., 71:815–902.

RIPLEY, S. D. 1961. Aggressive neglect as a factor in interspecific competition in birds. Auk, 78:360–371.

ROBINSON, A. 1956. The annual reproductory cycle of the magpie, *Gymnorhina dorsalis* Campbell, in southwestern Australia. Emu, 56:233–336.

ROWAN, M. K. 1966. Territory as a density-regulating mechanism in some South African birds. Ostrich, Suppl. 6:397–408.

ROWLEY, I. 1965. The life history of the Superb Blue Wren, *Malurus cyaneus*. Emu, 64:251–297.

SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. Univ. California Publ. Zool. No. 74:1–259.

SELANDER, R. K. 1965. On mating systems and sexual selection. Amer. Naturalist, 99:129–141.

SIEGEL, H. S. 1959. The relation between crowding and weight of adrenal glands in chickens. Ecology, 40:494–498.

SIEGEL, H. S. 1960. Effect of population density on the pituitary-adrenal cortical axis of cockerels. Poultry Sci., 39:500–510.

SKUTCH, A. F. 1935. Helpers at the nest. Auk, 52:257–273.

SKUTCH, A. F. 1961. Helpers among birds. Condor, 63:198–226.

SMITH, J. M. 1964. Group selection and kin selection. Nature, 201:1145–1147.

SMITH, R. L. 1966. Ecology and field biology. Harper and Row, New York.

SMITH, S. M. 1967. Seasonal changes in the survival of the Black-capped Chickadee. Condor, 69:344–359.

SNOW, D. W. 1958. A study of Blackbirds. Allen and Unwin Ltd., London.

SOUTHERN, H. N. 1959. Mortality and population control. Ibis, 101:429–436.

STEFANSKI, R. A. 1967. Utilization of the breeding territory in the Black-capped Chickadee. Condor, 69:259–267.

STENGER, J. 1958. Food habits and available food of Ovenbirds in relation to territory size. Auk, 75:335–346.

STEWART, R. E., AND J. W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir community. Auk, 68:471–482.

TINBERGEN, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. Arch. Néerlandaises Zool., 13: 265–343.

TINBERGEN, L., AND H. KLOMP. 1960. The natural control of insects in pine woods. II. Conditions for damping of Nicholson oscillations in parasite-host systems. Arch. Néerlandaises Zool., 13:344–379.

TINBERGEN, N. 1957. The functions of territory. Bird Study, 4:14–27.

TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. Auk, 79:687–698.

TOMPA, F. S. 1964. Factors determining the numbers of Song Sparrows *Melospiza melodia* (Wilson) on Mandarte Island, B.C., Canada. Acta Zool. Fennica, 109: 1–73.

VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Evolution, 18:252–261.

VERNER, J., AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. Ecology, 47:143–147.

WASHBURN, S. L., P. C. JAY, AND J. B. LANCASTER. 1965. Field studies of Old World monkeys and apcs. Science, 150:1541–1547.

WATSON, A. 1965*a*. A population study of ptarmigan (*Lagopus mutus*) in Scotland. J. Anim. Ecol., 34:135–172.

WATSON, A. 1965*b*. Research on Scottish ptarmigan. Scottish Birds, 3:331–349.

WEEDEN, J. S. 1965. Territorial behavior of the Tree Sparrow. Condor, 67:193–209.

WIENS, J. A. 1966. On group selection and Wynne-Edwards' hypothesis. Amer. Scientist, 54:273–287.

WILLLIAMS, G. C. 1966. Adaptation and Natural Selection. Princcton Univ. Press, Princeton, N.J.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr., 36:51–77.

WYNNE-EDWARDS, V. C. 1959. The control of population density through social behaviour: a hypothesis. Ibis, 101:436–441.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Hafner Publ. Co., New York.

WYNNE-EDWARDS, V. C. 1963. Intergroup selection in the evolution of social systems. Nature, 200:623–626.

ADDENDUM

The following significant works appeared after the review was written.

Brown, J. L. 1969. The buffer effect and productivity in tit populations. Amer. Naturalist. (in press).

Crook, J. H. 1968. The nature and function of territorial aggression. pp. 141–178 in Man and aggression (Montagu, M.F.A., Ed.). Oxford Univ. Press, New York.

Fretwell, S. 1968. Habitat distribution and survival in the Field Sparrow (*Spizella pusilla*). Bird-Banding, 39:293–306.

Horn, H. S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus cyanocephalus*). Ecol. Monogr., 49:682–694.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co. Ltd., London.

Lack, D. 1969. Population changes in the land birds of a small island. J. Anim. Ecol., 38:211–218.

Moss, R. 1969. A comparison of Red Grouse (*Lagopus l. scoticus*) stocks with the production and nutritive value of the heather (*Calluna vulgaris*). J. Anim. Ecol., 38: 103–122.

Watson, A. 1967. Population control by territorial behavior in Red Grouse. Nature, 215:1274–1275.

Watson, A., and D. Jenkins. 1968. Experiments on population control by territorial behaviour in Red Grouse. J. Anim. Ecol., 37:595–614.

DEPARTMENT OF BIOLOGY, UNIVERSITY OF ROCHESTER, ROCHESTER, NEW YORK, 31 MARCH 1967.

GENERAL NOTES

An apparent agonistic display of the Whistling Heron (*Syrigma sibilatrix*).— In view of the recent interest in relationships and behavior of herons (e.g., Bock, Amer. Mus. Novitates No. 1779, 1956; Meyerriecks, Nuttall Ornithol. Club. Publ. No. 2, 1960), I offer the following description of an apparent agonistic display of the Whistling Heron (*Syrigma sibilatrix*) observed at six kilometers southwest of Colonia Garabí, Corrientes, Argentina.

Whistling Herons are the herons most frequently noted in the pampas of Corrientes. They are most often seen along roads wherever there are small or larger pools of water. From the vicinity of a small pond between upland pampas and a small patch of woodland on 27 September 1967, I heard loud, squawking calls. I crept to the edge of the woods, from whence I saw across the pond (about 40 meters away from me) two Whistling Herons confronting each other, calling and obviously displaying. Because the display itself held my attention, it was several minutes before I detected another Whistling Heron in the grass only 10 meters from the displaying birds. This lone bird remained silent and inactive throughout the encounter, which it was facing; it seemed to be watching the encounter as intently as was I. The displaying herons were facing each other in close proximity, often only one-third of a meter apart. At times they stood motionless with heads held high and dark head plumes slightly erected. Suddenly one of the two (bird 1) would move its head forward, calling *ka-wee-ok*, until its head was fully extended and its head, neck and body were virtually parallel to the ground. Simultaneously the second bird (bird 2) would draw back its head, emit a call sounding like *se-wee*, and then, as the initiating bird's head and conspicuously reddish, dark-tipped bill were fully extended toward it, commence a forward motion of its head over that of its apparent antagonist. Bird 1 reacted to this by lowering its head, bill, and neck below the horizontal, and, synchronously with the advancing head of bird 2, by posteriorly withdrawing its head from under that of bird 2. When its head was sufficiently withdrawn, bird 1 would then rapidly raise its head, still withdrawing it posteriorly, and emit a *se-wee* call about coinciding with the most advanced position of bird 2's head, and the latter's *ka-wee-ok* call. The birds would then again reverse their actions in the manner just described. About seven to 12 such interactions took place over nearly a minute in a single bout. I observed six such bouts in eight to 10 minutes. Between bouts the interacting individuals were motionless and silent. Movements of the two birds forward and backward during a bout included some short steps and a gradual circling of the birds, during which each bird occasionally lost its balance and used one or both wings to right itself. I feel such movements were caused by the unevenness of the terrain, and that these movements were not a part of the displays. It did appear, however, that both birds had their wings slightly extended for the duration of each bout. One of the birds may have seen me, or not; at any rate, after the sixth bout all three birds flew abruptly off across the pampas.

I assume this to have been an agonistic encounter because of the nature of these displays (for example, the prominence of bill movements forward, and withdrawal of the bill, the relative lack of prominence of the head plumes, and the quite sleeked plumages of both birds). The third bird could have been a female (awaiting the outcome of the conflict?). It certainly appeared to be watching the encounter, and it flew away with the other two birds. Except for the observation that the Whistling Heron does not remind me very much of a night heron (*Nycticorax*), I am otherwise quite unprepared to discuss the significance of these displays in the behavior of this species, or with respect to its possible relationships (for recent comments on its systematics see P. S. Humphrey and K. C. Parkes, Proc. 13th Internatl. Ornithol. Congr. 1963:89–90).

These observations were made while I was conducting field studies of woodpeckers under a grant (N.S.F.—GB-5891) from the National Science Foundation.—LESTER L. SHORT, JR., *The American Museum of Natural History, New York, 1 April 1968.*

Use of man-made islands as nesting sites of the Common Loon.—Many species of waterfowl commonly nest on islands where nesting success is generally higher than at other sites. This has led waterfowl managers to provide islands as a habitat improvement measure (Hammond and Mann, J. Wildl. Mgmt. 20:345–352, 1956). A technique was developed on the Chippewa National Forest in north-central Minnesota to provide floating sedge-mat islands for nesting sites, especially for Ring-necked Ducks (*Aytha collaris*). An unexpected result was the immediate and frequent use of the islands as nest sites by Common Loons (*Gavia immer*). Of eight water areas containing groups of islands, six had an island occupied by loons. This would indicate that loon pairs find man-made islands highly desirable for nesting. The technique may provide a means of increasing nesting success of loons throughout much of their range, should this ever become a matter of concern.

FIG. 1. Typical island occupied by nesting loons.

The islands occupied by loons ranged in size from 36 ft^2 to 100 ft^2. Sedges (*Carex* spp.), leatherleaf (*Chaemeadaphne calyculatta*), bog birch (*Betula pumila*) and sphagnum (*Sphagnum* spp.) are typical of the plant community composing the islands. They are free-floating pieces of bog, cut away from the edge and anchored in open water (Fig. 1).—JOHN E. MATHISEN, *Chippewa National Forest, Cass Lake, Minnesota, 4 September 1968.*

Egg transportation by a female Mallard.—In late May of 1960 in the Bethany Bog, in Bethany, Connecticut I observed a female Mallard (*Anas platyrhynchos*) fly from its nest with its egg in its bill. At this time the water had receded below the sphagnum level leaving the area surrounding the nest dry.

Audubon (Ornithol. Biogr., 1:212, 1831) claimed that if the eggs of a Chuck-will's Widow (*Caprimulgus carolinensis*) were disturbed the bird would carry them off in its beak. This claim has been disputed by Ganier (Wilson Bull. 76:19–27, 1964). Dr. and Mrs. F. M. Baumgartner (in litt.) reported that they observed a Yellow-shafted Flicker (*Colaptes auratus*) fly off with its eggs after the breaking of a branch uncovered the nest. Truslow (Nat. Geographic, 882–884, 1966) observed a female Pileated Woodpecker (*Dryocopus pileatus*) carry off its eggs after the nest site was uncovered when the trunk above the nest broke off.

These examples suggest that egg carrying in bills by birds may be more widespread than has been reported. Conditions which seem to expose the nesting site may be a factor which motivates birds to move their eggs.—ALPHONSE AVITABILE, *The University of Connecticut at Waterbury, Waterbury, Connecticut, 19 February 1968.*

A record of the Tufted Duck for Connecticut.—A recent article (Gochfeld, Condor, 70:186–187, 1968) brings to mind a heretofore unreported record of the Tufted Duck (*Aythya fuligula*) for Connecticut. On 11 November 1956, a male was seen and photographed by the author and several members of the Hartford Audubon Society at Giant's Neck (about 2.5 miles southwest of Niantic), East Lyme County. The bird was on a small brackish pond in the company of Mallards (*Anas platyrhynchos*), Black Ducks (*A. rubripes*), and Mallard × Black Duck hybrids. This is the first Connecticut report of this species and one of the earliest for eastern North America.—GEORGE T. AUSTIN, *Department of Biological Sciences, Nevada Southern University, Las Vegas, Nevada 89109.* (*Present address: Department of Biological Sciences, University of Arizona, Tucson, Arizona*). *30 July 1968.*

Great Horned Owl nesting in a populated area.—The usual nesting habitat of the Great Horned Owl (*Bubo virginianus*) in the midwest is in rural woodlots or forests, occasionally near farm buildings, and well removed from human activity (Bent, U. S. Nat. Mus. Bull., 170, 1938; Baumgartner, Auk 56:274–282, 1939; Austing and Holt, The world of the Great Horned Owl, Lippincott, Philadelphia, 1966).

A Great Horned Owl was seen occasionally on the inhabited part of the campus of Western Illinois University in Macomb, Illinois, during January, 1968, and its nest was discovered there on 15 March. The nest was upon a deserted nest of a fox squirrel (*Sciurus niger*) 38 feet above the ground in a 51-foot-tall European larch (*Larix decidua*). The nest was positioned against the south side of the tree trunk, and contained one small nestling at the time of discovery.

The nest tree was located in mowed lawn nearly separated from other trees, and only 100 feet from the central administration building (Fig. 1). Based upon a few one-hour counts, the sidewalks near the nest tree carried a minimum of 3,400 persons past the nest each weekday between the hours of 08:00 and 17:00.

While almost continually brooding the nestling in the daytime during the period 15 March through 25 March, the parent owl (sex not ascertained) watched pedestrians with an alert but unalarmed posture. After the nestling was old enough not to require constant brooding, the parent bird spent little time at the nest during the daytime, but instead perched within view of it at the base of a dome atop the university administration building. The young bird left the nest about 15 April and remained in the nest tree until 24 April.

The selection of this nesting site in a congested area is especially puzzling since

FIG. 1. Nesting Tree of Great Horned Owl. Arrow marks location of nest.

a 3.8-acre woodlot is located 0.2 mile away, and a densely wooded, uninhabited river valley is within 0.8 mile of the nest site. We postulate that the nest site was selected when few people were on the campus (16 December 1967 through 2 January 1968), and that the psychological bond to the site was maintained in spite of the increased human activity.

Other casual observations included occasional harassment of the adult owl by crows (*Corvus brachyrhynchos*) and Blue Jays (*Cyanocitta cristata*); the tendency for the adult owl to roost on the shady north or northwest side of the dome during the daytime; and the tendency for the adult owl to spend more time brooding the nestling on relatively cool, windy days than on warm, calm days. Several searches on and near the campus failed to reveal the presence of more than one adult owl at any time.—EDWIN C. FRANKS AND JOHN E. WARNOCK, *Department of Biological Sciences, Western Illinois University, Macomb, Illinois 61455, 5 August 1968.*

The nest, eggs, and young of the Elepaio.—The Elepaio (*Chasiempis sandwichensis*) is an endemic Hawaiian species of the Old World flycatcher family (Muscicapidae). The three races exhibit a peculiar and unexplained distribution in that separate races occur on Kauai, Oahu, and Hawaii. There is no evidence to suggest that the species ever inhabited the islands of Molokai, Lanai, and Maui, even though Molokai and Lanai can be seen from Oahu on a clear day and Maui is readily visible from the island of Hawaii.

More is known about the life history of the Elepaio than of any other endemic Hawaiian land bird. Nevertheless, there appears to be no published photograph of the

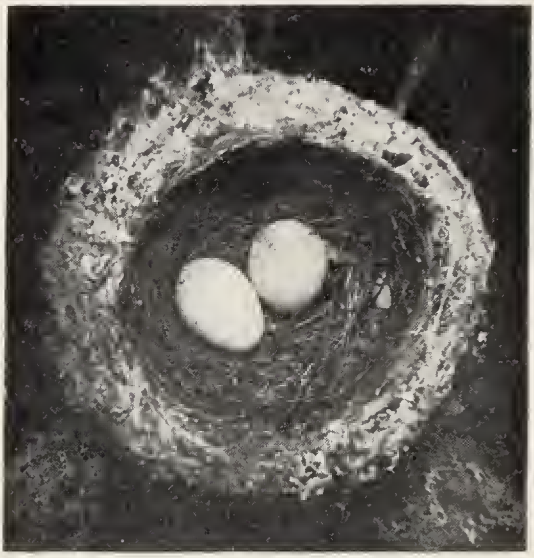


FIG. 1. Nest of the Hawaii Elepaio (*Chasiempis s. sandwichensis*) in a mamani tree; Kaohe Game Management Area, Mauna Kea, Hawaii; 30 April 1967.

FIG. 2. The same nest shown in Fig. 1 with its two eggs; 30 April 1967. This presumably is the first photograph ever taken of the eggs and an active nest of this species.

eggs or young of any race of this species. Alfred Newton (Proc. Zool. Soc. London:890–894, 1897) mentioned the eggs of an unspecified race of the Elepaio, stating that "it would be useless to figure them or to describe them otherwise than by saying that they might pass perfectly for eggs of *Parus* or *Sitta*," which is, indeed, somewhat of an exaggeration. S. B. Wilson and A. H. Evans (Aves Hawaiiensis: The birds of the Sandwich Islands, 1890–99) presented three paintings of Elepaio eggs, but these bear very little resemblance to the real eggs. W. A. Bryan (Bernice P. Bishop Mus. Occ. Papers: 37–49, 1905) presented photographs of three incompleted or deserted nests, but not of the eggs or young.

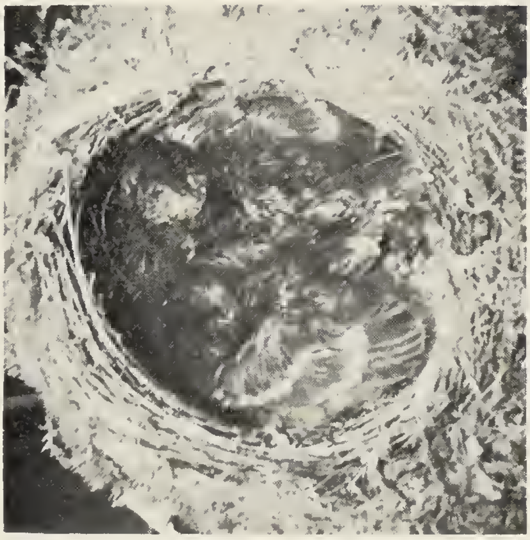


FIG. 3. Three well-feathered nestlings of the Kauai race (*C. s. sclateri*) of the Elepaio. Photograph taken 30 May 1966 in the Alakai Swamp region of Kauai. This is the first photograph taken of the nestlings of any race of this species.

On Kauai and Hawaii, the Elepaio is a fairly common permanent resident in the native ohia (*Metrosideros collina*) forests, which are areas of high rainfall. On Oahu, where much of the native forest has been replaced by exotic vegetation, the Elepaio is found in both introduced and mixed forests. By contrast, the Elepaio is one of the few endemic land birds that nests in the relatively dry (26.9 inches of rain in 1965; 15.6 inches in 1966) mamani (*Sophora chrysophylla*)-naio (*Myoporum sandwicense*) forest on the slopes of Mauna Kea at elevations of approximately 7000 to 9000 feet. Figures 1 and 2 were taken in this latter habitat, whereas Figure 3 is of a nest found in the Alakai Swamp region of Kauai. Over 600 inches (*50 feet*) of rain have been recorded in a single year on Mt. Waialeale, only a few miles from the site of the nest in Figure 3. (Work supported by NSF Grant GB-5612.)—ANDREW J. BERGER, *Department of Zoology, University of Hawaii, Honolulu, Hawaii, 9 September 1968.*

An unusual nest site of the Starling.—On 16 August 1967 Professor Emanuel Fritz of Berkeley, California, presented the Museum of Vertebrate Zoology with a live starling (*Sturnus vulgaris*) captured in his home. This bird (MVZ no. 15802), a male with an incompletely ossified skull, had testes two mm in length and weighed 76.6 g. It was obviously nearing completion of its post-juvenal molt, for the feathers of the entire head and neck, one primary on each wing, and all the secondaries were of the brown juvenile type.

The nest site from which this bird was obtained was in the basement of the Fritz's home, in the bottom of a vertical ventilating pipe nine inches in inside diameter and approximately 35 feet in height. The pipe, which was lined with unglazed terracotta, led directly to the chimney above the three-story house. Two other smaller pipes joined this one in the basement at five feet above the nest site, one coming from a gas furnace and the other from a gas water heater. By removing one of these side pipes, then by using a mirror and flashlight, the Fritz family was able to count six juveniles, though the brood may have been larger. One juvenile died of unknown causes and could not be removed from the bottom of the pipe; the others apparently fledged successfully.

According to Professor Fritz the young continued to roost with the parents in the nest for several days after fledging. They entered and left the nest by travelling the full length of the 35 foot pipe from the vent of the chimney to the nest, and vice-versa. On several occasions, both adults and juveniles exited into the basement via the two side pipe outlets. Each time they were captured and released into the garden; the one retained was collected in this manner. Locomotion was presumably achieved by a combination of fluttering and clinging to the rough-surfaced terra-cotta lining of the pipe.

That the two gas pipes entered the main outlet five feet above the nest no doubt accounted for the birds' not being asphyxiated (the dead juvenile may have been) since the noxious fumes were lighter than air and rose rather than descended the chimney. Fresh air probably entered via the chimney and the side vents described, permitting dilution of carbon monoxide and other gaseous wastes.

It is only in recent years that the Starling has been observed breeding in the San Francisco Bay region. On 14 May 1965 Gene M. Christman recorded in his field notes that two Starlings were seen in the fronds of a palm tree on Ridge Road near the Pacific School of Religion north of the University of California, Berkeley campus; later they were seen carrying food and the noises of begging young was heard. Banks (Bull. So. California Acad. Sci., 64:11–15, 1965) reports Starlings breeding in palm trees in San

Diego County. On 6 May 1967 I observed Starlings carrying food into palm trees in Ruth Hardy Park near Palm Springs, Riverside County, California.

The adaptability of these birds to new situations, as illustrated by these examples of choices of nest sites, no doubt contributes to their success in rapidly colonizing areas into which they are introduced or have spread.

My thanks to Drs. Emanuel Fritz and Ned K. Johnson who read this manuscript and offered helpful criticisms.—Luis F. Baptista, *Museum of Vertebrate Zoology, University of California, Berkeley, California, 17 May 1968.*

Fall and winter food habits of Red-winged Blackbirds and Brown-headed Cowbirds in western Oklahoma.—Since the establishment of the Washita National Wildlife Refuge on the upper portion of Foss Reservoir in western Custer County, Oklahoma, there has been a large increase in the number of wintering Red-winged Blackbirds (*Agelaius phoeniceus*) and Brown-headed Cowbirds (*Molothrus ater*). There have been several reports by local farmers of grain sorghum (*Sorghum vulgare*) depredations by blackbirds coincident with this buildup.

This paper deals with the food habits of Redwings and Cowbirds during the September through January period. The objectives were to determine: (1) frequency of various items in the diet; (2) significance of grain sorghum in the diet; and (3) effect of large winter concentrations of Redwings and Cowbirds.

Beal (U.S. Dept. of Agric. Biol. Surv. Bull., 13, 1900) reported that in the stomachs examined weed seeds occurred most frequently in Redwings and ragweed in Cowbirds.

Analysis of 92 blackbird stomachs collected in Okfuskee County, Oklahoma on 30 January 1950, showed that the eight food items which occurred most frequently had no commercial value. Grain sorghum ranked ninth and oats eleventh (Stebler, Oklahoma Coop. Wildl. Res. Unit Quarterly Report 5:20–24, 1952).

During the period September through January 1964 and 1965, 83 Redwings and 35 Cowbirds were shot in the evening at blackbird roosts on the refuge and adjacent terrain. Contents of the crops and gizzards of the specimens were examined and identified and frequency of each item determined.

The frequency of various items in the diets of Redwings and Cowbirds is presented in Table 1. Grain sorghum was the most frequently found food item in Redwings and Cowbirds, occurring in 93 and 71 per cent respectively of the crops and/or gizzards examined.

The importance of grain sorghum in the diets differed from that reported by Martin, Zim, and Nelson. (A guide to wildlife food habits. Dover Publ., 1951) for each species. They reported a greater preference for foxtail (*Setaria*), corn (*Zea mays*), oats (*Avena*), and panic grass (*Panicum*) for Redwings in the prairie region of the United States. In the southeastern United States, foxtail, panic grass, ragweed, oats, wheat, and doveweed were listed as important items in the diets of Cowbirds.

Redwings and Cowbirds had varied diets (about 15 items in each). Only five items were found in 20 per cent or more of the Redwings, while eight items were found in over 20 per cent of the Cowbirds examined. This apparently was due to the latter's habit of feeding in smaller, more dispersed groups over the study area in early fall. Cowbirds did not center their feeding on the refuge until later in the year. Most of the less important items were probably picked up while feeding on grain sorghum or other favored foods because these other grasses and weeds were usually found in or around sorghum fields.

TABLE 1

PERCENTAGE OCCURRENCE OF VARIOUS FOOD ITEMS IN CROPS AND GIZZARDS OF REDWINGS AND COWBIRDS

Food item	Redwings (83)	Cowbirds (35)
grain sorghum (*Sorghum vulgare*)	93	71
ragweed (*Ambrosia*)	75	63
insects	36	63
sunflower (*Helianthus*)	36	49
johnson grass (*Sorghum halepense*)	24	49
foxtail (*Setaria*)	10	46
lamb's quarter (*Chenopodium*)	10	26
doveweed (*Croton*)	7	20
pigweed (*Amaranthus*)	10	14
sand dropseed (*Sporobolus*)	2	14
panic grass (*Panicum*)	5	6
Paspalum	0	14
smartweed (*Polygonum*)	1	0
grama grass (*Bouteloua*)	2	0
bush-clover (*Lespedeza*)	1	3
bluestem (*Andropogon*)	1	3
wheat (green) (*Triticum*)	0	3
miscellaneous and unidentified	11	3

Damage to grain sorghum off the refuge was not significant if local farmers were able to complete their harvest by the middle of October. However, blackbirds did cause considerable damage in some fields close to the refuge when the harvest was delayed by late fall rains. Blackbird populations did not start to build up rapidly until the latter part of October (Goddard, Unpubl. Ph.D. thesis Oklahoma State University, 1967) at which time their feeding was centered in refuge sorghum fields. These fields were available because portions of them had been left unharvested to provide food for wintering waterfowl. The availability of this grain sorghum as a food supply is probably responsible for the increased populations of migrant blackbirds in the area.

Blackbirds competed with ducks for sorghum and depletion of this food source may have been responsible for the daily duck feeding flights in late December and January. A shortage of food may have accounted for the large duck and blackbird population movements away from the refuge in January both years and may have resulted in a reduced duck use of the refuge during spring migration.—STEPHEN V. GODDARD, *Department of Biology, Wisconsin State University, River Falls, Wisconsin, 5 September 1968.*

Sharp-tailed Sandpiper and Palm Warbler in Alaska.—On the afternoon of 28 June, 1967, together with my wife Helen and my daughter and son-in-law, Ann and Peter Wendt, I observed four Sharp-tailed Sandpipers (*Erolia acuminata*) on the tundra about three-quarters of a mile east of the lagoon bordering the airstrip at Kivalina, Alaska. They were feeding on the mud at the edge of a small pond, together with some Golden Plovers (*Pluvialis dominica*), Semipalmated Sandpipers (*Ereunetes pusillus*), a Bar-tailed Godwit (*Limosa lapponica*) and a Long-billed Dowitcher (*Limnodromus scolopaceus*). We watched them at a range of 20 feet for almost an hour with 9× binoculars.

The birds bore only a superficial resemblance to the Pectoral Sandpiper (*Erolia melanotos*), in spite of the remark of Gabrielson and Lincoln (Birds of Alaska, 1959, p. 372) that the Sharp-tailed Sandpiper "is so much like the Pectoral Sandpiper in size and general appearance that it can easily be overlooked." The two species are about the same size, but the Sharp-tailed Sandpiper has a much rudier overall coloration. The top of the head was rich chestnut. The breast and flanks were spotted with rufous, and the belly washed with light buff, whereas the Pectoral Sandpiper has brown streaks on the breast which contrast sharply with the white belly and flanks. The back had a scaly appearance, much like Baird's Sandpiper (*Erolia bairdii*), but with much more rufous tone. The bill of the Sharp-tails appeared to be entirely black, not yellowish-green at the base as in the Pectoral, and the legs were darkish-green rather than yellowish-green.

The status of the Sharp-tailed Sandpiper in North America was recently summarized by Stuart Keith (Canadian Field-Nat., 81:197–198, 1967). All previous occurrences of the bird in Alaska have been between 19 August and 26 October, and there is no breeding record for North America. Keith, who found the bird common at Hooper Bay, Alaska in September 1956, comments (loc. cit.) on the curious fact that some Sharp-tailed Sandpipers apparently leave their regular fall migration route down the coast of eastern Asia and fly east to Alaska. This regular action is not paralleled by any other Asian bird and is hard to explain. On the other hand, were there an as yet undiscovered breeding ground of the Sharp-tailed Sandpiper in Alaska, the bird's presence on the coast in fall would be easily accounted for. The presence of four birds in breeding plumage on the tundra in late June might indicate that there is such a breeding ground waiting to be discovered.

On 6 July 1967, I saw a Palm Warbler (*Dendroica palmarum*) on the Kenai Peninsula, Alaska, about 10 miles east of Ninilchik at the gravel pit on Kingsley Road at the point where state road maintenance ends. It was in some low bushes along the road, together with some Orange-crowned Warblers (*Vermivora celata*). I clearly noted the bright chestnut cap, yellow eyestripe, yellowish throat, white underparts with chestnut streaking, and bright yellow under tail coverts. It was singing its somewhat weak song, reminiscent of that of a Chipping Sparrow (*Spizella passerina*), and wagging its tail in typical Palm Warbler fashion.

The Palm Warbler has not previously been reported from Alaska. The nearest recorded localities for the bird are southwestern Mackenzie and northeastern British Columbia, roughly 1,000 miles to the east of the Kenai Peninsula.—JOSEPH W. TAYLOR, *590 Allen's Creek Road, Rochester, New York 14618, 3 June 1968.*

Responses of three avian species to burning.—Bobwhites (*Colinus virginianus*), Mourning Doves (*Zenaidura macroura*), and an American Woodcock (*Philohela minor*) were observed to respond positively to burning of the vegetation on a 2-acre field located on Stephen A. Forbes State Park, Marion County, Illinois. Vegetation on the field at the time of burning was an admixture of grasses and weedy forbs. Except for a narrow food patch planted 2 years previously, the field had been neither cropped nor pastured for about 5 years. Fertility was low and the soil acid. Vegetation tended to be rank although somewhat spotty.

At approximately 17:30 on 24 March 1967 fire was set around and through the field in a crude grid pattern with fire lines at approximate 100-foot intervals. There was little or no wind, dew was condensing on the vegetation, and the temperature was 50 to 55° F. Because of these conditions, and the somewhat scattered nature of the vegetation, burning proceeded slowly.

Shortly after the fire was set, about a dozen Mourning Doves, primarily in pairs, began to fly over the burning field and land on recently burned spots. The doves flew only 10 to 20 feet above the fire and landed that close to the flames, on the still warm ashes.

Three Bobwhites were heard giving covey calls, one east, one south, and one northwest, within 200–300 yards of the burning field. Two single and one pair of quail were observed to fly directly to the burning field and land within a few feet of the flames.

Earlier in the afternoon, on a different part of the study area, a covey of about 16 quail had been observed to flush less than 6 feet ahead of an earlier fire. When flushed, they flew approximately 80 yards and landed as a covey. There was neither covey disorganization nor calling behavior to indicate either alarm or fright exhibited by these birds. The following morning a covey, presumably the same one, was again flushed from this earlier burn; three more coveys were flushed from other new burns that morning. From these and other observations, we conclude that Bobwhites typically respond very quickly to burning and to newly burned fields.

Just before dark, when the 2-acre field first mentioned was about three-fourths burned, a single woodcock "peented" and made a song-flight from some brushy cover about 100 yards northeast of the field. He landed in the approximate area where he was first heard, "peented" again, and flew again. This time he flew directly to the burning field, circled once at an altitude of about 25 feet, and landed abruptly on a burned spot within 15 to 20 feet of flames which reached 2 to 3 feet into the air. After landing on the burn, he immediately initiated apparently normal courtship behavior, alternately peenting and making song-flights from the still burning field; he was still continuing these acts when we left the area at approximately 19:00.

The significance of these observations is that these three avian species appeared to respond positively rather than negatively to fire in their environment. These observations are in agreement with Komarek's hypothesis (Proc. Sixth Annual Tall Timbers Fire Ecology Conference, 6:143, 1967) that certain of our fauna may be fire adapted.

The study was partially supported by Federal Aid Project W-66-R, the Illinois Department of Conservation, the U.S. Bureau of Sport Fisheries and Wildlife, and the Illinois Natural History Survey, cooperating.—WILLIAM R. EDWARDS AND JACK A. ELLIS, *Illinois Natural History Survey, Urbana, 20 April 1958.*

Functional gonads in Peregrines.—Certain falconiform birds are considered to differ in their reproductive organs from birds of other orders in that the female may possess paired ovaries and reproductive tracts rather than the usual single left ovary (Van Tyne and Berger, Fundamentals of ornithology, Wiley and Sons, New York, 1959; A. J. Marshall, Ed., Biology and comparative physiology of birds, Vol. II, Academic Press, New York, 1961.). Van Tyne and Berger (op. cit.: 38) state that double ovaries is the usual condition in about 50 per cent of the individuals in the genera *Accipiter*, *Circus*, and *Falco*. Wood (Auk, 59:463, 1932) mentions some of the variability in the paired ovary condition in members of the Accipitridae and Falconidae. The two Peregrine Falcons (*Falco peregrinus*) he reported on had unpaired ovaries. Gunn (Proc. Zool. Soc. London, 1912:63–79) reported on one three-year-old adult Peregrine which had a left ovary about four times larger than the right; his plate shows enlarged follicles only in the left ovary. Fitzpatrick (Wilson Bull., 64:19, 1934) cited a case of one adult female with two ovaries and stated that in this case the right could be called vestigial. Finally, Storer (Auk, 83:423, 1966) pointed out that in *Accipiter* paired ovaries are the usual condition and that specimens, especially Goshawks (*Accipiter gentilis*), are not infrequently mis-sexed as a result of the collectors mistaking paired ovaries for testes. Of some 1200 museum specimens of Peregrines examined by me to date, I have found less than 4 per cent mis-sexed. Those that have been are usually immatures.

In the course of two somewhat independent studies, a biosystematic study of Peregrines and a study of pesticide residue concentrations in Peregrines, I have welcomed and sought out the opportunity to critically examine carcasses including those of captives owned by falconers as well as the occasional adult taken for pesticide studies from far northern breeding grounds. The data reported here come from 11 male and 17 female specimens taken in May, June, and early July 1961 to 1967. To obtain an index to the size of testes, both width and length were used. Of the 11 males in breeding condition only one had a right testis slightly larger than the left, two had testes approximately equal in size, while the remaining eight had the left testis slightly to significantly larger than the right. Data from the literature, where length and width of testes are recorded, also indicate the left testis indeed tends to be larger. Assuming that size is indicative of the relative degree of active spermatogenesis, the left testis would appear to be the more functional of the two.

Of the 17 females, all in breeding condition, 12 or 70 per cent possessed only a single left ovary. Four specimens had double ovaries of which three had the left larger than the right. In one case both were essentially equal in size. In a female from the Colville River, Alaska, obtained on 14 June 1964 the left ovary was markedly atrophied and appeared never to have been functional. The right ovary had five enlarged follicles about 2.5 mm in diameter and two visible ovarian scars from which follicles had ruptured. In an additional nine winter-taken females examined, only the left ovary was evident in 6 or 66 per cent while three possessed both ovaries. It appears from these data that the usual condition in the North American Peregrines is the possession of a single ovary with only about 30–35 per cent of the individuals having double ovaries. This is opposed to the usual (50 per cent or greater) paired condition in the genera *Accipiter*, *Circus* and perhaps other members of *Falco*. Although two ovaries may be present only one appears to be functional in egg production in any one season or perhaps throughout the life of the bird.—CLAYTON M. WHITE, *Department of Zoology, University of Utah, Salt Lake City, Utah 84112. (Present address: Section of Ecology and Systematics, Cornell University, Ithaca, New York), 22 May 1968.*

Insecticide residues in Least Bittern eggs.—The Least Bittern (*Ixobrychus exilis*) is sometimes found nesting in rice fields of southern Louisiana. Egg samples were taken from three nests in rice fields on the Louisiana State University Rice Experiment station in Crowley, Louisiana. One sample was collected in June, 1965 and two others in June, 1966.

These eggs were analyzed for chlorinated hydrocarbon insecticide residues at the Harry D. Wilson Laboratories, Louisiana State University, using electron capture gas chromatography with thin-layer chromatography used as a qualitative check. The results of the analyses are given in Table 1.

Dieldrin residues in the Least Bittern eggs were rather high. The contamination levels ranged from 0.49 to 5.39 ppm. Heptachlor epoxide, *p,p′*-DDE, and *p,p′*-DDT were also present at lower levels.

The rice fields in which these nests were located were planted with aldrin-treated seed which contained ¼ lb aldrin/100 lb seed. This was the only insecticide treatment applied during the two growing seasons.

TABLE 1

CHLORINATED HYDROCARBON INSECTICIDE RESIDUES IN LEAST BITTERN EGGS FROM RICE FIELDS NEAR CROWLEY, ACADIA PARISH, LOUISIANA.

Number Eggs	Date Collected	ppm Dieldrin	Heptachlor epoxide	*p,p′*-DDE	*p,p′*-DDT
4	June, 1965	5.39	0.02	0.15	1.94
1	June, 1966	0.49	0.07	0.42	0.38
2	June, 1966	2.25	0.05	0.33	*

* Not detected at 0.5 ppm.

The food of the Least Bittern is comprised mostly of animal matter such as frogs, fish, leeches, snails, etc. (Bent, U.S. Natl. Mus. Bull. 135:84, 1926; and Oberholser, The bird life of Louisiana. La. Dept. Conserv. Bull. No. 28:72, 1938). Therefore, it seems unlikely that the residues detected in these eggs came about through ingestion of treated rice seed. It is probable that these residues resulted from insecticides concentrated by organisms lower in the food chain that were ingested by the Least Bittern in its random feeding.

Purple Gallinules (*Porphyrula martinica*) and Common Gallinules (*Gallinula chloropus*) nesting in the same rice fields where these Least Bittern nests were found had an average dieldrin contamination in their eggs of 6.51 and 9.37 ppm, respectively (Causey, et al., Bull. Environmental Contamination & Toxicol., 3:274, 1968). The gallinules, unlike the Least Bittern, are highly granivorous and probably eat enough treated rice seed to accumulate such high residues. There is a distinct possibility, based on reports that the Least Bittern occasionally eats small birds and mammals, that residues of dieldrin could be acquired through ingestion of young Purple and Common Gallinule chicks which are fairly abundant in these rice fields during the summer months.

The effects of dieldrin and other insecticide residues present in eggs of the Least Bittern are unknown. It is hoped that this report may stimulate research in this area.—M. KEITH CAUSEY (Present address, *Department of Zoology-Entomology, Auburn University, Auburn, Alabama 36830*), AND JERRY B. GRAVES, *Department of Entomology, Louisiana State University, Baton Rouge 70803, 17 June 1968.*

On abnormally crossed mandibles in birds.—Among the kinds of manuscripts regularly appearing on the desks of editors of ornithological journals are those describing abnormalities of various types. Perhaps the favorite topic is variation in color; there appears to be a compulsion to place every albino or white-spotted bird on record. Readers of journals are less aware of this phenomenon than are editors and editorial committees, since relatively few of these notes are accepted for publication.

A close second to color abnormalities in popularity among aspiring authors seems to be bill deformities. Pomeroy (Brit. Birds, 55:49–72, 1962) published what must certainly come close to being the definitive paper on the subject of abnormal bills in birds, but, again, everyone who encounters a specimen of this type feels obliged to place it on record. Pomeroy (op. cit.:54) described "crossed mandibles" as "a relatively common abnormality which has been recorded in a wide range of species." He cited five passerine species merely as examples, and figured crossed bills in the Blue Tit (*Parus caeruleus*) and the Great Tit (*P. major*).

A search through any large museum collection will yield specimens of species for which abnormally crossed mandibles have not been specifically recorded in the literature. Among 700 birds from northern Argentina in Carnegie Museum, collected in 1961 by the late William H. Partridge, Philip S. Humphrey, and the writer, are at least four cross-billed specimens: a Short-billed Canastero (*Asthenes baeri*), a Larklike Brush-runner (*Coryphistera alaudina*), a Field Flicker (*Colaptes campestroides*), and a Plush-crested Jay (*Cyanocorax chrysops*), the latter two collected *on the same day.*

Any bird bander who regularly handles large numbers of birds will encounter individuals with abnormal bills, including crossed mandibles, almost every year. Such has certainly been our experience at our banding station at Powdermill Nature Reserve (near Rector, Pennsylvania); we note any such abnormality on our banding sheets and file cards, and release the birds routinely. Most of the reported birds with crossed bills (and those with other common abnormalities, such as extended and decurved upper mandibles), as well as those we have seen at Powdermill, have been adults, or at least full grown, and have thus obviously been able to feed in spite of their apparent handicaps.

I suggest that we take it as understood that these common bill abnormalities may occur in almost any avian species, and that there is little to be gained by devoting the valuable pages of our ornithological journals to descriptions and photographs of additional species. I except from my suggestion such thorough analyses as that of Threlfall (Auk, 85:506–508, 1968), with its careful anatomical description of an abnormal (and apparently non-viable) young Herring Gull (*Larus argentatus*). I prefer not to cite any examples of papers on bill abnormalities that, in my opinion, were *not* worthy of publication.—Kenneth C. Parkes, *Carnegie Museum, Pittsburgh, Pennsylvania, 4 September 1968.*

PUBLICATION NOTES AND NOTICES

Birds of Pennsylvania: When and Where to Find Them. By Merrill Wood. Pennsylvania State University, Agricultural Experiment Station, University Park, [1967]: 4-3/8 × 8-1/2 in., paper covered, [xvi] + 119 pp., 156 drawings by Dorothy L. Bordner. $1.00.

An introduction includes the topography of the area, migration seasons, and a calendar of birdlife. Pages 1–111 present a list of 423 species with brief remarks (when applicable) on frequency, abundance, seasonal occurrence, habits and status changes, and general breeding and wintering ranges.

ORNITHOLOGICAL NEWS

W. E. Clyde Todd, Curator Emeritus of Birds at Carnegie Museum, died on 24 June 1969 in his 95th year. Mr. Todd, who will be remembered for his two monumental works, "The Birds of Western Pennsylvania" and "The Birds of the Labrador Peninsula," had been a member of the Society since 1911, and was the senior member of the A.O.U.

The University of Miami announces the appointment of Oscar T. Owre to the Robert E. Maytag Chair of Ornithology.

The International Council for Bird Preservation, United States and Pan-American Sections, have limited funds available to assist research into the status, ecology and biology of rare and endangered species of birds. Qualified persons interested in carrying on such research, and needing funds for that purpose, are invited to submit proposals. Such proposals should be fully documented, indicating the plan of study, previous experience and training, what other financial assistance is being sought, a detailed expense estimate, and, if by a graduate student, a recommendation from his major professor.

Proposals relating to birds outside the Latin American area should be forwarded to Stuart Keith, Secretary, U.S. Section, I.C.B.P., American Museum of Natural History, New York, N. Y. 10024; if relating to birds in Latin America to Eugene Eisenmann, Secretary, Pan-American Section, I.C.B.P., at the same address.

During May through July of each year for a five year period, Ring-billed Gulls (*Larus delawarensis*) from three Great Lakes colonies will be wing-marked with 1.5 inch-diameter "Saflag" tags. Each colony is represented by a specific color. An attempt is being made to determine the dispersal pattern, migration route, and winter range for each population. Anyone observing such wing-marked gulls is asked to notify Dr. William E. Southern, Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115. Please report each observation of marked individuals even though the same bird may be sighted on different days. The following information is desired: date, exact location, marker color, and the observer's name. Your assistance in this aspect of the project will be greatly appreciated. Respondents will receive information pertaining to colony locations and the date of marking.

A study of the northward movement of the Cattle Egret is being made to determine the distribution and post breeding movements of this species throughout its range. The following information is requested: Name, address of observer, date, time, number, location of observation (state, nearest town, county and if possible township, range and section), habitat, activity, and weather. Please send records and observations to Alan B. Schroeder, $^{C}/_{O}$ Norman Bird Sanctuary, Third Beach Road, Middletown, Rhode Island 02840.

Cooperators will be sent proper forms and a report of the results, if requested.

ORNITHOLOGICAL LITERATURE

RADAR ORNITHOLOGY. By Eric Eastwood. Methuen & Co., London (distributed in the U.S.A. by Barnes and Noble, New York), 1967: 6¼ × 9½ in., xii + 278 pp., 24 pls., many figs. 75 s ($9.00).

Radar ornithology is still in its infancy, even though it has matured enough now to have a book devoted to it. Dr. Eastwood is in a delicate position. If not the father, he is at least a close family relative of the infant. He could be tempted to an excess of praise, or to a compensatory over-criticism. Remarkably, he has avoided either without bragging of this agile feat and has given us a very readable book.

The tendency of one intimately involved in any field is to describe the technical aspects of that field in glorious detail. In a book on radar this could result in a jungle of electronic mathematics impenetrable enough to stop all but the most persistent. The value of this book is that it presents no pyrotechnical display, but provides instead just about enough technical discussion so that the reader has some "feel" for the value of radar and some concept of the problems involved in using it. I suspect some readers will find too much, others will regard the description of "radar working" as too superficial. Dr. Eastwood does oscillate somewhat from detail to generality but I believe most readers will find the mean level quite satisfactory. The practicing researcher has technical information available, anyway, and eventually ends up with a sort of do-it-yourself approach which goes beyond the printed information available. The discussion of principles of radar, the extraction and display, and the interpretation of radar data are essential to the appreciation of the rest of the book (and the bulk of it) on findings of radar ornithology. Much of what is claimed in this central core of the book cannot be evaluated without some technical background (any hi-fi stereo bug will recognize the situation), so pages 1-78 should be read carefully and in sequence. I mention the latter because it is possible to sample the remaining sections of the volume as interest dictates. I rather recommend that the reader do this. Unless one has a particular interest in, say, patterns of migration over a certain area in the fall, I think it is hard to keep all the observations mentioned in mind and continue reading with sustained enthusiasm. As yet there are too few generalizations available to serve as memory pegs for the mass of data reviewed by Dr. Eastwood. Nevertheless, each case presented serves as a fascinating demonstration both of what migrating birds can do *and do* and of the detecting abilities of radar. Fortunately, Dr. Eastwood has set up bite-sized divisions under clear bold-faced headings which facilitate the sampling process. The following list of topics will give some idea of the scope of the book's main section: time variation, patterns in Europe and North America, flight behavior, wind drift, orientation, ring angels, altitudes of flight, soaring and gliding, counting, effects of weather. In one chapter Dr. Eastwood turns the tables and discusses the effect of radio waves on birds. He presents a remarkable amount of information in all the foregoing, yet does encourage further study by pointing out gaps in information and the ambiguity of some observations and by suggesting what information is still needed.

The final chapter is a brief but optimistic look at the future of radar ornithology. The author stresses the need for both coordinated studies covering large landscape units and intensive studies of individual birds in flight. He also points out the importance of defining and refining questions as hypotheses are generated and of considering the limitations of the instrument. New developments of radar now available only to the military, or anticipated, will reduce certainly the confines of the latter problem. As the author says, so much of radar ornithology has been "opportunistic," with ornithologists making use of what equipment they could and wherever it happened to be located. Now it is time to plan studies with respect to the biological problems requiring investigation with radar.

Dr. Eastwood's book is essentially a review, creative as well as critical, and suggests great promise for the infant subject.—JEFF SWINEBROAD.

BIRD GUIDE OF THAILAND. By Boonsong Lekagul. Privately printed with the advice of the Association for the Conservation of Nature, Bangkok, 1968: 5¼ × 7½ in., xxviii + 271 pp., 81 col. pls. of line drawings, 6 photos, 1 map. $7.50. Order from the author, c/o Association for the Conservation of Nature, 4 Old Custom Lane, Bangkok, Thailand; add $1.00 for mailing. (Also available for $8.50 from Pierce Book Company, Winthrop, Iowa).

Dr. Boonsong, by profession a physician, by devotion an ornithologist and conservationist, has produced a remarkably complete and useful field guide. All the 829 bird species known from Thailand (formerly Siam) are depicted in color—even the peculiar new River-martin (*Pseudochelidon sirintarae*) described in 1968, which provides the frontispiece. The illustrations are by the author, and, though not of professional caliber and on some plates dully printed, they should serve for identification of almost all species. The drawings are in field-guide style and show both sexes when markedly different. In the case of raptors and waders, the line drawings depict birds in flight. The distinguishing tail characters of the various snipe are illustrated on one plate. The text, in English, gives scientific name, English name, Thai name (both in Thai and Latin characters), length, field marks, and sometimes vocalizations; it briefly indicates the part of the country where the species occurs as well as its habitat and status as migrant visitor or resident. A map of Thailand shows major geographical and political divisions, tinted to reflect the type of vegetation of the area. This is supplemented by a chapter on zoogeography. The sequence and scientific nomenclature essentially follow Deignan's (1963) Thailand check-list, but after the plates and text had been prepared, additional species were found in the country, so text and illustrations covering these had to be included at the end.

There are said to be about fifty thousand North Americans currently, if temporarily, in Thailand. Adding the number in neighboring countries of southeast Asia, including Vietnam, the potential market for this little book is substantial. Its quality and present uniqueness should make the small edition go rapidly out of print. Dr. Boonsong merits great credit in preparing and publishing this work on his own. As a conservationist he felt that bird preservation required a book by which his countrymen could identify, and thus more fully appreciate, their immense and interesting avifauna. For Thai unfamiliar with English ornithological terminology, he has provided a glossary and special index. These, with the pictures and the Thai names, should suffice until an edition entirely in the Thai language can be financed. The present version serves as an inexpensive introduction to the bird life of an ornithologically rich area of the globe.—E. EISENMANN.

ORNITHOLOGY: AN INTRODUCTION. By Austin L. Rand. W. W. Norton & Company, New York, 1967: 6¾ × 9½ in., 311 pp., 51 figs. $8.50.

Publishers, like clothes designers, quickly learn to create modes and to capitalize upon them. The success of the Peterson Field Guides and *Life's* Nature Library Series has engendered a rash of popular science books for the "general reader"—a "ready-to-wear" form of learning that is fashionable, fairly inexpensive, and comfortable for even the most non-scientific reader.

Norton and Company have augmented this genre with "The World Naturalist Series," including Austin Rand's book on ornithology. The reader of this book will find the going uniformly easy and palatable. Technical jargon is eliminated here, but the text is larded with important aspects of bird biology. The author's preface was written in mid-1964. No references go beyond 1964. I wonder why, then, the book was not published until late 1967. A lot of exciting ornithology has been written in the intervening period on a variety of topics, especially ecology, behavior, migration, and orientation. It is a pity that none of this could have been included in the text.

The book covers almost all aspects of bird biology in 240 pages and 24 chapters. Five appendices describe briefly the different orders of birds, explain scientific nomenclature, list several references on techniques of studying birds, and provide notes and suggested readings for each chapter. Appropriately for this book, all scientific names are included in an appendix. Twenty-three pages very adequately index the book's contents.

The chapters cover such aspects of bird biology as characteristics of birds as a group, the bird body, sense organs, size and shape of birds, patterns of diversity, social feeding, food and water, breeding cycle, nest and eggs, parents and young, social nesting, homing and orientation, migration and hibernation, predation and parasites, coloration, feathers and molt, flight, bird song, behavior, geography, the nature of species, and birds and man. Scattered throughout the chapters are some of Rand's personal observations — all too few — from both the museum and the field. They considerably enhance the book's readability.

The writer who is imbued with the technicalities of his science must shift gears when writing for the public, translating scientific jargon into language that the public can not only assimilate but also enjoy. The author succeeded in this difficult task. The danger in such translation is obviously found in a tendency to generalize, to oversimplify ideas and conditions. Numerous exceptions to general statements cannot, of course, be included in a book of this nature.

The author maintains a consistent writing style throughout. But not all chapters are of consistent quality. Sections on the senses of birds, patterns of diversity, and the nature of species are especially well presented for the general reader. Others on activity and rest, behavior, and bird song are weaker, lacking in solid information. Too much space is devoted to the musical qualities of bird song, and not enough to some other topics, such as some of the recent theories of bird orientation. The author attempts to avoid the use of technical terminology as completely as possible. He succeeds very well, with the exception of a few lapses. Because of the delay between the writing and publication, several stated facts were no longer valid by the time this book was published.

If I am mentioning what appear to be shortcomings of this book, I emphasize that they are minor ones. The text of the book is lucid and informative. The most serious impediment to the book's likely success will be its illustrations. The publisher bears the onus for this deficiency. Seldom have I seen a book published with such poorly executed and inadequate illustrations. Drawings are few and inaccurate and the illustrative material poorly selected. The reader of such a popular science book, because he is a tyro, needs desperately good graphic teaching to augment the text. One wonders why the publishers went to the effort to get such a well-known ornithologist as Austin

Rand to write this excellent text, but failed to back up his effort with high quality art work. What a difference it would make in the sales of the book!—D. A. LANCASTER.

A NATURALIST IN TRINIDAD. By C. Brooke Worth. J. B. Lippincott Company, Philadelphia, New York, 1967: 6 × 9 in., 291 pp., 18 drawings, 2 maps. $7.95.

The island of Trinidad, about nine miles north of Venezuela, is more closely allied faunally to South America than to the West Indies. Like much of South America, its natural history is still in the pioneering stage.

In 1960, C. Brooke Worth, after serving as a medical parasitologist in India and South Africa, went to Port-of-Spain, the capital of Trinidad and Tobago, to join the staff of the TRVL (Trinidad Regional Virus Laboratory). Supported by the Rockefeller Foundation, this organization was created for research on viruses among various animals. Dr. Worth's position was that of field naturalist, and so he was expected to study the habits of local wildlife and obtain specimens of blood from the subjects under observation.

For field headquarters, he chose Bush Bush Island in the Nariva Swamp on the east side of Trinidad. Relatively untouched and remote, being accessible only by boat from the coast, Bush Bush was ideal. Here he had a small prefabricated building erected and named it We House from a local expression. Most of the book is centered on Bush Bush although it takes in trips to the Arima Valley in the northern range, Port-of-Spain, and Soldado Rock off the southeastern coast.

Dr. Worth's project encompassed practically the whole field of natural history, but his particular interest was ornithology. He sat up nets to capture birds for banding and bleeding. To obtain specimens in the upper canopy, he invented a method of raising the nets to tree-top level. The first species caught in this manner was the Black-tailed Tityra. Later species included the Palm Tanager, Sulphury Flatbill, Seven-colored Parrot, and several kinds of honeycreepers.

Dr. Worth gave attention to other creatures besides birds, as the headings of some of the book's chapters reveal: Monkeys, Small Mammals, Spiders and Bugs, Bees, Snails, Ants, Bats, Snakes, Lizards and Caymans, Butterflies and Boys.

One feature of special attraction was a cocorite palm in the yard of We House. The life, both plant and animal, associated with this tree is a summary in microcosm of the wildlife in the area.

While Bush Bush Island was retained essentially in its wild state, human occupation did initiate changes. Leon, Dr. Worth's helper, cultivated some plantains, the leaves of which bats found to be ideal places for roosting. A small beach lizard from the coast found its way to sections of exposed sand that resulted from the opening of the forest. A succession of animal and plant life, due to changes of this sort, is always of interest.

Since "A Naturalist in Trinidad" is primarily autobiographical, Dr. Worth makes no attempt to delve deeply into any one topic. However, he has a facility for effecting vivid descriptions. Thus the book is certain to please the armchair reader who desires a vicarious introduction to Central and South America, or the individual who wishes to travel retrospectively to Trinidad.

Don R. Eckelberry has greatly enhanced the book with 18 excellent black-and-white drawings, all done from personal observations during his many months in Trinidad. Two maps, one of Trinidad and one of Bush Bush Island, help to orient the reader.—MARGARET H. HUNDLEY.

Of Predation and Life. By Paul L. Errington. Iowa State University Press, Ames, 1967: 6 × 9 in., xii + 277 pp., 1 photo of author, many sketches by Dycie Madson. $6.95.

For more than 30 years Paul Errington labored to promote the appreciation of predators as part of the natural order of living communities and to develop a theory of predation. In simplified form, the theory states that most vertebrate predators consume surplus individuals from their prey populations—individuals that would die from some other cause if not eaten—and that predation is largely non-regulatory in determining the population levels of prey, although he did allow certain exceptions. This book is a posthumous attempt at popularization and elaboration of Errington's basic philosophy about predation. The first draft of the manuscript was complete at the time of his death in 1962, and we are indebted to his wife, Carolyn Errington, for undertaking the revision necessary for publication.

It is clear that Errington remained true to his early convictions right to the end of his life, despite increasing difficulties with some of the more recent findings of his own and other researches. The organization and chapter titles of this book reveal some of the problems that beset him in later years, as well as the clarity of his original insight. Part I consists of four chapters dealing with preliminaries and perspectives. In Part II there is a chapter entitled, "Predation and the Bobwhite Quail: some comfortable generalizations," followed by another headed, "More about predation and the Bobwhite Quail." Farther on there is a chapter headed, "Predation and the Muskrat: when the patterns still looked fairly simple," followed by, "More about predation and the Muskrat." In Part III, the final chapter about "Predation and life's wholeness" reveals Errington at his best as a writer, naturalist, and conservationist—not quite in the class of Aldo Leopold—but credible and appealing nonetheless.

Errington's influence on vertebrate population biology—particularly its management aspects—has been very great; and I suppose it is safe to say that most field biologists today accept the thesis that predation among vertebrate populations is epiphenomenal to other controlling factors. Only in the case of certain highly capable predators—such as canids and felids that prey on ungulates lacking important self-limiting mechanisms of population control—is predation thought to act as a true limiting factor, according to the Erringtonian theory.

Errington's ideas constituted a healthy reaction against the glib and shallow thinking about predation current before and during the time he was formulating his views in the 1930's and early 1940's. First, there was the attitude of the hunter and gamekeeper, who thought that all predators were "bad" because they kill game and that by eliminating predators the game would automatically increase. Then, there was the equally uncritical approach of the protectionists and economic biologists who attempted to prove how "beneficial" birds and some other animals are because of the great numbers of insects, rodents, and weed seeds they eat but who paid no attention to the dynamics of the populations involved in their calculations. The mere fact of eating was all that these groups emphasized. Errington gave a more balanced perspective to predation by considering it one among many factors that can influence the numbers of animals. For this reason his work remains important, but one should avoid the temptation to generalize his theory to cover all cases of predator-prey relations.

Some of the difficulty in understanding the details of Errington's thinking stems from his choice of subjects for study, as well as from his methods of research. It is no slight to recall that Errington was a local field-naturalist who worked on certain specific wildlife problems in the north-central United States (Wisconsin and Iowa), but it *is* important to examine his studies in the context of their limited geographic and ecological setting. His views about predation were formed early in his career from studies of Bobwhite (*Colinus virginianus*) and one of its less important predators, the Great Horned Owl (*Bubo virginianus*), but even more so, from his lifelong preoccupation with muskrats (*Ondatra zebethicus*) and their main predator, the mink (*Mustela vison*).

In Wisconsin the Bobwhite populations reside at the northern limits of the species range, in an environment that is climatically marginal for the existence of quail. There one would expect the overriding mortality on quail populations to be associated with hard winters or other climatic extremes that largely obscure biological regulation by factors such as predation. This is precisely the conclusion I reach from Errington's quail studies, and all the tedious recitation about the thousands of Great Horned Owl pellets that did not contain quail remains is beside the point. Moreover, the quail studies suffer from a lack of information about mortality during the late spring and summer period of breeding and development of the young quail. Much of Errington's puzzlement about the three different "thresholds of security" shown by the Prairie du Sac quail might have been erased by a detailed, month by month analysis of mortality, including the kill by owls *and other predators of quail.*

Errington's views were most strongly molded by his experience with the single predator-single prey interaction between minks and muskrats. Again, these mammals live in a special, marshland habitat that is often beset by environmental crises—drought years, hard winters with deep freezing, early spring thawing followed by re-freezing—that are likely to overshadow biological controls and reduce populations far below the spring capacity of the habitat to support muskrats during the more favorable years. The basic aggressive behavior of the muskrat—the intraspecific intolerance which Errington emphasized as the main regulator of population density—possibly has been selected as a response to the extremely variable and unpredictable nature of the animal's habitat. The effects of predation could easily be masked by such a meteorologically influenced population. It seems doubtful that one can generalize Errington's findings on muskrats to include other vertebrate prey populations, especially those that occupy more terrestrial habitats, which are less subject to extreme crises.

Errington emphasized that it is the "biological surplus" of transient, unsettled muskrats after dispersal to the spring breeding home ranges that are particularly subject to predation or other mortality, but that the settled rats are relatively safe. Other examples have come to light, however, in which the predators operate on settled, breeding populations of prey animals, such as European Sparrow Hawks (*Accipiter nisus*), on passerine birds (L. Tinbergen, 1946), an aggregation of avian and mammalian predators, on birds and mammals (Craighead and Craighead, 1956). Gyrfalcons (*Falco rusticolus*), on ptarmigan (Cade, 1960), and Northern Shrikes (*Lanius excubitor*), on passerine birds and microtine rodents (Cade, 1967). Errington never considered examples of this sort, and predation on muskrats may be atypical in respect to influences on resident, breeding populations, because few predators seem to be adapted to get at the rats in their optimum nesting habitat. The mink is about the only one, according to Errington.

What is a surplus animal? Errington said, the immature, ill-situated, sick, and handicapped. But many such individuals would doubtlessly survive if not caught by predators, and some would breed. In the case of territorial birds, it is probable that surplus animals are important in maintaining the "saturated" state of the breeding habitat. Therefore, a bird that is "surplus" one moment may become a functioning unit of the breeding population at the next. In a ptarmigan population, adult birds that are a non-breeding "surplus" one year may be breeding stock in another year, if they can survive. The extent of reduction in their numbers can have important results on the degree to which ptarmigan exploit optimum breeding conditions in a good year following several bad ones. Predation by Gyrfalcons, arctic owls, foxes, and other mammals looms as a factor of major importance in this equation.

At times, Errington stressed the randomness of the effect of predators on their prey. He thought compensatory mortality factors like predation are analogous to the reproductive behavior of bottled fruit-flies, or the molecules of a gas, in that they seem to be based on random contacts with dangers increasing with density. But this randomness does not prove out in nature as well as in theory, and some selective predators continue to catch prey at densities well below that which would be predicted by a theory of random contacts—for instance, Little Eagles (*Hieraetus morphnoides*) preying on rabbits in Australia (Calaby, 1951) and Gyrfalcons taking ptarmigan in northern Alaska (Cade, 1960). Errington did not pay enough attention to "vulnerability factors," which can drastically alter the randomness of predation based on simple density considerations, as L. Tinbergen showed for the vulnerability of different passerine species to predation by Sparrow Hawks.

Errington did not consider instances in which a host of predators that have virtually no alternate prey feeds on a single, abundant species, such as the brown lemming (*Lemmus trimucronatus*) in arctic Alaska (Pitelka, et al., 1955), or instances in which an aggregation of predator species, although having alternate prey, nevertheless is highly attracted to one or two conspicuous, easily caught species, such as ptarmigan in the low arctic tundras. Both these examples appear to represent nonrandom predation that may well exert important modifying influences on the population dynamics of the prey, from season to season and year to year.

Errington's methods of gathering and presenting data leave something to be desired. For instance, there are no tables, graphs, or any other convincing presentation of data in this book. Perhaps he thought these formalities unnecessary for a popular treatment of his subject, but in fact one must go back to papers mainly published before 1945 in order to find an acceptable accounting of the data upon which he based his generalizations.

Despite the thousands of Great Horned Owl pellets and mink scats he examined and despite his use of rather precise figures for estimates of Bobwhite, muskrat, and mink populations, Errington was not really quantitative, statistical, or systematic in his methods of study. He began his outdoor experiences as a hunter and trapper, and he remained naturalistic in his approach to biological study, relying heavily upon intuitive and impressionistic experiences. As far as one can tell, his only method of census was to wander around on his favorite marshes and to record observations on whatever animals happened to appear.

Errington was accomplished at "reading sign," and he was able to see much more than most of us. On page 23, for example, where he speaks about his examination of gunshot wounds on trapped mink, he says, "Another, a male, had healed wounds on head and neck suggesting that while peering out of a hole it had taken a shot charge at a distance of about thirty-five feet from a choke-bored, twelve-gauge shotgun." That is a terrific amount of detail to be able to infer from old scars on a pelt! Nor is this an isolated example of the inference Errington could generate from his observations of "sign." On page 184, he assigned 2,415 mink scats containing muskrat remains to the following categories of predation: 1600 to 1700 resulted from scavenging on muskrats that died from disease, 360 consisted of remains of muskrats that became vulnerable to predation because of intraspecific strife, 100 consisted of victims exposed by droughts and freezeout crises, and 210 were of "young muskrats caught by the minks under varying conditions of disadvantage." Most field biologists consider themselves fortunate to be able to identify the species represented by materials in carnivore scats, and they are absolutely overjoyed if they can also work out the sex and approximate age class of the food items. Errington was able to go far beyond these routine matters and actually determine the social status, health, and general welfare of the victims.

Like all of Errington's work, "Of Predation and Life" is highly provocative and stimulating, but equally difficult and unsatisfying because of conceptual vagueness and a lack of solid factual support. The book leaves me wanting to think that it is all true, but not quite satisfied that everything is just right.—Tom J. Cade.

Thorburn's Birds. Edited with an introduction and new text by James Fisher. Ebury Press/Michael Joseph, London, 1967; 7¾ × 10½ in., 184 pp., 82 col. pls. by Archibald Thorburn; endpaper maps. 50s ($6.00).

Anyone interested in bird painting will certainly want to have this re-issue of Thorburn's long out-of-print "British Birds," now presented in one volume including a completely new text.

The much smaller format was probably necessary to fit the modest price. But there has been a substantial loss of quality too. At least a dozen of the plates in the copy before me have a flat, "washed out" look, though the registration is consistently good. I am informed that the new plates had to be made from the earlier reproductions rather than from the original paintings long since dispersed and in private collections. That could account for any consistent loss of quality, but surely not for an inconsistent one. The publisher rather than the author is probably responsible for the decisions as to the makeup of this book. It is this reviewer's opinion that an opportunity was missed in not providing us with a volume, even at higher cost, that would have better displayed the work of one of Britain's finest bird painters.

And in larger format Mr. Fisher would have been able to give us more than his concise but excellent distributional paragraphs on each species, bibliography, index, and a two and one-half page introduction. We might have learned more about the artist upon whose work, after all, this book depends.

I first became acquainted with Thorburn's work at about the age of sixteen when an uncle gave me a small three-volume set of T. A. Coward's "Birds of the British Isles and their Eggs." I had by that time already determined to become a bird painter and I remember how I studied and studied the many fine illustrations in those books. It was then the only work I had seen which seemed to me to come up to that of Fuertes, or nearly so. Thorburn put much more effort into feather texture and had a much softer treatment of both bird and background than did Fuertes. Looking back, it was probably this misty atmospheric mood which I later learned was very much in the tradition of English watercolor, which kept Thorburn's work from being an influence on mine. There was something very foreign in his lighting to a boy viewing birds in an Ohio setting.

It is clear that Thorburn influenced Allan Brooks and others. He apparently worked on a toned ground, a practice which Brooks adopted early, but which Fuertes took up only rather late in his career, and then with much less delicacy in handling.

My respect for Thorburn's work has not lessened over the years. I particularly like his shorebirds, hawks, and upland game birds. And while his flying birds are not very authentic, some of his water birds seem to ride a bit high in the water and the proportions in some figures could be better, it is only with the facial expression of owls (due to his treatment of the shapes of the facial disks) that I feel he "missed" almost consistently.

All that aside, it can still be appreciated in these plates, which figure from one to eight species each (the text usually appearing on the facing page), that Thorburn really knew his birds in life and had a rare talent for making us experience his view of them.—DON R. ECKELBERRY.

PUBLICATION NOTES AND NOTICES

A Biology of Birds with Particular Reference to New Zealand Birds. By B. D. Heather. Issued by the Ornithological Society of New Zealand, 1966: 102 pp., many drawings and photos. Paper-covered. $2.00 (including postage). Available from OSNZ, Box 40-272, Upper Hutt, New Zealand.

Written for both the student of biology and the amateur ornithologist, with all illustrations and examples of principles based on New Zealand birds. Informative to anyone contemplating work with New Zealand birds; useful to any American or Canadian instructor in ornithology wanting different ideas and examples in presenting his subject.—O.S.P.

COMMUNICATION IN THE ANIMAL WORLD. By William F. Evans. Thomas Y. Crowell Company, New York, 1968: 5½ × 8½ in., x + 182 pp. illus. with drawings by Nancy Lou Grahan and photos. $5.95.

A "popular" review of the various kinds of signals used in communication. Following a brief introduction, seven chapters deal with communication in different animal groups, one being birds. A final chapter discusses methods and tools for study. The author is assistant professor of biology at Little Rock University in Arkansas.

EXTINCT AND VANISHING BIRDS OF THE WORLD. By James C. Greenway, Jr. Second revised edition. Dover Publications, New York, 1967: 5½ × 8½ in., paper cover with col. illus., xvi + 520 pp., 86 figs. $3.50.

Although this is mainly a reprint of the original edition published in 1958 (see review in Wilson Bull., 70:293–294, 1958), it is also a revised edition to the extent that "the status of the species and subspecies has been brought up-to-date wherever new information has become available" and a separate bibliography of new works cited has been added.

PROCEEDINGS OF THE FIFTIETH ANNUAL MEETING

JEFF SWINEBROAD, SECRETARY

The Fiftieth Annual Meeting of the Wilson Ornithological Society was held 1 May through 4 May, 1969, at the College of William and Mary, Williamsburg, Virginia. Co-sponsors were the College of William and Mary and the Virginia Society of Ornithology. The meeting was attended by two hundred and ninety registered members and guests.

The meeting started on Thursday with an informal coffee hour, followed by a viewing of the film "Mark Catesby, the Colonial Naturalist."

On Friday morning, the Society was welcomed by Dr. John H. Willis, Assistant Vice-President of the College of William and Mary. Dr. H. Lewis Batts, President of the Society, responded. The first business session followed the welcome and response and then the first of four paper sessions started. The third and fourth paper sessions were held on Saturday. The fourth session was a special symposium "An Ornithological Preview," chaired by Dr. Harrison B. Tordoff. The second business meeting of the Society was held Saturday mid-morning.

Friday evening a social hour was held at the Cascades Meeting Center of Colonial Williamsburg.

The business meeting of the Virginia Society of Ornithology was held Saturday afternoon at the close of the fourth paper session.

The annual dinner was on Saturday evening. Kenneth C. Parkes was toastmaster. The presidential address was presented by President H. Lewis Batts. The evening program concluded with an illustrated program, "The Storks of the World," filmed by Philip Kahl and presented through the courtesy of the National Geographic Society. For the first time an award was given for the best paper presented at the meeting by student or non-professional. The recipient was announced at the annual dinner, and was Mrs. Martha A. Whitson whose paper was "Breeding Behavior of the Roadrunner (*Geococcyx californianus*)."

Field trips were conducted to local areas on Friday and Saturday morning, and on Sunday trips visited Craney Island, Seashore State Park, and Cedar Island.

FIRST BUSINESS MEETING

The first business meeting was presided over by President Batts. The minutes of the previous meeting were approved as published in the Bulletin. The Secretary, Jeff Swinebroad, presented a brief summary of the meeting of the Executive Council of the Society:

1. The Council voted to accept an offer from Colorado State University to hold the 1970 meeting there as a joint meeting with the Cooper Ornithological Society sometime in late June of that year. The Council also approved the 1971 meeting site as Dauphin Island, Alabama, with the Mobile County Bird Club as hosts.
2. Dr. George Hall was reelected unanimously as Editor of the Wilson Bulletin.
3. Temporary committees were designated by President Batts as follows:
   Auditing Committee: C. Chandler Ross, Phillips B. Street;
   Nominating Committee: Olin Sewall Pettingill, Aaron Bagg, Phillips B. Street;
   Resolutions Committee: Burt Monroe, Jr., Chandler Robbins, Robert W. Storer;
   Special Award Committee: Andrew J. Berger, Kenneth C. Parkes, Olin Sewall Pettingill.
4. The Council accepted the Treasurer's Report and the reports of the Membership Committee, Trustee's Report, Student Membership Committee Report, Library Com-

mittee Report, Editor's Report, and Secretary's Report. The Council accepted the report and recommendations of the Research Committee, and through the generosity of a Wilson Society member was able to make two awards again this year. Richard E. Johnson was awarded a $200.00 Fuertes Award for his studies on the Biosystematics of Avian Genus *Leucosticte*. The second award of $100.00 went to G. Frederick Shanholtzer for his research on the food ecology and bioenergetics of the Cattle Egret.

5. The Council tendered its gratitude to Mrs. Hazel Bradley Lory for her long and fruitful tenure as Chairman of the Membership Committee.

6. The Council noted with sorrow the passing of two former officers of the Society who have contributed much to its growth: Burt L. Monroe, Sr., and Fred T. Hall.

At the first business meeting the Treasurer summarized his report which is included in full here for the record:

Report of the Treasurer for 1968

GENERAL FUND

Balance as shown by last report 31 December 1967			$ 8,962.41
RECEIPTS			
Dues			
Active Memberships		$ 6,656.78	
Sustaining Memberships		824.00	
Subscriptions to The Wilson Bulletin		2,397.50	
Sales of back issues of The Wilson Bulletin		1,206.49	
Interest and dividends on savings and investments		2,879.97	
Royalties from microfilming back issues of The Wilson Bulletin		171.30	
Total Receipts		$14,136.04	
DISBURSEMENTS			
The Wilson Bulletin (Printing & Engraving	$12,137.01		
Less contributions from authors	130.00		
and publication fund	1,220.45	10.786.56	
The Wilson Bulletin (Mailing and Maintenance of List)		1.496.80	
Editor's expense		159.91	
Secretary's expense		56.30	
Treasurer's expense		464.46	
Foreign discount and transfer fees		9.89	
Annual Meeting expense		253.21	
Committee expense		195.81	
Miscellaneous expense		31.72	
International Council for Bird Protection (1968 dues)		25.00	
Transfer to Research Fund		189.00	
Total Disbursements		$13,668.66	
Excess of Receipts over Disbursements for Year 1968			$ 467.38

GENERAL FUND CASH ACCOUNTS	
Checking Account	$ 5,459.99
Savings Account	3,969.80
Balance in National City Bank, Cleveland, Ohio, 31 December, 1968	$ 9,429.79

Josselyn Van Tyne Memorial Library Book Fund

Balance as shown by last report dated 31 December, 1967	$ 119.14
RECEIPTS	
Sale of duplicates and gifts	155.50
Total Balance and Receipts	$ 274.64
DISBURSEMENTS	
Purchase of Books	117.89
Balance in National City Bank, Cleveland, Ohio, 31 December, 1968	$ 156.75

Louis Agassiz Fuertes Research Fund

Balance as shown by last report dated 31 December, 1967		$ 10.00
RECEIPTS		
Contributions		27.50
Transfer from General Fund		189.00
Total		$ 226.50
DISBURSEMENTS		
Award to James J. Dinsmore	$100.00	
Award to Leon John Gorski	$100.00	
Total Disbursements		200.00
Balance in National City Bank, Cleveland, Ohio, 31 December, 1968		$ 26.50

Prepaid Student Dues

Balance in National City Bank, Cleveland, Ohio, 31 December, 1968	$ 115.00

Endowment Fund

Balance in Endowment Fund Savings Account as shown by last report dated 31 December, 1967		$ 5,887.73
RECEIPTS		
Life Membership Payments	$ 1,737.50	
Patronship Payments	350.00	
Stock Dividends and Exchanges (included below)		
29 shares Massachusetts Investors Trust	—	
210 shares Fund American Companies exchanged for 168 shares American Express $1.50 pfd.	—	
25 shares Owens-Illinois Glass 4% pfd. exchanged for 25 shares Owens-Illinois Fiberglass	—	
Total Receipts		2,087.50
		$ 7,975.23

DISBURSEMENTS

Purchase of securities		
$5000 Commonwealth Oil Refining Bonds		$ 4,368.23
Balance in Endowment Fund Savings Account		
National City Bank, Cleveland, Ohio, 31 December, 1968		$ 3,607.00
SECURITIES OWNED (listed at closing prices 31 December, 1968)		
United States Government bonds	$ 9,851.56	
Canadian Provincial bonds	4,500.00	
Corporate bonds	3,750.00	
Convertible Corporate bonds	5,675.00	
Convertible preferred stocks	24,904.50	
Common stocks	19,378.13	
Investment trusts	8,734.89	
Total Securities Owned		76,794.08
Total Endowment Fund 31 December, 1968		$80,401.08

Respectfully submitted,
William A. Klamm, *Treasurer*

Also for the record here are summaries of the Membership Committee's and Library Committee's reports:

Membership Committee (Hazel Bradley Lory, Chairman)—124 new members joined the Society this year as compared to 152 last year and 131 for the year before. As of 15 April, resignations and deaths had removed about 25 names from the roster and 121 others had been suspended for failure to pay dues.

Library Committee (William A. Lunk, Chairman)—During the year 48 gifts came in from 32 donors. Received were 8 books, 76 journals, 3429 reprints, 2 pamphlets, 1 translation, and 1 transcript of the president's annual address. Of the reprints, 3,300 made up an additional gift by Mrs. Van Tyne from the library of her late husband, Josselyn Van Tyne. There are many recent titles which are not yet on our shelves, and our New Book Fund remains at rather low ebb. Direct gifts of needed items, gifts of desirable duplicates which can be sold for the Society, or monetary donations, are always solicited.

Second Business Meeting

The president noted the Auditing Committee's report was favorable.

The proposed new members as posted by the Chairman of the Membership Committee were elected without dissenting vote.

The Nominating Committee presented the following slate for 1969: President, William W. H. Gunn; First Vice President, Pershing B. Hofslund; Second Vice President, Kenneth C. Parkes; Secretary, Jeff Swinebroad; Treasurer, William A. Klamm; Elective Member of the Council, Ernest P. Edwards.

The report of the Nominating Committee was accepted and the slate was elected without dissenting vote.

Chairman Burt Monroe, Jr., presented the following resolutions which were passed without a dissenting vote by members in attendance at the meeting:

Resolutions Committee Report

WHEREAS the College of William and Mary and the Virginia Society of Ornithology, as the co-hosts of the 50th annual meeting of the Wilson Ornithological Society, have graciously provided excellent facilities that were essential to a most successful meeting, have exhibited works of and a movie of the life of the renowned Mark Catesby, and have provided for enjoyable and instructive field trips.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society—its council, officers, and members—do extend a formal and warm-hearted expression of appreciation to College President Davis Y. Paschall and his staff and to the officers and members of the Virginia Society of Ornithology for their efforts on our behalf.

WHEREAS the selection of so delightful a meeting place in an inspiring natural and historical setting, and the selection of such a superior program as we have enjoyed at the meeting indicates much forethought, planning, and hard work by the officers of the Society.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and more particularly we members and guests who have benefited from these services do, at this 50th annual meeting of the Society held at Williamsburg, Virginia, this 3rd day of May, 1969, express our gratitude to all officers of the Society, and more particularly to its President and committee members and to Harrison B. Tordoff for arranging an informative symposium on the ornithological future.

WHEREAS the success of this 50th annual meeting stems from the dedication, planning, and patience of the local committee on arrangements.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society assembled in annual meeting at Williamsburg, Virginia, this 3rd day of May, 1969, does express its grateful appreciation to Chairman Mitchell A. Byrd and all the members of his local committee on arrangements for making possible an exceptionably enjoyable meeting.

WHEREAS Mrs. Hazel Bradley Lory has so unselfishly dedicated her time and talents as Chairman of the Membership Committee of the Wilson Ornithological Society for the past decade.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society expresses its sincere appreciation for her untiring efforts on behalf of the Society.

WHEREAS the success of the annual dinner was greatly enhanced by the entertainment and education provided by the film on the storks of the world.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society on occasion of its 50th annual meeting express its gratitude to the National Geographic Society for their courtesy in providing this film.

WHEREAS research in recent years has established the increasingly deleterious effects of persistent pesticides on our total environment, as notably demonstrated by a greatly reduced reproductive success in such birds as petrels, pelicans, birds of prey, and waterfowl, and WHEREAS the federal government has recognized that hazardous limits of concentration of these pesticides have already been exceeded in several organisms that are sources of food for man, and WHEREAS pesticide residues have been noticeably increasing in man himself, and WHEREAS there is no justification for continued use of these persistent chemicals in view of the availability of suitable substitutes.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society, on occasion of its 50th annual meeting, strongly urges the immediate banning of persistent, broad-spectrum, toxic pesticides.

PAPERS SESSIONS

Bertram G. Murray, Jr., Michigan State University. *The Origin of Seabird Colonies.*

Martha A. Whitson, University of Oklahoma. *Breeding Behavior of the Roadrunner* (Geococcyx californianus).

Lewis W. Oring, The University of North Dakota. *Nesting Behavior of Two Species of Arboreal Sandpipers.*

John P. Hubbard, Rockbridge Alum Springs Biological Laboratory. *The Relationships and Evolution of the* Dendroica coronata *Complex.*

Deborah V. Howard, Massachusetts Audubon Society. *A Population Study of Robins in an Urban Community.*

Nicholas L. Cuthbert, Central Michigan College. *Home Range of the Shiny Cowbird* (Molothrus bonariensis).

Paul W. Sykes and Thomas L. Quay, North Carolina State University. *Nesting-range Extension by the Cliff Swallow* (Petrochelidon pyrrhonota) *into the Piedmont of the Southeastern States.*

Jeff Swinebroad, United States Atomic Energy Commission. *Obvious and Concealed Declines in Local Bird Populations.*

Chandler S. Robbins, Migratory Bird Populations Station. *Progress Report on the Breeding Bird Survey.*

James D. Rising, Cornell University. *Adaptive Modifications of the Basal Metabolic Rate of the Black-capped Chickadee* (Parus atricapillus).

Nancy S. Mueller and Helmut Mueller, North Carolina State University and University of North Carolina. *Sex-specific Feather Coloration in* Anas platyrhynchos.

Elden W. Martin, Bowling Green State University. *Daily Variation in Deep-body Temperatures of Sparrow Hawks as Measured by Radio-telemetry.*

Olin Sewall Pettingill, Jr., Cornell University. *The Lesson of the Hornero.*

Symposium: An Ornithological Preview

Chairman: Harrison B. Tordoff, The University of Michigan

Introductory remarks by Chairman.

Paul C. Mundinger, The Rockefeller University. *Learning and Mimicry in Avian Vocalizations.*

Vance A. Tucker, Duke University. *Wind Tunnel Ornithology.*

Douglass H. Morse, University of Maryland. *Habitat Utilization by Spruce-wood Warblers.*

Frank B. Gill, The University of Michigan. *Evolution of White-eyes on a Small Island.*

Alan H. Brush, The University of Connecticut. *Pigments and Proteins.*

ATTENDANCE

Two hundred and ninety members and guests were registered. Twenty three states and two Canadian provinces were represented.

From **Alabama**: 1—*Clayton*, Ruth Berrey.

From **Connecticut**: 1—*Storrs*, A. H. Brush.

From **District of Columbia**: 3—*Washington*, Virginia Lee Roberts, Alexander Wetmore, Beatrice T. Wetmore.

From **Florida**: 1—*Winter Park*, Marjory Bartlett Sanger.

From **Hawaii**: 1—*Honolulu*, Andrew J. Berger.

From **Iowa**: 3—*Grinnell*, Marjorie Ramisch, Helen T. Stewart, Mildred Stewart.

From **Kentucky**: 4—*Louisville*, Burt L. Monroe, Jr., Rose S. Monroe, Ann L. Stamm, F. W. Stamm.

From **Maryland**: 15—*Beltsville*, Orrey P. Young; *Bethesda*, Shirley A. Briggs, Harriet S. Gilbert, John A. Pond, Mrs. J. A. Pond; *College Park*, Douglas H. Morse, Elizabeth K. Morse; *Laurel*, Larry L. Hood, Chandler S. Robbins, Jean Swinebroad, Jeff Swinebroad; *Owings Mills*, Jean R. Worthley, Elmer G. Worthley; *Silver Spring*, Donald H. Messersmith; *Towson*, Mrs. R. D. Cole.

From **Massachusetts**: 6—*Dover*, Aaron M. Bagg, Mrs. Aaron M. Bagg; *Middleboro*, Kathleen S. Anderson; *Petersham*, John Fiske, Rosalie Fiske; *West Newton*, Deborah V. Howard.

From **Minnesota**: 4—*Duluth*, Elaine Hofslund, Pershing B. Hofslund; *St. Paul*, Thomas C. Savage, Mrs. Thomas C. Savage.

From **Michigan**: 13—*Ann Arbor*, Dean Fisher, Frank Gill, Louise S. Storer, Robert W. Storer, Harrison B. Tordoff; *East Lansing*, Bertram G. Murray, Jr.; *Kalamazoo*, H. Lewis Batts, Jr.; *Mt. Pleasant*, Nicholas L. Cuthbert, Rose Husted, Ivan La Core, Harold D. Mahan; *Pinckney*, Sheldon Miller; *Saginaw*, Richard A. Wolinski.

From **New Jersey**: 13—*Cape May*, Ernest A. Choate, J. D'Arcy Northwood, W. Parker, Mrs. W. Parker; *Essex Fells*, Mildred Brydon, Norman F. Brydon; *Morris Plains*, Jack Stewart; *Princeton*, Charlotte A. DuBois; *Rutherford*, Alan J. Miller; *Wenonah*, Edward R. Manners, Rhoda L. Manners, William R. Middleton, Mrs. W. R. Middleton.

From **New York**: 13—*Bronxville*, Carolyn Dickerman, Robert W. Dickerman; *Ithaca*, Robert S. Gourley, Mrs. Robert S. Gourley, Eleanor Pettingill, Olin S. Pettingill, Jr., James D. Rising; *Milford*, Cora B. Wellman, Bertram Wellman; *New York*, Lester L. Short, Jr., Sheila C. Short; *Rye*, Paul C. Mundinger; *Waterloo*, Jayson A. Walker.

From **North Carolina**: 12—*Chapel Hill*, Helmut C. Mueller, Nancy S. Mueller; *Charlotte*, Edith Hague, Florence Hague, Alvalyn E. Woodward; *Durham*, Vance A. Tucker; *Hillsboro*, Charles H. Blake; *Laurinburg*, Robert A. Pedigo; *Oxford*, Paul A. Stewart; *Raleigh*, Thomas L. Quay; *Tarboro*, Edward H. Marrow, Thelma H. Marrow.

From **North Dakota**: 2—*Grand Forks*, Kay E. Oring, Lewis W. Oring.

From **Ohio**: 22—*Ashtabula*, Howard E. Blakeslee; *Bowling Green*, Elden W. Martin, Mary A. Martin, Carol L. Votava; *Canton*, Arnold W. Fritz, Mrs. Arnold W. Fritz; *Canfield*, G. William Ritcher; *Dayton*, Eleanore E. Meyers, Kenneth L. Meyers; *Delaware*, R. R. Greene, Mrs. R. R. Greene, William D. Stull, Mrs. W. D. Stull; *East Liverpool*, John T. Laitsch, Mrs. John T. Laitsch; *Gambier*, Robert D. Burns, Eugene S. Kleiner; *Lakewood*, Nancy R. Klamm, William A. Klamm; *Oxford*, David R. Osborne; *Painesville*, Mrs. Robert V. D. Booth; *Poland*, Betty A. Lovell.

From **Oklahoma**: 1—*Norman*, Martha A. Whitson.

From **Pennsylvania**: 10—*Chester Springs*, Phillips B. Street, Mrs. Phillips B. Street; *Philadelphia*, C. Chandler Ross, Gene Stern, Lillian Stern; *Pittsburgh*, Mary Heimerdinger Clench, Kenneth C. Parkes, Mrs. Kenneth C. Parkes; *Washington*, Judith Ickes, Roy A. Ickes.

From **South Carolina**: 6—*Chester*, Mrs. B. Clyde Carter, Mrs. James W. Crowder, Mrs. Spratt Moore, Mrs. W. S. Robinson, Mrs. W. Cornwell Stone, Sr., Mrs. E. M. White.

From **Tennessee:** 8—*Clinton*, Mrs. Billie Nickell, Walter P. Nickell; *Gatlinburg*, Arthur Stupka, Mrs. Arthur Stupka; *Maryville*, Ralph J. Zaenglein; *Nashville*, Mrs. Charles Cornelius, Mrs. Ernest W. Goodpasture; *Norris*, Frances B. Olson.

From **Vermont:** 1—*South Londonderry*, Mrs. James R. Downs.

From **Virginia:** 131—*Annandale*, Sylvia C. Johnson, J. Enoch Johnson; *Arlington*, M. Ralph Browning, Jane P. Church, Arthur H. Fast, Helen L. Goldstick, Grasty Crews, II, Robert J. Watson; *Barboursville*, Earl R. Andrew, Margaret N. Andrew; *Cape Charles*, Mrs. J. E. Guthrie; *Casanova*, Mrs. James Gulick, Janet D. Turnbull; *Charlottesville*, J. J. Murray, Jr., Charles E. Stevens; *Chester*, Ruth Jordan, Ann G. Miranian, Sally Weaver; *Cullen*, Edith Driskill; *Danville*, Mrs. Grasty Crews; *Durlington Heights*, Vera Copple, Margaret H. Watson; *Driver*, Ed Ames; *Fairfax*, Claire L. Eike, James W. Eike, *Ft. Eustis*, Sharon Sagerty; *Gloucester*, Brantley Peacock, Elizabeth D. Peacock; *Goshen*, Claudia L. Hubbard, John P. Hubbard; *Greenwood*, Paul S. Dulaney, Elizabeth Dulaney; *Hampton*, Walter P. Smith, Doris Smith; *Lexington*, Gillie W. Campbell, Mrs. Allen W. Moger, J. J. Murray, Dickson V. Murray; *Lynchburg*, John T. Cacciapaglia, Mrs. Myriam P. Moore, Phyllis Murphy, Wyatt Murphy, Mary H. Walker, J. W. Wiltshire, Jr., Mrs. J. W. Wiltshire; *Marshall*, James B. Barrett, Mrs. James B. Barrett; *Martinsville*, Catherine Sheffield Wallace, George L. Wallace, Pat B. Wallace; *Mechanicsville*, Joseph Trahan, Margaret W. Trahan; *McLean*, Benjamin B. Warfield, Lucile Warfield; *Newport News*, Ray J. Beasley, Violet Beasley, Charles W. Hacker, Mrs. Dorothy H. Silsby, Norman S. Silsby; *Norfolk*, Louise Bethea, David L. Hughes, Mrs. R. A. Lassiter, Virginia A. Miller, Kindred Trevillian, Mrs. Lawrence White; *Portsmouth*, Carolina K. Green, David D. Green; *Richmond*, Winifred E. Barksdale, Margaret H. Coleman, Margaret G. Finch, Mabel H. Holt, Mrs. H. A. Garber, H. A. Garber, Virginia P. Lacy, David Roszell, Elizabeth Roszell, Dorothy C. Rudd, Dorothy B. Schenck, Frederic R. Scott, Mrs. F. R. Scott, Jennifer Shopland, Lorna Shopland, Geraldine V. Smith, Warren M. Smith, Henrietta Weidenfeld, Patricia S. Yencer; *Roanoke*, Mrs. T. H. Cline, Cornelia T. Edmonds, Elleta Y. Thomas, William H. Thomas, Jerry Via; *Scottsville*, Carolina L. Whiteside, F. S. Whiteside; *Springfield*, Roxie Laybourne, Gale Monson, Sarah E. Monson, *Staunton*, John F. Mehner; *Suffolk*, Joy R. Dulaney, Middleton H. Dulaney; *Sweet Briar*, Jeanette Boone, Ernest P. Edwards, Mrs. Ernest P. Edwards, Gertrude Prior; *Troutville*, Carol Massart; *Virginia Beach*, Miss Mary T. Gwathmey, Raymond Long, Mrs. Peter Mediate, Mrs. Emma Jean Pointer, Mrs. Joseph Toth; *Warrenton*, Mrs. Tom Frost, Mrs. Nancy McCarty; *Waynesboro*, Mozelle W. Henkel, Ruth S. Snyder; *White Stone*, Mrs. W. A. Rothery; *Williamsburg*, Bill Akers, Kay C. Baker, Paul S. Baker, Ruth A. Beck, Sherwin Beck, Lois E. Byrd, Mitchell A. Byrd, Linda Chaflin, Sue Covington, Gustav Hall, I. L. Jones, Mrs. I. L. Jones, Edward Katz, Robert Kennedy, Mrs. F. L. Morris, Mrs. Jackqueline C. Lorensen, Mrs. E. Stubbs, Stewart R. Ware, Mrs. Stewart R. Ware, Tom Wieboldt.

From **West Virginia:** 10—*Harpers Ferry*, Orville Crowder, Mrs. C. A. Rathbone; *Inwood*, Clark Miller; *Morgantown*, Maurice Brooks, Mrs. Maurice Brooks, George A. Hall, Tanya Hall, Earl N. McCue; *Ona*, Maxine C. Kiff, Ben W. Kiff.

From **Wisconsin:** 2—*Madison*, George N. Allen; *Viroqua*, Margarette E. Morse.

From **Ontario:** 4—*Hamilton*, Eric W. Bastin; *Ottawa*, D. E. McAllister, Mrs. D. E. McAllister; *Toronto*, William W. H. Gunn.

From **Quebec:** 2—*Montreal*, George H. Montgomery, Mrs. George H. Montgomery.

This issue of *The Wilson Bulletin* was published on 30 September 1969.

SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subsequently identified. Summaries of major papers should be brief but quotable. Where fewer than five 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 "Style Manual for Biological Journals" (1964. AIBS). Photographs for illustrations should be sharp, 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. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A WORD TO MEMBERS

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

Plan now to participate in

THE FIFTY-FIRST ANNUAL MEETING

to be held at

COLORADO STATE UNIVERSITY

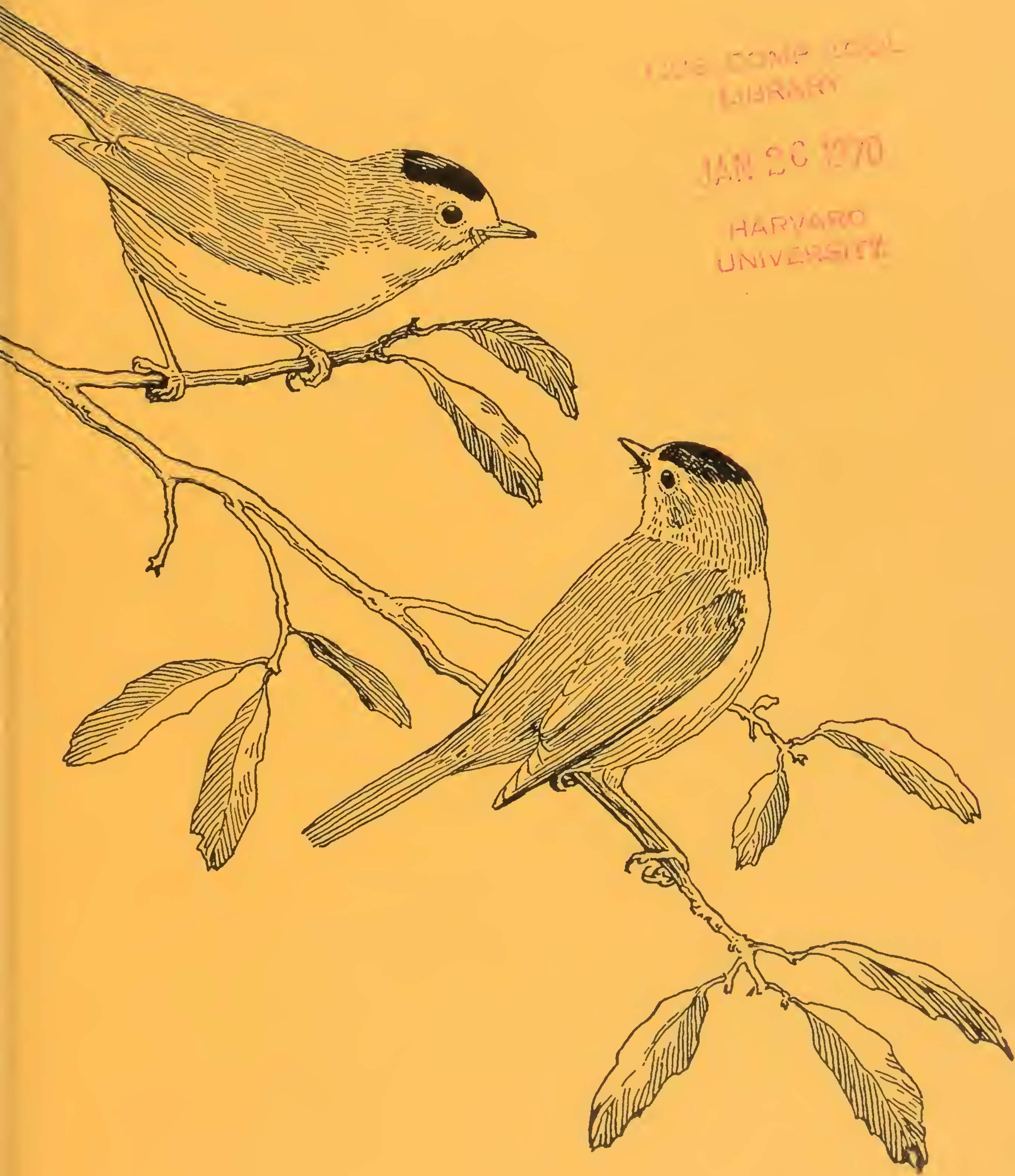
FORT COLLINS, COLORADO

June 1970

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY
WEST VIRGINIA U. · MORGANTOWN, W. VA.

VOL. 81, NO. 4 DECEMBER 1969 PAGES 361–496



THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—William W. H. Gunn, Apt. 1605, 155 Balliol Street, Toronto, Ontario.

First Vice-President—Pershing B. Hofslund, Dept. of Biology, University of Minnesota Duluth, Duluth, Minnesota 55812.

Second Vice-President—Kenneth C. Parkes, Carnegie Museum, Pittsburgh, Pennsylvania 15213.

Secretary—Jeff Swinebroad, 8728 Oxwell Lane, Laurel, Maryland 20810.

Treasurer—William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107.

Elected Council Members—Andrew J. Berger (term expires 1970); C. Chandler Ross (term expires 1971); Ernest P. Edwards (term expires 1972).

Membership dues per calendar year are: Sustaining, $10.00; Active, $5.00.
Life memberships, $150 (payable in four installments).
THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 104 periodicals as gifts and in exchange for *The Wilson Bulletin.* With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to "The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan." Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically.

THE WILSON BULLETIN

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December, at Morgantown, West Virginia. The subscription price, both in the United States and elsewhere, is $6.00 per year. Single copies, $1.50. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at $1.50 each) and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan.

Second class postage at Lawrence, Kansas, U.S.A. 66044

PRINTED IN U.S.A. Allen Press, Inc., Lawrence, Kansas 66044

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by The Wilson Ornithological Society

VOL. 81, NO. 4 DECEMBER 1969 PAGES 361–496

CONTENTS

ANTBIRDS OF THE GENUS *RHEGMATORHINA*, Painting by Guy Tudor Facing page 363

ON THE BEHAVIOR OF FIVE SPECIES OF *RHEGMATORHINA*, ANT-FOLLOWING ANTBIRDS OF THE AMAZON BASIN .... *Edwin O. Willis* 363

REPRODUCTIVE SUCCESS OF THE WOOD THRUSH IN A DELAWARE WOODLOT .... *Jerry R. Longcore and Robert E. Jones* 396

PHYSIOLOGICAL SUSCEPTIBILITY OF ROBINS TO DDT POISONING *L. Barrie Hunt* 407

ANNUAL ACTIVITY PATTERNS OF CAGED NON-MIGRATORY WHITE-CROWNED SPARROWS *Robert W. Smith, Irene L. Brown, and L. Richard Mewaldt* 419

ENERGY RESPONSES OF BIRDS TO THEIR THERMAL ENVIRONMENTS *S. Charles Kendeigh* 441

MORTALITY OF COOTS DURING SEVERE SPRING WEATHER *Leigh H. Fredrickson* 450

UNUSUAL NESTING HABITATS OF THREE BIRD SPECIES IN RONDEAU PROVINCIAL PARK, ONTARIO .... *Walter P. Nickell* 454

GENERAL NOTES

BIRDS OF ST. GILES ISLANDS, TOBAGO *James J. Dinsmore and Richard P. ffrench* 460

GLOSSY IBIS TAKEN IN INDIANA .... *Russell E. Mumford and Larry E. Lehman* 463

BREEDING STATUS OF WHISTLING SWANS NEAR CHURCHILL, MANITOBA *Allan J. Pakulak and Carroll D. Littlefield* 464

EIDER HATCHING GOOSE EGG .... *Bernard C. Lieff* 465

SHELL COLOR OF EGGS LAID BY YEARLING, 2-, AND 3-YEAR-OLD PHEASANTS
Ronald F. Labisky and Gary L. Jackson 466

THE DROWNING OF BOBWHITES IN A LARGE RESERVOIR
James W. Mullan and Richard L. Applegate 466

RENESTING BY BARN AND GREAT HORNED OWLS .... *Carl D. Marti* 467

FORAGING ASSOCIATION OF GREEN-BARRED FLICKERS AND CAMPO FLICKERS IN ARGENTINA .... *Lester L. Short, Jr.* 468

RED-BELLIED WOODPECKER FEEDS TUFTED TITMOUSE .... *James R. Curry* 469

A CAROLINA WREN SHADOW-BOXING .... *Hervey Brackbill* 470

ROBIN KILLS SNAKE .... *William F. Davis* 470

DOES THE ROBIN EAT DEKAY'S SNAKE? .... *M. Graham Netting* 470

RECURRENT USE OF TERRITORIES BY INDIVIDUAL AMERICAN REDSTARTS
Ruth M. Yarrow 471

UNUSUAL FEEDING BEHAVIOR OF THREE SPECIES OF BIRDS .... *Warren M. Pulich* 471

ORNITHOLOGICAL NEWS 473

ORNITHOLOGICAL LITERATURE 475

François Haverschmidt, *Birds of Surinam*, reviewed by Charles T. Collins; Oscar T. Owre, *Adaptations for Locomotion and Feeding in the Anhinga and the Double-crested Cormorant*, reviewed by Lowell Spring; Karen A. Grant and Verne Grant, *Hummingbirds and their Flowers*, reviewed by Larry L. Wolf; Louise de Kiriline Lawrence, *The Lovely and the Wild*, reviewed by Harold Mayfield.

PUBLICATION NOTES AND NOTICES 481

THE WILSON ORNITHOLOGICAL SOCIETY, OFFICERS AND COMMITTEE CHAIRMEN 483

INDEX TO VOLUME 81, 1969 .... *Mildred Stewart and Tanya Hall* 484


TUDOR

ON THE BEHAVIOR OF FIVE SPECIES OF *RHEGMATORHINA*, ANT-FOLLOWING ANTBIRDS OF THE AMAZON BASIN

Edwin O. Willis

In the rain forests of the Amazon, separated for the most part by giant rivers that forest-loving birds do not cross, live five little-known antbirds (family Formicariidae) of the genus *Rhegmatorhina.* All are plump, short-tailed birds somewhat larger than House Sparrows (*Passer domesticus*); all have large pale greenish or blue bare areas around the eyes and lengthened crown feathers that they can erect to form crests. They differ strikingly in the arrangement of black, brown, rufous, and white in their pied plumages (see frontispiece), but they are clearly closely related species.

J. Natterer (according to Pelzeln, 1868, p. 166) recorded that two Crested Antbirds (*Rhegmatorhina cristata*) he took in 1831 on the Uaupés River, Brasil, were following army ants. Riker (1891) noted that the pair of Bare-eyed Antbirds (*Rhegmatorhina gymnops*) he collected near Santarém, Brasil in 1877 were following a swarm of ants. On the specimen label of a Hair-crested Antbird (*Rhegmatorhina melanosticta*) from Avila, eastern Ecuador (Philadelphia Academy of Sciences no. 169629, collected by W. Clarke-Macintyre) is a note that the local name is "tamia añangu pishcu." At Limoncocha, nearby on the Rio Napo, the Quichua word for the army ant *Eciton burchelli* is "tamia añangu." Nothing else has been recorded about the behavior of birds of this genus. In the course of studies of birds that follow army ants, I visited the Amazon briefly in 1962 and for seven months in 1965 and 1966. These studies show that all five *Rhegmatorhina* are "professional" ant-followers, birds that forage most of the time over swarms of army ants and capture arthropods flushed by the ants.

DESCRIPTIONS AND DISTRIBUTIONS

The Crested Antbird (*R. cristata*) was the first species described (Pelzeln, 1868). There are three known specimens, Natterer's pair from São Jeronimo (Cachoeira Ipanoré, Rio Uaupés, northwestern Brasil) and a male from Mitú (Olivares, 1964), upstream on the

---

←

Frontispiece: Antbirds of the genus *Rhegmatorhina*, from a painting by Guy Tudor. Males in slight alarm poses at left, females loafing at right. Top pair, Bare-eyed Antbirds (*R. gymnops*). Second pair, Harlequin Antbirds (*R. berlepschi*). Central pair, White-breasted Antbirds (*R. hoffmannsi*). Fourth pair, Crested Antbirds (*R. cristata*). Lowest pair, Hair-crested Antbirds (*R. melanosticta*).

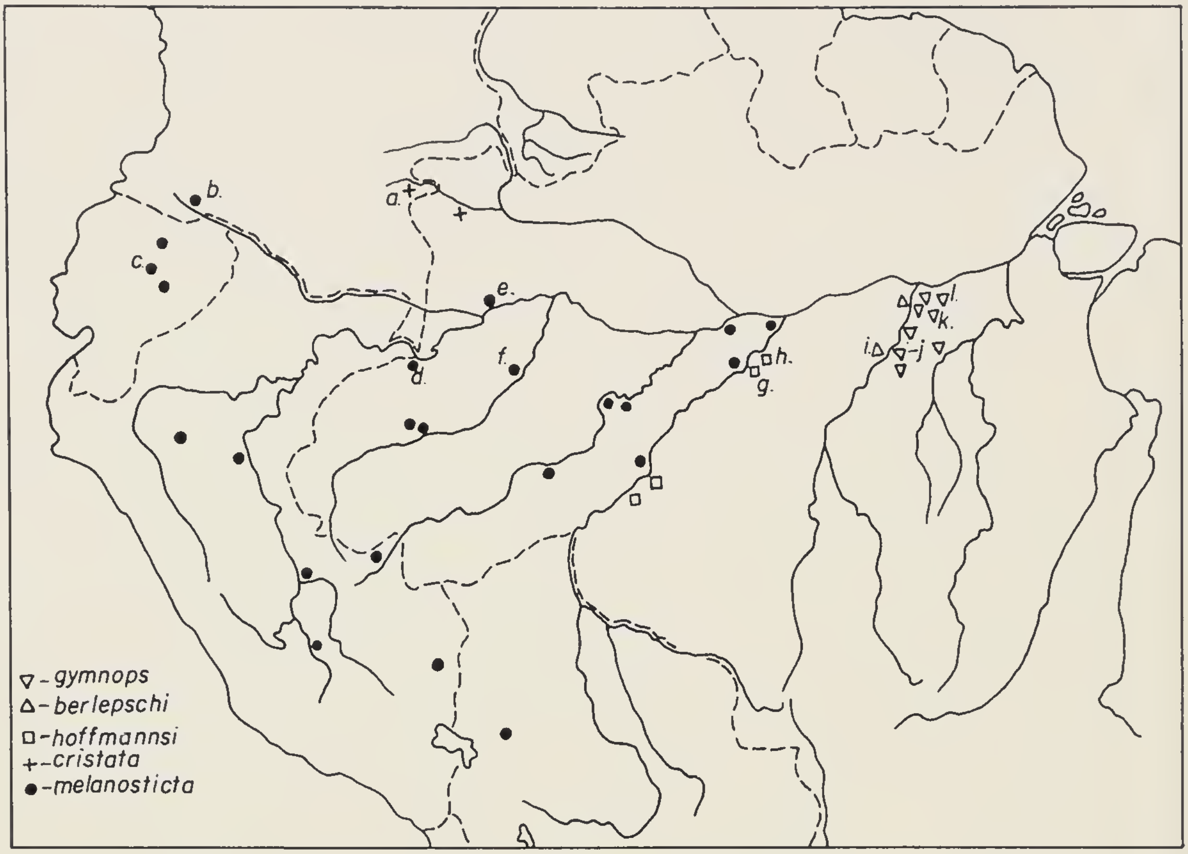


FIG. 1. Ranges of the five species of *Rhegmatorhina*. a, Mitú. b, Umbria. c, Zatzayacu. d, Benjamín Constant. e, Tonantins. f, Carauarí. g, Borba. h, Coatá. i, Maloquinha. j, Itapucurá. k, Palhão. l, Barreirinha.

same river in southeastern Colombia (Fig. 1). Males are black, rufous, and olive-brown (frontispiece); females have small dark marks on the back and perhaps on the wing coverts but are otherwise like males. Hellmayr, who examined the immature female taken by Natterer, says (1924, p. 306) it lacks the elongated crest and has a darker, blackish-chestnut crown as well as a more russet-brown back than does the male.

Natterer (fide Pelzeln, 1868, p. 167) states that the eye-ring of the adult male he took was "blaulich weiss," but that the eye-ring of the young female was "schwarzlich, nackte Haut, um die Augen sehr hellgrau, bloss gegen das Ohr in Violett ziehend." Young birds in this and related genera commonly have duskier and smaller bare faces than do adults. Young commonly have short crests and tend to be brown in areas where adults are brightly colored. Olivares (1964) suggested that the male from Mitú must have had a red face in life; however, among antbirds only three species of *Phlegopsis* have red faces, and it is nearly impossible to guess facial color in life from any antbird specimen once postmortem changes have set in. All Crested Antbirds I saw at Mitú had pale bluish-white faces.

The type species of the genus is the Bare-eyed Antbird (*R. gymnops*). It is known from many localities from the west bank of the Rio Xingú to the east bank of the Rio Tapajoz. Male Bare-eyed Antbirds are sooty black, with contrasting large pale bluish-green faces and brown mantles and tails. Females are dark brown, varying to blackish around the bill and bare eye-ring.

Harlequin Antbirds (*Rhegmatorhina berlepschi*) live on the west bank of the lower Tapajoz. Males are strangely pied birds (see frontispiece). Except for a chestnut breast-splotch, gray underparts, and blackish borders of the crest, the male Harlequin Antbird is rather like the male Crested Antbird. The females differ strongly, as female Harlequin Antbirds are barred black and buff on the underparts and barred black on the upperparts.

To the west of Harlequin Antbirds, on the east bank of the Rio Madeira, live Hoffmanns' or White-breasted Antbirds (*Rhegmatorhina hoffmannsi*). The female looks like a female Harlequin Antbird, but has wider bars underneath and a darker, dusky-rufous crown; the whole lower face and throat and bib below a pale greenish face are white. Male White-breasted Antbirds also are white from eye-ring to chest; the underparts are gray and the upperparts greenish-brown, much as in *berlepschi*. There is less rufous on the wings and much less in the crest of *hoffmannsi*, which is black-crested and black-naped.

The Hair-crested Antbird (*Rhegmatorhina melanosticta*) lives south of the Amazon from the west bank of the Rio Madeira west to the Andean foothills in Bolivia and Perú, thence north across the smaller branches of the upper Amazon into eastern Ecuador and southeastern Colombia. At Tonantins, on the north bank of the Amazon in western Brasil (Fig. 1, e), the Ecuadorean subspecies occurs (fide Kenneth C. Parkes). Presumably *R. m. melanosticta* occurs down the length of the Putumayo River, from Colombia into Brasil. Possibly it meets the Crested Antbird somewhere between the Vaupés and Putumayo Rivers, or is separated from it by the rather small Caquetá or Japurá.

Instead of the long, pointed, shiny crest feathers of adults of other species of *Rhegmatorhina*, Hair-crested Antbirds have whitish crown feathers that separate like aigrettes into hairlike filaments. In the Andean foothills west of the Rio Ucayali and south of the Rio Marañon, Hair-crested Antbirds have buff crown feathers. The range of the buff-crested subspecies (*R. m. brunneiceps*) separates the ranges of the white-crested subspecies (*melanosticta*) north of the Marañon and the similar subspecies (*badia* and *purusianus*) southeast of the Ucayali. All the subspecies have dark brown bodies and dark, velvety faces around large, pale blue eye-rings. Females are spotted above with small, black, reddish-tipped crescents.

THE STUDY AREAS

Table 1 lists places where I studied the five species of *Rhegmatorhina*. The forests of all these areas are very similar in general aspect, but differ in detail. They are tropical to upper tropical forests, moderately hot and very humid, with dense canopies and fairly uncluttered undergrowth. As in most mature forests, occasional treefalls break the canopy and grow up to dense thickets of saplings and sprouts around tangles of fallen limbs and lianas. The ground is covered with a thin layer of recently fallen leaves, which in wet weather are decomposed by invertebrates and reused by plants so fast that there is relatively little humus or evidence of decay except in treefalls.

The very wet forests at Mitú, Colombia, rest almost directly on the rocks of the pre-Cambrian Guianan Shield, in an area of creeks stained red by humic acids and of rivers of clear, blackish water. Rainfall is probably about 3500 mm a year, with slightly lower monthly totals in April and September. The extremely thin soil is seldom visible, for it is interlaced by a carpet of roots and rootlets over the rocks and under

TABLE 1
STUDY AREAS

Locality[a]	Elevation (Meters)[a]	Dates
COLOMBIA		
Mitú, Vaupés (1°5′N, 70°04′W)	150	29 Apr.–9 May 1966
Umbria, Putumayo (0°53′N, 76°34′W)	350	18 May–2 June 1962
ECUADOR		
Zatzayacu, Napo-Pastaza (1°6′S, 77°52′W)	550–950	20–23 Oct. 1965
BRASIL		
Benjamín Constant, Amazonas (4°22′S, 70°02′W)	75	16–18 Apr. 1966
Carauarí, Amazonas (4°52′S, 66°54′W)	75	15–20 Mar. 1966
Borba Road, Amazonas (4°28′S, 59°35′W)	75	28–29 Mar. 1966
Coatá Ridge, Amazonas (4°15′S, 59°18′W)	75	2–11 Apr. 1966
Coatá-Madeira Trail (4°12′S, 59°20′W)	75	12 Apr. 1966
Itaituba Road, Pará (4°14′S, 56°04′W)	75	3 Mar. 1966
Maloquinha, Pará (4°18′S, 56°05′W)	75	20 Feb.–1 Mar. 1966
Itapucurá, Pará (4°21′S, 56°04′W)	75	2 Mar. 1966
Palhão, Pará (2°47′S, 54°17′W)[b]	75	25 Jan.–9 Feb. 1966
Barreirinha, Pará (2°35′S, 54°01′W)	75	11 Feb. 1966

[a] Latitudes, longitudes, elevations from available maps, are approximate.
[b] Just above Cachoeira do Portão.

the fallen leaves. Trees with tangled stilt roots perch on the rocky soil. The lush and moss-covered undergrowth resembles that of a wet montane or cloud forest. However, it is obvious that the poor soil and rocky basement make living conditions difficult for trees, despite the high rainfall and moderate temperatures. From the air, one sees elevated mesas and ridges, covered with rocky to bushy savannahs or scrubby woodland, interlacing these forests of the Vaupés. The variety provided by the stilt-rooted trees and the lush undergrowth of these patchy forests may explain why Crested Antbirds can live along the Rio Vaupés. However, the interlacing forests and savannahs of the Guianan Shield extend from the Cordillera Macarena, a huge table mountain against the Colombian Andes, past great mesas like Roraima in the Gran Sabana of Venezuela, into the Guianas. If conditions like those at Mitú are found over much of this region, the narrow range of Crested Antbirds is puzzling.

I studied Hair-crested Antbirds in less peculiar but similarly lush forests. The annual rainfall varies from four or five meters in the Andean foothills at Zatzayacu, Ecuador, and four or so at Umbria, Colombia, to 2742 mm at Benjamím Constant and 2534 mm at Carauarí in Brasil. The rain is distributed over the year, with slight dry seasons about July and January.

Richards (1952) and others have emphasized that the undergrowth of mature tropical forests is relatively open and uncluttered, and that dense "jungle" is generally a sign of second growth after man or floods or other natural catastrophes have removed the natural canopy. However, such very wet forests as these of upper Amazonia have fleshy-leaved plants crowding the undergrowth, moss on trees and fallen logs, and large numbers of epiphytes. The trees are usually less tall and magnificent than in areas with two to three meters of rainfall per year and with strong dry seasons, as in central Amazonia.

The forests of upper Amazonia look somewhat like the lower montane rain forests (where low evaporation leads to similarly humid conditions, despite low rainfall) of Trinidad, Colombia, and Panamá. Perhaps, with very high rainfall, trees fall to fungus and insects and weather so frequently that rain forests are actually lower and thicker than "monsoon" forests, such as the magnificent forests of northern Colombia and of central Amazonia. However, Indians and others may have cut most of the forests of upper Amazonia; it is difficult to get away from human interference and second growth anywhere in Amazonia. I have seen occasional patches of fairly uncluttered and tall forest in eastern Ecuador, suggesting that really mature rain forest may be nearly as uncluttered as mature seasonal or monsoon forests.

Since Hair-crested Antbirds range eastward into relatively dry forests near the Madeira and to strongly seasonal forests in Bolivia, they may live in open forests with little undergrowth in some regions. However, I found them only where the undergrowth is lush. At Carauarí, near an oxbow lake of the meandering yellow Rio Juruá, there are swampy oxbows and cutoff channels dissecting the rather swampy lowland forests. At Benjamín Constant I found them in wetter but less swampy forests back from the Amazon, which is too large and fast to form oxbows. At Zatzayacu the steep lower montane forests east of the Baños-Napo highway are rain-drenched but not swampy. Umbria is in rolling foothills just out from the Andes, and the forests are swampy only along the nearby Rio Guineo.

I found the other three species of *Rhegmatorhina* in less cluttered and more typical lowland forests south of the Amazon in central Brasil. Rainfall is lower in central Amazonia than in upper or lower Amazonia, or two to three meters annually; there is a strong dry season from June to October or later. An unusually severe dry season had extended into January when I arrived on the Tapajoz Plateau near Santarém in 1966. The crackling dead leaves on the forest floor and the dry lower levels of the forest were protected by the evergreen canopy, except in areas where colonists had turned the region to a semi-desert, but it was evident why there were few epiphytes and little moss.

The Tapajoz Plateau or "planalto," home of the Bare-eyed Antbird, is an undulating forested plateau, generally less than 100 meters above the sandy plains along the rivers. Bounded to the north by the immense yellow Amazon, to east and west by the great blue Xingú and Tapajoz Rivers, it rises gradually to savannahs on the low Serra do Cachimbo to the south. It is a northern extension of the pre-Cambrian Brasilian Shield. I was unable to find Bare-eyed Antbirds at the type locality of Diamantino, about eleven kilometers out the Palhão road from Santarém. The forests there have been cut into patches by refugees from northeastern Brasil, and the diversity of forest-inhabiting birds has decreased since the time of Riker (1891). Beyond Diamantino, the wave of cutting and burning has reached about fifty kilometers from Santarém, but from there to the end of the road at Palhão, about eighty kilometers from Santarém, the forest is little disturbed. Palhão, the future site of a hydroelectric plant for Santarém on the falls or Cachoeiras of Palhão and Portão, was an airstrip scrape and a few shacks by the clear little Rio Curuá-Una when I visited it. The tall forest was quite open underneath. Stilt roots, buttressed trees, and epiphytes were uncommon. I was reminded of the open and magnificent older forests in Panamá and northern Colombia, in areas that also have a strong dry season. Similarly well-drained and tall forests covered the planalto inland from Barreirinha, the forestry and research center of the United Nations (FAO) down the Curuá River below Palhão. There were similar forests at Itapucurá, behind a pasture and a few houses on the Tapajoz River. Despite the tall forests and the deep soil of the Tapajoz Plateau, Indians seldom used it for crops; Americans and Brasilians, from Civil War slave-owning refugees at Diamantino to Henry Ford and his rubber plantations and Brasilians who are trying to resettle refugees, have spent fortunes finding that modern man is no more successful than the Indians in using this poor-soil region.

At Maloquinha, a few kilometers across the blue Tapajoz from Itapucurá, one steps into the different world of *Rhegmatorhina berlepschi.* "Maloquinha" means "little maloca" or "little Indian site," and there are evidences of Indian and later use everywhere in the forest. The huge brasilnut trees (*Bertholletia excelsa*), each cleared out underneath by castanheiros who gather and open fallen pods each January and February, are probably the only remaining trees of the original forest. Otherwise trees are small to medium in size, often densely capped with vines. The undergrowth is fairly dense in many areas, as is usual in secondary forest. It is difficult to tell how different this forest would be from the relatively undisturbed forests across the river had man not interfered.

There is no plateau on the west side of the Tapajoz, so the river in flood does most of its work on this side. Swampy watercourses and sloughs break the forest. Behind Maloquinha Cupituã Creek, which flows south to meet the Tapajoz going north, had magnificent floodplain forest or "varzea." The varzea, at the time I visited, was not yet flooded; dead leaves littered the very open undergrowth among huge buttressed trees and swampy or incised channels of the Cupituã. Since leaves began on the saplings at about head height, I suspect annual flooding normally reaches a meter or so. Between the Cupituã and Maloquinha there are low, rolling hills with very irregular forest, cut by swampy little creeks with an undergrowth of palms.

The road west and south from Itaituba cuts behind Cupituã Creek, crossing at least one of its upper branches. After passing through several kilometers of cutover and burnt-over poor farmland, the road passes a ridge where the forest seemed little disturbed. The forest was open underneath, with numerous large trees. The presence of ropy-trunked and other unusual trees suggested that the natural forests of this area may differ from those across the river in some tree species as well as in dozens of bird species.

In general, forests along the east bank of the Madeira in the range of *Rhegmatorhina hoffmannsi* seem much like forests at Itaituba. There is a greater difference in birds and plants across the Tapajoz, three to fifteen kilometers wide, than in the 440 kilometers from Itaituba to Borba or Coatá.

Near Borba I found no White-breasted Antbirds, for the forests have been cut to shreds by colonists. There is an area of sandy soil, a "campo" with savannah vegetation; it must be an outlier of savannahs that break the Madeiran forests in two to the south. A new road south from Borba skirts the campo and passes into open forests very like those on the ridge south of Itaituba; near the road, at about 10 kilometers south of town, I saw some White-breasted Antbirds. Later I briefly visited similar but more swampy forests behind Nova Olinda do Norte on the island of Tupinambaranas, but found none of these antbirds. Tupinambaranas is cut off by a channel or "paraná" from the wide, muddy Madeira to the wide blue Rio Canumã, and from there the mixed waters of both flow east past the Rios Abacaxis and Maués to the Amazon.

Between the lower Canumã and the muddy Madeira, I studied White-breasted Antbirds near Coatá, a village of the Mundurucú Indians. The blue Canumã floods wide bays and creek valleys around Coatá, so that scrubby varzea woodland nearly surrounds the town. Low ridges of "terra firme" to the south and west are covered with fairly old forest. These forests, extending past many flat, swampy areas and small creeks, are characterized by large palms as well as brasilnuts and other giant trees. There are few epiphytes and moss-covered trees, so the dry season must be severe. Near the Madeira to the west the forest drops to flooded swampy creeks, full of water plants and shrubs dripping with epiphytes. Yellow soil washed off the Bolivian highlands nourishes a rich aquatic and swamp vegetation on the Madeira, while the dark waters of such "rivers of hunger" as the Canumã and Tapajoz support little life.

THE ARMY ANTS

Rettenmeyer (1963) discusses the activities of army ants. *Eciton burchelli*, the most important species of ant for birds, has been studied by Schneirla (1957). In tropical lowland forests from México to Argentina, these ants send out huge raiding parties that flush large numbers of roaches, spiders, and other arthropods from the leaf litter and from tangles of vegetation on or above the ground. Numerous species of parasitic flies lay eggs on the leaping insects, while many species of birds chase the fleeing arthropods. Birds less often follow a smaller swarming ant, *Labidus praedator*, in forests and scrub from México to Argentina. In the upper Amazon, *Eciton rapax* forms straggling swarms that sometimes attract birds.

Most *Rhegmatorhina* followed swarms of *Eciton burchelli.* I also saw *melanosticta* at a swarm of *Labidus praedator* at Carauarí, *cristata* at two swarms of *praedator* at Mitú, and *gymnops* at a swarm of *praedator* at Itapucurá. I encountered no swarms of *praedator* at all within the ranges of *berlepschi* and *hoffmannsi.*

CALLS

Antbirds of the genus *Rhegmatorhina* are so like Bicolored Antbirds (*Gymnopithys bicolor*) in calls and movements that the terminology used for the latter (Willis, 1967) can be applied to the species of *Rhegmatorhina*. Many calls are so similar to those of related species of *Gymnopithys* or *Phlegopsis* at the same swarms that one can tell which species is calling only after long practice.

Chirring.—All five species utter a deep buzz or *chirrrrrr* when disturbed by the observer or others, including insect-eating hawks. The chirr of Hair-crested Antbirds is slightly deeper than the chirring of the White-cheeked Antbirds (*Gymnopithys leucaspis*) and White-throated Antbirds (*Gymnopithys salvini*) that forage with it in different regions, but I was often unable to tell the chirrs of *melanosticta* from those of *salvini* or *leucaspis.* Crested Antbirds have chirrs intermediate between the hissing chirrs of White-fronted Antbirds (*Pithys albifrons*) and the deeper chirrs of White-cheeked Antbirds, both of which forage with it at Mitú. Black-spotted Bare-eyes (*Phlegopsis nigromaculata*), which forage at swarms of ants with the other three species of *Rhegmatorhina*, have a similar but more nasal chirr; Pale-faced Antbirds

(*Skutchia borbae*), which I found with *Rhegmatorhina hoffmannsi* at Coatá, have chirrs almost exactly like those of the five species of *Rhegmatorhina.*

Chipping.—Alarmed or excited *Rhegmatorhina* of all five species call *chip* sharply and loudly. The chip is doubled or tripled to a *chip-ip* or *chip-ip-ip* only rarely; in this respect these species are unlike the double-chipping *Gymnopithys leucaspis* and its relatives. However, Crested Antbirds, which forage with *G. leucaspis*, double-chip more frequently than do other species of *Rhegmatorhina.*

Keening.—Keening, a thin *teeeeeee* whistle when a bird freezes in alarm, was noted only for *gymnops, berlepschi,* and *hoffmannsi.* This sound is faint and difficult to hear, and is widespread among related genera; *melanosticta* and *cristata* may well have it.

Songs.—It is convenient to divide the wide spectrum of songs into "loud-songs, why-songs, faint-songs, and serpentine-songs" as I did for Bicolored Antbirds. The basic pattern of the "loud-song" in *Rhegmatorhina* is a loud, pure *heeeeee* followed by several shorter whistles at a lower pitch or descending in pitch. The loud-song is most commonly used when mates are distant from each other, when birds search for a swarm of ants, and when birds dispute with each other. In the last case, the song often descends to rough, snarling noises like the word "why" as a "why-song." These species seem to use the loud-songs and why-songs more frequently in disputes than do Bicolored Antbirds, which use snarling.

At Benjamín Constant, a typical why-song of *melanosticta* was a loud "*Wheeeeer, whee-whee-whee-ee-ai-aihh*!" At Zatzayacu, one why-sang "*Wheeeh, wheep, eep, why*!" A typical loud-song of *cristata* was "*Eeeee, HEEER, you-you-you-you*!", the last notes successively lower in pitch, length, and volume; the second note is sharply inflected in both pitch and volume. Why-songs add one to several snarling "*hraah*" noises to the loud-song in *cristata.*

A loud-song of *gymnops* at Palhão was "*Heeeeee, hew-hew-hew-hew*!" The last notes are on the same low pitch or fade into snarling "*whaihh*" noises if the song becomes a why-song. The bird raises and extends the neck and opens the beak for a loud-song, but there is otherwise little change from standard postures. The loud-song of *berlepschi* at Maloquinha was like that of *gymnops*, but the "*hew*" notes were repeated more rapidly. Harlequin Antbirds also used long songs, with five to ten or more "*hew*" notes, more often than did *gymnops.* The posture for a song is much the same as in *gymnops*; in *berlepschi*, I noted that the crest is raised during the snarls at the end of a why-song.

The loud-song of *hoffmannsi* is much like that of *gymnops* or *berlepschi*, but the "*hew*" note is rarely repeated more than twice. However, *hoffmannsi* often adds as many as 15 snarls to the end of a song. One day when it was raining, I noted that the song of *hoffmannsi* sounded like that of *berlepschi*. Apparently the "white noise" of the rain drowned out the rough overtones of the snarls, leaving only their pure tones and making them sound like "*hew*" notes. All these species vary their loud-songs and why-songs widely in length and volume, and they occasionally drop out introductory notes or other distinctive characteristics, so that their songs sometimes resemble those of the allopatric species of *Rhegmatorhina* or even the songs of species of *Phlegopsis* and *Gymnopithys* that occur at the same swarms with them.

When several rhegmatorhine antbirds of a species are at a swarm, they keep up a cross-talk of chirping little "faint-songs," which usually are faint versions of loud- or why-songs. At Zatzayacu, Carauarí, and Benjamím Constant the faint-songs of *melanosticta* were a hissing whistle followed by one to five or so hissing notes: "*wheeeec, whihh whihh*!" or the like. These songs were very like the faint-songs of *Gymnopithys salvini* at Carauarí and Benjamín Constant, although unlike the less sibilant faint-songs of *Gymnopithys leucaspis* at Zatzayacu and Umbria. The faint-songs of *cristata* were a "*whreeeeeer, wheer-whih*!" or the like, the second note generally emphasized. The faint-songs of *gymnops* were faint versions of the loud-songs or why-songs, often shortened to one or two notes. The faint-songs of *berlepschi* were similar to those of *gymnops*, although often longer and faster. Faint-songs of *hoffmannsi* were like those of *gymnops*, except that the "*hew*" note was seldom repeated before it graded into one or more snarls or the song ended. The faint-songs of these three species thus differ in about the same ways as do their loud-songs.

Serpentine-songs are faint ditties when a bird is leading its mate or young. Usually the serpentine-songs are repeated faint-songs, often with inflected notes and punctuated with faint "*chup*" or "*chup-up-up*" grunts. A male *melanosticta*, leading his mate past me to a swarm at Zatzayacu, whispered "*whreer, whee'eep wheer chup chup chup*" over and over. A lone male *cristata* muttered to himself "*wh'yurr, wh'yeer-whree chuf-uh-uh-uh-uh-uh-uh-uh*" as he wandered around a swarm near me. Another chirped "*chip-ip-whseep-whseep*" over and over when he arrived at a swarm. At Palhão, male *gymnops* occasionally warbled "*hew, hew, hew chip-ip-ip*" over and over as they led their mates in to swarms. A male *berlepschi* showing a nest-site to a female at Maloquinha muttered "*chuc-chuc-chuc-uc-u-u-u*" over and over. A male *hoffmannsi* arriving at a swarm warbled "*chericriew chup, chup-up-up*" over and over. Otherwise I noted no serpentine-songs for these three species, which usually alternate "*chup*" and faint-songs at rather long intervals as they lead their mates more often than they warble serpentine-songs.

Snarling.—Loud, snarling hisses like those at the ends of why-songs are often given separately, one to fifteen times in a row, when birds are feuding with others of their own species: "*whahh, whahh, whahh*" or the like. In *hoffmannsi*, I noted that snarls seemed different when given separately rather than with loud-songs or faint-songs; however, there is so much variation in snarls in such species as Bicolored Antbirds that this could occasionally be true for any species. Hoffmanns' Antbirds snarl more times in a sequence and more frequently, on the average, than do other species of *Rhegmatorhina*; they are like the similarly white-bibbed *Gymnopithys bicolor* in this respect.

Bugling.—The battle cry, uttered before or as a bird chases its rival, is a rapid and musical "*Chrrrrrrrt!*" in all species, with about the speed and tone of the word "*chert*" if the "r" is rolled as a Scotsman would. The bugling of *melanosticta*, at Benjamín Constant, descended in pitch and was somewhat slow compared to the bugling of other species. I recorded the bugling of *gymnops*, at Palhão, as "*chew'ew'ew'ew'ew'ew!*" or "*r'r'r'r'rew!*," but I remember it as very similar to the bugling of other species; it may be slightly slow. All five species have a bugling call that is much faster than bugling in any species of *Gymnopithys* or *Phlegopsis.* Although rhegmatorhine bugling can be written like chirring, bugling has much slower and more musical notes than the rapid clicks that make up a chirr; chirring and bugling are easily told apart even if one has not had experience with related species, in which bugling and chirring are extremely different.

Peeping.—A fledgling *hoffmannsi*, just out of the nest April 3 at Coatá, called "*Pee pee pee!*", two to five notes, loudly in the hand. A well-grown young *melanosticta*, following its parents at a raid at Zatzayacu 20 October, had a "*Whee, pee pee peep!*" that was intermediate between the peeping of young and the loud-singing of adults. I was not able to discover if young antbirds in this genus have squeaking notes when they are fed, as do young Bicolored Antbirds (Willis, 1967). In the latter species, squeaking and peeping are different notes, and peeping eventually becomes the loud-song as young grow up.

Chirping.—Antbirds of the genus *Rhegmatorhina* commonly chirp "*cheup*" or "*chup*" when the mate is nearby. A similar "*chup*" is used by tame antbirds when the observer is nearby. However, I have not established whether this note is like the "grunting" of Bicolored Antbirds, which repeatedly use the notes whenever supplantable competitors are nearby and crowding their foraging zones. I rather think that rhegmatorhine antbirds lack the "grunt" or use it rarely, for I have been close to them when competitors of other species moved nearby and have failed to detect grunting.

Snapping and Hissing.—When rhegmatorhine antbirds supplant others of their own or other species, they generally give a single "snap!" of the bill. Double or multiple snaps are less common than among birds of related genera.

Often a rhegmatorhine antbird hisses "*whiahh*" as, before, or after it snaps and sends the competitor flying. I recorded hissing for all species except *cristata*, a bird for which I had few records of supplantings.

Growling.—A female *berlepschi* gave growling "*chauhh*" series, three to five notes, very faintly on three occasions when her mate fed her. Once he had to call "*chee*" faintly several times before she accepted his gift. Courtship feedings in *melanosticta* and *gymnops* seemed to be silent, but I was too far away to be certain the birds were not growling faintly. In Bicolored Antbirds, growling is used by the female mainly when the male holds back with the food; he may chirp or growl if she refuses his gift; feedings are often silent.

BASIC POSTURES AND MOVEMENTS

The standard posture for all five species of *Rhegmatorhina* is like that for Bicolored Antbirds (Willis, 1967). However, all species except *melanosticta* are heavier than Bicolored Antbirds and stand closer to the perch (Fig. 2) than do the latter. The various *Rhegmatorhina* are adept at clinging to vertical saplings, common near the ground in tropical forests. These antbirds are similar to Bicolored Antbirds in the clinging posture: the upper leg of the bird is flexed, the lower leg extended, and toe II on the lower foot angles 20 to 40 deg above the closely appressed toes III and IV.

The various simple movements are about the same as in Bicolored Antbirds. The tail is "flicked," or lowered to as much as 80 deg below the angle of the body and jerked back suddenly to as much as 30 deg above body level, when a rhegmatorhine antbird is excited. Compound movements like yawing and pitching on or around a perch, pivoting and reversing on or along a perch, and hopping from perch to perch or on the ground, are performed easily in much the same ways as in Bicolored Antbirds. Generally rhegmatorhine antbirds fly rather than hop progressively. Flight is usually slow and fluttery, and it is often started by a powerful jump with the big legs and feet. Most *Rhegmatorhina* seem heavy and slow compared to Bicolored Antbirds, but all can be quick and agile when chasing prey or excited by predators or competitors.

WANDERING

I never saw antbirds of the genus *Rhegmatorhina* foraging away from army ants. One group of *berlepschi* at Maloquinha were disputing busily at 17:20, but they may have been near an inactive ant colony. One pair of *hoffmannsi* at Coatá were with a poorly-flying fledgling. All others seen away from ants were wandering through the forest undergrowth as if looking for ants.

A wandering antbird generally travels between one and two meters above the ground, higher than it forages at swarms. It leaps and flutters from one

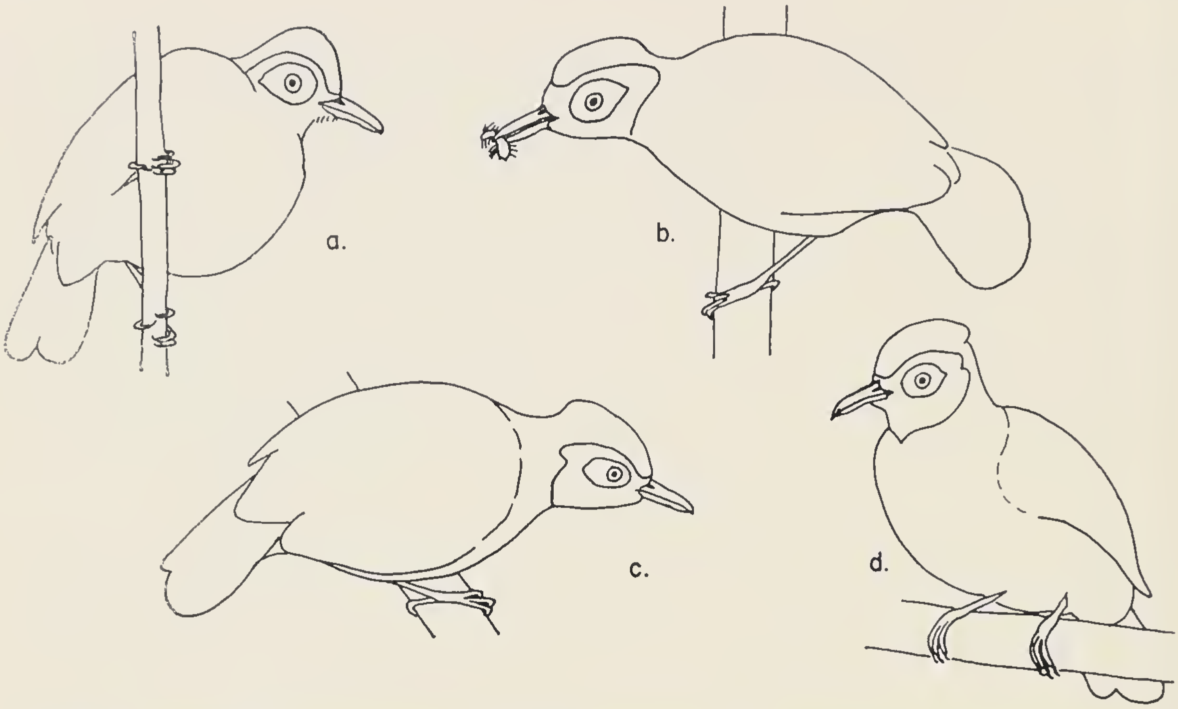


FIG. 2. Typical foraging postures for *Rhegmatorhina*: a, loafing-foraging *melanosticta*; b, *melanosticta* head down chewing prey; c, d, *cristata*. From field sketches.

vertical sapling to another, one to fifteen meters at a time, and alights precisely and easily. It looks around at each perch, but it seldom cocks the head as if looking at the ground for food.

Often an antbird loud-sings periodically as it wanders. Ones that encountered me chirred, reversed a few times, flew up higher, and circled around me before continuing in the general direction they had been traveling. When a wandering antbird encounters a trail of army ants or nears a swarm, it often chips excitably between faint-songs. Males with females commonly serpentine-sing as they precede their mates to the raid along the trail of ants.

Birds wander and loud-sing or wait and preen near a swarm that has been stopped by rain, at least until they find spots where the ants are active.

FORAGING

Birds of the genus *Rhegmatorhina* forage over the ants in much the same way as does *Gymnopithys bicolor*. All spend most of their time between 0.1 and 0.5 meters above the swarming ants, generally on the slender vertical saplings or more or less horizontal fallen branches so common in the lowermost layers of a tropical forest. They pitch and yaw, pivot and look about, or cock their heads at the ants below them. They hop or flutter to new perches if no prey appears in a minute or two, thus keeping above the active parts of the advancing swarm. They seldom hop on the ground, but they readily hop over logs and fallen twigs. At times one flies up to one or two meters above the ground, looks about, flies to another part of the swarm, and drops to near the ground again.

Most of the prey is captured by sallying to or near the ground. The bird leaps or leap-flutters after a fleeing arthropod and bounces back up to a perch with it so rapidly that army ants seldom have a chance to attack either the arthropod or the bird. At times the antbird yaws or pitches from a low perch and pecks the prey out of the air or off the ground. At other times one tosses leaves by grasping them between the mandibles and flicking one away at a time until the hiding prey is uncovered and pecked. Occasionally a bird flutters up rather clumsily and catches prey on a tree trunk or other low vegetation. I never saw them hopping through tangles of fallen limbs or lianas one to five meters above the ground as subordinate Bicolored Antbirds sometimes do. However, there were seldom enough rhegmatorhine or larger antbirds at swarms I watched to force subordinate birds to forage above the ground.

Both *melanosticta* and *cristata*, which forage in the lush and cluttered undergrowth of the wet forests of upper Amazonia, spent much time hopping about the stilts of stilt-rooted trees or the buttresses of mossy or vine-covered trees, through rotten tangles of fallen limbs, and from perch to perch in low sprouts. They searched more actively than did the smaller *Gymnopithys leucaspis* at the same swarms. However, *melanosticta* and *cristata* also spent much time waiting for prey to jump, and they promptly supplanted nearby *G. leucaspis* as if to eliminate competition. Differences between *Rhegmatorhina* and *Gymnopithys* in foraging are as slight as differences in calls and morphology.

The other three species of *Rhegmatorhina* live in less moist and cluttered forests, in regions where there are no competing species of *Gymnopithys*. As one might expect, they forage almost exactly like the species of *Gymnopithys* that live in similarly uncluttered forests across the equator, such as *G. bicolor* in Panamá. These three *Rhegmatorhina* did seem a bit slow and prone to take horizontal perches compared to *bicolor*, but one might expect this from the slightly larger size of the three. The sudden sallies of *Rhegmatorhina* were as quick or quicker than the sallies of *bicolor* when the former did move.

The prey of *Rhegmatorhina* were almost always insects, spiders, and other arthropods. Roaches, crickets, and orthopterans in general were favored prey. I never saw a bird eat army ants. In upper Amazonia there are black ants that, when the army ants invade, grab their white larvae and stream up nearby vegetation in a frantic race to escape. One such stream of ants at Benjamín Constant attracted a male *melanosticta*, who pecked 10 larvae and tossed away the adult ants from a nearby petiole as fast as he could, as if working on an assembly line; he ignored a similar stream of ants with larvae up another petiole near him, then relinquished the job to a pair of *Gymnopithys salvini.*

Most of the prey seems to be one-third to one and a half times the length of the exposed bill (one bill length = about 16 mm). The largest prey seen was a centipede three times the length of the bill of the young male *hoffmannsi* that captured it.

Large prey may be taken to the ground or to a broad, horizontal perch for dismembering. The bird shakes and chews the prey, drops it to the ground and looks at it, then takes it up again. The bird usually flies off a few meters if other birds or the ants are nearby. The prey is never held by the foot or hammered against the perch.

One female *hoffmannsi* performed anting. She flew up to two meters over the ground with prey half as long as her beak, chewed it and repeatedly poked it into the under sides of her remiges and rectrices. She finally ate the prey and wiped her beak energetically. She did not raise the crest, although such noncrested relatives as the Bicolored Antbird commonly do so after bill-wiping or billing a distasteful prey.

OTHER MAINTENANCE ACTIVITIES

Periodically antbirds of the genus *Rhegmatorhina* preen over the ants, even if they have just arrived and are foraging busily. At times one loafs and preens in a sheltered spot near the swarm.

Loafing and preening resemble the same activities in Bicolored Antbirds. All pick horizontal perches, sit or half-sit, and fluff the feathers of the body. The preening bird looks about every second or two. One preening female Hair-crested Antbird gave a head-shaking nibble at the base of each feather preened, then a sweep of her head as she ran the rest of the feather between the tips of her mandibles. When one *berlepschi* turned the head to preen the upper breast, the scanty feathers of the neck parted from those of the body in the same way as do the neck feathers of Bicolored Antbirds.

"Underwing-looking" was noted for *hoffmannsi* and *cristata.* The latter displayed a cinnamon wing-lining as he stretched one wing laterally and peered under it as if mesmerized; this behavior is so frequent among birds with plain wing linings that the birds are probably looking for parasites rather than displaying.

In all *Rhegmatorhina*, the head is scratched over the wing. However. one young female *gymnops* scratched repeatedly under the wing at a spider web plastered on her bill. Related antbirds usually scratch over the wing, but nearly all scratch under the wing at times.

Stretching movements are much the same in *Rhegmatorhina* as in Bicolored

FIG. 3. Two-wing stretch, juvenile Bare-eyed Antbird. From field sketch, Palhão.

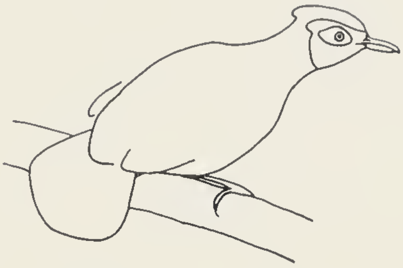


FIG. 4. Panicking Crested Antbird. From field sketch, Mitú.

Antbirds and other birds. Full side-stretches (wing, leg, and tail on one side of the body) were noted for *melanosticta*, *gymnops*, and *hoffmannsi*. Two-wing stretches over the back, as in a stretching human, were noted for *melanosticta* and *gymnops* (Fig. 3). Toe-standing was recorded for *melanosticta* and *berlepschi*. All these stretching movements, and yawning as well, are so widespread in birds that they probably occur in all species of *Rhegmatorhina*.

Frequently these antbirds twitch the rear end of the body or shake the head from side to side. Often the twitching includes a sudden flit of the wings. One Hair-crested Antbird jabbed down at her ventral apterium after a flitting twitch. Since isolated antbirds as well as ones close to other antbirds or to me perform such motions, I suspect the persistent mosquitoes rather than the presence of observers incite these movements. On a few occasions when sunlight outlined the hovering parasites, I saw that alighting mosquitoes provoked similar twitches and head-shakes in related antbirds, *Pithys albifrons* and *Gymnopithys bicolor*. To the birds, I must have seemed similarly twitchy.

REACTIONS TO DANGER

I observed freezing only for *berlepschi*, although it is to be expected in all species of *Rhegmatorhina*. The bird crouches, sleeks the body, and stays immobile for a few seconds. Keening, the sound that characteristically accompanies freezing in Bicolored Antbirds, was noted for *gymnops*, *berlepschi*, and *hoffmannsi*.

Chipping, panicking, and hyperactivity were noted for alarmed birds of all five species. The panicking antbird sleeks the body, flexes the femora as it extends the next two joints of each leg, and extends the neck and head (Fig. 4). It often angles the front of its body downward. It flicks the spread tail rapidly. It darts from perch to perch or into cover with sharp "chip!" notes. Panicking and hyperactivity were difficult to see clearly in other respects, but seem to resemble the same activities in Bicolored Antbirds.

One male Hair-crested Antbird at Benjamín Constant was very sleeked and flicked his tail rapidly as he wandered in the exposed branches atop a treefall. An arriving male Crested Antbird at Mitú sleeked his head and body and flicked his tail when he saw me. His throat was ruffed, his crest folded (Fig. 4). Throat-ruffing is often a sign of mobbing in this group of birds, but the other movements suggest panic.

Bare-eyed Antbirds chipped and panicked when hawks arrived: *Leucopternis kuhli* once; *Leucopternis albicollis* once; *Micrastur gilvicollis* twice. One Bare-eyed Antbird chipped and fled when a Scale-backed Antbird (*Hylophylax poecilonota*) gave its alarm call, and two other *gymnops* chipped and became hyperactive when a squirrel started chattering above the ants. On three occasions, Harlequin Antbirds chipped and fled when *Micrastur gilvicollis* arrived at swarms. One White-breasted Antbird double-chipped and fled when a big Hoffmann's Woodcreeper (*Dendrocolaptes hoffmannsi*) glided down from above. Several other *R. hoffmannsi* started a chipping panic when a White-chinned Woodcreeper (*Dendrocincla merula*) started chattering. Another *R. hoffmannsi* chipped at the distant alarm call of a nunbird (*Monasa morphoeus*). An arriving hawk (*Micrastur gilvicollis*) caused another chipping panic among White-breasted Antbirds.

One Bare-eyed Antbird chipped once, then chirred twice when a tayra (*Eira barbara*) wandered past. Antbirds of the genus *Rhegmatorhina* generally performed mobbing and chirring when I appeared at the swarms. After chirring from behind cover for a time, they converged on the swarm again. Finally one or more flew up to two meters or so above the ground or to some other place where they were in plain sight. Still chirring, they flicked the partly spread tails and stared at me with one eye and then the other.

The large, seemingly glowing greenish-blue bare area around the dark eye, set as it is in a black face against the dark undergrowth, resembles at such times the eye of a large cat. Perhaps this bare area is used as the "iris" in an "eyespot" design, frightening potential predators or competitors of the same or other species. The bare area is very prominent when the bird is mobbing and when it is displaying to an opponent of its own species, hence may serve both purposes.

Mobbing antbirds commonly extend the head and neck as they flex the femora, thus presenting the bare facial area to the object of mobbing. One occasionally swings round and around a vertical perch, 30 to 100 deg at a pitch, displaying the face before darting behind cover again. Perhaps the bird is uncertain whether to approach or flee. Bare-eyed Antbirds, which have unusually large bare areas in otherwise rather unmarked bodies, were very prone to swing around perches and stare at the observer (Fig. 5). The related Harlequin and White-breasted Antbirds were less prone to do this. I did not note such behavior for Hair-crested or Crested Antbirds, and it is rare in related species unless they have bright blue facial areas.

Foraging but nervous antbirds of the genus *Rhegmatorhina* flick their closed tails, dart behind cover periodically, or chirr. Slightly tamer birds stay but have their throats ruffed, at least in *cristata*, *gymnops*, and *hoff-*

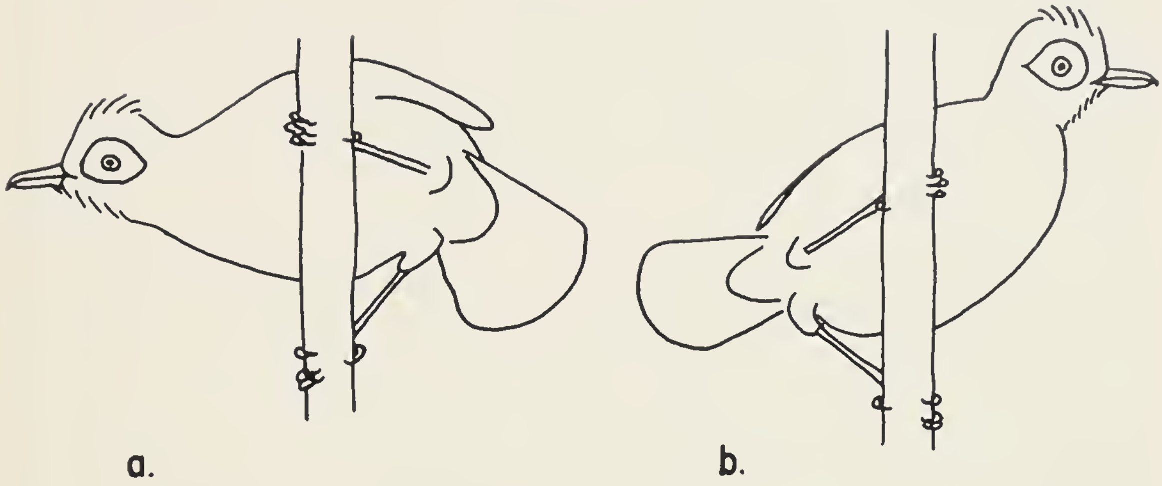


FIG. 5. Mobbing Bare-eyed Antbirds, probably showing signs of panicking. From field sketches, Palhão. See also males on frontispiece.

mannsi. Throat-ruffing is common in semi-tame Bicolored Antbirds and other species of *Gymnopithys*, but in addition the half-tame *Rhegmatorhina* of all species raise their crests now and then. Occasionally when I was near them, the tame antbirds popped up to two meters or so above the ground, stared and crest-raised, and dropped down again even though they did not chirr or show other signs of mobbing. One *berlepschi* flew up in this fashion when a brocket (*Mazama* sp.) wandered through the swarm. Semi-tame *Rhegmatorhina* often call "chup" or faint-sing, as do semi-tame Bicolored Antbirds. I recorded some body fluffing from one semi-tame *melanosticta.*

Semi-tame *Rhegmatorhina* often perform displacement activities when they forage near me. They crest-raise, wipe their beaks, toe-look, flit the wings, flick the closed tail, reverse repeatedly, hop up and down perches. One moderately tame *hoffmannsi* was sleeked and high on his legs, his femora flexed so his body angled down, and his head extended and up, when he came near me. Perhaps he was performing a mixture of foraging and panicking.

Rhegmatorhine antbirds watched for long periods mobbed, panicked, or froze less and less strongly when I came near. However, none became very tame. Some young birds, changing from the juvenal to the adult plumage, approached and investigated me. Presumably, if I had been able to stay with the birds more than a week or two, they would become as tame as do the related Bicolored Antbirds when I watch them repeatedly. The *Rhegmatorhina* species became tame less rapidly than do Bicolored Antbirds, or about as rapidly as does the Amazonian *Gymnopithys leucaspis.*

At Palhão and later at Curuá, *R. gymnops* chipped as they readily but rapidly darted across dirt roads 10 to 15 meters wide. Crested Antbirds readily used low second growth, two years old or so, when following swarms in a largely forested area. Otherwise these species seem as restricted to forest as are members of related genera. Since the army ants also avoid open areas, it is probably very unlikely that rhegmatorhine antbirds cross large rivers like the Tapajoz and Madeira even if they can fly well enough to do so.

Occasionally a rhegmatorhine antibird forages in rather open situations, although it shows signs of panicking. One male *berlepschi* at Maloquinha followed ants for several days in the very open undergrowth of the varzea along Cupituã Creek. He stayed by fallen logs and near tree trunks or groups of saplings whenever they were available. Other males there flew down and worked in a tractor trail through second growth when ants swarmed along the trail. They hopped or stood on the road briefly, feet splayed and tails up slightly, and pecked here and there before fleeing to the roadside thickets for a time. One male hop-fluttered over the grass in the center of the tractor trail and resumed hopping in the other rut. When these antbirds crossed the road, they generally flew out from 1.2 to 1.5 m up. The *Phlegopsis nigromaculata* foraging with them crossed at various levels, suggesting that they were not moving to special heights before crossing. The Black-spotted Bare-eye is more of a bird of second growth than is *berlepschi*, and the Tapajoz and Madeira Rivers only separate the Bare-eye into subspecies.

When swarms passed over the open mounds of leaf-cutter ants at Coatá, most *hoffmannsi* waited at the periphery; however, an occasional bird worked over the ants. At Mitú, Crested Antbirds worked the edges but not the centers of clearings in the undergrowth below a species of sapling that either kills the other vegetation or has ants that do this for it.

AGONISTIC BEHAVIOR

As in an earlier paper (Willis, 1967), I shall use "agonistic behavior" to mean such competitive behavior as fighting, supplanting, aggressive display, and submissive display.

I saw fighting only once, when two White-breasted Antbirds fluttered up and had a brief aerial peck and scrabble duel. Fighting is so rare in the related Bicolored Antbirds that I could easily miss it in such short-term studies as these. I saw no submissive displays in *Rhegmatorhina*, perhaps because I did not watch them long enough to get them really tame. These displays are best observed when birds are very tame, since wary dominant birds tend to flee rather than persecute subordinate ones persistently enough to start submissive displays in the latter.

Supplantings and Displacings.—One male Hair-crested Antbird ducked his head and raised his crest as a woodcreeper dove past. A juvenile *gymnops* jumped and ruffed its crest and throat strongly when a Rufous-capped Ant-thrush (*Formicarius colma*) ran past and snapped up an insect. A male *hoffmannsi* jerked up when a woodcreeper (*Dendrocincla merula*) sallied to the ground for an insect in front of him. A female *hoffmannsi* raised her crest when a smaller female antbird (*Myrmoborus myotherinus*) hopped nearby. Crest-raising at a competitor of another species was seen on several other occasions.

When several birds of various species work over the swarms of army ants, a rhegmatorhine antbird keeps away from competitors by moving away or by supplanting any birds that come closer than a meter or two. The antbird supplants a competitor by flying at it and taking its perch with a snap of the beak. Once I saw that a *hoffmannsi* supplanting another had its beak open until the terminal snap. A *melanosticta* supplanting a *Gymnopithys leucaspis* at Zatzayacu had the tail and wings partly spread and somewhat tented as it alighted. One female *hoffmannsi* snapped as she alighted above a larger woodcreeper (*Dendrocincla merula*), then pitched around the perch pecking repeatedly at the dodging woodcreeper. It flew but returned; she flushed but supplanted it successfully on her next try. Generally larger birds supplant smaller ones at ant swarms, so that *D. merula* is about the largest bird a rhegmatorhine antbird can supplant.

Hair-crested Antbirds twice supplanted White-plumed Antbirds (*Pithys albifrons*) and five times supplanted White-cheeked Antbirds (*Gymnopithys leucaspis*) at Zatzayacu. White-throated Antbirds (*Gymnopithys salvini*) lost to *melanosticta* seven times at Carraurí and seven times at Benjamín Constant. The large Rufous-winged Bare-eye (*Phlegopsis erythroptera*) supplanted *melanosticta* once at Zatzayacu and once at Benjamín Constant. By contrast, I saw *melanosticta* supplant *melanosticta* twelve times, all at Benjamín Constant.

Crested Antbirds at Mitú supplanted White-cheeked Antbirds thirteen times, White-plumed Antbirds three times, a Scale-backed Antbird (*Hylophylax poecilonota*) once, and a White-chinned Woodcreeper (*Dendrocincla merula*) once. Rufous-winged Bare-eyes supplanted *cristata* three times.

At Palhão, Black-spotted Bare-eyes (*Phlegopsis nigromaculata*) supplanted Bare-eyed Antbirds twice, a Concolor Woodcreeper (*Dendrocolaptes concolor*) supplanted one once, and a Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) displaced one once.

At Maloquinha, Harlequin Antbirds once supplanted a Spot-backed Antbird (*Hylophylax naevia*). On twenty occasions, Black-spotted Bare-eyes supplanted *berlepschi*. By contrast, I noted 46 supplantings of *berlepschi* by *berlepschi*.

At Coatá, White-breasted Antbirds supplanted a Scale-backed Antbird once, a Saturnine Antshrike (*Thamnomanes saturninus*) once, and White-

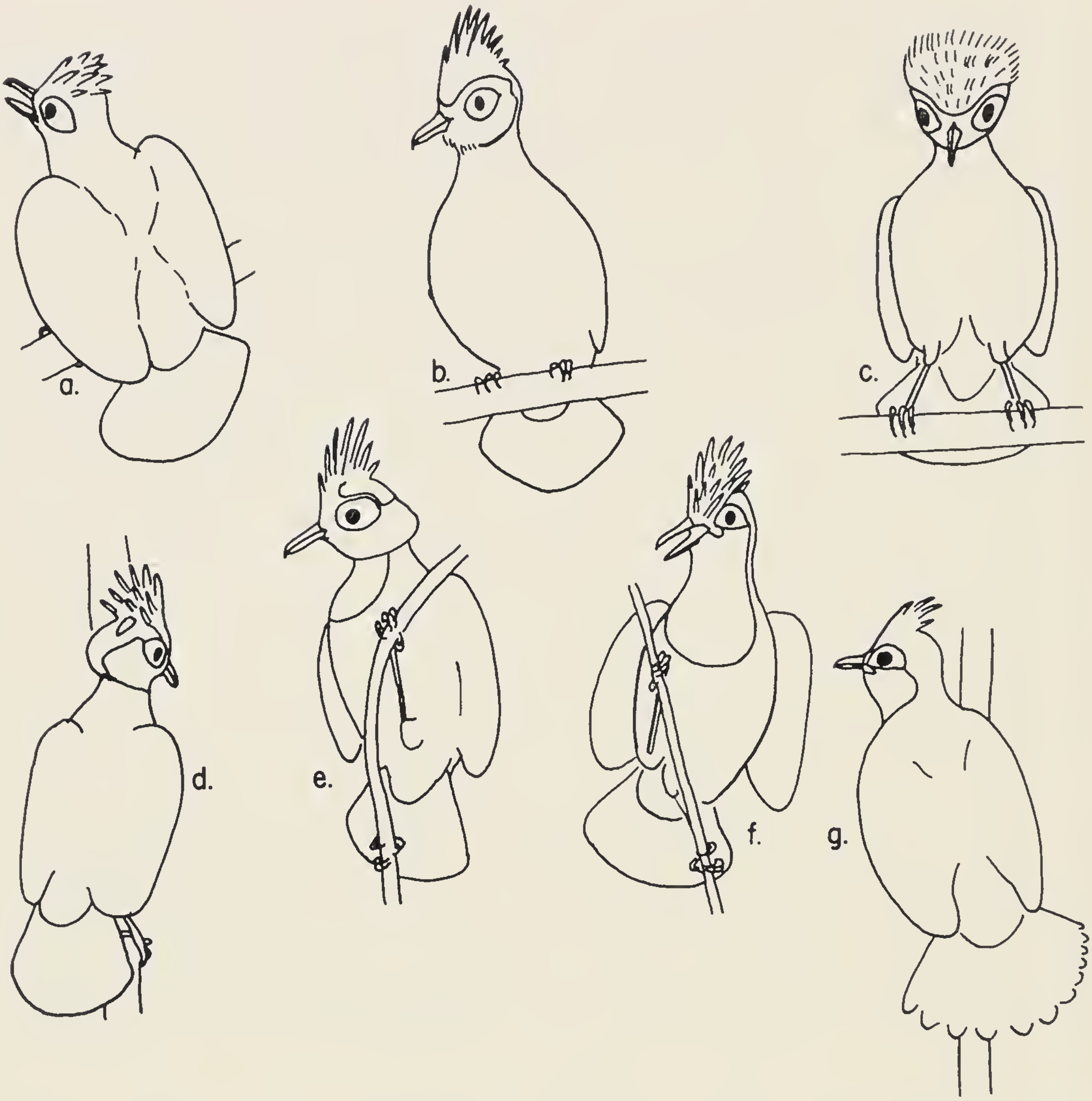


FIG. 6. Challenging in *Rhegmatorhina*, from field sketches; a, *gymnops* at Palhão; b, *cristata* at Mitú; c, *melanosticta* at Benjamín Constant (note the "giant-eyed" appearance caused by bare facial areas, also the "hair-crested" look); d, e, *berlepschi* at Maloquinha (note the "*Bucephala*-like" head and the exposed skin on the hind crown); f, g, *hoffmansi* at Coatá.

chinned Woodcreepers fifteen times. The woodcreeper returned the favor three times. Black-spotted Bare-eyes supplanted *hoffmannsi* thirteen times, and Pale-faced Antbirds (*Skutchia borbae*) supplanted *hoffmannsi* twelve times. By contrast, *hoffmannsi* supplanted *hoffmannsi* 112 times.

Aggressive Display.—The aggressive display of rhegmatorhine antbirds is very like the "challenging" display of Bicolored Antbirds, except that all rhegmatorhine antbirds raise and spread their crests very strongly. The challenging display (Fig. 6) is graded: postures passed through on the way to the maximum display are often the full display at other times. All species of *Rhegmatorhina* extend their legs so that their bodies rise as far as the vertical, whether the birds are on vertical or horizontal perches. The tail is spread more or less strongly, and flicking stops. The wings are often partly spread, and form with the spread tail a "tented" appearance. I have not seen the wings completely spread, but I may have missed the maximum form of challenging. Unlike Bicolored Antbirds, the rhegmatorhine antbirds do not part or fluff the interscapular feathers noticeably. I noted expansion of body feathers, due to fluffing or to inflation, only for female *hoffmannsi.* Her expansion displays barred feathers rather strongly. However, inflation and body fluffing are hard to detect, so I may have missed the movements in other species.

The neck is extended in challenging, but not strongly so. In *berlepschi* the neck-extending causes the feathers to part so that the rufous nape shows on a head shaped somewhat like that of a male American Goldeneye (*Bucephala clangula*). In *berlepschi, hoffmannsi,* and *cristata* and probably others the bill is pointed down at the chest during the strongest displays—that is, the head is strongly flexed. The bare eye areas become large and conspicuous as the crest is raised, and the bill-down posture displays both bare areas conspicuously against the black face. One female *hoffmannsi* turned her head so as to keep the bill and both facial areas toward a male flying past.

In *cristata* the throat of one challenging bird was fluffed (Fig. 6b). In that species and in all but *melanosticta* the raised crest is pointed. In Hair-crested Antbirds, the whole whitish crown seems to expand evenly, like a large hairy petal pushed up by a bee. In *cristata* the center of the crest is full and jaylike, but in *berlepschi* and *hoffmannsi* the long front feathers rise high over the few short feathers of the rear of the crown. In one male *berlepschi* the frontal crest was raised so strongly it left a bare blue spot at the center of the crown (Fig. 6d).

Even when they are no longer rising in indignant challenging poses at trespassers, the rhegmatorhine antbirds continue to raise their crests at competitors. Even a male *hoffmannsi* that was defeated and retreated from an encounter crest-raised before he wiped his bill. The crest, which is the best distinguishing characteristic for this genus of antbirds, is used far more in agonistic encounters than it is during bill wiping or as a reaction to competitors of other species or to the observer.

Once a male *hoffmannsi,* separated from another by a large Pale-faced Antbird, was utterly silent as he jerked into several upright challenges. Normally a challenging antbird snarls or bugles vigorously at the opponent, or why-sings loudly or faintly at the very least.

A snarling or bugling challenge is likely to start an outburst of supplantings, challenging displays, snarls, more bugling, loud why-singing, chipping and even chirring. Challenge-flying, when one bird flutters with spread wings and tail after another, is often associated with bugling and with a series of supplantings. Eventually the defeated bird leaves, loud-singing, or wanders on the periphery of the ant-swarm, faint-singing. Songs seem more frequent than in the otherwise similar outbursts of Bicolored Antbirds; however, in the similarly white-bibbed *hoffmannsi* snarling is frequent, as it is for Bicolored Antbirds.

I saw only a few such outbursts for *melanosticta*, *cristata*, and *gymnops*. At the seasons I visited them there were rarely more than one pair at each swarm of ants. I saw many outbursts from *berlepschi* at Maloquinha in February and from *hoffmannsi* at Borba and Coatá in late March and early April. There were many young of the year out of the nest and two or even three pairs at some swarms, so there were many disputes. At times, however, birds foraged near each other with little sign of agonistic behavior. I suspect that they had determined the peck order and had habituated to each other, as is generally the case when Bicolored Antbirds tolerate each other.

The frequent outbursts, the muted snarling why-songs, and the supplantings back and forth reminded me of the frequent feuding when two or more pairs of Bicolored Antbirds attend a swarm of ants. In Bicolored Antbirds, the pair on its own territory dominates other pairs and wandering birds but permits them to remain at peripheral sites at a swarm. The rhegmatorhine antbirds probably have a similar form of territoriality, although I could not be certain without banding pairs and following them from one territory to another to see if there are reversals of dominance.

One male *melanosticta* waited to supplant another male until the latter finished chewing a prey item. A male *hoffmannsi*, food in his beak, did a bugling upright with his back toward a female who had supplanted him; she held her upright pose and then bill-wiped as he made his getaway. Another male *hoffmannsi* supplanted a juvenile male as it captured a long centipede; both faced in bill-down upright poses and the adult male retreated. I have recorded similarly polite conduct from Bicolored and other antbirds. The general rule seems to be that a bird dissecting food or with food in its beak is rarely attacked, except at the moment of prey capture.

One male *berlepschi* raised his crest now and then as a dominant male approached; then the first male bill-wiped, preened his belly, and shook his body. Eventually he was supplanted and moved away to forage, calling "chup" faintly. Retreating *hoffmannsi* were occasionally sleeked.

One male *berlepschi* gave several "*chuc*" notes as his mate approached, but she supplanted him anyway. I occasionally saw males supplant nearby females and vice versa, but could seldom tell if they were mated or not.

There were two other definite records: a male *gymnops* supplanted his mate; and a female *berlepschi* supplanted her mate after a courtship feeding.

At swarms, a pair converse with faint chirps, chup notes, and short faint-songs. They sometimes forage a meter or two apart, but closer approach is permitted only for courtship feedings. In this respect these birds are like the species of *Gymnopithys* and unlike *Phaenostictus*, *Phlegopsis*, and *Skutchia*, which tolerate the foraging mate within a centimeter or two.

REPRODUCTIVE BEHAVIOR

Adult females of all five species of *Rhegmatorhina* always seemed to be paired. One young female *hoffmannsi*, with brown feathers still along her malar region and on the side of her breast, had a male attending her at Coatá. Female Bicolored Antbirds of about this age (10 to 20 weeks since hatching) occasionally pair with wandering males for short periods, but the definitive pair bond is normally formed only after the female has lost all her brown juvenal feathers. There is a surplus of males among Bicolored Antbirds and perhaps among rhegmatorhine antbirds: there always seemed to be unmated adult males in all five species. However, it was not possible to be certain without banding birds.

Probably the pair bond is formed by courtship feeding, which is the pairing and precopulatory ritual in many genera of antbirds. In related antbirds, the female often gets nearly all her food from the male during the period when she is forming the eggs. I have seen courtship feeding only for *melanosticta* at Carauarí, *gymnops* at Palhão, and *berlepschi* at Maloquinha. Perhaps I arrived at Coatá too late in the breeding season (young out of the nest were common in early April) to see feeding in *hoffmannsi*. However, I watched many pairs for many hours; and such related species as Bicolored Antbirds occasionally perform courtship feeding even during the non-breeding season (the dry season). I watched the few pairs of *cristata* so briefly that they did not become tame enough for courtship feeding.

I watched two feedings of *melanosticta*. The female preened and loafed after the first one. On the second, she flew below the male, he bent down, and she took the prey. When she lowered her head he pecked at her, so she dropped into cover.

For the one observed feeding of Bare-eyed Antbirds, the male faint-sang and chirped as he wandered with food in his beak. Finally he found the female, loafing in cover as she had been at various times that morning. As she took the prey to the ground, he flicked his spread tail and returned to the swarm.

I observed seven feedings of Harlequin Antbirds. On three the female growled faintly. On the last of these three the male backed off when she

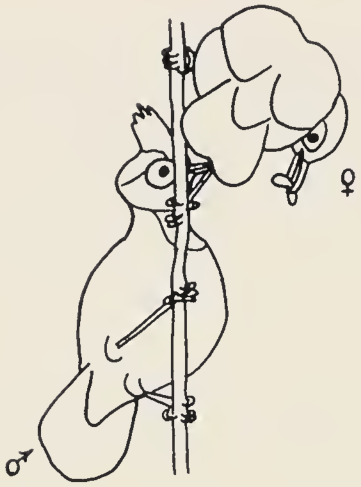


Fig. 7. Male Harlequin Antbird watching female eat after feeding her. Note his raised crest and spread tail. After a field sketch, Maloquinha.

gaped; he raised his crest and spread his tail. Finally he gave her the food and she stopped growling. Later she supplanted him. Just after she had captured her own prey later that morning, he arrived with food. He called "*chee*" faintly several times and presented the food to her twice before she gulped down her own prey and accepted his without growling. Another male spread his crest as he watched his mate eat the food nearby (Fig. 7). Another female, her head and body low in the usual food-chewing pose, spread her tail when her mate waited beside her and watched her eat his gift.

Males often lead their mates to swarms. The male flicks his tail and looks down at the trail of ants repeatedly as he flies along it toward the swarm. Faint chipping and chirping notes are interspersed with his faint-singing and serpentine-singing. The female usually tags along behind, but she may leapfrog with him as the two close in on the swarm. For *cristata* I recorded only "*chup*" and two-note faint-songs ("*whierr, whew*") as the male led his female (calling "*whier*," a one-note faint-song) about a swarm; however, an unmated male called serpentine-songs persistently one day.

The nests of these birds are unknown, but probably are inside low rotten stubs or similar sites as is the case for Bicolored Antbirds. One male *berlepschi* at Maloquinha performed "nest-showing" by flying to the top of a low stub, peering in as he flicked his spread tail, and calling repeatedly.

YOUNG

On 3 April a young *hoffmannsi* at Coatá, out of the nest and away from an ant swarm, fluttered short distances near the ground but was relatively easy to catch. It was dark brown all over, with a grayer belly, and had a dusky bare eye-ring and pale yellow gape angles. About half the size of the adult, it had a short black bill and blackish feet. The throat and neck were rather bare. The half-length tail had wedge-shaped brown feathers with rather dusky tips. The young flicked the tail busily as it clung to a vertical sapling after release. It peeped loudly in the hand, bringing the adult female up. She had arrived, fed the young, and departed several times before I found it. The male arrived when the young was peeping loudly and the female chirring, but he soon departed. In related species, the female feeds one fledgling and the male feeds the other; this male may have been caring for another young bird off in the forest.

A nearly full-sized young *hoffmannsi* at an ant swarm with its parents near Borba, 29 March, was plain brown with pale gape angles and a dusky face. Other young at Borba and Coatá were catching at least part of their own food. One young female at Borba, 28 March, was brown but had a small bluish bare ring around the eye. She was barred on the back and underparts, and had a few white feathers among the brown ones on the lower cheeks, throat, and bib. A young male at Borba was similar, but lacked the barring and had large patches of white on the throat and bib. Several independent young males and females at Coatá showed various stages of the transition from the dusky faces and brown heads of young to the greenish-faced, white-bibbed adult stage, April 5 to 11.

These young birds were always supplanted by adults, and had to take the poorest foraging positions when adults were present. Young of many related species of antbirds are subordinate to adults, but young often supplant adults in the related *Gymnopithys lunulata*.

One nearly grown young *melanosticta*, giving a peeping song, followed two adults at Zatzayacu, 20 October. It had pale gape angles, a small bluish bare area around the eye, and a speckled back. It flew up and looked me over before following the adults off.

One young *gymnops*, with pale gape angles and a small bare bluish face area, followed the male of a pair at Palhão from 28 January to 3 February. The face was brownish-black, not dark black as in adults, and the body was dark brown. The bill was dark plumbeous, the iris dark reddish, as in adults. There was no sign of speckling. It fluttered the wings as it begged from the male on several occasions, but it was capturing some prey itself. On 31 January the male fed it and then pecked it.

Specimens of these birds in various museums (AMNH, American Museum of Natural History; CM, Carnegie Museum at Pittsburgh; CMNH, Chicago Museum of Natural History; MCZ, Museum of Comparative Zoology at Harvard; MG, Museu Goeldi at Belém, Brasil; PANS, Philadelphia Academy of Natural Sciences; examined by courtesy of the curators of the Departments of Ornithology) show the change from the juvenal to adult plumage and indicate that the first adult plumage is like following ones. The "immatures" of specimen labels and faunal lists generally are birds molting from juvenal to adult plumage in this and related genera of antbirds.

Adult *gymnops* are so plain that it is difficult to tell the juvenal feathers from adult ones in young birds. A juvenile of "one third" the adult tail length (as one looks at it from the normal field distance of ten meters) from Miritituba, 20 March 1920 (CM-77563) has blackish from the dark and tiny bill to the auriculars, but the other feathers are dark reddish-brown. The throat is mostly bare, and new feathers at the sides are paler. The crest is fairly long and fluffy.

Older juvenile males (Santa Julia, Rio Iriri, 8 June 1914, MG-10834; Miritituba, 20 March 1920, CM-77558) show brown feathers along the sides of the chest and brown-tipped, blackish feathers on the belly to a greater extent than do adult males. The crown is mostly brown; the old feathers are short and broad and rather rufous, with darker centers, but new black sheathed crown feathers are scattered about. The back is a more russet brown than in the adult, the tail is browner, and the auriculars browner and less well feathered than in the adult. Several other males (AMNH-286724, Caxiricatuba, 16 May 1931; AMNH-286725, Caxiricatuba, 17 May 1931) seem young males finishing wing and body molt into the adult plumage. There are still a few brown-tipped feathers on the lower belly and crown, and the new inner primaries have duller, less rufous edges than do the old outer ones. The male taken on 17 May has a brown feather on the chest.

A juvenile but nearly full-sized female from Miritituba (20 March 1920, CM-77561) has short and broad crown feathers, uniformly brown or rufous-brown and colored like those of the back, instead of the long and pointed brown crown feathers of the adult female. The throat is well feathered in soft, pale brown rather than in the mottled blackish-brown of the adult female. The breast feathers form a band of a peculiar shiny and very dark rufous brown, not a plain brown with pale shaft streaks as in the adult female. The new feathers below the breast-band are paler and buffier brown, from the center of the chest down to the belly. Another young female (Miritituba, 20 March 1920, CM-77562) is slightly further in molt, with a few tiny blackish chin feathers and more brown feathers on the rufous-brown chest. Probably a similar bird from Caxiricatuba (12 May 1931, AMNH-286729) and one from Tauary (11 April 1931, AMNH-286730) are also juvenile females. All these young birds have black bills rather than the pale lower mandibles of adults; in life, the lower mandible of the adult is dark, but the pigment seems to disappear from specimens.

The young male *gymnops* thus seems to be browner than the adult male, especially on the short crown and on the belly and sides; but the black feathers appear on the face and chest very early. There is a rufous tinge to the dark brown areas of the plumage in both the juvenile male and female, especially on the pectoral band of the female. Certain adult females, taken in October to March, show a rather rufous tinge to the edges of crown feathers; it may be that these are first-year females. However, the juvenal plumage differs from the adult so subtly that I hesitate to attempt further separation of adults, which probably show individual variation.

The 30 specimens examined indicate that young *gymnops* appear in the early months of the year, or in the final months of the rainy season. They molt the body and then the wing feathers into an adult plumage in March to June. Molting adults have been taken March to November, and moderately worn adults from October to March. The schedule of molt and nesting is probably much the same as in Bicolored Antbirds, which start nesting with the rains but rarely get young out (because of nest predation) until near the center or end of the rains several months later. Bicolored Antbirds have a protracted molt, from the middle of the rainy season to early in the dry season.

Of 30 available specimens of *berlepschi*, presumed adults in molt have been taken July to January, ones with slight or moderate wear from December to June. Three changing juveniles are available, a female from Vila Braga (21 January 1920, CM-76400) and males from there (1 July 1917, MG-13612) and Igarapé Bravo (16 June 1931, AMNH-286731). This species probably nests late in the rainy season, slightly later than do the *gymnops* across the river, and delays its molt to the dry or nonbreeding season and the beginning of the nesting season.

The young male from Vila Braga has double-barred feathers of the juvenal plumage among the new gray feathers on the center belly and lower chest. The brown bases and buff tips of single-banded feathers of the upper back and wing coverts are somewhat more rufous in hue than in the adult female, and other wing feathers are also somewhat more rusty. The black bars on dorsal and ventral feathers are narrower and smaller than in the adult female. The breast is rusty brown, the belly feathers and feathers of the lower back dull brown. The crown feathers are short and rusty, and lack the blackish sheen and edges of the feathers of the adult crest.

The young male from Igarapé Bravo has some dull brown juvenal feathers on the rufous chest and a few brown ones in the gray areas of the sides of the upper chest; the brown breast-band of many young antbirds of this and related genera was evidently being replaced. The underparts are otherwise as in the adult male, except that the throat and cheeks are a dull sooty black rather than pure black. The rusty crown and barred back and covert feathers seem juvenal; however, the scapulars are greenish-brown and adult.

The juvenile female from Vila Braga is scrubby-plumaged and small. Although russet feathers are appearing on the chest, the feathers of the belly are a loose, fluffy brownish rather than double-barred as in the adult; however, the undertail coverts are doubly banded with blackish. The juvenal chest feathers are tinted buffy-brown, with blackish central spots. The face and loral feathers are a dirty blackish. The crown has short rufous feathers, darker in the center and paler toward the nape. The tail is dusky brownish with a black subterminal band and pale buff tips, quite lacking in the adult. (However, the adult has a slight whitish-buff tip to each tail feather when it is new.) Feathers of the upper back and scapulars are marked like the tail feathers, and are duller than in the adult female. The juvenile female is thus less strongly barred than the adult female, except for the tail band and the chest feathers, while the juvenile male has dorsal and ventral barring that the adult male lacks.

Among the 14 available specimens of *hoffmannsi*, there are two juvenile males from Calama (AMNH-491346, 28 June 1907; AMNH-156290, 1 August 1907). The first has brown rather than gray underparts, many rufous feathers over the nape, one brown feather on the forecrown, and russet-brown upperparts and tail; it is otherwise adult. The second has a few brown feathers at the sides of the chest and on the gray underparts. The axillars are brown rather than gray as in the adult, and the under surfaces of the wings are duller and less rufous than in the adult. The mantle and tail are more rufous than in the adult. The feathers of the hind crown are very dark rufous brown and rather long; new sheathed black feathers are on the forecrown. There are a few brown feathers on the black auriculars and nape. There are some brown feathers on the lower cheeks, and a few yellowish-stained feathers on the white bib. On the new labels of two females with a few yellowish-stained bib feathers (AMNH-491347 and AMNH-

491353) C. E. Hellmayr has marked "juv.," but they may be adult. All juvenile females I saw in the field had brown feathers, especially on the underparts.

One male from Borba (AMNH-491342, November 29, 1906) is in wing molt, suggesting that this species molts before the breeding season in the fashion of *berlepschi*. June to August adults are not in molt. My records and the two juvenile males above indicate that young are out of the nest at least February to July, or in the final months of the rainy season.

The 56 available specimens of *melanosticta* are too widely scattered to tell much about molt and breeding. June to August specimens from Rosarinho and Humaitá, across the Madeira from the range of *hoffmannsi*, are in molt. Seven juveniles molting into adult plumage, taken from Humaitá north to the Amazon, span the period from April to August. Molt probably follows breeding, which is concentrated in the rainy season, rather than preceding breeding as in *berlepschi* and *hoffmannsi*. Closer to the Andes the seasons of molt and breeding are uncertain. On the Purús a juvenile was taken 11 November, and birds in molt have been collected from August to February. In Perú, both molting and nonmolting birds have been taken from July to October. The breeding seasons of birds in this and related genera are so closely tied to rainfall that I would expect breeding in the southern rainy season (January to June) toward the south and east and breeding with two annual peaks (April and October), corresponding to the two equatorial rainy seasons, in northern Perú to southern Colombia. Presumably *cristata* also shows the latter pattern, although the only known juvenile was taken in July.

Although adult male *melanosticta* are unspotted, juvenile males are spotted on the back like females. A young male from Santo Antonio de Guajará, near Borba on the Madeira (11 April 1930, AMNH-280637) has even larger black subterminal bars and rufous tips on the back feathers than does an adult female, although he has fewer and smaller spots on the wing coverts than do females. This young male has a very dull brownish crown, the feathers shorter and less filamentous than in the adult. There is a breast-band of deep rufous-brown, while the rest of the underparts are the grayer brown of the adult plumage. The face is black, much as in the adult. The tail and wings of this and a similar young male (11 November 1922, CM-93968) from Arimã on the Purús are more russet, less brown, than in the adult male. Some birds sexed as females (such as AMNH-491330, Humaitá, 17 August 1906) are quite like young males.

The russet or dull brown breastband and the dull crest feathers are among the last of the juvenal feathers to be replaced; in the above young female and one other (AMNH-282110, Rosarinho, 28 June 1930) the new whitish feathers are restricted to the front of the crown, indicating replacement from front to back. For young *Rhegmatorhina*, the dull and short crests and the brown feathers on the breast, as well as the dull and small eye rings, perhaps reduce attacks by adult birds, as probably is the case for the brown chests of the related Bicolored Antbirds (Willis, 1967). However, the differences between young and old are difficult to detect when the adult is mostly brown, as is true for *melanosticta* and *gymnops*.

DISCUSSION

In behavior, rhegmatorhine antbirds are very much like Bicolored Antbirds and ant-following birds in several other related genera (*Phlegopsis*, *Skutchia*, *Phaenostictus*, and *Pithys*). The major peculiarity of *Rhegmatorhina* is the behavior pattern of crest-raising, associated with strong development of a crest in all five species. One could argue that the genus *Rhegmatorhina* should be a subgenus of *Gymnopithys*, for the two genera are morphologically very close. However, *Pithys albifrons* and species of the other genera are also closely related to these in behavior and morphology. Through *Hylophylax*, these genera grade into *Myrmotherula* and into *Thamnophilus*. There has been more evolutionary divergence in plumage and morphology than in reproductive and vocal behavior in the ant-following antbirds. It is uncertain whether they should all be put in one genus (*Pithys* has priority) or left in the present narrow genera. I prefer to wait for a revision of the Formicariidae. There is not much point in lumping two genera at a time, such as *Rhegmatorhina* with *Gymnopithys*, and creating several successive combinations of names, if all are eventually going to be lumped as the large genus *Pithys* or eventually into *Thamnophilus*.

The species of *Rhegmatorhina*, so far as is known, are allopatric. They differ mainly in color pattern, so that some might wish to consider them well-marked forms of one species. *R. melanosticta* clearly diverges from the others in the structure of the crown feathers. It probably should not be placed as a subspecies unless it is found to hybridize with *cristata* in Amazonian Colombia. *R. cristata* looks more like the other species of the genus, despite its rather long crest and its different song. However, it is more isolated geographically and morphologically than are the other three.

The forms *gymnops*, *berlepschi*, and *hoffmannsi* are practically identical in behavior. Oddly, *berlepschi* looks like a hybrid between *gymnops* to the east and *hoffmannsi* to the west. However, no intergrades have yet been discovered, and the juvenal plumages of the three are very different. At Maloquinha and along the wide Tapajoz, *gymnops* and *berlepschi* are separated by the river. If savannahs or other unsuitable habitats do not prevent their spread, the two may occur together around the headwaters of the Tapajoz.

The relationship of *berlepschi* and *hoffmannsi* is even more puzzling. Both species occur between the Tapajoz and Madeira, without any large river or other unsuitable habitat to prevent their meeting. How could two forms or species have evolved? There are isolated species on the west bank of the Tapajoz in several other genera of antbirds, and in marmosets as well (Hill. 1957). There are several theories that could account for evolution of these species.

One theory (Haffer, 1969) suggests that such species evolve in isolated forest "islands" when savannah areas widen during dry interglacials, then spread to meet relatives when forests increase during wet glacial periods. Another theory is that high sea levels during interglacials flood the river basins of the lower Amazon, cutting off islands because of the peculiar river pattern between the Madeira and Tapajoz. De Boer (1966) reports marine

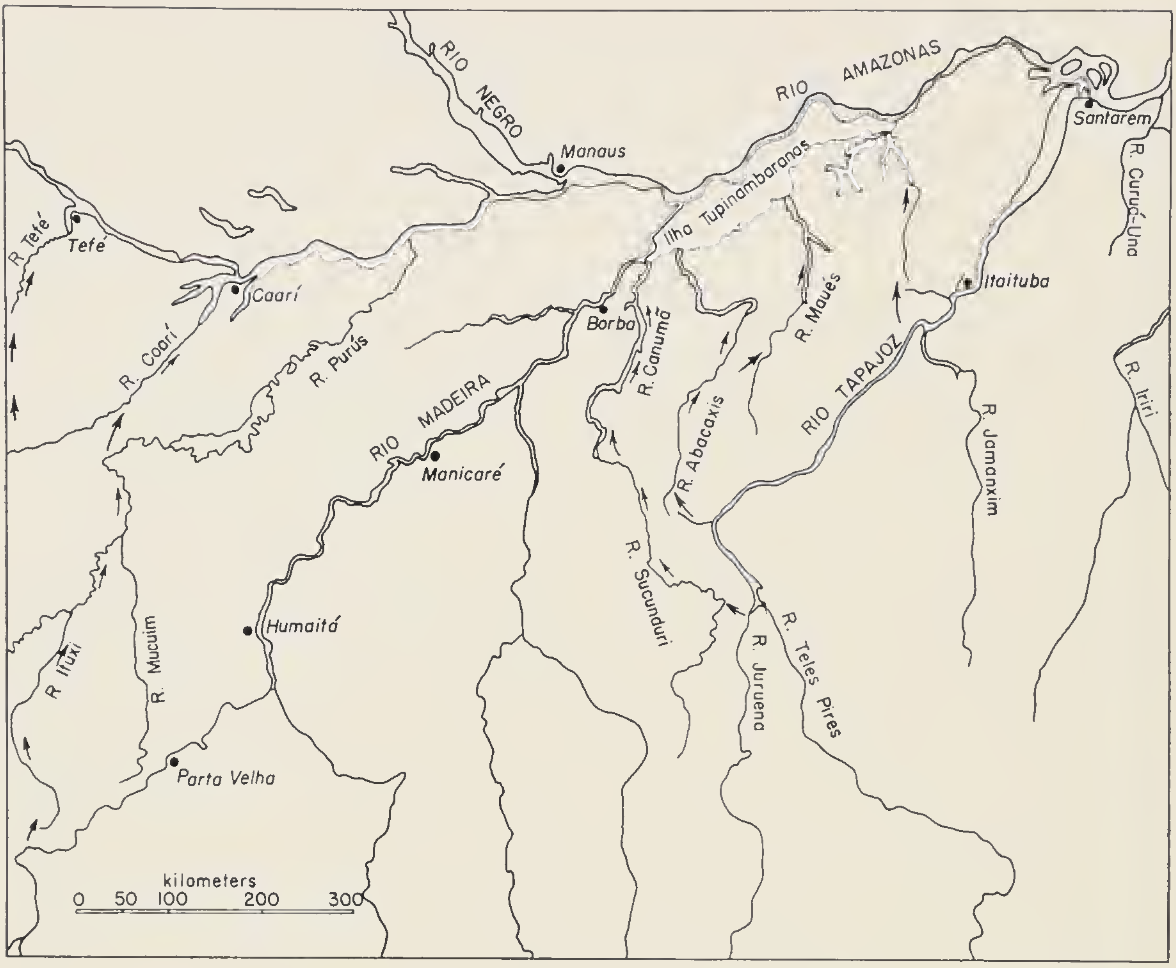


FIG. 8. Central Amazonia, showing possible former courses of the Rio Madeira (arrows on left of present-day Madeira) and Rio Tapajoz (arrows on right).

sediments well up the lower Amazon in the Tertiary and earlier. The peculiar river pattern probably derives in part from a crisscross fracture pattern that seems to develop in river basins where there is considerable sedimentation (Sternberg, 1950) but in part may derive from what may be called the third theory, that of river piracy creating islands as the Tapajoz and Madeira shifted their lower courses eastward after the Andes rose in the late Tertiary.

Probably the Tapajoz and Madeira flowed northwest off the Brasilian Shield until well after the Andes rose, and did so even after the Amazon became a strong river rather than an occasionally flooded lowland between the Guianan and Brasilian Shields. On a map of Amazonia, one sees huge finger lakes along the Amazon, pointing toward sharp bends in the upper courses of the Tapajoz and Madeira (Fig. 8): Lagoa de Tefé, Lagoa de Coarí west of the Madeira; and the lagoons of Canumã, Abacaxis, Maués-Acu, Uaicurapá, and Arapuins between the Tapajoz and Madeira. Possibly small rivers cutting back from the northeast captured the headwaters of the Madeira and Tapajoz by a series of river piracies. If so, the Madeira may once have flowed to the Amazon at Tefé and jumped to its present exit near Nova Olinda do Norte by way of a temporary exit at Coarí. The lower Tapajoz, which once flowed out through the Canumã to the mouth of the present-day Madeira, may have jumped eastward from lagoon to lagoon and ended flowing out from its present exit at Santarém. In this way the Madeira and Tapajoz, which probably feathered west into the Amazon when it first became a strong river, now feather east into it. After seeing the Lagoa de Tefé several times from the air and traveling the lower Canumã by boat, I doubt that these wide, steep-sided lagoons were carved by the tiny rivers that now flow to them. From the air, the upper end of the Tefé Lagoon, now silted in by the winding little Rio Tefé, seems the swampy former channel of a large river far to the south of the present lake.

Glacial periods, when sea levels were low and the cutting powers of rivers great because of high rainfall, are likely times for shifts in the lower courses of these rivers. River channeling or river subsidence because of deposits in glacial periods could allow flooding in interglacials, creating islands; or the Tapajoz may have had two exits at times, creating a large forested island on which *berlepschi* and other animals now restricted to the west bank of the Tapajoz could have evolved. Investigation of the geologically and ornithologically unknown region between the Tapajoz and the Madeira may show whether or where *berlepschi* and *hoffmannsi* come near each other and thus specify what the western boundary of such an island may have been.

J. Haffer (1969) suggests that the Amazonian rivers are poor barriers unless competing species occupy different banks. Changes in river courses and occasional flights across have permitted some colonizations even for poor-flying antbirds. Gene exchange could make the origin of species on separate banks unlikely unless wide marine or savannah areas added to isolation. I agree that competition from related forms may help keep rhegmatorhine and other antbirds from successfully crossing rivers, but think that clearing-avoiding species like these probably are effectively isolated by large rivers and could evolve separate species on the two sides because active crossings would be very rare. However, it is likely that evolution of species has involved both riverine and savannah "forest islands" in this region, and it may be difficult to compare the relative effects of the two kinds of isolating processes.

Even if evolution of these birds and others may be difficult to trace, comparison of ant-following and other "guilds" of species on the different banks of the Madeira and Tapajoz and Xingú should be very exciting for ecologists. The ant-following guild to the west of the river is in each case slightly more complex in numbers of species, yet geological and climatic conditions on the two banks often differ less than conditions 100 kilometers apart along the same side of a river. Evidently the rivers are a strong barrier to spread even when there is no competing species beyond. The banks of these tropical rivers, often infertile for agriculture, should be fertile ground for ecologists and others interested in sudden changes in species diversity with little environmental diversity.

SUMMARY

All five allopatric species of plump, short-tailed antbirds of the genus *Rhegmatorhina* follow army ants and capture arthropods flushed by the ants low in the undergrowth of lowland forests along the Amazon. The most common foraging motion is sallying to the ground, as in birds of the related ant-following genera *Gymnopithys* and *Phlegopsis*.

Rhegmatorhine antbirds chirr and mob the observer. Freezing, and a sound of "keening" in some species, seem a reaction to distant danger. Single-note chipping, panicking, and hyperactivity result from the appearance of hawks and other nearby danger. The tail is flicked when a bird is excited.

Submissive behavior has not been noted, but there is a strong aggressive display, "challenging." The bird stands upright, ruffs up the crest (characteristic of the genus), and partly spreads the wings and tail. The bright blue bare areas around the dark eyes then show prominently against black faces, reminding one of the eyespot patterns of moths and other animals. Supplantings are frequent when several individuals of a species attend a swarm of ants. Two pairs or more attend a swarm at times, suggesting that there is a territorial system in which the pair on its own territory dominates other birds.

Interspecific aggression is frequent. Rhegmatorhine antbirds supplant smaller species, up to the size of woodcreepers of the genus *Dendrocincla*. Larger woodcreepers and large antbirds, such as members of the genus *Phlegopsis*, exclude rhegmatorhine antbirds from the best places over the ants.

Courtship feeding has been seen in three species and probably is the main courtship ritual in all. All adult females seemed to be paired, for there is apparently a surplus of males. Males lead their mates to swarms. A "nest-showing" display was noted for one male *berlepschi*.

In most behavioral aspects other than crest-raising, these antbirds resemble the noncrested antbirds of the related genus *Gymnopithys*. These and other ant-following genera have diverged less in behavior than in morphology.

Of the five species of *Rhegmatorhina*, *melanosticta* (ranging through upper Amazonia) is the most distinct in morphology and behavior. The isolated *R. cristata*, from the Uaupés River in northern Brasil and nearby Colombia, differs from other species in its loud-song but in few other respects. *R. berlepschi*, the Harlequin Antbird of the west bank of the Tapajoz in central Brasil, looks like but probably is not a hybrid between the white-throated *R. hoffmannsi* of the east bank of the nearby Madeira and the black-and-brown *R. gymnops* from the east side of the Tapajoz; juvenal plumages differ strongly. Possibly the presence of *berlepschi* and *hoffmannsi* rather than one species of the genus in forests between the Madeira and Tapajoz resulted from river piracies shifting the mouth of the Tapajoz eastward, creating for a time a forested island on which *berlepschi* evolved. The forested island may have been additionally isolated during dry interglacials by savannahs or by marine flooding up former and present river channels.

The different banks of the Tapajoz and Madeira and Amazon, with their rather

different species and guilds and communities, should be fertile ground for ecological studies of changes in species diversity in areas of low environmental diversity.

ACKNOWLEDGMENTS

A fellowship from the Frank M. Chapman Fund of the American Museum of Natural History sponsored most of my studies. I gratefully acknowledge also the hospitality and help of many people, especially: Dr. Djalma Batista and the staff of the Instituto Nacional de Pesquisas da Amazônia in Manaus; Bishop James Ryan of Santarém; the Brothers of the Holy Cross at Diamantino; the Franciscan friars at Maloquinha; W. E. Knowles and Jean DuBois of the FAO unit at Barreirinha and Santarém; Mr. and Mrs. Gerald Wood, missionaries at Borba; Mr. and Mrs. Albert Spieth, missionaries at Nova Olinda do Norte; Jack Looney, missionary at Benjamín Constant. The visit to Umbria in 1962 was sponsored by a National Science Foundation predoctoral fellowship.

LITERATURE CITED

De Boer, N. P. 1966. The tectonic framework and history of the sedimentary basins of northern Brazil. Anais da VI Conferência Geológica das Guianas. Ministério das Minas e Energia, Divisão de Geologia e Mineralogia, Avulso no. 41:78–82.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science, 165:131–137.

Hellmayr, C. E. 1924. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist. Publ. 223, Vol. 8, Part 3.

Hill, W. C. O. 1957. Primates, comparative anatomy and taxonomy. 3, Pithecoidea, Platyrrhini. Edinburgh: University Press.

Olivares, A. 1964. Adiciones a las aves de la Comisaria del Vaupes (Colombia), II. Caldasia, 9:151–184.

Pelzeln, A von. 1868. Zur ornithologie Brasiliens. A. Pichler's Witwe and Sohn, Wien.

Rettenmeyer, C. W. 1963. Behavioral studies of army ants. Univ. Kansas Sci. Bull., 44:281–465.

Richards, P. W. 1952. The tropical rain forest. Cambridge University Press.

Riker, C. B. 1891. A list of birds observed at Santarém, Brazil. Auk, 8:24–31.

Schneirla, T. C. 1957. A comparison of species and genera in the ant subfamily Dorylinae with respect to functional pattern. Insectes Sociaux, 4:259–298.

Sternberg, H. O'R. 1950. Vales tectônícos na planicie Amazônica? Rev. Brasileira de Geografía, 12:511–534.

Willis, E. O. 1967. The behavior of bicolored antbirds. Univ. California Publ. Zool., 79:1–132.

AMERICAN MUSEUM OF NATURAL HISTORY, CENTRAL PARK W AT 79TH STREET. NEW YORK, NEW YORK 10024, 31 MAY 1967 (PRESENT ADDRESS: OBERLIN COLLEGE, OBERLIN, OHIO.)

REPRODUCTIVE SUCCESS OF THE WOOD THRUSH IN A DELAWARE WOODLOT[1]

JERRY R. LONGCORE AND ROBERT E. JONES

WOODLAND habitat in northern Delaware is being altered considerably by urbanization (Catts et al., 1966). These habitat changes are not confined to Delaware but encompass most of the Atlantic seaboard. Changes in land-use priorities stemming from the increasing human population are resulting in the destruction of wooded areas. To evaluate the effects of these changes on wildlife populations, an ecological study of suburban woodlots is under way in the Department of Entomology and Applied Ecology at the University of Delaware.

Birds, being conspicuous and common, seemed a logical choice on which to undertake studies. Initially a 35.6-acre relatively undisturbed woodlot was chosen as a basic study unit so that a base line of breeding bird success could be established. Information gained on this unit is to be used for comparative purposes with breeding bird success obtained for greatly disturbed, remnant woodlots scattered throughout suburban developments.

This paper deals only with the Wood Thrush (*Hylocichla mustelina*) in the 35.6-acre study unit. In addition to the standard information on breeding success; i.e., per cent of nests successful, per cent of eggs hatching, per cent of young fledging, etc., an attempt is made to relate reproductive success to the interplay of the physical and biological factors at work in the woodlot. An analysis of the 142 Wood Thrush nesting attempts recorded over a two-year period is presented.

METHODS

Systematic nest searches were initiated in mid-May, 1965, and in late April in 1966. Searches were continued through mid-August. Grid lines located at 150-ft intervals were traversed at least once every three days except for a two-week period in July, 1965. As nests were located the following information was noted: plant species in which the nest was located, nest height above ground level, degree of nest completion, and number of eggs and young. Data on eggs and nestlings and their development were recorded until each nest was vacated. Heights of nests above ground were measured to the nearest half-foot. The contents of high nests were observed, using a mirror attached to a 10-foot length of ¾-inch thin-wall conduit.

Forty-six Wood Thrushes were banded and handled a total of 84 times during a concurrent netting operation that was conducted for approximately 36 hours every 2–3 weeks in the 1966 breeding season. The birds were weighed and measured, and when possible they were sexed and aged. This was the continuation of a less regular

---

[1] Published as Miscellaneous Paper No. 567 with the approval of the Director of the Delaware Agricultural Experiment Station. Publication No. 372 of the Department of Entomology and Applied Ecology.

banding effort carried on by J. T. Linehan of the U. S. Fish and Wildlife Service in the study woodlot during the previous 10 years.

Vegetation of the study area was sampled in three ways. A tally of all overstory tree species two inches DBH (diameter breast height) and above was made on 40 per cent of the study area using a 66 foot wide strip transect. Line-intercept transects (10 m in length) were employed to measure understory shrub and sapling tree species, while 0.25 m^2 plots were used to sample herbs.

Climatological data were obtained from the records of the U. S. Department of Commerce for the Greater Wilmington Airport official weather station located approximately six miles from the study area.

STUDY AREA

Physical Features.—The study area is located within the city limits of Newark, Delaware, on the University of Delaware Agricultural Experiment Station Farm. The wooded area is mitten-shaped, covering 35.6-acres. The topography is slightly hilly with a slope from north to south. Elevations range from 77 to 103 feet above sea level. Soils are variable, with loam, silt loam, and sandy loam represented. An intermittent stream drains the lower portions of the area.

Weather.—The average monthly temperature varied, but precipitation readings during 1965 and 1966 were all well below the long-term normal. Although a cold, damp period (13–19 June) occurred during the 1965 breeding season, neither Wood Thrush eggs nor nestlings appeared to have been affected by the inclement weather. However, two rain storms accompanied by strong winds on 10 June and 21 July 1966, blew a few nests to the ground.

Vegetation.—The study area is located near the fall line between the Piedmont Region and Coastal Plain, and consequently includes plant species common to both physiographic areas.

Two relatively distinct vegetational types, based on species composition and related to site and soils, were recognized; an upland type (23.2 acres) and a lowland type (12.4 acres).

The upland type was well stocked with 121 ft^2 basal area per acre and 322 stems per acre. Overstory trees present in the upland type included tulip poplar (*Liriodendron tulipifera*), sweet gum (*Liquidambar styraciflua*), oaks (*Quercus* spp.) and hickories (*Carya* spp.). Flowering dogwood (*Cornus florida*), an important nest site species, accounted for little basal area but ranked sixth in number of stems. Tree diameters were rather evenly distributed among size classes. Predominant understory species were sweet pepperbush (*Clethra alnifolia*), blue beech (*Carpinus caroliniana*), spicebush (*Lindera benzoin*), arrowwood (*Viburnum dentata*), Japanese honeysuckle (*Lonicera japonica*) and Virginia creeper (*Parthenocissus quinquefolia*). The principal herbaceous plants in the upland type were mayapple (*Podophyllum peltatum*), false Solomon's seal (*Smilacina racemosa*), and enchanter's nightshade (*Circaea quadrisulcata*).

Much of the lowland type was even-aged secondary growth but with scattered mature red maples (*Acer rubrum*), sweet gums and pin oaks (*Quercus palustris*). The basal area per acre (130 ft^2) was relatively high because of the large, mature trees. There were 390 stems per acre with secondary growth accounting for much of this total. Predominant understory plants included spicebush, arrowwood, sweet pepperbush, greenbrier (*Smilax* spp.), and Japanese honeysuckle. Herbs commonly found in the lowland type were mayapple, jack-in-the-pulpit (*Arisaema triphyllum*), touch-me-not (*Impatiens biflora*), and skunk cabbage (*Symplocarpus foetidus*). Plant names follow Gleason and Cronquist, 1963.

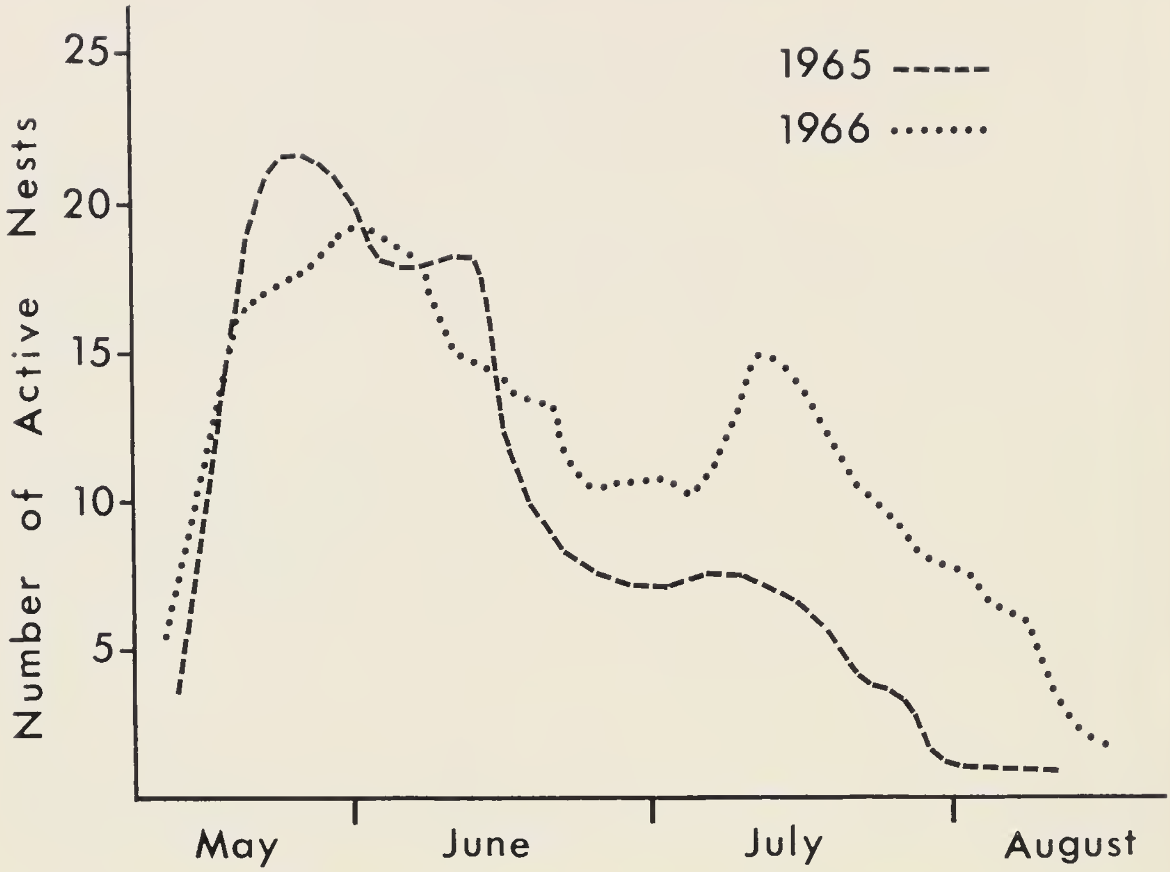


FIG. 1. Three point floating average curves for the daily number of active Wood Thrush nests, 1965–1966.

NESTING SEASON

Peaks of nesting activity.—The duration of use for any given active nest was approximately 30 days. Included in this 30-day period were 3–4 days for nest-building, 2–5 days for egg-laying, 13–14 days for incubation and 12–13 days for nestling growth before fledging. Nest-building was usually completed in four days but on one occasion extended for eight days. Brackbill (1958) states that generally the nest is complete after three days, but that some building may occur even up to seven days. Weaver (1939) reported that about five days were required for nest building in New York.

Interpolation and extrapolation of the nest survey data revealed the approximate day of initiation and termination of each nest. From these data the number of nests active on each day of breeding seasons (Fig. 1) was determined. The earliest active nest was started on 14 May and the latest on 13 July and vacated on 12 August. The primary nesting peak in both years occurred during the last two weeks of May, and a secondary peak was attained in the second week of July. Although the number of nests active during the primary nesting peak in 1965 (23 nests) was greater than the 1966 peak (20 nests), there were more nests concurrently

TABLE 1

ANALYSIS OF 142 NESTING ATTEMPTS OF THE WOOD THRUSH IN A DELAWARE WOODLOT, 1965–1966

	1965			1966			Totals		
		Per cent			Per cent			Per cent	
	Number	1*	2*	Number	1	2	Number	1	2
Nests									
Incomplete	19	29	—	18	24	—	37	26	—
Fate Unknown	4	6	—	8	11	—	12	8	—
Active	43	65	—	50	66	—	93	65	—
Successful	13	20	30	22	29	44	35	25	38
Total Nesting Attempts**	66	—	—	76	—	—	142	—	—
Cause of Failure									
Predation	30	—	70	19	—	38	49	—	53
Weather	0	—	—	4	—	8	4	—	4
Desertion	0	—	—	5	—	10	5	—	5

* 1, Per cent of total nesting attempts; 2, Per cent of active nests; ** Successful nests are included in active nests.

active over a longer portion of the breeding season in 1966. The 1966 secondary peak was more than double the 1965 peak, suggesting more renesting or double nesting.

Analysis of nesting attempts.—An analysis of the 142 nesting attempts is presented in Table 1. A "nesting attempt" includes incompleted nests, active nests (any nest having received one egg), and "fate unknown" nests (outcome could not be determined). Thirty-five (38 per cent) of the 93 active nests were successful (at least one young fledged); 37 nests were incomplete and 12 nests were classified as "fate unknown."

Nice (1957) summarizing 7,788 nests for 24 studies found that success rate of open nests of altricial birds in the North Temperate Zone ranged from 38 to 77 per cent, averaging 49. Potter (1915) reported tree and bush nesters to have 43 per cent nest success. Kendeigh (1942) reported a 63 per cent success for 16 Wood Thrush nests observed during the period 1921–1939. Brackbill (1958) found 17 of 26 active nests (65 per cent) successful, with desertion, storms, predation and the intrusion of the Brown-headed Cowbird (*Molothrus ater*) affecting success.

In the present study, nest failures were attributed to predation, weather, and desertion. From examination of disturbed nests and the presence of egg remains, 49 nests were listed as destroyed by predators. Strong winds caused the loss of four nests and five other active nests were deserted.

TABLE 2

DISTRIBUTION OF WOOD THRUSH NEST SUCCESS BY YEAR AND MONTH FOR ACTIVE NESTS, 1965–1966

	Successful Nests		Unsuccessful Nests		Total Nests		Probability of Success in per cent		
Month *	1965	1966	1965	1966	1965	1966	1965	1966	(Both Years)
May	5	10	23	15	28	25	18	40	28
June	6	6	6	8	13	14	54	43	48
July	1	6	1	5	2	11	50	55	54
Totals	13	22	30	28	43	50	30	44	38

* Nest assigned to month in which first egg laid.

Probable avian predators on Wood Thrush eggs and young included the Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*) and Robin (*Turdus migratorius*). On one occasion a Blue Jay was observed taking a Wood Thrush egg from a nest. A Robin was flushed from another nest containing freshly punctured eggs.

Sizable populations of the eastern gray squirrel (*Sciurus carolinensis*) (three per acre) and the southern flying squirrel (*Glaucomys volans*) (two per acre) were present on the study area. These animals are thought to have destroyed some nests.

FACTORS ASSOCIATED WITH NEST SUCCESS

The success of active nests was related to advance of the breeding season (month), plant species in which the nest was located, height of nest above ground level, and vegetational type. The lack of Brown-headed Cowbird parasitism may have contributed to nest success. The inevitable disturbance caused by the investigators is acknowledged but the extent to which this disturbance affected success is unknown.

Advance of the season.—The probability of nest success increased from one month to the next as the season progressed (Table 2). For both years combined, success of nests initiated in June and July was considerably greater than success of nests started in May. Nest success in June 1965, however, was slightly higher than success in July.

Plant species in which nest located.—Wood Thrush nest success apparently was associated with the plant species in which the nest was located. Seventeen plant species were used as nesting sites for the 93 active nests (Table 3). Plants of five species, including two shrubs; arrowwood (26 nests), spicebush (11 nests), and three saplings, black gum (*Nyssa sylvatica*) (14

TABLE 3

DISTRIBUTION OF WOOD THRUSH NEST SUCCESS IN PLANT SPECIES BY MONTH, 1965–1966

	May *			June			July			Totals		
Plant Species	A	S	% S	A	S	% S	A	S	% S	A	S	% S
Shrubs												
Arrowwood	18	5	28	5	1	20	3	3	100	26	9	35
Spicebush	6	2	33	4	2	50	1	1	100	11	5	45
Black haw	2	0		–	–		1	1		3	1	33
Sweet pepperbush	–	–		–	–		1	1		1	1	100
Buttonbush	–	–		1	0		–	–		1	0	0
Saplings												
Black gum	4	1	25	7	4	57	3	1	33	14	6	43
Red maple	9	3	22	1	0	0	–	–	–	10	2	20
Flowering dogwood	4	1	25	3	2	67	1	0	0	8	3	38
American beech	3	1		1	1		–	–		4	2	50
Blue beech	2	1		–	–		1	0		3	1	33
Sweet gum	1	0		2	0		–	–		3	0	0
Black oak	–	–		2	2		1	0		3	2	67
Black cherry	1	1		–	–		1	0		2	1	50
Pignut hickory	–	–		1	1		–	–		1	1	100
White oak	1	0		–	–		–	–		1	0	0
Magnolia	1	0		–	–		–	–		1	0	0
Vines												
Japanese honeysuckle	1	1		–	–		–	–		1	1	100

* A = Number of active nests; S = Number of successful nests; % S = Per cent successful.

nests), red maple (10 nests) and flowering dogwood (eight nests) were used for 69 of the nesting sites. Of these five species, spicebush and black gum were most often associated with successful nesting attempts.

Nest height.—Nest heights above ground level, grouped into four categories for comparative purposes are given in Table 4. Nest success was inversely proportional to nest height; the greatest success (53 per cent) occurred in the lowest nest-height class and the least success (15 per cent) in the highest nest-height class. The two lower height divisions span the usual heights of shrubs while the higher divisions are more representative of the saplings.

Vegetational type.—Over the two year period the ratios of active to successful nests in the two vegetational types were similar. In the upland type 22 of 54 active nests were successful and in the lowland type 13 of 39 were successful for ratios of 2.5 : 1 and 3.0 : 1, respectively.

Table 4

Distribution of Wood Thrush Nest Success by Nest Height and Month, 1965–1966

	Nest Heights Above Ground—(nearest 0.5 ft)											
	< 5.5 *			5.5–8.5			9–16			16.5–25		
Month	A	S	% S	A	S	% S	A	S	% S	A	S	% S
May	19	8	42	20	6	30	8	1	13	6	0	0
June	6	3	50	11	6	55	4	2	50	6	2	33
July	2	2	100	6	4	67	4	1	25	1	0	0
Totals	27	3	48	37	16	43	16	4	25	13	2	15

* A = Number of active nests; S = Number of successful nests; % S = Per cent successful.

Influence of Brown-headed Cowbirds on success.—While other authors (Weaver, 1939; Brackbill, 1958; and Friedmann, 1963) report that cowbird parasitism is a factor in the nesting success of the Wood Thrush, no such parasitism was observed in this study. Cowbirds were present and were found to have laid eggs in the nests of the Red-eyed Vireo (*Vireo olivaceus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Yellowthroat (*Geothlypis trichas*), and Kentucky Warbler (*Oporornis formosus*). Friedmann (ibid.) lists the recorded frequency of parasitism for these four species as 875, 300, 250 and 150, respectively. In contrast, only 75 records have been noted for the Wood Thrush. Perhaps the availability of the more "preferred" host species tended to exclude the use of less frequently parasitized hosts such as the Wood Thrush.

Interactions.—Nest success did not increase progressively during the season for any given plant species, except spicebush, because usage of certain species changed with the season. Red maple and spicebush were used mostly in early season, black gum in mid-season, and arrowwood supported a disproportionately higher number of successful nests in July.

Monthly differences in success may be partially explained by: (1) the phenological changes of the vegetation are such that foliage is denser and affords more cover for nest concealment later in the season, (2) the amount of parental care available per nestling is probably greater in July during re-nesting when clutches are smaller than during early nesting attempts, and (3) the functional response of predators (Leopold, 1933; Holling, 1961) is to destroy a higher proportion of prey (eggs or young in nests) when more are available. These variables, singly or in combination, may explain the higher nest losses in May and lower losses in June and July when fewer nests were active.

Of the five predominant plant species used, success was lowest in red

TABLE 5

CLUTCH SIZE OF 74 COMPLETED WOOD THRUSH CLUTCHES BY MONTH FOR 1965–1966

Eggs per clutch	Number of clutches by month for both years			Totals
	May	June	July	
2	0	6	3	9
3	13	14	10	37
4	24	2	0	26
5	2	0	0	2
Totals	39	22	13	74
Average clutch size	3.7	2.8	2.8	3.3

maple. This low success appeared related to the high average nest-height and the early average time of the season for nests in this plant species. In addition, nests at these heights before complete development of foliage, were quite conspicuous, at least to the investigators. Nine of the 10 active nests in red maple were initiated in May and six of the 10 nests were over nine feet above ground level. Although Weaver (in Bent, 1949) states that "there seems to be little choice in selecting the kind of tree, shrub or vine used," Preston and Norris (1947) theorize that "we are so accustomed to thinking of tree-tops as a relatively safe place for birds that it may be difficult to envisage them as a highly dangerous place, only to be used as a last resort." Our data tend to support the latter idea with respect to the sapling understory.

Nest success varied among nest heights between months of the breeding season. The two lower nest-height classes show increasing nest success from May through July, but the two higher nest classes show greater nest success in June than in May or July. The two trends are most pronounced in the extreme height classes, i.e., < 5.5 feet and 16.5–25 feet.

PRODUCTIVITY

Clutch size.—Mean clutch size decreased as the breeding season progressed (Table 5). Four-egg clutches were common in May and absent in July. Average clutch size was determined from 74 completed clutches. Two-egg clutches and many three-egg clutches in June and July were most likely from re-nesting pairs as success was low in May. Only one adult, out of 14 Wood Thrushes captured in late June was a new unbanded bird, compared to 16 new birds of 26 captured (62 per cent) in May and early June, indicating that the breeding population had stabilized, and the June–July nests were not likely built by newly arrived birds.

An effort was made to determine the extent of double nesting among Wood Thrush in the study woodlot. Nine adult Wood Thrushes which were thought to be residents of the woodlot because they were banded during a previous breeding season or because they were caught repeatedly during 1966, were color marked and observed when possible. Only one color marked bird was observed at a nest; this bird, a female banded the previous August, was observed three times at or near a nest which contained five eggs. The nest blew down during the period 7–11 June and the marked bird built another nest nearby on 13 June, from which three birds were fledged between 12–15 July. Brackbill (1958) observing nine color banded pairs, found two broods per year to be the rule near Baltimore, Maryland. Weaver (1939) recorded a second successful nesting for a color marked pair near Ithaca, New York. Eaton (1914) states that the eggs are usually laid from 17–30 May but later sets are frequently found as late at 25 June and 10 July. Forbush (1927) states: "One brood yearly in New England though said to rear two in the west and south." Sprunt and Chamberlain (1949) reporting for South Carolina indicate the interval between the two broods is very brief. One record, for example, makes note of young leaving a nest on 6 June, while one parent was still feeding them and of the other adult carrying nesting material two days later and settling into the completed second nest by 11 June.

Success of eggs and nestlings.—Fifty-two per cent of the 276 Wood Thrush eggs hatched (Table 6). On the basis of the total eggs hatched, 65 per cent fledged. However, on the basis of total eggs laid, only 33 per cent fledged. By considering both ways of calculating success, a more exact estimate can be obtained for nests in which there is only partial success of a clutch but in which the nest is considered successful.

Other workers have reported varying rates of nest success with which our findings are generally in accord. In 29 studies involving 21,951 eggs, fledging success of altricial birds ranged from 22–70 per cent, averaging 46 (Nice, 1957). Weaver (1939) found that of 51 eggs laid in 15 Wood Thrush nests, 33 (65 per cent) produced young, and 22 fledged. This was a survival of 43 per cent of the eggs laid and 66 per cent of the young hatched. Brackbill (1958) observed that of 44 eggs laid in 15 nests, 39 hatched (89 per cent), and 35 young fledged (80 per cent of eggs laid and 90 per cent of the eggs which hatched). Kendeigh (1942) reported that of 14 Wood Thrush eggs laid in 10 successful nests, 79 per cent hatched, while 58 per cent of the eggs which hatched, survived to fledge. Kendeigh further stated that in successful nests 46 per cent of the eggs laid became fledglings, but in successful and unsuccessful nests combined only 29 per cent of the eggs laid developed into fledglings.

TABLE 6

FATE OF WOOD THRUSH EGGS AND NESTLINGS FROM 93 ACTIVE NESTS, 1965–1966

	1965	1966	Total
Active nests	43	50	93
Eggs laid	124	152	276
Mean/Active nest	2.9	3.0	3.0
Eggs hatched	54	88	142
Mean/Active nest	1.3	1.8	1.5
Young fledged	27	65	92
Mean/Active nest	.6	1.3	1.0
Eggs lost			
Infertile or addled	5	3	8 (3)[1]
Predation	63	43	106 (38)
Weather	0	9	9 (3)
Desertion	0	5	5 (2)
Unknown	2	4	6 (2)
Nestlings lost			
Predation	26	13	39 (27)
Weather	0	8	8 (6)
Unknown	1	2	3 (2)

[1] ( ) Per cent.

Reproductive success also may be expressed as the mean number fledged per either active or successful nest. In this study an average of 2.6 young was fledged from 35 successful nests and an average of 1.0 young from 93 active nests (which includes both successful and unsuccessful nests). Regardless of various interactions affecting success, egg and nestling attrition in successful nests is not extensive. Of the 111 eggs produced in 35 successful nests, 92 eggs (83 per cent) hatched and subsequently fledged.

Predation was the largest mortality factor, apparently causing a loss of 38 per cent of the total eggs laid and 27 per cent of the nestlings which hatched. In open nesting songbirds over three-quarters of the losses of eggs and young are due to predation (Lack, 1954).

SUMMARY

A study of the reproductive success of the Wood Thrush in a suburban area was conducted near Newark, Delaware during 1965–1966.

Nesting peaks occurred in the last week of May and in the second week of July. A total of 142 "nesting attempts" was recorded with 93 active nests; 35 (38 per cent) of which were successful. Destruction of 49 nests (58 per cent) was attributed to predators. Inclement weather and desertion caused some nest failures.

In general, the greatest nest success was associated with (a) late season nests

(June and July), with (b) spicebush and black gum vegetation, and with (c) the lower heights of nests above ground level (below 8.5 feet). Low nest success was associated with May nesting, red maple, and heights above nine feet. There was little difference in success between the two vegetational types: upland and lowland.

Arrowwood, black gum, red maple, spicebush, and flowering dogwood were the most commonly used plant species of the 17 used to support active nests.

Mean clutch size decreased from May to July. The average clutch size was 3.3 eggs per nest with clutches ranging from 2–5 eggs. Thirty-three per cent of the total eggs laid, hatched while 65 per cent of the hatched birds survived to leave the nest.

ACKNOWLEDGMENTS

We gratefully acknowledge the support of the University of Delaware Research Foundation and McIntire Stennis funds administered by the Cooperative State Research Service, U. S. Department of Agriculture.

We also sincerely thank Dr. E. P. Catts for aiding in field work and in the presentation of data. Mr. J. T. Linehan rendered many helpful criticisms during the course of the study and generously made available his pertinent unpublished banding data. To him we are indebted. Many students gave freely of their time and enthusiasm during field work; their help was appreciated.

LITERATURE CITED

Bent, A. C. 1949. Life Histories of North American thrushes, kinglets and their allies. U.S. Natl. Mus. Bull., 196:101–123.

Brackbill, H. 1958. Nesting behavior of the Wood Thrush. Wilson Bull., 70:70–89.

Catts, E. P., R. E. Jones and J. R. Longcore. 1966. Trees, woods, urbanization and you. University of Delaware, Agr. Expt. Sta., Circular 3.

Eaton, E. H. 1914. Birds of New York. Univ. State of New York. New York State Museum. Memoir 12, Part II.

Forbush, E. H. 1927. Birds of Massachusetts and other New England States. Commonwealth of Massachusetts. Part III:387–389.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull., 233.

Gleason, H. A. and A. Cronquist. 1963. Manual of vascular plants of Northeastern United States and Canada. Van Nostrand, Princeton, New Jersey.

Holling, C. S. 1961. Principles of insect predation. Ann. Rev. Entomol., 6:163–182.

Kendeigh, S. C. 1942. Analysis of losses in the nesting of birds. J. Wildl. Mgmt., 6:19–26.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

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

Potter, J. K. 1915. Egg and nestling destruction. Cassinia, 19:30–32.

Preston, F. W., and R. T. Norris. 1947. Nesting heights of breeding birds. Ecology, 28:241–273.

Sprunt, A., Jr. and E. B. Chamberlain. 1949. South Carolina bird life. Univ. South Carolina Press, Columbia.

Weaver, F. G. 1939. Studies in the life history of the Wood Thrush. Bird-Banding, 10:16–23.

DEPARTMENT OF ENTOMOLOGY AND APPLIED ECOLOGY, UNIVERSITY OF DELAWARE, NEWARK, DELAWARE, 22 JUNE 1967.

PHYSIOLOGICAL SUSCEPTIBILITY OF ROBINS TO DDT POISONING

L. BARRIE HUNT

LARGE numbers of Robins (*Turdus migratorius*) occupy major portions of their breeding range in the northern United States from March until at least October (Bent, 1949), but published records of Robin deaths attributed to DDT used for Dutch elm disease control are confined mostly to the months of April and May (Barker, 1958; Hickey and Hunt, 1960; Bernard, 1963; Boykins, 1964; Wallace et al., 1964; Wurster et al., 1965). I have previously described how peak Robin mortality on the Madison campus of the University of Wisconsin during late April coincided with maximum availability of DDT-laden earthworms influenced by moderating soil conditions (Hunt, 1968). Such observations suggested that the chronology of DDT poisoning in these birds was extrinsically influenced if not controlled by phenological responses of their toxic food supply, but counter-evidence was also presented indicating that few or no avian deaths were associated with other periods of mild climate and high worm activity. In one of the first reports of bird kills associated with elm (usually *Ulmus americana*) spraying, Blagbrough (1952) expressed the view that birds in spring were especially susceptible to poisoning if their food was highly contaminated and if their body fat, which could store high DDT concentrations, was at a minimum. It would appear that appreciable mortality will occur only when these two conditions are concurrent.

Using measurements taken on both poisoned and normal specimens from Wisconsin as well as comparisons involving data collected by others, I have as my objective in this study the presentation of quantitative support for the following argument: adult male and female Robins show a differential tolerance to DDT, and in at least the males, changes in body weight which occur naturally during the spring season are inversely correlated with changes in susceptibility to this insecticide.

METHODS AND MATERIALS

Most, but by no means all, birds dying on the Madison campus after the elm spraying began were collected; all reasonably fresh specimens were weighed, labeled, and immediately frozen in plastic bags. Most birds were later measured and examined internally, and a representative sample was chosen for chemical analysis on the basis of species, age, sex, condition, collection date, and exposure to insecticide. Of 27 adult Robins analyzed, two represented controls, 21 had known exposure to DDT, and four had known exposure to both DDT and methoxychlor, the latter group being discussed elsewhere (Hunt and Sacho, 1969). From each bird the brain and breast muscle were removed, weighed, oven-dried to constant weight at 49°C, reweighed, and individually frozen in glass jars until analysis. All tissue analyses were made at the Wisconsin Alumni Research Foundation Insecticide Laboratory, with extraction procedures reported by Hunt and Sacho (1969). Residue concentrations of DDT, DDE, and TDE (DDD) were detected by gas chromatography and are reported here in parts per million wet weight.

Since the sample of Wisconsin Robins to be analyzed was restricted by the expense involved, residue figures from other published sources are included for purposes of comparison. Thus trends suggested by the Wisconsin material might be either confirmed or refuted. Ideally, such borrowed data should involve specimens comparable to those analyzed from Wisconsin—adult Robins of known sex presumed to have died from DDT poisoning during April or May in a Dutch elm disease-control environment. Birds matching these criteria were collected in Michigan in 1959–60 (Bernard, 1963), in Michigan in 1962–63 (Boykins, 1964; and Wallace, et al., 1964), and in New Hampshire in 1963 (Wurster, et al., 1965). The New Hampshire specimens, although not oven-dried, were analyzed by the same Wisconsin laboratory using identical procedures, while residues in all Michigan birds were determined by the Schechter-Haller colorimetric method which is apparently quantitative for DDT and TDE but not DDE (Stickel, et al., 1966). Because differences in drying and analytical procedures may have affected the retention or detection of the original insecticide content, I will use these additional data to emphasize trends and differences within individual studies rather than to stress quantitative comparisons between studies.

Body weights of apparently normal, adult Robins were obtained at my banding station in Kenosha, Wisconsin, during 1964–66. Each bird was color-banded so that its presence and nesting activities could be followed through the breeding season. Additional weights for Wisconsin Robins banded in 1963-66 were provided by E. W. Peartree of Oconomowoc, Wisconsin. Based upon my measurements and internal sexing of 170 male and 85 female Robin specimens, I chose to omit Mr. Peartree's unsexed birds with wing lengths of 124–127 mm; larger birds I called males and smaller ones females.

RESULTS AND DISCUSSION

The problem of providing proof that Robins were poisoned by DDT residues has been considered by Stickel et al. (1966) and by Hunt (1968) with only a resumé of evidence presented here. Elms on the Madison campus were first sprayed with 22.5 lb DDT/acre in 1959 and at half that dose in 1960 and 1961. The die-off of songbirds following the initial application was considerable (Hickey and Hunt, 1960), although no dying birds had attracted attention the previous year nor were specimens being reported from adjacent unsprayed sites. A single campus tally of 15 dead and dying Robins on 23 April 1959 indicated a highly lethal environment. Insecticide concentrations in the brains of 21 campus Robins were similar to those from other DDT-contaminated areas and from experimentally poisoned birds, but were 100 times the average concentration in two Wisconsin Robins from unsprayed habitat. Tissue residues in birds found dead did not differ significantly from those in specimens found with tremors thought to be caused by DDT. Absolute assurance that certain concentrations of specific chemicals were lethal to

TABLE 1

ADULT ROBIN MORTALITY ON THE DDT-SPRAYED MADISON CAMPUS. Shown as a percentage of the season total

Specimens Sampled	Sample Size	April 1–15	April 16–30	May 1–15	May 16–31	June 1–30
All Robins*	232	5	52	30	12	2
Males	119	9	60	20	10	1
Females	52	6	46	35	14	0

* Includes unsexed birds not examined internally.

individual animals is beyond the realm of expectation, but an objective evaluation of the above findings will likely lead to the conclusion that most adult Robins picked up on the Madison campus during spring of 1959–61 were victims of DDT.

Seasonal pattern of mortality and residues.—From 1959 when DDT was first used on Madison campus elms until 1962 when methoxychlor was substituted in an effort to reduce songbird mortality, more than 340 apparent-DDT victims were picked up. Robins, which formed the bulk of this collection, began returning to nesting areas during late March with males preceding females by one or two weeks. The earliest tremoring Robin was seen on 6 April and the latest on 20 June, but the majority were found dead or dying during late April (Table 1). The pattern was repeated each spring with 51, 59, and 47 per cent of the season's total Robin kill appearing during the same two-week period. This expression of Robin mortality should not be confused with *mortality rate* as derived from life-table computations. Treatment of these data by the latter method appeared unjustified since considerable recruitment to the initial population occurred during the spring season. As evidence of such ingress, one closely watched territory yielded a succession of seven dead. adult Robins before becoming totally vacated. While the rate of mortality may have remained consistently high through May, the magnitude noticeably declined with the approach of summer.

Other trends became apparent when the results of tissue analyses were also separated on a seasonal basis (Table 2). In the sequence from early April through May, there were considerable increases among individual and total insecticide residues in both brain and breast muscle and in breast muscle fat content as the season progressed. Only the per cent of fat in the brain failed to follow the trend. The early-April and late-April measurements did not differ significantly ($P > 0.05$), but total brain residues were significantly higher ($P < 0.05$) in May than in late April, and breast fat in May was significantly higher than in early April. When the pooled April

TABLE 2

SEASONAL TISSUE DIFFERENCES IN ROBINS FOUND DEAD AND DYING ON THE MADISON CAMPUS

Tissue Component	April 1–15	April 16–30	May 1–31
	x̄ ± SE (N = 6)	x̄ ± SE (N = 8)	x̄ ± SE (N = 7)
Brain			
Fat (per cent)	6.7 ± 0.4	6.1 ± 0.1	6.9 ± 0.3
Residues (ppm)			
DDT	5.0 ± 1.3	6.3 ± 1.0	9.1 ± 2.4
DDE	27.9 ± 6.7	33.1 ± 3.9	63.3 ± 9.4
TDE	38.2 ± 2.6	45.1 ± 6.5	50.7 ± 9.5
Total	71.1 ± 7.4	84.5 ± 8.0	123.1 ± 11.7
Breast Muscle			
Fat (per cent)	1.2 ± 0.2	1.8 ± 0.3	2.1 ± 0.3
Residues (ppm)			
DDT	0.9 ± 0.2	3.0 ± 1.5	4.0 ± 1.4
DDE	35.8 ± 9.1	57.8 ± 8.2	133.1 ± 17.0
TDE	63.3 ± 9.5	125.8 ± 45.7	184.6 ± 45.8
Total	100.0 ± 15.7	186.5 ± 53.9	321.7 ± 54.0

data were compared with May data, differences in the total insecticide residues in both brain and breast muscle were highly significant ($P < 0.01$). It is thus apparent that birds collected later in spring contained higher fat reserves and tolerated higher tissue levels of poison before succumbing, but it is not obvious whether these increases were due to actual seasonal changes or rather to changes relating to the sex ratio of specimens as the weeks passed.

Analyses of male and female Robins.—The disproportionately high number of males occurring in my collection (Table 1), as well as in other DDT studies, suggested the tendency for excess males to repopulate rapidly vacated territories where a breeding population had been depleted (see discussions in Stewart and Aldrich, 1951; Hensley and Cope, 1951), but it might also indicate a greater susceptibility among males to DDT poisoning. Similarly the lag in female mortality could be the result of later arrival in the contaminated environment, or it could point to physiological differences in the reproductive roles of the two sexes resulting in unique stresses conducive to insecticide poisoning.

The tissue analyses for Wisconsin specimens, along with residue data from sources cited earlier were grouped according to sex (Table 3). In all seven comparisons, the concentrations in the females exceeded those in the males

TABLE 3

TOTAL DDT-COMPLEX RESIDUES IN ROBINS SUSPECTED OF DYING FROM DDT. Shown in parts per million wet weight.

Tissue Where Studied	DDT Complex	Males Mean ± SE (N)	Females Mean ± SE (N)
Brain			
Michigan-1963	DDT-TDE	79.5 ± 6.1 (25)	110.9 ± 17.7 (11)*
Michigan-1964	DDT-TDE	96.5 ± 9.6 (23)	120.5 ± 8.4 (19)
New Hampshire	DDT-TDE-DDE	119.4 ± 16.7 (25)	169.7 ± 27.3 (9)
Wisconsin	DDT-TDE-DDE	81.0 ± 5.1 (14)	118.6 ± 15.1 (7)**
Breast Muscle			
Michigan-1963	DDT-TDE	108.3 ± 12.6 (21)	120.8 ± 17.0 (10)
New Hampshire	DDT-TDE-DDE	96.5 ± 11.2 (25)	194.5 ± 36.0 (9)**
Wisconsin	DDT-TDE-DDE	149.5 ± 26.0 (14)	321.6 ± 68.2 (7)**

* Difference is significant ($P < 0.05$).
** Difference is highly significant ($P < 0.01$).

although only four comparisons were statistically significant. Wurster et al. (1965) did find significant brain differences in their New Hampshire birds when two June specimens were included in the tests. On the other hand, when Bernard (1963) limited his comparisons in Michigan to tremoring birds only, he found higher breast residues among males, but the differences were not significant. From insecticide tests on penned Ring-necked Pheasants (*Phasianus colchicus*), both Genelly and Rudd (1956) and Azevedo, Hunt, and Woods (1965) found males to be more vulnerable than females to DDT in the diet.

Comparisons of fat content in tissues submitted for insecticide analysis help to shed some light on possible reasons for higher DDT tolerance among the females (Table 4). While brain lipids from New Hampshire birds did not differ significantly, fat content in the three remaining comparisons was significantly greater among females. Since fats serve as reservoirs where insecticides may temporarily accumulate, even seemingly insignificant changes in the lipid balance of various tissues might have a direct bearing on the immediate fate of ingested toxins. Furthermore, the following studies revealed that stored poisons could later be released when fats are metabolized to meet energy demands. A rise in the DDT level of body tissues during periods of stress was shown to be lethal in starvation experiments with rats by Dale, Gaines, and Hayes (1962), with House Sparrows (*Passer domesticus*) by Bernard (1963), and with American Woodcock (*Philohela minor*) by Stickel et al. (1965). Although no DDT deaths were noted, Mussehl and Finley (1967) reported that residue-laden, fatty tissues in male Blue Grouse (*Den-*

TABLE 4

FAT CONTENT IN MALE AND FEMALE ROBINS EXPOSED TO DDT. Shown as a per cent of tissue wet weight.

Tissue Where Studied	Males Mean ± SE (N)	Females Mean ± SE (N)
Brain		
New Hampshire	5.4 ± 0.3 (25)	4.8 ± 0.5 (9)
Wisconsin	6.3 ± 0.2 (14)	7.0 ± 0.3 (7)*
Breast Muscle		
New Hampshire	0.6 ± 0.0 (25)	1.1 ± 0.2 (9)**
Wisconsin	1.4 ± 0.1 (14)	2.3 ± 0.4 (7)**

* Difference is significant ($P < 0.05$).
** Difference is highly significant ($P < 0.01$).

dragapus obscurus) were heaviest early in the breeding season but declined at the breeding peak, while lipid content in females was highest at peak laying with rapid declines during incubation and hatching. Breitenbach and Meyer (1959) presented evidence that fat reserves in hen pheasants became so depleted during incubation and brooding that these females would be highly vulnerable to stress factors; previously sublethal concentrations of stored DDT could well impose such stress late in the breeding cycle.

Seasonal changes in Robin tissues.—When male Robins from the several studies were separated according to collection date (Table 5), there was a tendency for May victims to contain higher insecticide residues, although the

TABLE 5

TOTAL DDT-COMPLEX RESIDUES (PPM WET WEIGHT) IN MALE ROBIN VICTIMS.

Tissue Where Studied	April Mean ± SE	(N)	May Mean ± SE	(N)
Brain				
Michigan-1963	75.5 ± 9.1	(13)	83.8 ± 8.3	(12)
Michigan-1964	98.8 ± 17.5	(12)	94.0 ± 7.3	(11)
New Hampshire	90.5 ± 7.0	(12)	146.1 ± 30.2	(13)
Wisconsin	77.4 ± 5.1	(12)	102.6 ± 8.6	(2)
Breast Muscle				
Michigan-1963	105.1 ± 21.2	(9)	110.8 ± 15.9	(12)
New Hampshire	68.0 ± 9.2	(12)	122.9 ± 17.1	(13)*
Wisconsin	117.0 ± 11.7	(12)	344.1 ± 91.5	(2)**

* Significant difference ($P < 0.05$).
** Highly significant difference ($P < 0.01$).

TABLE 6

TOTAL DDT-COMPLEX RESIDUES (PPM WET WEIGHT) IN FEMALE ROBIN VICTIMS.

Tissue Where Studied	April Mean ± SE	(N)	May Mean ± SE	(N)
Brain				
Michigan-1963	140.0 ± 35.7	(5)	86.7 ± 6.6	(6)
Michigan-1964	117.0 ± 16.2	(9)	123.7 ± 7.2	(10)
New Hampshire	109	(1)	177.3 ± 29.7	(8)
Wisconsin	86.9 ± 33.4	(2)	131.4 ± 14.9	(5)
Breast Muscle				
Michigan-1963	130.0 ± 21.6	(5)	111.6 ± 28.1	(5)
New Hampshire	38.1	(1)	214.1 ± 34.3	(8)
Wisconsin	343.8 ± 211.6	(2)	312.7 ± 72.2	(5)

results were far from conclusive. The probability of significant brain differences between most monthly pairs was reduced by the considerable variability in both periods, and in the second Michigan group even the general trend was reversed. Changes in male breast residues were more convincing, especially with the New Hampshire results approaching a highly significant difference. Among the females represented in Table 6, there was a high degree of variability within most subgroups; neither common trends nor significant differences were present. It appeared that residue levels from different females may have varied with the particular stage and metabolic demands of the individual nesting cycles rather than exhibiting seasonal tendencies as such.

These seasonal comparisons were based upon the premise that some time after their arrival on northern breeding grounds, resident Robins would gradually accumulate fat reserves enabling them to store greater toxicant concentrations before the dosage became lethal. This assumption was not entirely borne out by seasonal comparisons of the fat content in analyzed tissues of either males or females, but there was reason to suspect that tissue lipids from DDT victims might be a poor index to normal body fat prior to the onset of poisoning symptoms. First, when Wisconsin Robins found in tremors and dispatched were compared with those already dead, tissue insecticides did not differ significantly, but the dead birds had significantly lower brain fat and also lower breast muscle fat which approached significance. Such findings suggested that fat reserves were being metabolized as energy demands increased during periods of violent terminal tremors. Second, for 170 Robins, body weights at death for each sex were remarkably constant with 118 males averaging 69.4 ± 0.4 g and 52 females averaging 72.8 ± 0.8 g.

TABLE 7

SPRING BODY WEIGHTS IN WILD-TRAPPED, BANDED ROBINS.
Shown in grams ± standard error and (sample size).

Period	Males Kenosha	Males Oconomowoc	Females Kenosha
March 16–31	89.3 ± 2.0 (13)	—	—
April 1–15	82.5 ± 2.0 (5)	85.3 ± 2.6 (6)	82.5 ± 2.1 (5)
April 16–30	78.6 ± 2.3 (7)	75.0 ± 1.6 (8)	88.9 ± 3.1 (9)
May 1–15	82.8 ± 3.7 (3)	77.6 ± 1.5 (2)	86.1 ± 3.6 (3)
May 16–31	78.6 ± 1.3 (9)	79.1 ± 1.7 (4)	85.3 ± 2.2 (7)
June 1–30	80.1 ± 1.3 (14)	—	78.7 ± 2.0 (4)

These differences were highly significant, but within each sex there were no significant differences between any two intervals in April or May. All 21 analyzed Robins and 94 per cent of the 223 Robin specimens examined were assigned to fat class "none," the rest being judged as having "little" fat according to the criteria of Wolfson (1954). Together, these observations point to a situation where a series of birds, regardless of sex or collection date, underwent such a reduction in fat reserves prior to death that all may have approached the homeostatic, fat-free, body weight described by Odum, Rogers, and Hicks (1964), even though these authors excluded from their remarks severely stressed birds. If changes in DDT susceptibility were to be correlated with changes in fat deposits, then clues to this relationship should logically be taken from apparently healthy Robins showing no poisoning symptoms.

Body weights of normal Robins.—Robin weights from both Kenosha and Oconomowoc are shown in Table 7 since the distance of some 50 air miles separating the two Wisconsin stations was not considered sufficient to interfere with seasonal comparisons. Peartree's Oconomowoc data included no repeat weights from the same year, and the weights of females were too few and unequally distributed to be useful here. Kenosha totals did include repeat weights but only those taken more than 48 hours after the previous capture, since Rogers and Odum (1966) attributed rapid weight losses in several species to stress from handling. Among Kenosha males, the high mean weight for late-March birds did not differ significantly from that for the first half of April, but taken in pairs, differences between March males and males weighed during each of the entire later months were highly significant. From Oconomowoc, the heaviest males were trapped in early April, and the weight difference between these and the late-April males was also highly significant.

For females in Table 7, the early-April mean weight was identical to that

TABLE 8

INITIAL AND REPEAT WEIGHTS OF MALE ROBINS TRAPPED IN KENOSHA.

Year Bird	March 16–31	April 1–15	April 16–30	May 1–15	May 16–31	June 1–30
1964						
*	80.7		72.4			
2	78.1		69.9			
3			81.0		81.6	83.1
1965						
4		78.4	88.1		84.1;79.4	
5		76.9				82.4
6*			80.4		83.1	
1966						
7	98.6	88.5				
8	91.7	84.4;84.4		89.2		

* Banded but not weighed in 1963.

of Kenosha males, but there followed a sizable weight increase in late April during the period of greatest egg laying on a Kenosha study area in both 1964 and 1965 (no census in 1966). This same relationship between peak weight and peak egg production was also detected in hen pheasants (Breitenbach and Meyer, 1959). From early to late April, when mean weights of two male populations declined 3.9 and 10.3 g, the mean weight for females increased 6.4 g. A portion of this female change would result from the process of ovulation, for a fully formed, 5.1-g egg found in the lower oviduct of one DDT specimen added appreciably to the total weight of that individual. Nevertheless, it is unlikely that all late-April females were ready to lay when weighed, and an important part of the additional weight must be explained as increases in adipose deposits. Due in part to small sample size, the only statistically significant weight difference in Kenosha females was between pooled, monthly samples representing May and June.

It could be argued that weight differences shown in Table 7 represented different populations rather than seasonal changes within a population, even though many of the color-banded, Kenosha birds were seen repeatedly during the nesting season. To insure that only a post-migratory, resident population was involved, individual males that were weighed during more than one spring period were tabulated (Table 8); again, repeat weights after less than 48 hours were omitted. Of 21 usable weights for eight different individuals, only one bird (4) and its four weights deviated from the previously established trend of appreciable April declines from March highs followed by partial recovery in May and June. It was possible that hourly weight changes could have influenced apparent seasonal patterns, because Nice (1937) noted daily fluctuations of less than 5 per cent with afternoon increases in the Song Sparrow (*Melospiza melodia*), but only the June weight for Robin 3 or the May weight for Robin 6 could have reflected diurnal rather than seasonal gains. All others were either reweighed during the same half-day interval or would have demonstrated improbable morning to afternoon losses. Nesting females were rarely recaptured, and the few repeat weights were trendless.

Earlier studies of bird weights and weight changes by Baldwin and Kendeigh (1938) involving over 13,500 measurements showed a pattern of annual rhythm showing a weight decline from spring to a trough in July probably caused in part by energy requirements for reproduction. These data included 28 adult Robin weights scattered over a span of eight months, and Nice (1938) reported 39 Robin weights by sex and season, pointing out the confusion caused by high and low figures during the nesting season. Wolfson (1954) warned that mean weights can obscure individual differences or changes having real meaning, and Odum (1960) stressed the significance of lipid reserves in relation to migration for, as he explained, fats are both the most variable and the most economical form of stored energy, giving useful indices to "the metabolic status of populations." Odum's research and that of King et al. (1963) was primarily concerned with pre-migratory fat accumulation, but these writers commented on the selective advantage of possessing fat reserves at the termination of migration that would permit survival during times of adverse weather or food scarcity.

Certainly, Robins nesting in the northern United States could often benefit from an adaptive store of reserve energy. For example, I observed that male Robins first appearing on my Kenosha study area on 14 March were exposed to snow showers on 25, 26, and 29 March; a Robin was not seen feeding on earthworms before 3 April. That same year two males trapped on 18 and 19 March had weight losses of 10 per cent when retrapped on 16 April (included in Table 8). The data I have presented indicate that apparently normal, male Robins were undergoing weight losses and reached their lowest body weight of the season during the same two-week period that peak male deaths associated with DDT exposure occurred in three earlier years. The frequency of dying males increased as weight representing stored fat decreased, and mortality decreased as weight began to increase. With the increasing weight in normal males went increasing concentrations of insecticide residues in Robin tissues until some higher tolerance level was apparently exceeded. Among females the relationships involving date, tissue residues, and body weight were apparently complicated by the particular stage of nesting activity, but greater fat reserves probably allowed them to accumulate and tolerate higher insecticide concentrations and to survive later than males in the contaminated nesting environment.

SUMMARY

Following elm spraying on the Madison campus of the University of Wisconsin in 1959–61, at least 232 adult Robins apparently died of DDT poisoning between the extreme dates of 6 April and 20 June with peak mortality occurring each year during late April. Males died earlier and in greater numbers than females, and male specimens from several similar studies contained lower insecticide residues and tissue fat in both brain and breast muscle. Male specimens tended to die with lower tissue toxicants in April than in May, although the percentage of brain and muscle fat was similar in male victims of both months. Most dead and dying Robins contained almost no subcutaneous body fat, males averaging 69.4 g and females 72.8 g. Normal wild males banded soon after arrival in late March averaged 89.3 g, reached a low weight in late April, and increased slightly by June, while female weights reached a mean of 88.9 g during peak egg laying in late April before declining gradually. The seasonal loss of fat reserves in male Robins appeared to increase their susceptibility to DDT poisoning with fatter females showing greater tolerance.

ACKNOWLEDGMENTS

I wish to express my thanks to J. J. Hickey for his supervision of the research and constructive criticism of the manuscript and to L. B. Keith for his comments. I am also grateful to my wife, Shirley, for helping with trapping and weighing operations, and to E. W. Peartree for offering me his banding data. Original residue analysis reports for New Hampshire Robins were received through the courtesy of C. F. Wurster, Jr. Many fellow students assisted me in collecting campus specimens. This study was partially supported by the Bureau of Sport Fisheries and Wildlife, Fish and Wildlife Service, U.S. Department of the Interior, and by the Research Committee of the Graduate School, University of Wisconsin, with funds provided by the Wisconsin Alumni Research Foundation.

LITERATURE CITED

Azevedo, J. A., Jr., E. G. Hunt, and L. A. Woods, Jr. 1965. Physiological effects of DDT on pheasants. California Fish and Game, 51:276–293.

Baldwin, S. P., and S. C. Kendeigh. 1938. Variations in the weight of birds. Auk. 55:416–467.

Barker, R. J. 1958. Notes on some ecological effects of DDT sprayed on elms. J. Wildl. Mgmt., 22:269–274.

Bent, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull., 196.

Bernard, R. F. 1963. Studies on the effects of DDT on birds. Michigan State Univ., Mus. Publ., Biol. Series, 2(3):155–192.

Blagbrough, H. P. 1952. Reducing wildlife hazards in Dutch elm disease control. J. Forestry, 50:468–469.

Boykins, E. A. 1964. DDT residues in the food chains of birds. Unpubl. Ph.D. thesis, Michigan State Univ., East Lansing.

Breitenbach, R. P., and R. K. Meyer. 1959. Effect of incubation and brooding on fat, visceral weights and body weight of the hen pheasant (*Phasianus colchicus*). Poultry Sci., 38:1014–1026.

Dale, W. E., T. B. Gaines, and W. J. Hayes, Jr. 1962. Storage and excretion of DDT in starved rats. Toxicol. and Appl. Pharmacol., 4:89–106.

Genelly, R. E., and R. L. Rudd. 1956. Chronic toxicity of DDT, toxaphene, and dieldrin to Ring-necked Pheasants. California Fish and Game, 42:5–14.

Hensley, M. M., and J .B. Cope. 1951. Further data on removal and repopulation of the breeding birds in a spruce-fir forest community. Auk, 68:483–493.

Hickey, J. J., and L. B. Hunt. 1960. Initial songbird mortality following a Dutch elm disease control program. J. Wildl. Mgmt., 24:259–265.

Hunt, L. B. 1968. Songbirds and insecticides in a suburban elm environment. Ph.D. thesis, Univ. Wisconsin.

Hunt, L. B., and R. J. Sacho. 1969. Response of Robins to DDT and methoxychlor. J. Wildl. Mgmt., 33:336–345.

King, J. R., S. Barker, and D. S. Farner. 1963. A comparison of energy reserves during the autumnal and vernal migratory periods in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii.* Ecology, 44:513–521.

Mussehl, T. W., and R. B. Finley, Jr. 1967. Residues of DDT in forest grouse following spruce budworm spraying. J. Wildl. Mgmt., 31:270–287.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linnaean Soc. New York, 4:1–247.

Nice, M. M. 1938. The biological significance of bird weights. Bird-Banding, 9:1–11.

Odum, E. P. 1960. Lipid deposition in nocturnal migrant birds. Proc. 12th Intern. Ornithol. Congr., 563–576.

Odum, E. P., D. T. Rogers, Jr., and D. L. Hicks. 1964. Homeostasis of the nonfat components of migrating birds. Science, 143:1037–1039.

Rogers, D. T., Jr., and E. P. Odum. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. Wilson Bull., 78: 415–433.

Stewart, R. E., and J. W. Aldrich. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. Auk, 68:471–482.

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.

Stickel, W. H., W. E. Dodge, W. G. Sheldon, J. B. DeWitt, and L. F. Stickel. 1965. Body condition and response to pesticides in woodcocks. J. Wildl. Mgmt., 29:147–155.

Wallace, G. J., A. G. Etter, and D. R. Osborne. 1964. Spring mortality of birds following fall spraying of elms. Massachusetts Audubon, 48:116–120.

Wolfson, A. 1954. Weight and fat deposition in relation to spring migration in transient White-throated Sparrows. Auk, 71:413–434.

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.

DEPARTMENT OF WILDLIFE ECOLOGY, UNIVERSITY OF WISCONSIN, MADISON AND DEPARTMENT OF BIOLOGY, UNIVERSITY OF WISCONSIN CENTER, KENOSHA (PRESENT ADDRESS: DEPARTMENT OF ZOOLOGY, EASTERN ILLINOIS UNIVERSITY, CHARLESTON, ILLINOIS 61920), 13 MAY 1968

ANNUAL ACTIVITY PATTERNS OF CAGED NON-MIGRATORY WHITE-CROWNED SPARROWS

Robert W. Smith, Irene L. Brown, and L. Richard Mewaldt

Night restlessness (locomotor activity) in caged night-migratory birds during the season of migration is generally equated with migratory restlessness (*Zugunruhe*) while caged non-migratory birds usually exhibit no such night restlessness (Farner, 1955). None was found in the House Sparrow (*Passer domesticus*) (Eyster, 1954) or the Clark Nutcracker (*Nucifraga columbiana*) (Farner and Mewaldt, 1953). On the other hand, Farner, King, and Wilson (1957) report vernal night restlessness in a non-migratory race of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). They state, however, that such activity was of relatively low intensity (13 per cent of total activity) compared to substantial night activity (51–69 per cent of total activity) in three migratory taxa of the same genus (*Z. leucophrys gambelii, Z. atricapilla,* and *Z. querula*). Mewaldt, Kibby, and Morton (1968) found that nocturnal activity, as a per cent of total activity, was lower in the non-migratory *Z. l. nuttalli* than in the closely related, but migratory, *pugetensis.*

Our objective is to characterize the relatively weak, but none-the-less present, night activity of this non-migratory race (*nuttalli*) of *Zonotrichia.* We have examined the circadian activity patterns and the orientation of day and night activity of several individuals over a period of more than a year. If night restlessness may be equated with an expression of migratory behavior in migratory birds, what is the significance of night restlessness in this non-migratory taxon?

MATERIALS AND METHODS

1. *Experimental Birds.*—Six immature male White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) were captured in June 1961 with Japanese mist nets near the mouth of the Pajaro River, Monterey County, California. From capture until this study began in December 1961 they were kept in Hendryx flight cages, in an outdoor aviary, on the roof of the Natural Sciences Building, San Jose State College, San Jose, California. During this time prior to our study they were used in a crown plucking experiment reported by Morton (1962). In addition, four adults which had been captured, banded, and released in June 1961 were recaptured in the same area in December 1961 and used for this investigation. Three were males; bird 843 was a female. Birds captured as immatures will consistently be referred to as immatures even though by the end of the experiment they were in adult plumage and over two years old.

Ground dry commercial dog food and water were provided ad libitum, and supplemented weekly with chick scratch, red millet, grit, and fresh lettuce. Once a week the birds were weighed and examined for molt. Molt readings were taken by examining the retrices, body, crown, dorsal wing coverts, and remiges. Each bird was then rated as having no molt, or to be in light, medium, or heavy molt. These designations were then used in the following formula to provide a mean numerical index to the intensity of molt:

$$\text{Molt Index} = 10 \times \frac{(\text{no. light} \times 1) + (\text{no. medium} \times 2) + (\text{no. heavy} \times 3)}{\text{total number of birds}}$$

2. *Activity cages and recording apparatus.*—Two (864, 879) of the 10 birds were kept in reserve in a large walk-in cage. The others were placed in one of two kinds of cages we used in studying activity patterns. All cages were outdoors; however, the small cages were sheltered from wind and rain under an overhanging roof which permitted these birds to see a small portion of the sky.

Four birds (Adults, 843, 875; Immatures, 867, 869) were placed individually in small cages (41 × 22 × 26 cm) with a centrally located activity-sensitive perch, adapted from the design of Farner and Mewaldt (1953). Each time the bird depressed the centrally located perch, which extended across the width of the cage (22 cm), a microswitch was closed and an impulse sent to a recorder. The activity was monitored on four channels of a remotely located 20-pen, Esterline-Angus event recorder.

Four birds (Adults, 845, 850; Immatures, 840, 866) were placed individually in activity-orientation cages of the type used by Mewaldt and Rose (1960) and by Mewaldt, Morton, and Brown (1964). These circular cages were 94 cm in diameter and 15 cm high. A masonite screen 58 cm high and 152 cm in diameter surrounding each cage provided a homogenous circular horizon and screened off most of the local environment. However, the birds could see the top of a nearby tree and a small portion of the surface of the roof through the hardware cloth floor of the cage. Each cage had a central circular perch attached to the circular foodcup. Around the periphery of the cage were eight activity-sensitive perches each occupying just under 45 degrees of the 360 degree circle. For example, the activity in an easterly direction represents activity from 68° to 112° and was recorded on the appropriate channel on the Esterline-Angus tape. Activity on the four sets of eight perches was monitored by two remotely located 20-pen, Esterline-Angus recorders.

Continuous 24-hour activity recordings for an entire year were begun on the eight birds (four in activity cages and four in activity-orientation cages) in early December 1961. The birds were occasionally switched among the four single-perch activity cages to check for differences in the characteristics of perch-microswitch assemblies. No significant differences were detected. Although the four circular activity-orientation cages were also nearly identical the birds were occasionally switched from one cage to another to minimize the effects of any minor differences among the cages or the possibility of preference for or fixation on a particular perch.

3. *Analysis of data.*—Tapes in the Esterline-Angus recorders were run at three inches per hour. When a bird was very active, the ink marks ran together and the actual number of perch registrations could not be determined. For such times, each two-minute interval filled with pen marks was counted as fifteen perch registrations. This allowed a maximum count of 450 per hour. Experience with faster moving tapes, with direct observations, and with digital print-out recorders established that fifteen registrations for a two-minute interval was a conservative estimate. This interpretation appeared not to affect the circadian patterns of activity except to reduce the amplitude of peak activity periods.

Because we recorded approximately 111,000 bird-hours during the twenty months of the investigation on up to 36 channels simultaneously it was not practical to make actual counts of all data obtained. Since the night activity was judged to be of greater interest, all night activity for the first 12 months was analyzed. Daytime activity was usually heavy and in the activity-orientation cages tended to be random, making data reduction more time consuming and, most likely, less rewarding. Therefore, day activity was sampled by counting perch registrations per hour only one day each week for each bird. Wednesday was chosen because it was well removed from the weekly disturbance of weighing done on Fridays or Saturdays. If there happened to be undue disturbances or recording troubles on a Wednesday, either Tuesday or Thursday was substituted as the "typical day" of the week.

For the period December 1961 through November 1962 circadian activity patterns were calculated for four birds. These consisted of one adult and one immature in the activity cages and for one in each age class in the activity-orientation cages. Data for these patterns by months consisted of the arithmetic means of each hour's locomotor activity for each of the four or five Wednesdays of each month.

In December 1962 we transferred the birds in the four activity-orientation cages to individual single-perch activity cages. These were placed next to the cages of the four birds that had been in the single-perch cages since December of 1961. We continued to monitor the circadian activity patterns of all 8 birds until the end of July 1963. Beginning in December 1962 locomotor activity of each of the eight birds was accumulated hourly on digital print-out recorders (Elmeg). During periods of intense activity, hourly counts of perch registrations on the Elmeg recorders exceeded the 450 arbitrary maximum on the Esterline-Angus recorders running at three inches per hour. We have attempted to equate graphically (Fig. 4) the quantitative aspects of locomotor activity monitored by the impulse markers (Esterline-Angus) and impulse counters (Elmeg).

Data from the eight peripheral perches of each activity-orientation cage were analyzed according to the method of Mewaldt, Morton, and Brown (1964). The mean azimuth is expressed in degrees from north. North equals 0°, east equals 90°, south equals 180°, and west equals 270°. These azimuths are presented plus or minus the angular deviation(s) in degrees, calculated according to Batschelet (1965) where $s = \sqrt{2(1\text{-}r)}$ in radians and $s = 57.296\ \sqrt{2(1\text{-}r)}$ in degrees. ("Vector value" in the 1964 paper of Mewaldt, Morton, and Brown is equal to 100r.) Batschlet's "s" for circular distributions is roughly analogous to the standard deviation of a linear distribution.

We tested these circular distributions for randomness with an approximate test which we devised and which is independent of the total number of perch registrations in each distribution. We agree with Hamilton (1966) that the number of perch registrations is not the number of independent choices and thus should not be used as "N" in statistical determinations. Our test is similar in principle to that of Emlen (1967*a* and *b*) but much simplified. By taking the algebraic sums of the frequencies of the perch registrations in opposing directions starting with the direction with maximum frequency, we establish a situation where the theoretical line for randomness has both zero slope and zero origin. For the circular normal distribution the theoretical line for orientation is essentially a straight line with slope and origin significantly greater than zero. (In a badly skewed distribution only the origin exceeds zero.) For each distribution tested we calculated the slope and origin of the line described by the 4 points resulting from the summing of opposing directional frequencies. Using the method of Simpson, Roe, and Lewontin (1960:226) we tested for orientation by testing whether zero fell outside the 95 per cent confidence interval of either the slope or the origin.

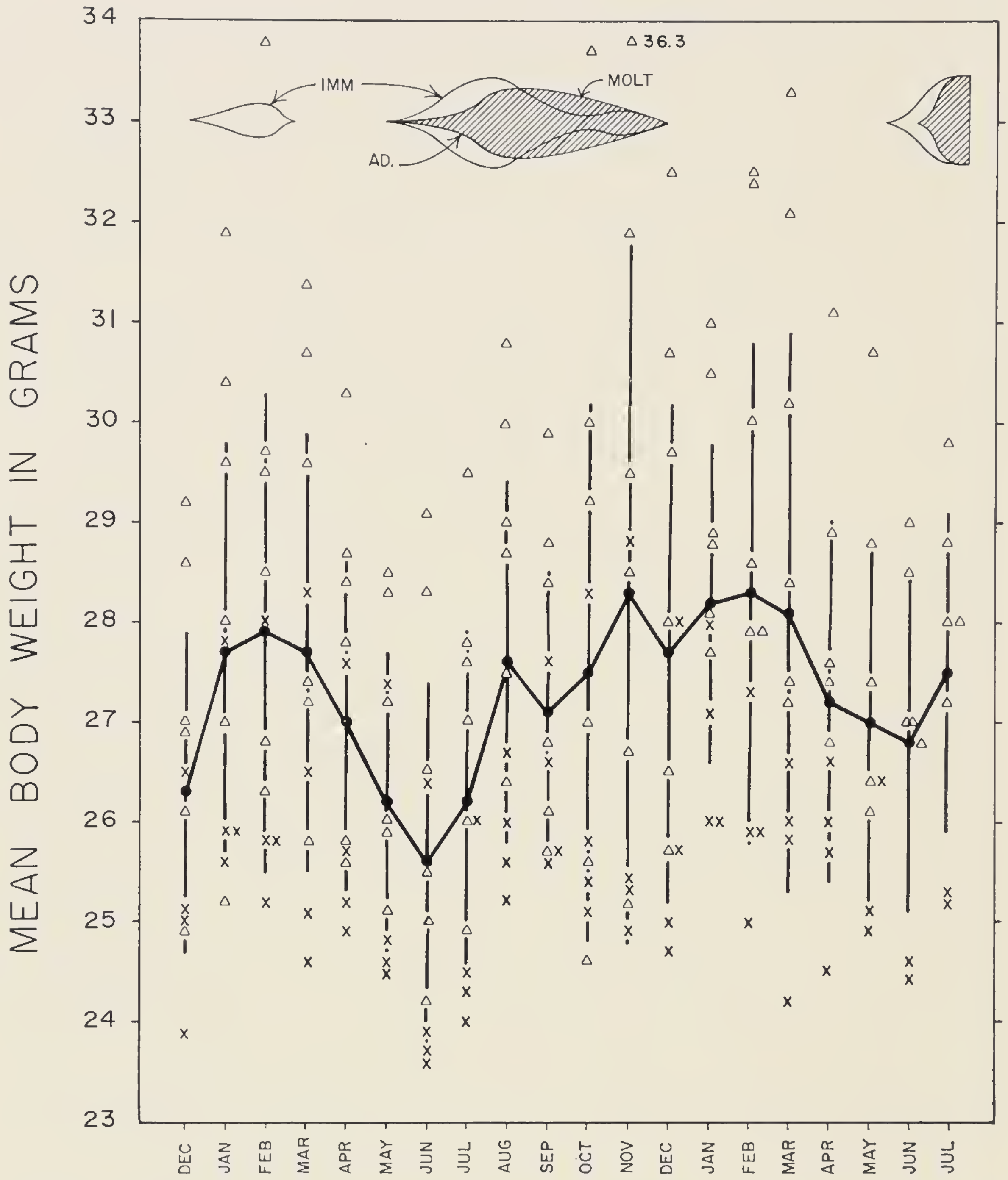


FIG. 1. Individual monthly mean body weights of four adults (x's) and six immature (Δ's) *Z. l. nuttalli*, December 1961 through July 1963. The large dark circles represent the combined means and the lines the standard deviations. Weekly means of body molt indices are represented graphically at the top of the figure.

BODY WEIGHT

Quite unexpectedly we found that the body weight of birds removed from their habitats as adults was consistently lower than that of those removed as immature birds (Fig. 1). This difference was not significant in individual months (e.g. $t = 1.706$, $d.f. = 8$ for March 1962, one of the times of greatest variance). However, the 52 week mean weights of adults and immatures were significantly (barely) different at the 5 per cent level ($t = 2.3$, $d.f. = 8$). Data from the papers of Weise (1956), Odum and Perkinson (1951), and Blanchard (1941) and extensive data from our laboratory (including Mewaldt, Kibby, and Morton, 1968) indicate that male *Zonotrichia* are slightly larger than female *Zonotrichia.* The adult group consisted of three males and one female whereas the immature group consisted of six males. The lower weight of the single female in the adult group accounts for some of the low weights in the adult group. Although the rest of the differences probably represent a vagary of sampling, the consistently higher body weights of the immatures might suggest a favorable energy balance in these individuals.

Seasonal fluctuations were similar in the two groups; therefore, we have plotted (Fig. 1) the combined means. For both groups, highest weights were attained during the winter months and lowest weights during the spring and early summer. Similar seasonal fluctuations in body weight have been demonstrated for other species of birds (Nice, 1937; Baldwin and Kendeigh, 1938). It has been suggested that this seasonal cycle is correlated, roughly at least, with temperature, since individual birds usually gain weight during cold weather (provided adequate food is obtained) and lose weight during warm weather (Baldwin and Kendeigh, 1938). For our data, the correlation coefficient (r) of monthly mean weight and monthly mean temperature is –0.35, a definite, but small, negative correlation. This weight fluctuation should not be confused with the premigratory fat deposits of migratory birds. Odum and Perkinson (1951), working with migratory White-throated Sparrows (*Zonotrichia albicollis*), found that though changes in body lipids accounted for most seasonal changes in total body weight, the lean weight varied somewhat independently, being highest in the winter rather than spring. The increase in weight in July and August is probably due to the heavy annual molt and the subsequent high water content of the growing feathers. Odum and Perkinson (1951) found that molting birds had greater total weight, but lower lipid content than non-molting post-migratory birds.

MOLT

Some *nuttalli* exhibit a partial prenuptial molt beginning in late January and extending through February. When this molt occurs it is usually light and involves feathers of the crown and, to a lesser extent, those of the body (Blanchard, 1941; Mewaldt, Kibby, and Morton, 1968). In this study only the immatures exhibited this prenuptial molt with five out of six birds showing some molt during the first spring of the study (Fig. 1). These six birds showed no prenuptial molt in their second spring. No adults showed prenuptial molt. The postnuptial molt of the adults started later and was completed

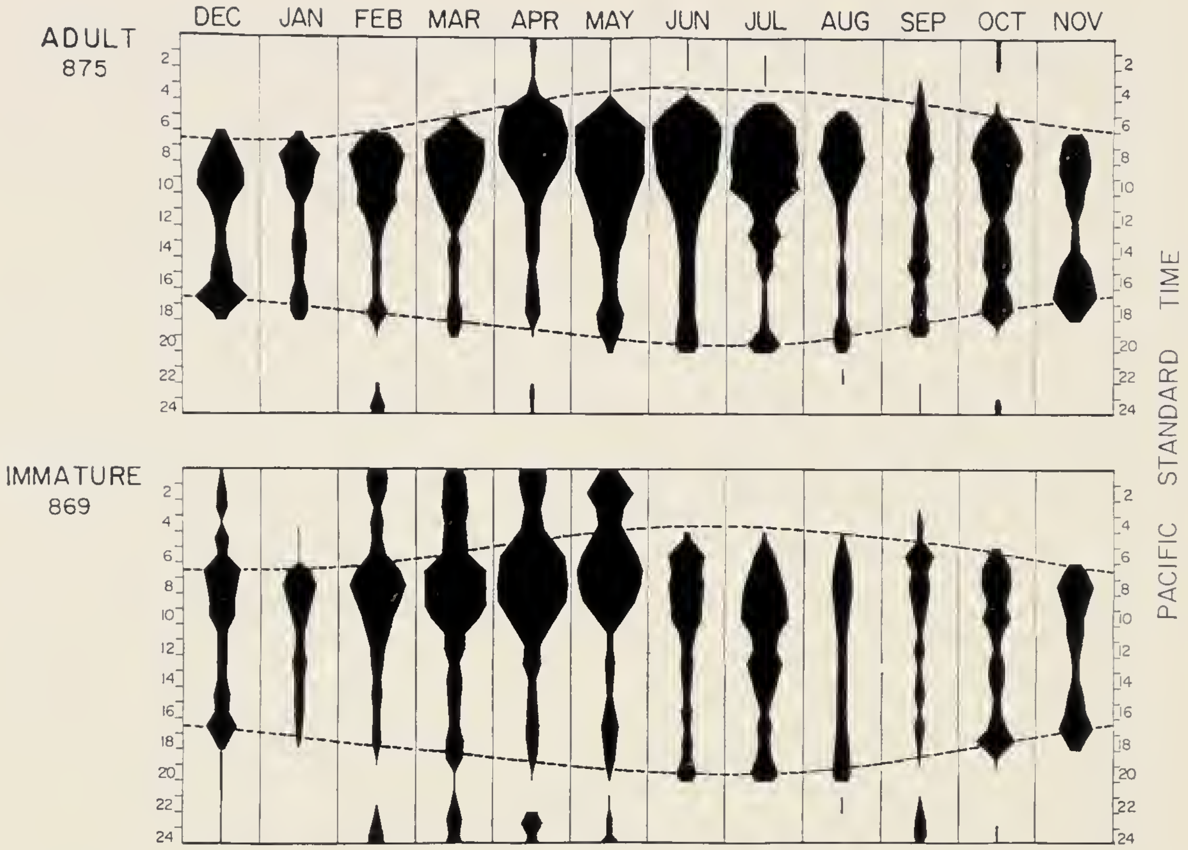


FIG. 2. Circadian patterns of an adult and an immature *Z. l. nuttalli* in activity cages. Dashed line indicates twilight. Full width of each month = 500 perch registrations per hour.

later than the postnuptial molt of the immatures. The six immatures began their first postnuptial molts between 9 June and 9 July. Between 3 and 17 August all six were in heavy molt. The four adults began their postnuptial molts between 16 June and 20 July and were all in medium or heavy molt between 17 August and 7 September. By 14 September all but one immature had completed the molt; however, the first adult to finish the molt did not do so until 14 October. The second summer only two of the original adults were still alive. They again started their molt a little later (Fig. 1) than the immature group which by now was about 2½ years old.

CIRCADIAN PATTERNS OF ACTIVITY

The data for the circadian activity patterns (Figs. 2 and 3) were obtained by taking the arithmetic means of the respective hours from the "typical days" for a given month. Each hour was plotted in the middle of the hour; e.g., the plot of the arithmetic mean for the eighth hour (08:00) is between 07:00 and 08:00. The birds generally showed high morning activity diminishing toward midday and exhibited another peak of lesser intensity at sunset. Many different bird activities follow this pattern: for example: feeding, nest

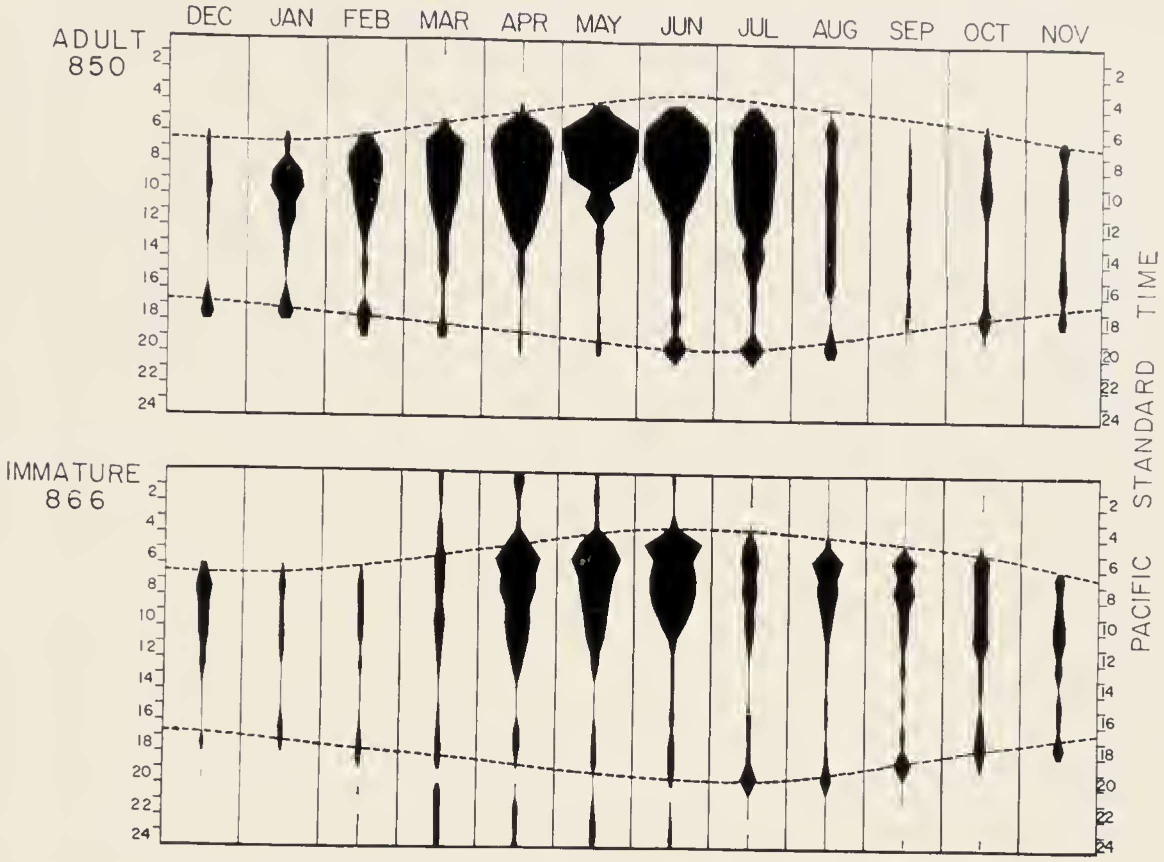


FIG. 3. Circadian patterns of an adult and an immature *Z. l. nuttalli* in activity-orientation cages. Dashed line indicates twilight. Full width of each month = 3000 perch registrations per hour.

building, and singing (Eyster, 1954). The evening peak is usually reduced or absent when the bird shows night activity (Palmgren, 1949; Mewaldt, Morton, and Brown, 1964.) It should be noted that no evening peak is shown for immature 869 in January (Fig. 2). This bird did display sporadic night activity during January but never on Wednesday—the arbitrary "typical" day. Also adult 850 (Fig. 3) lacks both morning and evening peaks in the month of September. This bird was in heavy molt in September and possibly the high energy demands of this molt resulted in reduced activity. Eyster (1954) reported a conspicuous decrease in the daily activity of the White-crowned Sparrow (*Z. l. leucophrys*) during molt.

Most of the night activity began several hours after sunset and continued on through the early morning hours until sunrise. There appeared to be a period of rest between sunset and the onset of nocturnal unrest. Eyster (1954) confirmed the results of other workers that, in migratory birds rest pauses usually occur before and after nocturnal activity during the migratory period.

Migratory *Zonotrichia*, which are night migrants, tend to exhibit less daytime activity in spring when they become active at night (*Zugunruhe*) (Eyster, 1954 and Mewaldt, Morton, and Brown, 1964). The unusually high

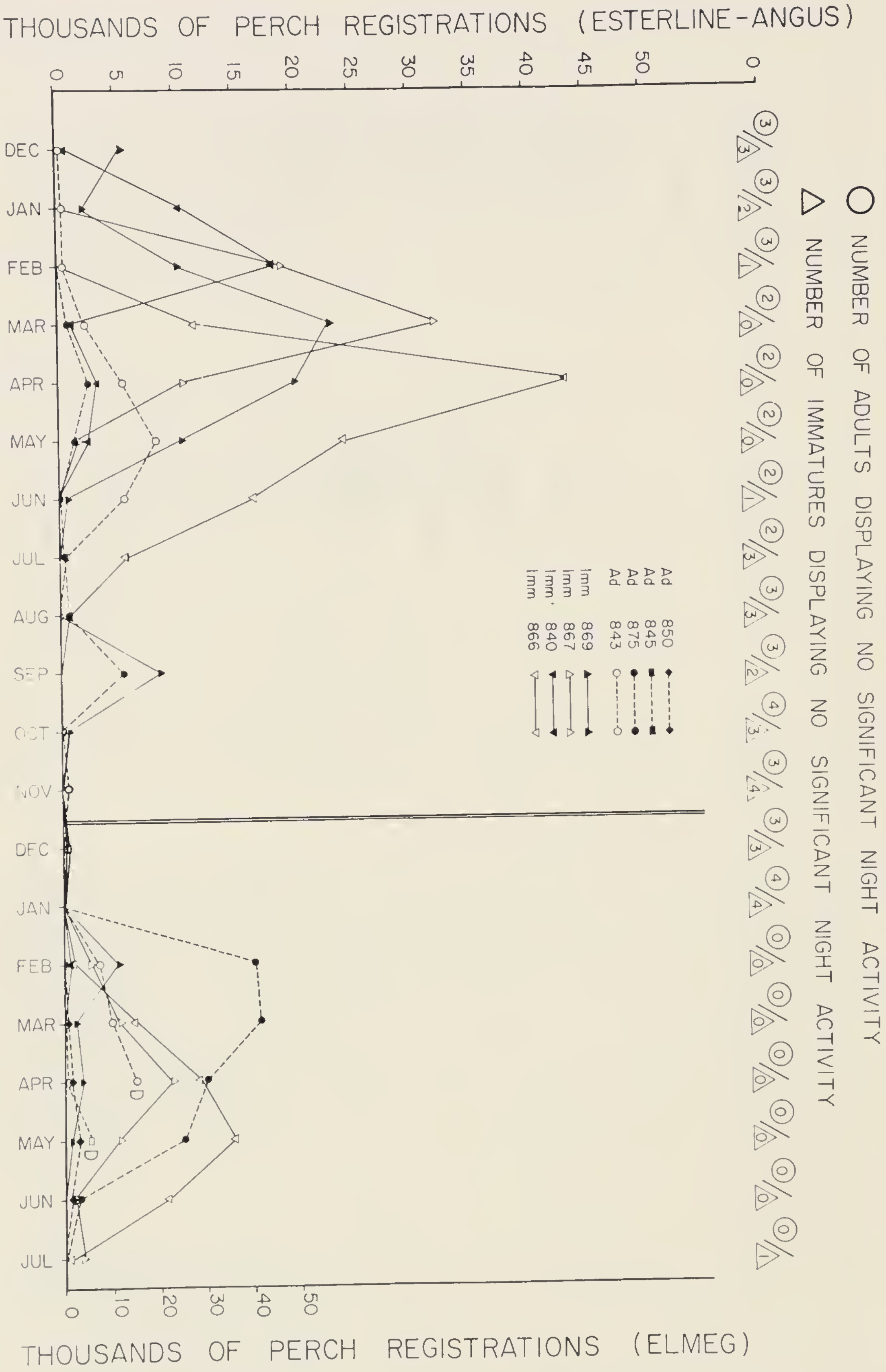


FIG. 4. Total night activity by months of four adult and four immature *Z. l. nuttalli.* Ordinate change in December 1962 reflects change from ink-marking to digital counter monitors for locomotor activity. Records of two birds were terminated by death (D) in 1963.

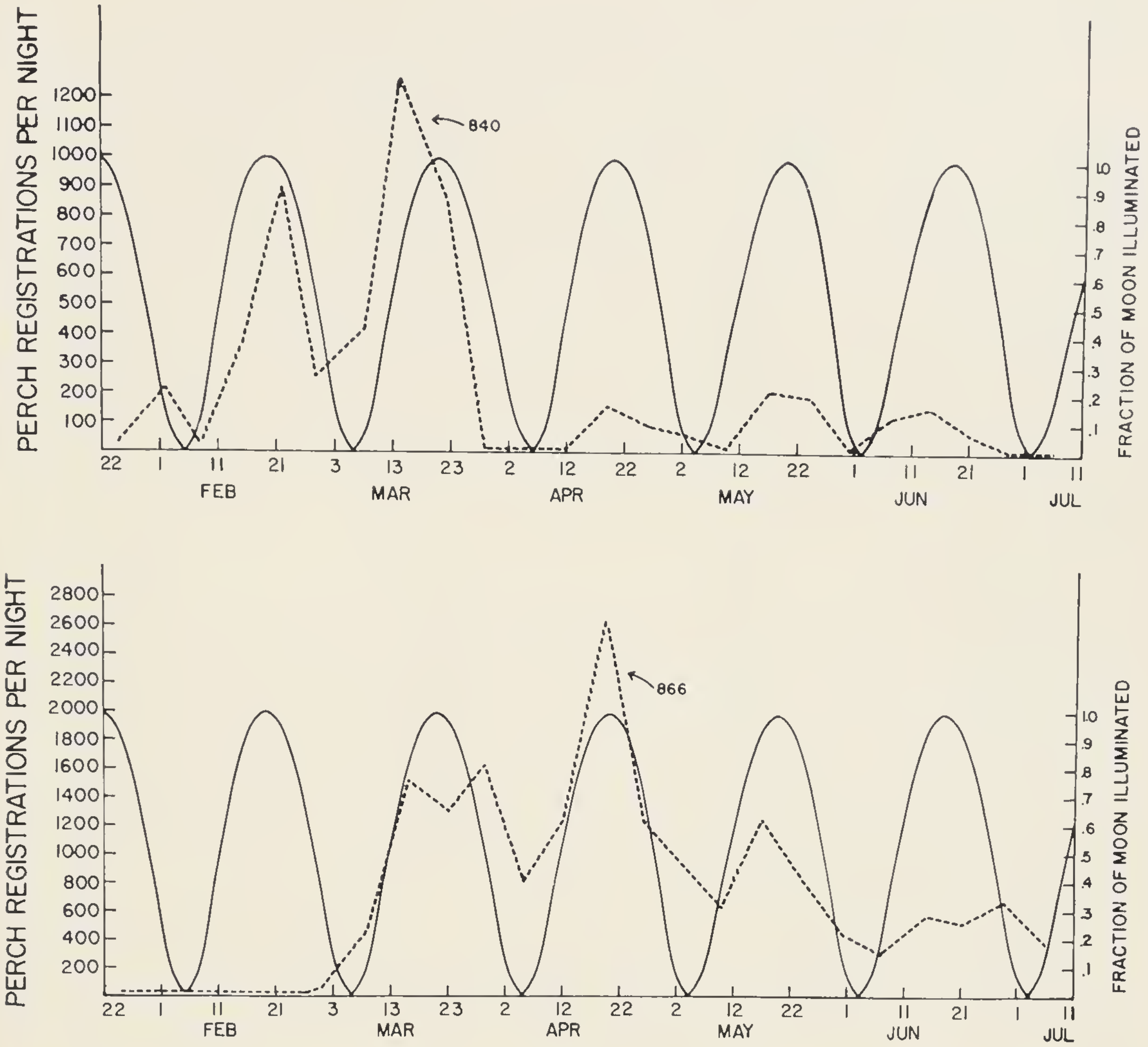


Fig. 5. Moon influence on quantity of night activity of two immature *Z. l. nuttalli* in activity-orientation cages. Solid lines indicate the fraction of the moon's disk illuminated as a convenient index of the brightness of the moon.

morning locomotor activity exhibited by our non-migratory *nuttalli* in February and March is probably associated with the development of the gonads and may be equated with breeding activity. Blanchard (1941) reports that breeding behavior in *nuttalli* begins with establishment of territory in mid-January. The circadian activity patterns of our *nuttalli* were similar throughout the year and resemble those of non-migratory birds. However, when night activity was present the evening peak disappeared, a phenomenon characteristic of night migrants.

NIGHT ACTIVITY

The records of night activity for each night for all eight birds in recording cages for a year and a half are summarized by monthly totals (Fig. 4). The data for the first year (December 1961 to November 1962) were recorded

TABLE 1

NIGHT ACTIVITY OF ADULT *Z. L. NUTTALLI* IN ORIENTATION CAGES.

Bird Date	Fraction of Moon Illuminated	Activity Index	Mean Azimuth ± Angular Deviation
Bird #845			
May 18–19	0.99	49	91 ± 50
19–20	1.00	98	127 ± 36
20–21	0.98	18	127 ± 18
June 12–13	0.75	64	128 ± 58
		229	120 ± 47
Bird #850			
Mar. 26–27	0.72	124	35 ± 41
27–28	0.62	305	000 ± 45
Apr. 20–21	0.99	155	339 ± 40
21–22	0.96	62	341 ± 36
23–24	0.85	110	352 ± 27
May 03–04	0.00	39	333 ± 26
21–22	0.94	135	339 ± 26
		930	353 ± 41

by Esterline-Angus recorders and the data for the second year were recorded by Elmeg print-out counters. Counts obtained by the Elmeg counter were at least 2 to 2½ times greater during periods of peak activity than the counts obtained by our method of analyzing the Esterline-Angus data. Figure 4 represents this difference graphically.

During the first spring all four immatures (now nearly one year old) displayed substantially more night activity than any of the four adults. Whereas three immatures showed greatest night activity in March, one immature and the two adults, showing any significant night activity, reached peak activity in April and May.

The birds in the orientation cages were directly exposed to moonlight whenever the moon was approximately 25° or greater above the horizon. Since the night activity of migratory birds is sensitive to changes in light intensity (Wagner, 1957) we investigated the possible effect of moonlight on these birds' activity. We found (Fig. 5) that both of the immatures had a remarkably strong positive correlation of peaks of night activity with nights of bright moon. Moon brightness is presented as the fraction of the moon's disk illuminated (data from American Ephemeris and Nautical Almanac, U.S. Naval Observatory, 1962). The highest peaks of night activity are in the spring in both immatures; however, the maximum of bird 840 is one month ahead of bird 866. The two adults in the orientation cages had a total of 11 nights when they had night activity, all but one of these nights occurred during a period of bright moonlight (see Table 1).

The birds in the small cages were partially sheltered from moonlight by an overhanging roof. However, they also showed peaks of activity coinciding with the full moon. Immature bird 869 had peaks of night activity which coincided with the full moons of February, March, and April. Immature bird 867 showed his first significant night activity in February as the moon began to increase in brightness. His peak of activity spanned the full moons of February and March and a smaller peak coincided with the full moon of April. Night activity was much less in the adults; however, a peak of activity of bird 843 was apparently related to the full moon of May and bird 875 had three small peaks of night activity related to the full moons of March, April, and May.

In the second spring (1963) the comparative amounts of activity exhibited by the original immatures and the adults were not separable. The two adults (875 and 843) again showed significant amounts of night activity but 875 showed relatively higher activity the second spring. Other than personal observation that this bird became increasingly nervous and cage worn as it remained in captivity, we cannot explain the high night activity of the second spring. The high amounts of activity exhibited by immature 866 in both years and the timing of its peak in April and May suggests that this individual bird possessed response characteristics of the migratory race *pugetensis* (Mewaldt, Kibby, and Morton, 1968). During the fall period only one adult and one immature showed appreciable night activity.

Most difference in vernal night activity between adults and the immatures disappeared the second spring probably because the immatures were in their second year and should by then be considered adults. The difference does not appear to result from the fact that our immatures were in captivity longer than the adults since most adults remained low the second year as well. The data for the fall period were collected when the immatures were in their second year. If the birds had been tested during their first fall period it is possible that we could have found night activity.

The overall picture of night activity, even among individuals of the same age and locality, is one of great variation. The only real consistencies are that the main onset of vernal night activity occurred in late January and early February and terminated with the annual molt which began in mid-June.

ORIENTATION OF ACTIVITY

Daytime orientation.—Because the orientation of daytime activity was very much alike in the four birds tested, data from one adult (850) and one

FIG. 6. The orientation of the daytime activity of an immature *Z. l. nuttalli*, bird 866. Number in circle is the total number of daytime perch registrations in "typical day." Arrow represents mean azimuth which is also presented beneath each circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

immature (866) were examined in detail (Figs. 6 and 7). Angular deviations were generally high (maximum possible is 81). The 52 week mean angular deviation for adult 850 is 72 (SD ± 5.52) and for immature 866 it is 71 (SD ± 5.76). Over all, the day angular deviations of these two *Z. l. nuttalli* were higher than those of migratory *Zonotrichia* in similar experimental conditions (Fig. 8) indicating that the *Z. l. nuttalli* have less tendency than their migratory relatives to orient their day activity. These high angular deviations suggest very poor orientation and our test for randomness (see methods) confirms this conclusion by indicating that almost half of the days of each of these birds are not significantly directed (azimuths in parentheses in Figs. 6 and 7).

FIG. 7. The orientation of the daytime activity of an adult *Z. l. nuttalli*, bird 850. Number in circle is the total number of daytime perch registrations in "typical day." Arrow represents mean azimuth which is also presented beneath each circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

Of those azimuths which were significantly directed, over 70 per cent in both birds fell in the range between 170° and 270°. This predominately southwest orientation might possibly be homing behavior since these birds were captured 40 miles almost directly south of San Jose. No homing ability has been previously reported for *Z. l. nuttalli.* Immature 866 was removed from its natal area well before it began its post-juvenal molt when it would normally have been imprinted with its home area (unpublished data in our laboratory); however, adult 850 might be expected to exhibit homing tendencies. We also examined the possibility that the birds' daytime orientation was related to a preference for the sunny or shady portions of the cage in relation to the time of day and/or the time of year. We found no progres-

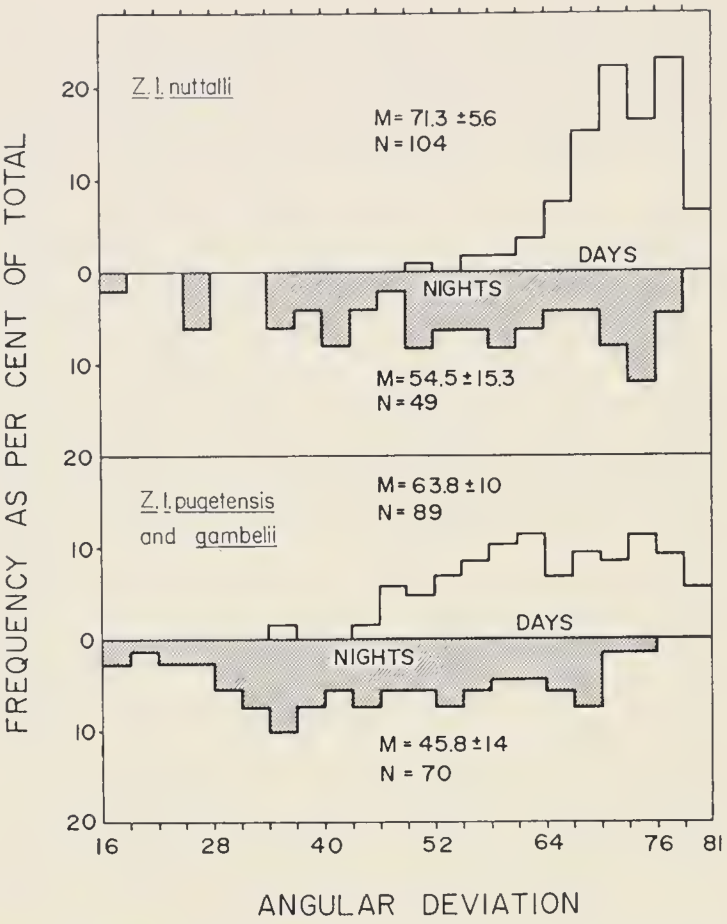


FIG. 8. Frequency distributions of day and night angular deviations on azimuths for *Z. l. nuttalli* (non-migratory) and *Z. l. pugetensis* and *gambelii* (migratory). All data included for *Z. l. nuttalli.* Data from two *Z. l. pugetensis* and two *Z. l. gambelii* under similar experimental conditions.

sive change in frequency of perch usage to correlate with the passage of the sun.

In April, May, and June adult 850 (Fig. 7) directed more activity to the north-northwest perches while continuing strong activity on the south perch. This change to a bimodal distribution of perch registrations was accompanied by a pronounced increase in daytime activity (Fig. 3) which persisted until the post-nuptial molt was well under way in late July. During the 8-week period from 6 February to 27 March, mean daily activity was 8,566 perch registrations with range from 4,713 to 10,334. Mean daily activity abruptly increased to 16,678 perch registrations with a range of 13,507 to 19,502 perch registrations per "typical" day during the 16-week period (5 April to 17 July). Because of the bimodal orientation during much of this 16-week period, angular deviations were high and in most of these weeks activity on the test day was random by our criterion. This does not, however, permit dismissal of possible functional significance of the persistent, if weak, change in directional choice during 16 weeks of very heavy activity coincident with the natural season of reproduction. Very little night activity was recorded for this bird during this, its first year in captivity. What night activity did occur, however, was significantly oriented north (see Table 1).

Behavior of immature 866 (Fig. 6) nearly paralleled that of adult 850. During April, May, and June, daytime activity was more than triple what it had been in the four previous months. Just prior to this increase in locomotor activity, the north perch was seldom used (13, 20, and 27 March). Coincident with the increase in day activity, the north perch was heavily used (4, 11, and 17 April), suggesting a carryover from night activity during those days. However, there was also considerable use of the perches in the north sector during August and September.

Nighttime orientation.—The adult birds in the activity-orientation cages showed little night activity. During the first spring, adult 850 was active only on the nights of 26 and 27 March, 20, 21, and 23 April, and 3 and 21 May (mean of perch registrations per night = 135) with a concentration of activity to the north (over-all angular deviation = 41) (Table 1). Adult 845 displayed night activity on 18, 19, and 20 May and on 12 June (mean of perch registrations per night = 56) with the activity oriented strongly to the southeast (over-all angular deviation = 47). The night activity of these two birds was strongly related to the presence of the moon and was of very low intensity; however, what little night activity each bird displayed was significantly oriented. The angular deviations compare favorably with those of the night activity of migratory *Zonotrichia* (Fig. 8). In both birds, night restlessness ocurred during the season when caged migratory *Zonotrichia* exhibit night restlessness (Mewaldt, Morton, and Brown, 1964). In neither case was the orientation phototaxic to the city lights, westerly in our experimental situation; however, the southeast orientation of bird 845 may have been phototaxic to the moon (see Brown and Mewaldt, 1968).

Immature 866 (Fig. 9) exhibited significant night activity during 22 weeks of the year. Its activity was oriented to the northwest beginning immediately after completion of the light prenuptial molt at the end of February. After four weeks it switched to a north-south pattern which persisted until the end of July. The angular deviations tend to be high (22 week mean = 66.1, SD ± 9.5) especially when the north-south components are nearly equal. This strong north-south tendency appeared even in the daytime activity (Fig. 6) during certain periods. Whenever this bird was disturbed for feeding, weighing, or cage cleaning it would rapidly jump from the perch to the floor, to the center perch and straight across to the opposite perch. These "across the cage" movements constituted a pattern of activity peculiar to this bird. When the data are analyzed, by the method employed here, the north and south

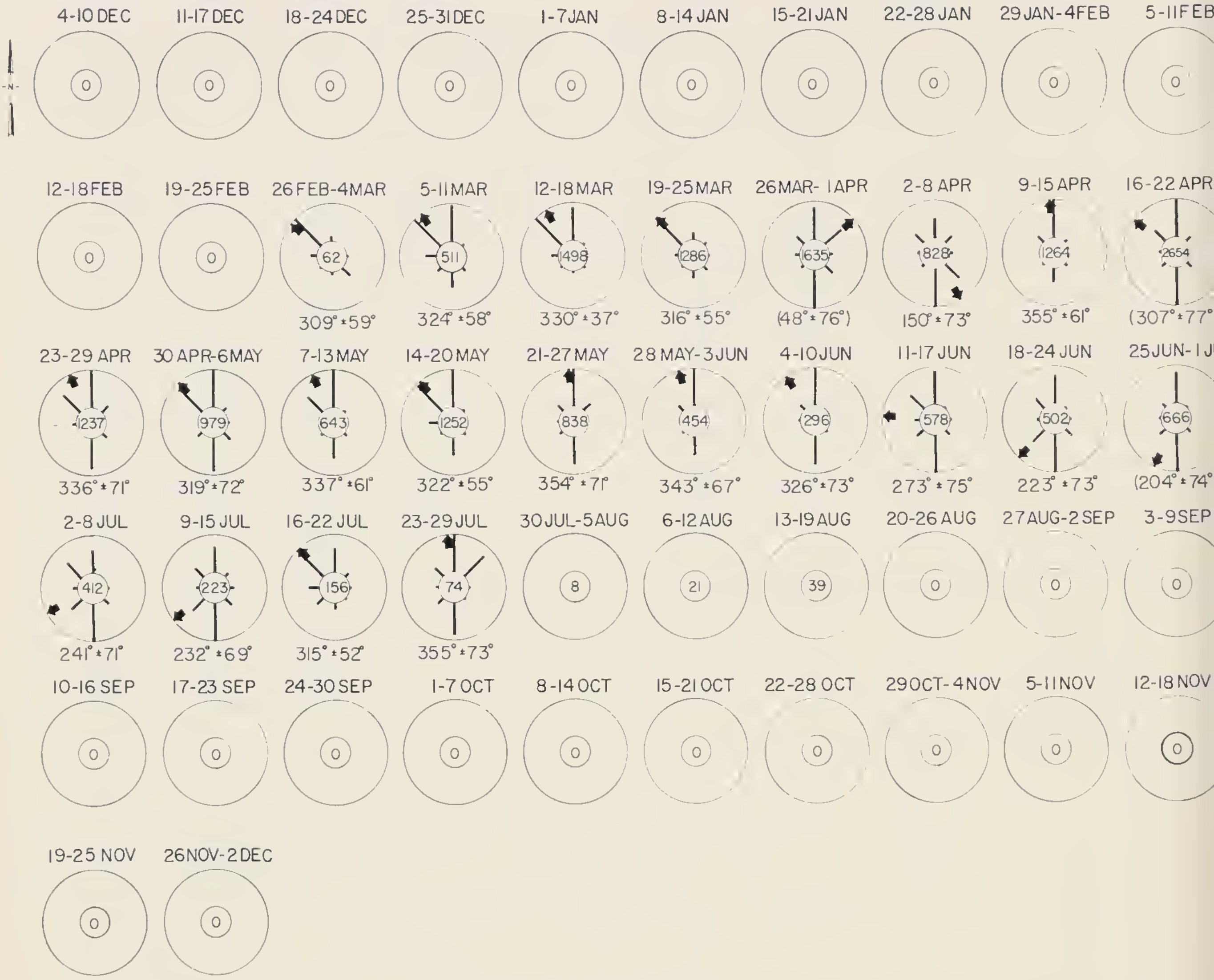


FIG. 9. The orientation of the night activity of an immature *Z. l. nuttalli*, bird 866. Number in circle is mean number of perch registrations per night. Arrow represents mean azimuth which is also presented beneath the circle with its angular deviation. Azimuths in parentheses were not significantly directed by our criterion.

components tend to cancel each other. Nevertheless, most week distributions were significantly directed by our criterion. The angular deviations do not reflect a true picture of what has occurred in this case. Such behavior is not without precedent; we have occasionally found "across the cage" responses in migratory *Zonotrichia.* Hamilton (1962) found alternation between north and south directional choices in two hand-reared Bobolinks. Lorenz and Tinbergen (1957) have indicated that organisms whose orienting responses have become stimulus-satiated often respond with an averting reaction to a previously positive stimulus. In spite of these bimodal distributions, the azimuths of bird 866 (Fig. 9) suggest that there was a greater tendency to orient toward the north than toward the south.

FIG. 10. The orientation of the night activity of an immature *Z. l. nuttalli*, bird 840. Number in circle is mean number of perch registrations per night. Arrow represents mean azimuth which is also presented beneath the circle with its angular deviation. All azimuths were significantly directed by our criteria.

City lights, visible to the birds as reflected light from clouds in the west on cloudy nights, did not seem to affect the northerly orientation of this bird. Likewise, the moon did not appear to influence the overall orientation of this bird. However, since most of its activity occurred during periods of bright moon, it is possible that some of its southward movements were phototaxic to the moon which is, of course, highest when it is due south. Night angular deviations sometimes increased during periods of bright noon. We propose that this bird was significantly orienting its night activity to the north. Closely related free-flying *Z. l. pugetensis* migrate to the north in late March and in April coincident with the period when this bird showed its greatest night activity. This bird (866) apparently possessed innate atavistic migratory behavior which was appropriately expressed as northerly oriented nocturnal activity during the spring and early summer months. Persistence of nocturnal activity in caged migratory birds during the early summer months is characteristic (Merkel, 1958; Mewaldt, Morton, and Brown, 1964).

Beginning in late January, after a light prenuptial molt, immature 840 displayed sporadic night activity until mid-June (Fig. 10). This activity correlated strongly with the lunar cycle (Fig. 5). During 15 of the 16 weeks that the bird showed night activity it was strongly oriented to the east (mean angular deviation = 50.8, SD ± 8.93). The week of 30 April–6 May the bird was only active two nights and all of the orientation to the west occurred during one night. This primarily eastward orientation probably results only from the variation among individual birds. Mewaldt, Morton, and Brown (1964) found considerable spread of directional choices among migratory *Zonotrichia* in spring. It would be necessary to test many more individual *nuttalli* in order to determine the mean orientation azimuth for the taxon. The important thing is that these immature non-migratory birds had oriented night locomotor activity. In fact, their night locomotor activity is almost as strongly oriented as that of a representative group of migratory *Zonotrichia* under similar conditions (Fig. 8). In both the non-migratory birds and the migratory birds night angular deviations are more variable than day angular deviations and tend to be lower.

DISCUSSION

Matthews (1961) discussed the fact that two non-migratory taxons, *Anas platyrhynchos* and *Columba* sp. exhibited orientation when displaced geographically and released. He suggested that this orientation may function in keeping flocks together or in post-fledgling dispersal. It is possible that the night activity and orientation we have discovered in the non-migratory White-crowned Sparrow might also be related to post-fledgling dispersal. Dispersal of immature birds has been reported for many non-migratory species. Some examples are the Black-capped Chickadee (*Parus atricapillus*) (Odum, 1942), Pygmy Nuthatch (*Sita pygmaea*) (Norris, 1958), Wrentit (*Chamaea fasciata*) (Erickson, 1938), and the Song Sparrow (*Melospiza melodia*) (Johnston, 1956). Immature *nuttalli* flock after fledging but wandering may be confined to the period preceding the post-juvenal molt (Blanchard, 1941). Of 58 nestling *nuttalli* which were banded and successfully fledged, only 12 were seen or reported after they had left their parents' territory. Eleven were seen within 400 yards of their birthplace during the nine months following fledging. Four of these eleven actually bred within 200–525 yards of their parents' territory. Remaining survivors, probably numbering another dozen birds if we allow a 40 per cent survival, probably dispersed to a greater distance. This is suggested by the recovery (by shooting) of one bird the following spring 1½ miles from its birthplace. The post-fledgling dispersal of the Song Sparrow (*Melospiza melodia*), a very sedentary bird, was studied by Johnston (1956) and Nice (1937). Johnston found that only 10 per cent of the young sparrows moved to distances greater than 360 meters from their nests and that the direction of distribution was random when suitable habitat was available in all directions.

However, if the significantly oriented locomotor activity of *Z. l. nuttalli* were related to post-fledgling dispersal it seems unlikely that it would be exhibited in spring, occur at night, appear in adults, or be consistently oriented over a period of time. Because night activity peaks during the period of migration of the closely related migratory *Z. l. pugetensis*, we propose that the night activity and its orientation in *nuttalli* are atavistic remnants of an ancestral instinct to migrate. The non-migratory *nuttalli* are still in genetic contact with migratory *pugetensis* over a small geographic region from Westport to Capetown, California (Banks, 1964; Mewaldt, Kibby, and Morton, 1968). Certainly there is no doubt that spontaneous locomotor activity can have a genetic base since in rats it has been possible, by selective breeding, to initiate "active" and "inactive" strains with respect to spontaneous running activity (Rundquist, 1933; Brody, 1942 and 1950).

The display of night activity (= *Zugunruhe* ?) was weaker in the adult birds than in the immatures. It has been found in learning experiments that immature birds show more spontaneous activity than adults (Vince, 1961). Perhaps the establishment of territory by the adult further weakens an already vestigial instinct. It would be interesting to know if *nuttalli* are restless at night in their native habitat during the migratory season. Residents of San Francisco and Berkeley report that *nuttalli* commonly sing at night during the spring and summer months. Some suggest this "unrest" is caused by a relatively high incident light level from the city lights. Certainly our birds were much influenced by moonlight. Perhaps an innate tendency toward night restlessness is accentuated by conditions of capivity since the opportunity to expend energy is greatly lessened within the confines of a cage. The night activity of the immatures may be related to their higher body weights which suggest a favorable energy balance with more energy available to expend in activity.

Wagner (1930) states that "we recognize two extreme groups of birds; permanent residents which spend all of their life within a narrow range of their breeding grounds and migratory birds whose breeding grounds and wintering grounds are far apart. Between these two extremes there are various transition groups." The races of *Zonotrichia leucophrys* found in central western California (*gambelii, pugetensis,* and *nuttalli*) represent all three of these categories to a certain extent. The strongly migratory *gambelii* might be placed at one extreme, whereas the "weaker" migratory *pugetensis* may represent a transitional stage. Although the *nuttalli* can be considered near Wagner's permanent resident extreme, individual birds apparently retain some characteristics of the transition group.

SUMMARY

We investigated body weight, molt, and locomotor activity of caged non-migratory White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) over a period of one and one half years including two springs. The four adults and six immatures used were captured in 1961 from the population which is permanently resident of the sand dune area near the mouth of the Pajaro River in Monterey County, California.

Locomotor activity patterns of two immatures (♂♂) and two adults (♂ and ♀) were continuously (24 hours per day) recorded in cages with single activity-sensitive perches from December 1961 to August 1963. The orientation of the locomotor activity of two imatures (♂♂) and two adults (♂♂), each in eight-perch activity-orientation cages, was monitored 24 hours per day from December 1961 to December 1962. In December 1962 these four birds were transferred to single-perch activity cages where their activity patterns were monitored until August 1963. Two additional immatures (♂♂) were held in a walk-in aviary. All ten were weighed and inspected for molt at weekly intervals. All birds were exposed to the natural weather at San Jose, California.

Body weight was inversely related to the mean environmental temperature. The weight of the fluids in the growing feathers probably accounted for an increase in weight in August. The mean body weight of the immatures was consistently, but not significantly, higher than the mean body weight of the adults in all months. Five of the six immatures showed a light prenuptial molt their first spring but not in their second spring. None of the four adults showed a prenuptial molt. The adults' postnuptial molt was about two weeks later than that of the immatures.

The circadian locomotor activity patterns of these birds displayed characteristic morning peaks and somewhat lesser evening peaks. The evening peaks were generally reduced or absent when the birds showed night activity. The morning peaks of activity increased greatly during the spring and early summer months. This increased restlessness during the day seems related to an increased availability of energy associated with a readiness to breed.

During the spring of 1962 all four immatures, but only two of the four adults, showed significant amounts of night locomotor activity. There was a remarkably strong positive correlation of peaks of night activity with nights of bright moon in all birds displaying night restlessness. The night activity of the two adults was of comparatively low intensity. In the fall only one adult and one immature showed night activity and that was very light in quantity. In the spring of 1963, by which time the original immatures were also adults, night activity levels of the two groups were broadly overlapping.

In the activity-orientation cages one immature showed a preference at night for north during the spring and summer months, whereas the other immature showed a definite preference at night for the east sector of the cage during the same period. No significant night activity was registered in the activity-orientation cages in the fall months. The very limited (less than ten nights combined) night activity of the two adults in activity-oriented cages was none-the-less strongly oriented. The moon appeared to have little effect on the orientation of night activity, but it may have contributed to north-south "across the cage" movements in one bird. The angular deviations of both day and night activity compared favorably with those of migratory *Zonotrichia.* We propose the night restlessness of these non-migratory sparrows is a vestige of ancestral migratory behavior. The possible significance of weakly but frequently oriented daytime activity is also discussed. The possible importance of post-fledgling dispersal is discussed but judged to be unimportant in the behavior of these captive birds. It is possible that the quantity of night activity was somewhat influenced (presumably increased) by a surplus of metabolic energy incident to the restrictions of life in a cage.

ACKNOWLEDGMENTS

We gratefully acknowledge assistance from Martin L. Morton, George Tengan, Dennis King, Raymond Marsh, Mildred Tomooka, Daryl Webb, Bill Mewaldt, Reneé Knoch, Mike Mayberry, and Judith L. Smith in the execution of the experiments and/or the analysis of data. We greatly appreciate the clerical assistance of Laura Erickson and Erica Heath. The project was supported in part by National Science Foundation grants G-20745 and GB-7031.

LITERATURE CITED

Baldwin, S., and S. Kendeigh. 1938. Variations in bird weights. Auk, 55:416–467.

Banks, R. C. 1964. Geographic variation in the White-crowned Sparrow Zonotrichia leucophrys. Univ. California Publ. Zool., 70:1–123.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S., Washington, D. C.

Blanchard, B. D. 1941. The White-crowned Sparrows (Zonotrichia leucophrys) of the Pacific Seaboard: environment and annual cycle. Univ. California Publ. Zool., 46:1–178.

Brody, E. G. 1942. Genetic basis of spontaneous activity in the albino rat. Comp. Psychol. Monogr., 17:1–24.

Brody, E. G. 1950. A note on the genetic basis of spontaneous activity in the albino rat. J. Comp. Physiol. Psychol., 43:281–288.

Brown, I. L., and L. R. Mewaldt. 1968. Behavior of sparrows of the genus, *Zonotrichia,* in orientation cages during the lunar cycle. Z. Tierpsychol., 25:668–700.

Emlen, S. T. 1967*a* Migratory orientation in the Indigo Bunting, *Passerina cyanea* Pt. I: Evidence for use of celestial cues. Auk, 84:309–342.

Emlen, S. T. 1967*b* Migratory orientation in the Indigo Bunting, *Passerina cyanea* Pt. II: Mechanism of celestial orientation. Auk, 84:463–489.

Erickson, M. M. 1938. Territory, annual cycle, and numbers in a population of wrentits (Chamaea fasciata). Univ. California Publ. Zool., 42:247–334.

Eyster, M. B. 1954. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. Ecol. Monogr., 24:1–28.

Farner, D. S. 1955. The annual stimulus for migration: experimental and physiologic aspects. *In* Recent studies in avian biology (Wolfson, A., Ed.), Univ. Illinois Press, Urbana, pp. 198–237.

Farner, D. S., and L. R. Mewaldt. 1953. The recording of diurnal activity patterns in caged birds. Bird-Banding, 24:55–65.

Farner, D. S., J. R. King, and A. C. Wilson. 1957. The development of vernal migratory behavior in caged individuals of several taxa of *Zonotrichia.* Anat. Rec., 128:546.

Hamilton, W. J., III. 1962. Bobolink migratory pathways and their experimental analysis under night skies. Auk, 79:208–233.

Hamilton, W. J., III. 1966. Analysis of bird navigation experiments. *In* Systems analysis in ecology. (Watt, Kenneth E. F., Ed.), Academic Press, New York.

Johnston, R. 1956. Population structure in Salt Marsh Song Sparrows, Part I. Environment and Annual Cycle. Condor, 58:24–44.

Lorenz, K., and N. Tinbergen. 1957. Taxis and instinctive action in the egg-retrieving behavior of the Greylag Goose. *In* Instinctive behavior. (Schiller, Claire H., Ed.), Internat. Universities Press, New York, pp. 178–208.

Matthews, G. V. T. 1961. "Nonsense" orientation in Mallard (*Anas platyrhynchos*) and its relation to experiments on bird navigation. Ibis, 103a:211–230.

Merkel, F. W. 1958. Untersuchungen über tages- und jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. Z. vergl. Physiol., 41:154–178.

Mewaldt, L. R., S. Kibby, and M. L. Morton. 1968. Comparative biology of Pacific coastal White-crowned Sparrows. Condor, 70:14–30.

Mewaldt, L. R., M. L. Morton, and I. L. Brown. 1964. Orientation of migratory restlessness in *Zonotrichia*. Condor, 66:377–417.

Mewaldt, L. R., and R. C. Rose. 1960. Orientation of migratory restlessness in the White-crowned Sparrow. Science, 131:105–106.

Morton, M. L. 1962. A plucking experiment with White-crowned Sparrows. Condor, 64:327–328.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linnaean Soc., New York. 4.

Norris, R. A. 1958. Comparative biosystematics and life history of the nuthatches. Univ. California Publ. Zool., 56:119–300.

Odum, E. 1942. Annual cycle of the Black-capped Chickadee. Auk, 59:499–531.

Odum, E., and J. D. Perkinson, Jr. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., 24:216–230.

Palmgren, P. 1949. On the diurnal rhythm of activity and rest in birds. Ibis, 91:561–576.

Rundquist, E. A. 1933. The inheritance of spontaneous activity in rats. J. Comp. Psychol., 16:415–438.

Simpson, G. G., A. Roe, and R. Lewontin. 1960. Quantitative zoology. Harcourt, Brace, New York.

U. S. Naval Observatory. 1962. American ephemeris and nautical almanac. Ephemeris for physical observations. U. S. Government Printing Office, Washington, D. C.

Vince, M. A. 1961. "String-pulling" in birds, III. The successful response in Greenfinches and canaries. Behaviour, 17:103–129.

Wagner, H. O. 1930. Über Jahres-und Tages rhythmus bei Zugvögeln. (I. Mitteilung) Z. vergl. Physiol., 12:703–724.

Wagner, H. O. 1957. The technical basis of experimental research on bird migration. Ibis, 99:191–195.

Weise, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. Ecology, 37:274–287.

AVIAN BIOLOGY LABORATORY, SAN JOSE STATE COLLEGE, SAN JOSE, CALIFORNIA 95114. 21 NOVEMBER 1967.

ENERGY RESPONSES OF BIRDS TO THEIR THERMAL ENVIRONMENTS[1]

S. CHARLES KENDEIGH

THE ability of a species to mobilize energy under different environmental conditions may greatly affect its responses and behavior, as shown by the limits it can extend its distribution, the size and fluctuations in its population in any area, whether or not it is a permanent resident, the time of year at which it initiates migration, nesting, and molt, the length of single migratory flights, the size of egg clutches, etc. Energy metabolism is well known to vary with ambient temperature, but these interrelations are complex. There is need of a generalized physiological model, applicable to all species, to show the interrelations between food intake, standard metabolism, existence metabolism, productive energy, limits of tolerance, evaporative cooling, body temperature, and the thermal environment.

Kleiber and Dougherty (1934) were among the first to make such a figure model based on their work with baby chicks (Fig. 1). This original figure was later greatly modified both by Kleiber (1961) and by King and Farner (1961) in ways with which I cannot agree. West's (1960) figure for the Tree Sparrow (*Spizella arborea*) is more nearly correct but omits consideration of several of the above mentioned parameters. The present study is my attempt at a generalized model (Fig. 2) based largely on information developed in this laboratory for the House Sparrow (*Passer domesticus*) but with additional data from other species where pertinent.

Standard metabolism, or the heat production of the fasting bird at complete rest, appears to have a zone of thermal neutrality with a lower critical temperature at 21°–22°C in three northern populations of House Sparrows, when measurements are made at night (Fig. 2). During the daytime, however, the zone disappears and the regression line of metabolism on temperature becomes curvilinear (Hudson and Kimzey, 1966) or linear with an upper critical temperature at 37°C (Kendeigh, 1944). Similarly in the Evening Grosbeak (*Hesperiphona vespertina*) the zone of thermoneutrality present at night disappears during the day (West and Hart, 1966). Above 37°C, metabolism increases, correlated with a rise in body temperature, to about 47°C ambient temperature, a short exposure to which is lethal to the bird. At the other extreme, standard metabolism increases to at least –40°C, although this temperature can be tolerated for only 5 or 6 hours.

---

[1] Supported by several National Science Foundation grants. This paper is a contribution to the objectives of the Working Group on Granivorus Birds, Terrestrial Productivity Section, International Biological Program.

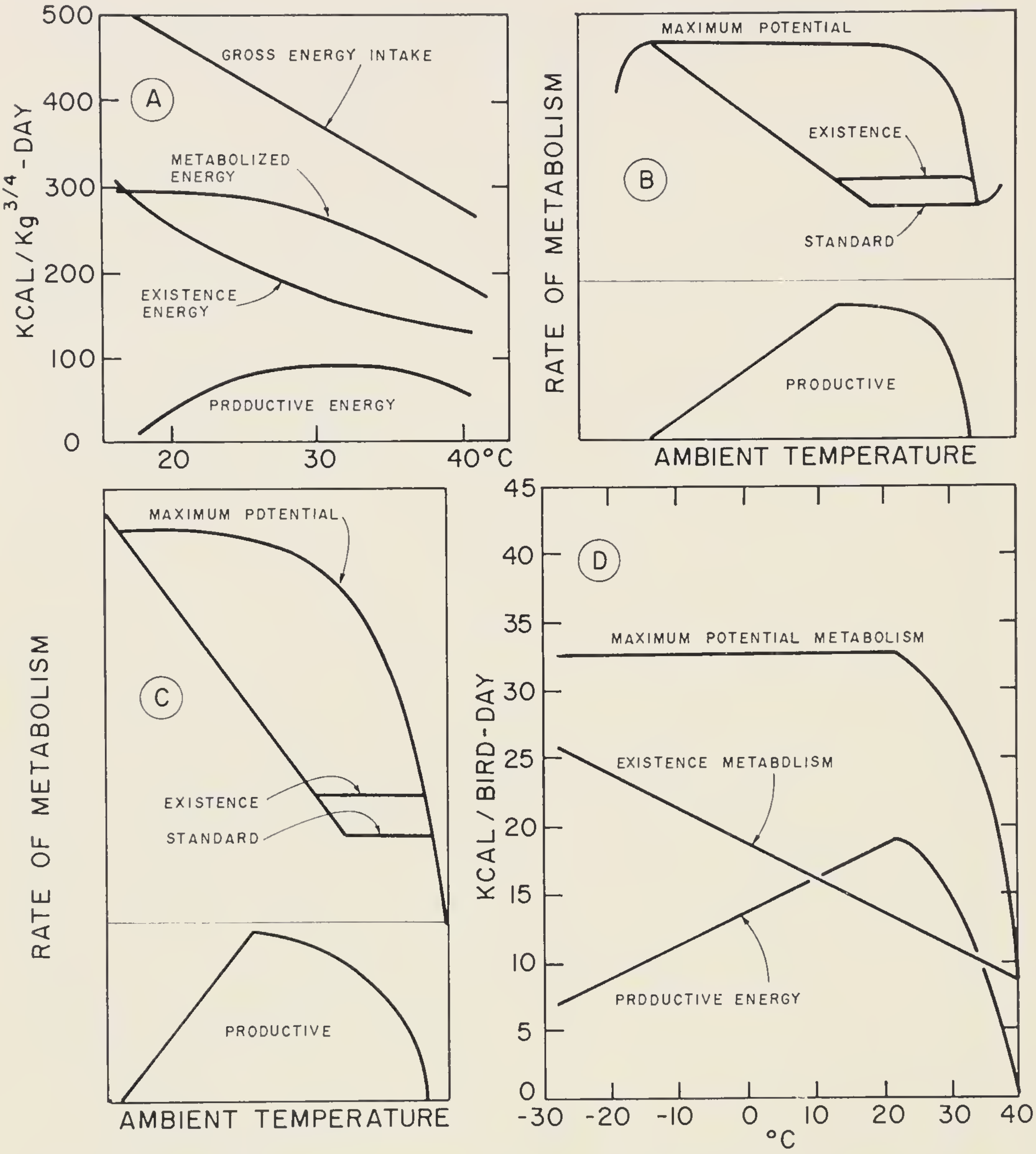


FIG. 1. Physiological models of previous workers: (A) Kleiber and Dougherty (1934) for baby chicks, (B) King and Farner (1961), (C) Kleiber (1961), and (D) West (1960) for the Tree Sparrow. These figures and terminology have been modified from the originals to make them comparative to Figure 2. It should be understood that A is for growing chicks while in the other models the birds are maintaining constant weight.

Body temperature is unaffected by fluctuations in medium ambient temperatures, and in several passerine species standard temperature, or core temperature at standard metabolism, averages about 40.5°C (Baldwin and Kendeigh, 1932). Winter acclimatized caged House Sparrows do not live indefinitely at temperatures below about –35°C, and there is a

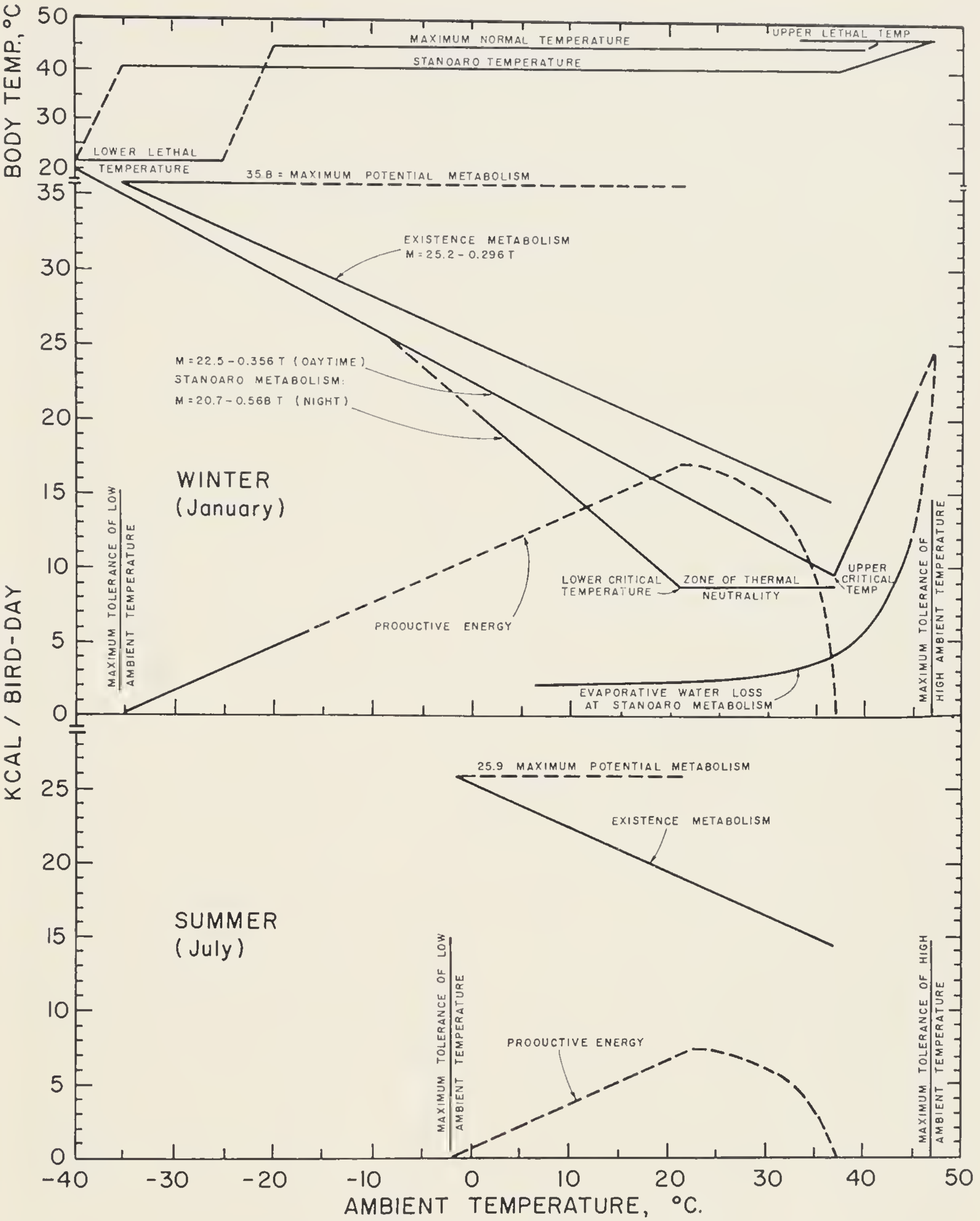


FIG. 2. Energetics of the House Sparrow: full lines are based on experimental data, broken lines on extrapolations or calculations.

drop in body temperature until death (Giaja and Gelineo, 1933). The House Wren (*Troglodytes aedon*) may recover from a body temperature of 23.7°C but dies at 21.7°C. At the other extreme, a body temperature of 46.8°C is fatal (Baldwin and Kendeigh, 1932), this commonly occurring at ambient temperatures between 42° and 47°C.

When extremely excited or active, body temperatures in passerine species may rise to 45°C. The margin between 45° and the upper lethal temperature (1.8°C) is narrower than between the standard temperature and lower lethal temperature (18.8°C). Kontogiannis (1968) has shown for the White-throated Sparrow (*Zonotrichia albicollis*) that birds subjected to forced activity, compared with quiet birds, tolerated 5°C less extreme high ambient temperature and about 15°C less extreme low ambient temperature. The same relation in the House Sparrow would mean that deaths would occur at ambient temperatures of 42°C instead of possibly 47°C and hypothermy at –20° instead of –35°C (Fig. 2).

Existence metabolism is determined by measuring the amount of food consumed by caged birds over periods of three or four days while maintaining constant weight. The caloric equivalent of the excreta voided is subtracted from the caloric equivalent of the food consumed to give the actual energy metabolized (Kendeigh, 1949; Davis, 1955). Existence metabolism increases linearly from the upper critical temperature of 37°C to the lower limit of temperature tolerance. There is no zone of thermal neutrality as shown in the models of Kleiber (1961) and King and Farner (1961) (Fig. 1). Existence metabolism at ambient temperatures above 37°C has not been studied in this species. Probably the birds become nearly or entirely aphagic as King and Farner (1961) suggest.

The slopes of the regression lines for existence metabolism and daytime standard metabolism converge, in agreement with Rubner's (1910) law of compensation. The difference in elevation of the two lines is accounted for by the heat increments of feeding (specific dynamic action) and cage activity. According to Rubner's "law," the heat increment of feeding contributes toward temperature regulation at low ambient temperatures. This heat is not available in the fasting bird, hence standard metabolism must increase more rapidly at low temperatures to compensate for the absence of the specific dynamic action. That the two lines do not actually intersect within the range of tolerated ambient temperatures may be due to the heat production of the cage activity being additive rather than compensatory (Kontogiannis, 1968).

Maximum potential metabolism occurs at the lower limit of temperature tolerance. Hypothermy and eventual death develops at lower ambient temperatures because heat production cannot be increased sufficiently to balance heat loss. Recent experiments demonstrate that this same maximum energy can be mobilized at 18° higher temperature under stress of forced exercise (Kontogiannis, 1968) and presumably it could also be mobilized for other purposes. West's (1960) diagram is confusing because existence energy is drawn for birds on a 10-hour photoperiod and the maximum potential metabolism is shown for birds on a 15-hour photoperiod involving nightly activity.

Existence metabolism subtracted from this maximum metabolism gives the potential *productive energy* available for other functions, such as locomotor activity, reproduction, molt, etc. The potential amount of productive energy available, as calculated for caged birds, increases linearly with rise in ambient temperature (Fig. 2), except that at very high temperatures the bird comes under heat stress and is not able to utilize all of this potential energy.

The maximum ability of birds to utilize their potential productive energy at high ambient temperatures may be indicated by the extent of their daily changes in weight. Birds decrease in weight between the time they stop feeding in the evening and begin feeding in the morning and gain in weight during the daytime. White-throated Sparrows, both those given a standard amount of forced exercise at night and those resting quietly on their roosts, varied least in weight between the late afternoon maximum and the early morning minimum at 22°C than at any other temperatures (Kontogiannis, 1968). Research now in progress indicates that this may also be true for the House Sparrow. Hence 22°C may represent the ambient temperature at which the species can carry on its activities most effectively. Although this temperature was not precisely determined, its apparent agreement with the lower critical temperature of thermal neutrality may be significant. Kleiber (1961) indicates maximum usable productive (net) energy as occurring at the lower critical temperature of well fed birds but below the lower critical temperature of birds at standard metabolism (Fig. 1). West (1960) estimated maximum productive energy as occurring within the range of 20° to 25°C. Calculations from King and Farner's (1961) figure indicate that productive energy would be maintained at a maximum level from the lower critical temperature of well fed birds well into the zone of thermal neutrality.

The daily fluctuation of weight is greater at low ambient temperatures because of the increased energy utilization for heat production and consequent greater depletion of body fat reserves. The greater daily fluctuation of weight above 22°C is because of increased vaporization of moisture from the respiratory tract for temperature regulation. Kontogiannis (1968) has shown that exercised birds utilize more water at these high temperatures because of the extra heat production of muscular activity and consequently cannot tolerate as extreme high ambient temperature. The decrease in work capacity between 22° and 37°C is probably inversely proportional to the increasing need for evaporative cooling and the energy expended to bring this about. West (1960), Kleiber (1961), and King and Farner (1961) all agree that there can be no sustained activity above the upper critical temperature, 37°C in the House Sparrow, without hyperthermy occurring.

The rate of evaporative cooling has been measured in the House Sparrow with birds at the resting standard metabolic level (Kendeigh, 1944) and is shown in Figure 2. These measurements were made at a relative humidity of about 18 per cent, hence at a high vapor pressure gradient between the evaporative surfaces of the bird and the environment. At the higher relative humidities of the species' natural environment, the vapor pressure gradient would be decreased, evaporative cooling would be more difficult, and the curve would be shifted downward on the temperature scale. Likewise the increase in rate of water loss as the result of activity, noted above, would shift the curve downward.

The regression lines for evaporative cooling loss and standard metabolism above 37°C were fitted to the measured data by eye, and the great variation in the data do not give their precise slopes statistical significance. It is of interest, however, that their intersection comes at the extreme upper limit of temperature tolerance, 47°C, where ambient temperature equals body temperature and all heat production in the bird can be lost only by evaporative cooling. Perhaps this precise agreement of points is fortuitous, but it emphasizes the basic principles involved.

In order to obtain a first approximation of utilizable productive energy or work capacity at high ambient temperatures, the curve of evaporative water loss was shifted 10°C down the temperature scale so that the precipitous increase in water loss comes at 37° instead of 47°C. The reciprocal of this curve, or its mirror image, was then drawn between 22° and 37°C to indicate work capacity. The accuracy of these energy relations at high temperatures should of course be tested by experimentation.

Potential productive energy is reduced during the summer in this species as the maximum energy which it is capable of metabolizing for existence is approximately 25.9 kcal instead of 35.8 kcal/bird-day (Fig. 2). Perhaps such seasonal changes in energetics are typical of permanent resident species in temperate zones. House Sparrows do not tolerate ambient temperatures much below 0°C in the summer compared with –35°C in mid-winter (Kendeigh, 1949; Davis, 1955). Maximum productive energy at 22°C will therefore be 7.2 kcal instead of 17.1 kcal/bird-day. There is no evidence that the upper critical temperature changes appreciably from 37°C throughout the year. Actually the greater potential productive energy available at 22°C is seldom realized during the winter because this ambient temperature is seldom reached. Using mean monthly temperatures, Davis (1955) calculated that the productive energy available to the bird is approximately 7.5 kcal/bird-day throughout the year, but further study may show that this figure is not a constant.

Energy balance is the relation between energy intake and outgo, the latter being the existence and productive levels already considered. If the total energy metabolized is less than the intake, the bird draws upon its reserves, loses weight, and dies. On the other hand, when intake is greater than outgo, there is deposition of energy, partly carbohydrates but mostly fats, and the bird gains weight. When a drop in ambient temperature persists over one or more days, the gain in weight with feeding during the daytime becomes greater than the loss at night, so that an increase in weight occurs until a new balance is attained (Kontogiannis, 1968). In permanent resident species, bird weights during the winter average higher than during the summer; in the House Sparrow this amounts to six per cent (Davis, 1955).

Gross energy intake may vary in total amount and rate dependent on photoperiod. In the House Sparrow, the average daily amount of food consumed at five different temperatures (0°–34°C) was nearly identical on a 10-hour and 15-hour photoperiod but on the 10-hour period the hourly rate was 31.5 per cent higher (Kendeigh, 1949; Davis, 1955). The amount of feeding during the daytime is determined largely by the amount of energy lost during the preceding night that needs to be replaced (Kontogiannis, 1968) and not by the number of daylight hours available for feeding. However, long photoperiods are usually correlated with greater amounts of activity and longer maintenance of high body temperature, so one would expect a greater total amount of food consumption. In other species where a significant difference between the two photoperiods can be demonstrated, the greater food consumption on the longer photoperiod is never, however, proportional to the increased number of daylight hours. One would also expect greater tolerance of extremely low ambient temperatures on a long photoperiod, both because it allows the bird a longer time for feeding and because the period of darkness when it cannot feed is shorter. However, the difference in tolerance is small or absent (West, 1960; Cox, 1961; Zimmerman, 1965).

Not all energy taken in as food is digested nor is all the energy that is absorbed from the alimentary tract actually metabolized. As yet, no attempt has been made to determine the loss of energy in the digestive tract to bacteria but the percentages due to these losses are probably very small. There appears to be no significant loss of energy in gases voided (Blem, 1968). The *metabolic coefficient* (metabolized energy/gross energy intake) in the House Sparrow at low temperatures, 0°–10°C, averaged 77.4 per cent on the 10-hour photoperiod and 83.8 on the 15-hour photoperiod, while at 18°–34°C the coefficients were almost identical averaging 80.8, not significantly different from 83.8 (Kendeigh, 1949; Davis, 1955). The higher coefficient on the longer photoperiod and at higher temperatures may result from a slower movement of food through the digestive tract.

Several physiological variables shown in Figure 2 are of ecological importance. The species extends northward to central British Columbia and Saskatchewan, northern Manitoba and Ontario, and southern Quebec. The mean monthly temperature in January at Churchill in northern Manitoba is –28°C with a photoperiod of only 7 hours and 18 minutes, and the species is probably able to survive the frequently lower daily temperatures that occur because it utilizes the local grain elevators for shelter and food. In June the photoperiod reaches 18 hours and mean monthly temperatures in July climb to +12°C. If the species loses as much of its tolerance to cold during the summer at Churchill as it does farther south it would have only about 4 kcal/bird-day available for reproduction, although 7.5 kcal is required (see above). Very probably the seasonal loss of temperature tolerance is not so great as at southern latitudes. Hudson and Kimzey (1966) have demonstrated a geographic difference in the standard metabolism of House Sparrows, and a recent study in my laboratory shows geographic differences in existence metabolism, seasonal variations in the limits of temperature tolerance, and other parameters. (Charles R. Blem, Ph.D. thesis.)

In the other direction, the species' range extends to the shores of the Gulf of Mexico and the West Indies. Mean July temperatures are about 28°C with maxima to 38°C (Reichelderfer, 1941).

In Illinois, near the center of its range, the species begins nesting in April when the normal mean monthly temperature is about 11°C and continues at an accelerated rate into the summer while mean temperatures go to 24°C. This range of temperatures on either side of 22°C would seem optimum for reproduction. Toward the periphery of the species' distribution, abundance decreases, correlated with temperatures falling either too far below 22°C or going too far above.

The determination of these variables in other species may go far towards giving an understanding as to what limits distribution and controls time of nesting and migration, extent of reproduction, etc. Thus, there is no seasonal change in the lower limit of temperature tolerance (–28°C) in the migrant Tree Sparrow, a species that nests abundantly at tree line in northern Canada (for instance, Churchill, Manitoba) and winters in the northern States. Compared with the 7.5 kcal/bird-day of productive energy available to the House Sparrow (27–29 grams) throughout the year, the Tree Sparrow, a smaller bird (18–20 grams), has from 8 kcal in the winter to as much as 12 kcal/bird-day in the summer (West, 1960). It appears a more efficient metabolic machine in harmony with its more northern nesting distribution and its common occurrence in open country throughout the winter.

SUMMARY

Critical features of ecological significance in the energy balance of the House Sparrow include 1) the lower limit of ambient temperature tolerance (–35°C in winter, –2°C in

summer) where existence metabolism is maximum (35.8 kcal in winter, 25.9 kcal/bird-day in summer), 2) the temperature at which there is the greatest work capacity (22±°C, the lower critical temperature), 3) the potential productive energy available throughout the year (7.5 ± kcal/bird-day), 4) the upper critical ambient temperature (37°C) beyond which activity leads to hyperthermy, and 5) the extreme upper limit of ambient temperature tolerance (47°C). This information correlates well with the apparent environmental control over distribution, time of nesting, and extent of reproduction.

LITERATURE CITED

Baldwin, S. P., and S. C. Kendeigh. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 3.

Blem, C. R. 1968. Determination of calorie and nitrogen content of excreta voided by birds. Poultry Sci., 47:1205–1208.

Cox, G. W. 1961. The relation of energy requirements of tropical finches to distribution and migration. Ecology, 42:253–266.

Davis, E. A., Jr. 1955. Seasonal changes in the energy balance of the English Sparrow. Auk, 72:385–411.

Giaja, J., and S. Gelineo. 1933. Sur la résistance au froid de quelques homéothermes. Arch. intern. Physiol., 37:20–34.

Hudson, J. W., and S. L. Kimzey. 1966. Temperature regulation and metabolic rhythms in populations of the House Sparrow, *Passer domesticus*. Comp. Biochem. Physiol., 17:203–217.

Kendeigh, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English Sparrow. J. Exp. Zool., 96:1–16.

Kendeigh, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk, 66:113–127.

King, J. R., and D. S. Farner. 1961. Energy metabolism, thermoregulation and body temperature. *In* A. J. Marshall, Biology and Comparative Physiology of Birds, II, 215–288.

Kleiber, M. 1961. The fire of life. John Wiley & Sons, New York.

Kleiber, M., and J. E. Dougherty. 1934. The influence of environmental temperature on the utilization of food energy in baby chicks. J. Gen. Physiol., 17:701–726.

Kontogiannis, J. E. 1968. Effect of temperature and exercise on energy intake and body weight on the White-throated Sparrow, *Zonotrichia albicollis*. Physiol. Zool., 41:54–64.

Reichelderfer, F. W. 1944. Climate and man. U. S. Dept. Agr. Yearbook: 705, 706.

Rubner, M. 1910. Über Kompensation und Summation von funktionellen Leistungen des Körpers. Sitzungsber. Konigl. preuss. Akad. Wissensch., 16: 316–324.

West, G. C. 1960. Seasonal variation in the energy balance of the Tree Sparrow in relation to migration. Auk, 77:306–329.

West, G. C., and J. S. Hart. 1966. Metabolic responses of Evening Grosbeaks to constant and to fluctuating temperatures. Physiol. Zool., 39:171–184.

Zimmerman, J. L. 1965. Bioenergetics of the Dickcissel, *Spiza americana*. Physiol. Zool., 38:370–389.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS, CHAMPAIGN 61820. 19 FEBRUARY 1968.

MORTALITY OF COOTS DURING SEVERE SPRING WEATHER[1]

LEIGH H. FREDRICKSON

AMERICAN Coots (*Fulica americana*) suffered extensive mortality in Iowa during severe spring weather in 1964. On 5 March, coots were first sighted on Little Wall Lake near Jewell (Hamilton County) after a period of warm weather freed the lakes of ice. No accurate counts were made of coot numbers, but thousands were present in central Iowa by 25 March when the minimum temperature suddenly dropped to about 10° F for six days (U.S. Weather Bureau, Climatological Data, Iowa Section 75:224, 1964). Many lakes refroze and hundreds of coots on Little Wall Lake and other Iowa marshes died during the cold weather. The first indication of extensive coot mortality on Little Wall Lake was encountered 30 March when large numbers of dead birds were found along the edge of the small area of open water. Some were frozen in the ice, others were dead on shore, and several weakened birds could not fly. On 31 March and 1 April, 235 dead coots were collected and placed in a freezer at Iowa State University. Similar mortality of coots and Anatidae was reported on several lakes in northern Iowa, and 64 coots were collected from Trumbull Lake in Clay County by Glenn Jones of the Iowa State Conservation Commission.

Coots were stored in a freezer until examined. Birds were weighed to the nearest gram. Breast contours were classified (from drawings) in three categories: rounded, v-shaped, or sharp. The gizzard was removed and opened, and the presence of food, lead shot, and grit was recorded.

RESULTS

Frequency distribution of weights of coots collected during the die-off is shown in Fig. 1. The mean weight of male birds was 419 grams, compared with a mean of 341 grams for females (Table 1). Although coots were not collected in a normal spring for a comparison of body condition, weight data are presented on 47 coots taken during the 1964 waterfowl hunting season. Weights in the fall were nearly twice the weight of birds collected during the spring die-off. The extreme difference in weight was indicative of the emaciated condition of the ice-trapped coots. There appear to be no data in the literature on weights of coots in spring, but winter weights taken in California by Gullion (J. Wildl. Mgmt. 7:191–197, 1943) are similar to weights of birds collected in the fall in Iowa. In California, the mean weight of coots in winter was 598 grams (range = 379–666) for females and 706 grams (range = 567–829) for males.

---

[1] Journal Paper No. J-5860 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project 1504.

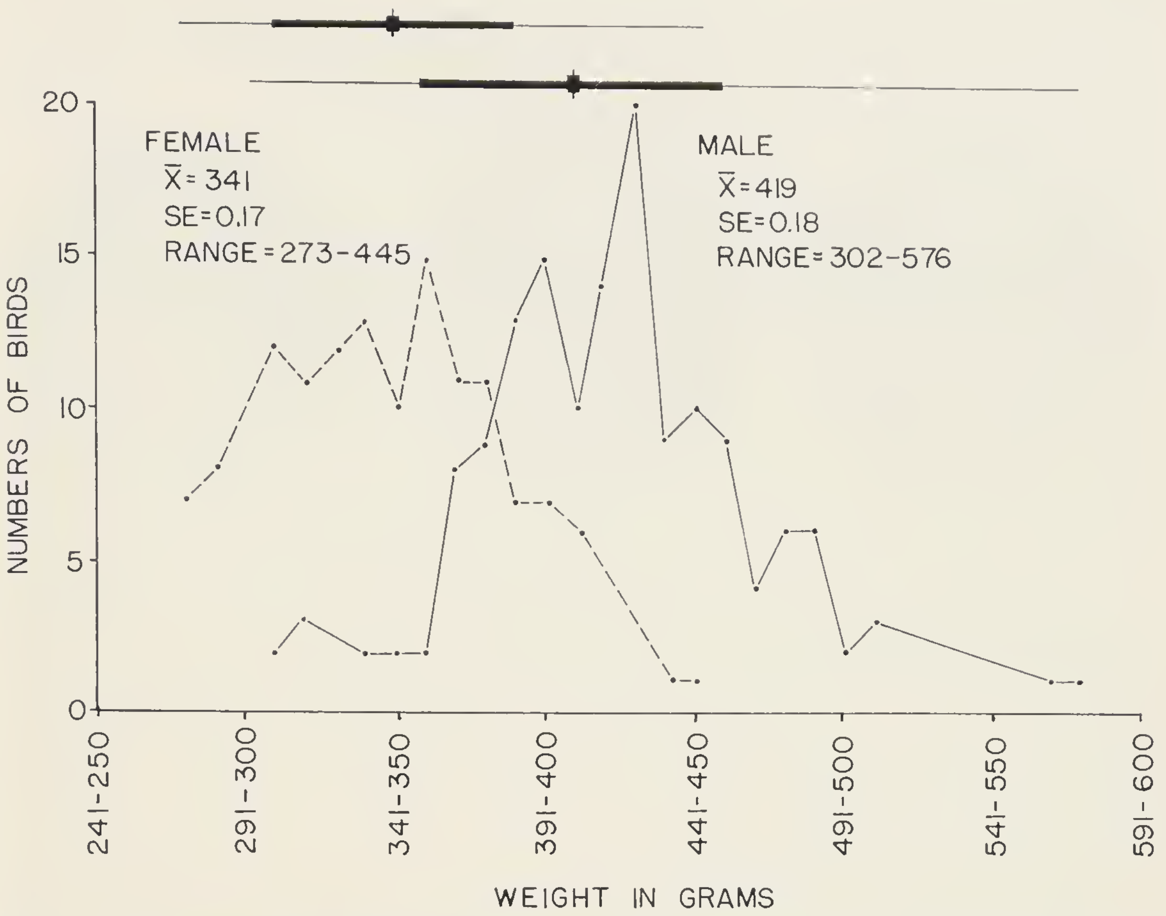


FIG. 1. Frequency distribution of weights of American Coots which died during severe weather, based on 141 females and 150 males.

Only 10 per cent of 293 coots collected during the spring die-off in Iowa had rounded breast contours (Fig. 2). Thirty-one per cent of coots of both sexes had v-shaped contours. The remaining 59 per cent of the birds had a sharp contour suggestive of utilization of breast muscle, indicating that over half were suffering from severe starvation. On the basis of breast

TABLE 1

COMPARISONS OF AVERAGE WEIGHTS (GRAMS) OF COOTS OF BOTH SEXES THAT DIED DURING ADVERSE WEATHER IN SPRING WITH THOSE COLLECTED DURING THE FALL WATERFOWL SEASON

(Ranges are shown in parentheses)

	Spring		Fall	
	139 Males	149 Females	27 Males	20 Females
Weight	419* (302–576)	341 (273–445)	725 (576–848)	560 (427–657)

* Mean

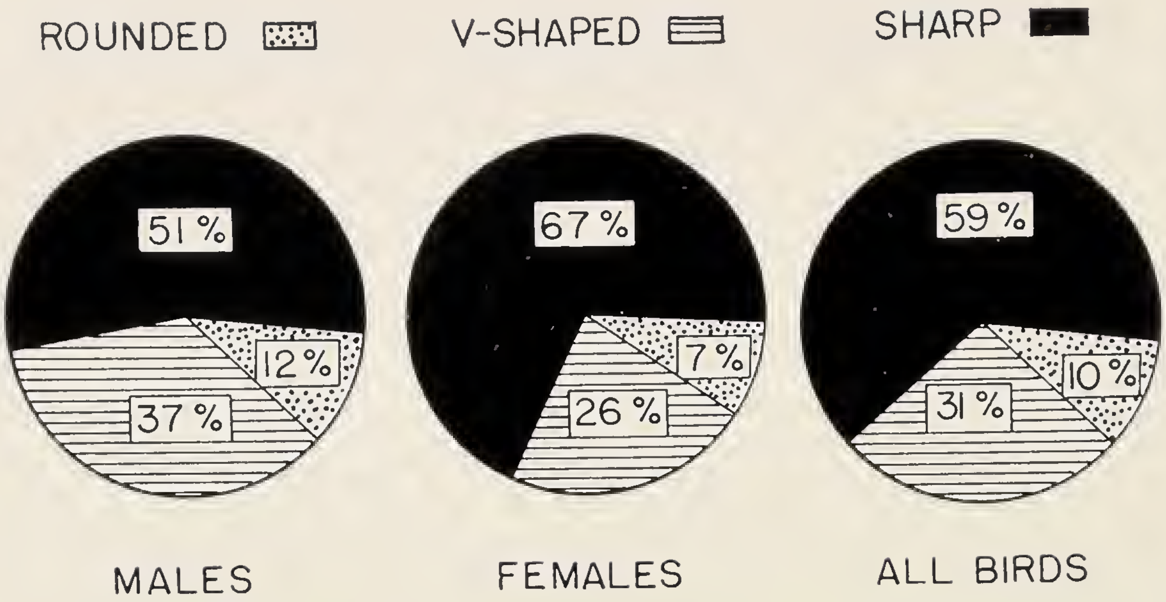


Fig. 2. Per cent of three types of breast contours found on 293 coots (141 females and 152 males) following a period of severe weather.

contours, females appeared more emaciated than males. Females had 16 per cent more sharp contours, 11 per cent fewer v-shaped contours, and five per cent fewer rounded contours.

On the average, male coots that died in the spring were 306 grams (42 per cent) lighter than those collected in fall. Females averaged 219 grams (39 per cent) lighter in spring than in fall. The sex ratio of the entire population in spring was unknown, but the sexes were almost equally represented among the dead birds (48 per cent males). Assuming that birds of both sexes arrived concurrently, they lost about the same percentage of body weight as they starved. However, as females apparently utilized a higher proportion of breast muscle than did males, the manner in which weight was lost differed by sex.

All gizzards contained grit, and all were free of lead shot, indicating that lead poisoning was not a factor in the die-off. Although 92 per cent of the gizzards contained some food, large quantities of food were never present. *Scirpus* seeds were found most commonly. No heavy helminth infestations were noted.

DISCUSSION

The high mortality experienced by coots during the abnormal period of freezing temperatures probably resulted from several factors. Coots in spring migration do not appear to return south to avoid adverse weather. Unseasonably cold temperatures refroze much of the water along the shallow shores, which restricted coots to feeding in deep water where submergent vegetation was scarce. Because of snow and cold, upland areas were devoid of grasses normally used as food. In addition, the plumage of coots may not provide adequate protection during prolonged periods of cold weather. Although no information is available on heat loss in Rallidae, it seems possible that an unusually large caloric intake may be necessary for survival during severe weather. This combination of factors probably induced starvation and the severe mortality. This die-off provides an example of the climatic limitations that affect the evolution of the chronology of spring migration.

ACKNOWLEDGMENTS

Milton Weller and Frederick Vande Vusse assisted with field collections and laboratory examination. Many students at Iowa State University provided assistance throughout the study. Thomas Neal, Douglas Thompson, Dale Hein, David Roslien, Jerry Horak, and Gerald Kaufman deserve special thanks. Thomas Baskett and Milton Weller made helpful suggestions on the manuscript.

DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, IOWA STATE UNIVERSITY, AMES, IOWA. (PRESENT ADDRESS: GAYLORD MEMORIAL LABORATORY, UNIVERSITY OF MISSOURI, PUXICO, MISSOURI), 2 FEBRUARY 1968.

NEW LIFE MEMBER

Dr. Alice M. Briant, Emeritus Professor at Cornell University has recently become a Life Member of the Wilson Society. Dr. Briant holds degrees from McGill University and Cornell University. She is a member of Sigma Xi and Phi Kappa Phi. Her interests in ornithology have been those of a serious amateur student, and she has other hobbies in travel, and a variety of handcrafts.

UNUSUAL NESTING HABITATS OF THREE BIRD SPECIES IN RONDEAU PROVINCIAL PARK, ONTARIO

Walter P. Nickell

Rondeau Provincial Park in Kent County, Ontario, consists of a total area of 11,450 acres. About 5000 acres consists of a triangular peninsula with its base and sides along the shores of Lake Erie and its apex about six miles to the north. The remaining 6450 acres consist of buttonbush, cattail, a phragmites marsh, and the open waters of Rondeau Bay. The larger portion of the 5000-acre land area consists of an unusual distribution of mature beech-maple forest transected by a number of parallel, narrow, tree-filled sloughs (Fig. 1). These sloughs and higher ridges represent successive old beach lines, which were formed when Lake Erie was higher than at present. Running parallel with these sloughs are old, narrow roads, over which maple sap was hauled in the past.

Many of the larger broad-leaved trees in Rondeau Park, such as beeches, maples, and tulip poplars, are up to four feet in diameter as this portion of the park was never systematically logged. Pines, walnuts, and other valuable trees were logged in the 1800's, but since the park was set aside in 1894 little but salvage cutting has been permitted, according to Richard Ussher, present naturalist in the park. Apparently, the most recent cutting has been largely in the sloughs where Dutch elm disease has killed many of the elms. Within recent years the old access roads have been allowed to grow up in small trees and shrubs, so that the forest canopy is closing over them.

I carried out studies both during and after the nesting season in the park from the fall of 1952 through the nesting season in 1954. A total of about 150 hours during 22 days were occupied with finding, tagging, and collecting nests. The longest continuous period spent in the park was from 15 June to 27 June 1954, when Dr. William B. Stapp and I worked from dawn to dusk in all parts of the land area, including the buttonbush and other types of marshes. During this period 242 active nests of 24 species were found and studied.

In low trees with canopies of wild grapes along these roads and into the adjacent sloughs and forest nest the Catbird (*Dumetella carolinensis*) and the Yellow Warbler (*Dendroica petechia*). In these same habitats as associates and extending into the understory of the thick forest nest such species as, in order of abundance, the American Redstart (*Setophaga ruticilla*), the Wood Thrush (*Hylocichla mustelina*), the Veery (*Hylocichla fuscescens*),

FIG. 1. Section of Beech-Maple Forest in Rondeau Park, Ontario.

the Prothonotary Warbler (*Protonotaria citrea*), and several less numerous species.

In this situation the Brown-headed Cowbird (*Molothrus ater*) is found in considerable abundance, parasitizing at least 10 other species. The Cowbird is more generally distributed in all types of habitats than are the Catbird and the Yellow Warbler, being found in the densest part of the beech-maple understory as well as in the narrow edge areas along the roads and sloughs. I have found no mention in the literature of these three species nesting in mature beech-maple habitats.

Although the mature beech-maple habitat for these three species differs markedly from the usual ones, several factors common to the habitats of the three species are present. These are adequate edge, density of foliage at the immediate nest site, and proximity to wet situations. I believe that low wind velocity in such a protected area is another favorable factor. I have often observed that many small birds apparently avoid building nests in shrubbery or trees along the edges of large bodies of water or other exposed situations where winds are often strong and continuous for long periods.

According to my survey, the Yellow Warbler was the most abundant nesting species in the park in 1954. A total of 207 nests of this species was found in both the smaller and larger beech-maple portion and in the buttonbush marshes among the colonies of Red-winged Blackbirds (*Agelaius phoeniceus*). Table 1 shows the sites of 207 nests of this species and the

TABLE 1
SITES OF 207 YELLOW WARBLER NESTS IN RONDEAU PARK

Plant Species	No. Nests	% of Total	Avg. ht. in feet	% parasitized
Wild grape (canopies)	45	22	7.4	18
Sugar maple	32	15	6.0	38
Beech	9	4	10.6	44
Gray dogwood	32	15	5.1	0
Buttonbush	9	4	5.0	0
Red raspberry	28	14	2.8	39
Meadowsweet	16	8	3.8	13
Miscellaneous (16 sp.)	36	17	5.0	25
Total	207	100	5.7	20.3

degree of Cowbird parasitism. Note that no Cowbird eggs or young were found in the 41 nests (nearly 20 per cent) with sites in gray dogwood and buttonbush. This lack of parasitism appears to be due to the presence of a number of Red-winged Blackbirds which were nesting in the same area. Bent (1953:174) states that Dr. George M. Sutton found only one parasitized nest out of 43 in Pymatuning Swamp, Pennsylvania. Sutton stated that this was due "to the protection against these parasites afforded by the Red-winged Blackbirds which would not tolerate a Cowbird anywhere about the marshes." On several occasions in recent studies of Yellow Warblers and Traill's Flycatchers I have found a very low degree or no parasitism where these birds were nesting along with Red-winged Blackbirds in the marshes.

Of the 200 Catbird nests found in the park (Table 2) 161 (80 per cent) were placed in species of trees and shrubs characteristic of the beech-maple complex. The other 20 per cent were built in trees and shrubs, including hawthorn and gray dogwood, outside the mature forest. Wild grapes, listed

TABLE 2
SITES OF 200 CATBIRD NESTS IN RONDEAU PARK

Plant Species	No. Nests	% of Total	Avg. ht. in feet	% parasitized
Wild grape (canopies)	132	66	7.6	0
Beech	14	7	5.2	0
Sugar maple	9	5	7.1	0
Hawthorne	7	4	5.4	0
American hornbeam	6	3	7.3	0
Miscellaneous (13 sp.)	32	16	6.1	0
Total	200	100	7.1	0

TABLE 3

SITES OF 123 AMERICAN REDSTART NESTS IN RONDEAU PARK

Plant Species	No. Nests	% of Total	Avg. ht. in feet	% parasitized
Sugar maple	64	52	8.9	16
Beech	10	8	6.5	20
Wild grape (canopies)	15	12	9.6	0
Ashes (sp.)	8	7	6.2	0
Ironwood	4	3	10.0	50
Miscellaneous (15 sp.)	22	18	6.4	14
Total	123	100	8.2	13.8

as sites for 66 per cent of these nests, were growing as canopies on saplings of typical beech-maple forest species, mostly beech, sugar maple, and basswood. No cowbird's eggs or young were found in any Catbird nests in the park. This species is generally intolerant of interference by the parasite and normally punctures and removes the Cowbird's eggs.

The third most abundant species in the park (Table 3), and a close nesting associate of the other three, is the American Redstart. One hundred twenty-three nests of this species were found. A comparison of the vegetation in which the nests were found shows 93 nests (76 per cent) were in four species which are characteristic of beech-maple forests. This habitat is more normal for the Redstart. The lack of Cowbird parasitism in wild grape canopies and ash trees is something for which I have no explanation, in that Yellow Warblers in the same situation showed 18 per cent parasitism. However, a total parasitism for the Yellow Warbler was 20.3 per cent, while the total parasitism for the Redstart was 13.8 per cent.

DISCUSSION

The question arises as to the factors involved in the appearance of the Yellow Warbler, Catbird, and Brown-headed Cowbird in a habitat such as has been described. Richard Ussher, in detailing some of the history of the park (Judd and Speirs, 1967:167–169), states that "White-tailed deer have played a prominent part in the recent life of the park" and for a period of 30 years (1912–1942) seedlings of most species of trees and undergrowth were destroyed by deer browsing. This, of course, opened up most of the understory of the park to such species as the three in question. as did the old sugar roads and the dying of many of the trees in the sloughs. About 1,800 deer were shot in the park during this 30-year period, reducing the herd to approximately 100 head at the present time. Since 1942 much of the understory has grown back and the forest canopy has gradually closed over the more open areas. All three species normally are found in much more open areas, and in such open areas bear about the same relationships to one another as they do in Rondeau Park.

It is probable that the Cowbird entered the region in which Rondeau Park is located at about the same time it entered much of Ohio and southern Michigan, about a 100 years ago or a little more. Mayfield (1960:145) states that in the first check-list of the birds of Ohio (1838) the Cowbird was admitted to the catalogue on somewhat doubtful authority. Further, he states that in the first check-list of the birds of Michigan for the southern portion of the state, Sager (1839) listed the Cowbird without comment, and that Fothergill's careful notes on birds seen in southern Ontario did not record the Cowbird in 24 years of field work there (1817–1840). Friedmann (1929:150) states that "deforestation has not been the only factor resulting from civilization that has been instrumental in enlarging the range of the cowbird, although it unquestionably has been the most potent one." Further, he states that "another factor synchronous with the deforestation and settling of the country was the added impetus for the cowbird to wander beyond its former limits, supplied by the presence of cattle on the newly cleared homesteads. The cowbird originally attended and followed the herds of buffalo, and possibly the antelope and other large game."

It appears probable that the Cowbird, Yellow Warbler, and Catbird actually entered the mature forest in Rondeau Park at about the same time (1912–1942) during the previously mentioned period of overbrowsing by white-tailed deer, to which the Cowbirds transferred their relationship from the cattle in the surrounding farmlands. Only very recently, as far as I can find in the literature, has the white-tailed deer been mentioned as a substrate-host of the Cowbird. McNeil (1967:37) describes having seen Cowbirds perched on the backs of deer and walking the full lengths of their backs on several occasions in 1965 and 1966 in Roscommon County, Michigan. He clinches his observation with a photograph of a Cowbird perched on the back of a white-tailed deer. In recent conversation with the naturalists in Rondeau Park they informed me that they had several times seen Cowbirds associating with deer in the park, and had seen them perched on the animals' backs on several occasions.

It will be interesting to know whether these three species (Yellow Warbler. Catbird, and Cowbird) maintain their numbers, or whether they will gradually disappear as the forest canopy covers and shades their present habitat in the future.

LITERATURE CITED

Bent, A. C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.

Friedmann, H. 1929. The Cowbirds. Charles C. Thomas, Springfield, Illinois.

Judd, W. W., and J. M. Speirs. 1967. A naturalist's guide to Ontario. Univ. Toronto Press, Toronto.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

McNeill, R. 1967. Cowbirds and white-tailed deer. Jack-Pine Warbler, 45:37.

CRANBROOK INSTITUTE OF SCIENCE, BLOOMFIELD HILLS, MICHIGAN, 48013, 2 FEBRUARY 1968.

NEW LIFE MEMBER

A recent addition to the roll of Life Members of the Wilson Society is Dr. Larry C. Holcomb, Associate Professor of Biology at Creighton University. Dr. Holcomb is an alumnus of Olivet College and holds two graduate degrees from Michigan State University. His scientific interests include the behavior and physiology of bird reproduction, the development of structure and behavior, and the origin of cowbird parasitism, and he has published 30 papers in ornithology and mammalogy. Dr. Holcomb is currently president of the Nebraska Ornithologists Union, and is a member of several scientific societies including the A.O.U., the Cooper Society, and the Ecological Society. He is married and has five children.

NEW LIFE MEMBER

Dr. William F. Davis, a surgeon of Ashtabula, Ohio has recently become a Life Member of the Wilson Society. Dr. Davis is a member of the A.O.U., the American Society of Mammalogists, and the Ottawa Field-Naturalists Club. His ornithological interests extend to ecology and nesting behavior, and he has published papers in these fields. He is also interested in botany and mammalogy. After graduating from Michigan State College with a major in wildlife management his interests turned to medicine and he holds an MD. degree from Ohio State University.

GENERAL NOTES

Birds of St. Giles Islands, Tobago.—The St. Giles Islands (= Melville Islands), at 11° 21′ N, 60° 31′ W support one of the most important seabird breeding colonies in the southern West Indies. The group consists of the 75-acre St. Giles Island, ½ mile off the northeast coast of Tobago, and several small outlying rocks. All are steep-sloped and rocky, the highest point being just over 350 feet, and are covered with thick masses of cactus, low brush, and trees, some as tall as 30 feet. None has a steady source of fresh water.

The seas around St. Giles are rough much of the year and landing is hazardous, a small cove at the west end of the main island being the only accessible point. Once on the island the thick vegetation and steep slopes make it difficult for a person to get to lower slopes where some seabirds nest.

Mr. Charles Turpin of Charlotteville, Tobago, longtime owner of the islands, recently offered them to the Government of Trinidad and Tobago on condition that they be maintained as a wildlife sanctuary and properly wardened. On 26 April 1968, St. Giles and all adjacent islands were proclaimed the St. Giles Game Sanctuary and closed to landing without special permission.

Protection may reduce the poaching by local people. Frigatebirds probably suffer most but boobies, terns, and perhaps other species are affected. As the St. Giles Islands contain the only nesting colonies of Magnificent Frigatebirds (*Fregata magnificens*) and Red-footed Boobies (*Sula sula*) in Trinidad and Tobago, their continued existence in this country is dependent on effective protection at St. Giles.

Several ornithologists have visited the islands and published records of the birds found there. E. A. Armstrong (1947) wrote briefly of his visit to the islands on 23 March 1932, and C. F. Belcher (Belcher and Smooker, 1934, 1935) visited the islands on 27 March 1932. L. Brown (1947, in litt.) visited the islands on 2 February 1940. Recent summaries of the avifauna of Trinidad and Tobago (Junge and Mees, 1958; Herklots, 1961) apparently have relied mainly on Belcher's observations. Much remains to be learned about the birds of the St. Giles Islands, especially the timing of the nesting cycles of the seabirds and the status of several species, notably *Sterna dougallii*, *S. anaethetus*, and *Larus atricilla*.

Since 1958 we visited the islands separately seven times and noted a total of 34 species. On 4–5 April 1958 ffrench spent 31 hours there; he visited them on 3 April 1959, 10 April 1963, and 21 August 1968. He was accompanied by D. W. and B. K. Snow in 1959 and by M. ffrench in 1959, 1963, and 1968. Dinsmore circled the main island by boat on 9 and 23 October 1965 and landed there on 4 May 1966. Most of our observations pertain to the main island of the group.

Our observations are mainly of seabirds but we also recorded the land birds we saw. The proximity of Tobago facilitates passage between it and St. Giles, and doubtless other land birds and some shorebirds visit the islands. We have used the nomenclature given by Meyer de Schauensee (1966).

Mr. Turpin generously gave us permission to land on the island. Dinsmore's stay in Tobago was financed in part by the Forestry Division, Ministry for Tobago Affairs and by graduate fellowships from the University of Wisconsin, Madison.

Audubon's Shearwater (*Puffinus lherminieri*).—ffrench found both eggs and small young in early April. Dinsmore found a young bird just starting to get flight feathers and otherwise covered with gray down on 4 May 1966. Neither of us was able to estimate numbers but ffrench heard many adults on the night of 4 April 1958 and the colony must number in the hundreds.

Red-billed Tropicbird (*Phaethon aethereus*).—On 3 April 1959, ffrench photographed an adult with one egg and saw several other nests. He saw several adults but no nests on 21 August 1968. Dinsmore saw this species on all three visits but found no nests. Belcher and Smooker (1934) listed *P. lepturus* nesting on the island, but neither of us has seen this species in the area (ffrench, 1961; see also Bond, 1962). Brown (1947) also saw *aethereus* here. Perhaps 200 tropicbirds nest on the islands.

Red-footed Booby (*Sula sula*).—Several hundred Red-footed Boobies frequent the islands, building their nests 8–12 feet up in the low trees on St. Giles and several of the outlying rocks. Both color phases are present, the brown with a white tail comprising over 90 per cent of the birds. They seem to have an extended nesting season. ffrench found all stages from eggs to nearly fledged young on all of his visits in early April, and all nests he examined on 21 August 1968 had eggs. Dinsmore saw downy young in October and downy to nearly fledged young in May. Belcher saw eggs on 27 March 1932 and Brown (1947, in litt.) saw nests with single eggs or downy chicks on 2 February 1940. Thus eggs apparently hatch any time from August to April and perhaps for a longer period.

Brown Booby (*Sula leucogaster*).—Although not so abundant as the previous species, the Brown Booby is common on St. Giles. It too has an extended breeding season although peaks of hatching seem to occur in early fall and again from February through March. Belcher and Smooker (1934) say that many young were away from the nests by 27 March 1932. Brown (in litt.) found this species nesting on 2 February 1940. ffrench found many nests containing eggs on 21 August 1968.

Magnificent Frigatebird (*Fregata magnificens*).—Perhaps 2000 frigatebirds nest or roost at St. Giles. ffrench found both eggs and young in April 1958 and 1959 but on 10 April 1963 he could locate only a few young birds in the nest. On 21 August 1968 he saw no nests but did see ballooning males. Dinsmore saw only young capable of flight on 4 May 1966. Armstrong (1947) saw well-grown young in late March while Belcher and Smooker (1934) report eggs on 27 March 1932. Brown (1947, in litt.) found eggs or occasionally small young on 2 February 1940. Poaching may affect the size of the colony considerably as the local people raid it for both eggs and young birds.

Yellow-crowned Night Heron (*Nyctanassa violacea*).—ffrench saw one adult on the island on 10 April 1963 and another 21 August 1968.

Black Vulture (*Coragyps atratus*).—Dinsmore saw one circling over St. Giles on 4 May 1966 and a vulture was reported at St. Giles during the summer of 1965. ffrench saw one over the island on 21 August 1968. Although this species is abundant on Trinidad, it was unknown on Tobago until recently. Herklots (1961) reports the birds being recently introduced to Tobago (about 1959) and the local story is that they were released there by people filming a movie for Walt Disney.

Peregrine Falcon (*Falco peregrinus*).—ffrench saw one in April of 1958 and 1959.

Laughing Gull (*Larus atricilla*.)—ffrench saw many flying by the islands in April and a few there on 21 August 1968. Dinsmore saw 300–400 there on 4 May 1966. They may nest on St. Giles although we have not found eggs or young. Belcher and Smooker (1935) reported “many” on St. Giles on 27 March 1932 and seeing many flying in that direction on 23 June 1934.

Roseate Tern (*Sterna dougallii*).—Dinsmore saw white *Sterna* terns around St. Giles on 4 May 1966. On 2 June he landed on a rocky slope on Tobago just opposite St. Giles and found downy young and eggs. About 200 adults were present with a steady line returning to the colony carrying fish in their bills. Unfortunately no specimen was collected. On 30 April 1967 ffrench and C. T. Collins saw adult Roseate Terns carrying fish toward the location of the 1966 colony but rough seas prevented them from locating the colony. ffrench saw a few *dougallii* near St. Giles on 21 August 1968. Thus it seem likely that the 1966 birds were *dougallii* in which case it would be the first nesting record for Trinidad and Tobago. Still the status of this species is uncertain and needs clarification.

Bridled Tern (*Sterna anaethetus*).—Dinsmore saw several fly out from low on the steep slopes of St. Giles on 4 May 1966. ffrench saw several, including some in immature plumage, along the coast on 21 August 1968. They may nest on St. Giles but we have found neither eggs nor young.

Sooty Tern (*Sterna fuscata*).—We both have found this species common around St. Giles in April and May and ffrench saw a few as late as 21 August 1968. It may nest here but we have not searched suitable nesting habitat at the probable time of nesting (April–June).

Brown Noddy (*Anous stolidus*).—At least 1000 noddies frequent the island, nesting in the low trees and thick masses of cactus. ffrench found many nests with eggs on all of his April visits. Dinsmore found several nests on 4 May 1966, most with eggs but one containing a young bird just hours old. He saw only a few in the area in October 1965. ffrench found them still abundant on 21 August 1968 and behavior suggested they may have been nesting but he didn't see any active nests. Belcher and Smooker (1935) reported it breeding here in April.

Pale-vented Pigeon (*Columba cayennensis*).—We both found this species fairly common on the island. ffrench found nests with eggs on 21 August 1968.

Ruddy Ground-Dove (*Columbina talpacoti*).—Dinsmore saw several on 4 May 1966.

White-tipped Dove (*Leptotila verreauxi*).—ffrench saw a few on each of his visits and found a nest with 2 eggs on 21 August 1968.

Smooth-billed Ani (*Crotophaga ani*).—We both have seen this species on St. Giles, 15–20 being present on 4 May 1966. Armstrong (in litt.) saw this species there in March 1932.

Copper-rumped Hummingbird (*Amazilia tobaci*).—ffrench saw one on 4 April 1958.

Tropical Kingbird (*Tyrannus melancholicus*).—ffrench saw several on 21 August 1968.

Brown-crested Flycatcher (*Myiarchus tyrannulus*).—ffrench saw several on each of his April visits.

Fuscous Flycatcher (*Cnemotriccus fuscatus*).—ffrench and Snow saw one at St. Giles on 3 April 1959 and ffrench saw two on 21 August 1968. It is common in similar dry habitat on the northwestern peninsula of Trinidad and the Bocas Islands off Trinidad.

Yellow-bellied Elaenia (*Elaenia flavogaster*).—ffrench saw several in April 1958 and 1959.

Caribbean Martin (*Progne dominicensis.*)—ffrench saw a few over St. Giles in April 1958 and 1959 and 21 August 1968.

Barn Swallow (*Hirundo rustica*).—ffrench saw one on 4 April 1958.

House Wren (*Troglodytes aedon*).—Both of us found this species common on the island. ffrench saw an adult feeding a young Shiny Cowbird (*Molothrus bonariensis*) on 21 August 1968.

Tropical Mockingbird (*Mimus gilvus*).—Both of us found this species abundant on St. Giles and saw it on all of our visits.

Bare-eyed Thrush (*Turdus nudigenis*).—ffrench saw one on 5 April 1958.

Northern Waterthrush (*Seiurus noveboracensis*).—ffrench saw one on 10 April 1963.

Shiny Cowbird (*Molothrus bonariensis*).—ffrench saw this species on 5 April 1958, 10 April 1963, and a young bird being fed by a House Wren on 21 August 1968.

Crested Oropendola (*Psarocolius decumanus*).—ffrench saw about 20 on the island on 5 April 1958.

Bananaquit (*Coereba flaveola*).—We both have noted this species on the island. ffrench found it nesting on 4 April 1958 and 21 August 1968.

Blue-gray Tanager (*Thraupis episcopus*).—ffrench found a dead chick on the ground on 21 August 1968.

Blue-black Grassquit (*Volatinia jacarina*).—ffrench saw several on 21 August 1968.

Yellow-bellied Seedeater (*Sporophila nigricollis*).—ffrench heard a male singing on St. Giles on 21 August 1968.

Although most of the land birds we saw at St. Giles are common in Trinidad and Tobago, the seabirds have a more restricted distribution. Red-footed Boobies and Magnificent Frigatebirds nest only at St. Giles. The Audubon's Shearwater, Red-billed Tropicbird, Brown Booby, Laughing Gull, Roseate Tern, Bridled Tern, Sooty Tern, and Brown Noddy all occur along the coast of Tobago or nearby islands during the breeding season and the last two also nest on Soldado Rock west of Trinidad.

LITERATURE CITED

ARMSTRONG, E. A. 1947. Bird display and behaviour. Oxford Univ. Press, New York.

BELCHER, C., AND G. D. SMOOKER. 1934. Birds of the colony of Trinidad and Tobago. Ibis, 1934:572–595.

BELCHER, C., AND G. D. SMOOKER. 1935. Birds of the colony of Trinidad and Tobago. Ibis, 1935:279–297.

BOND, J. 1962. The hypothetical element of the avifauna of Tobago. Caribbean J. Sci., 2:113–118.

BROWN, L. 1947. Birds and I. Michael Joseph, London.

FFRENCH, R. P. 1961. The Red-billed Tropic-bird. J. Trinidad Field Naturalists' Club, 1961:9–10.

HERKLOTS, G. A. C. 1961. The birds of Trinidad and Tobago. Collins, London.

JUNGE, G. C. A., AND G. F. MEES. 1958. The avifauna of Trinidad and Tobago. Zool. Verhandl., 37:1–172.

MEYER DE SCHAUENSEE, R. 1966. The species of birds of South America and their distribution. Acad. Nat. Sci., Philadelphia, Penna.

—JAMES J. DINSMORE, *Department of Zoology, University of Wisconsin, Madison, Wisconsin (Present address: Department of Zoology, University of Florida, Gainesville, Florida)*, AND RICHARD P. FFRENCH, *St. Peter's School, Texaco Trinidad Inc., Pointe-a-Pierre, Trinidad, 2 November 1968.*

Glossy Ibis taken in Indiana.—On 17 April 1968, Lehman saw two Glossy Ibises (*Plegadis falcinellus*) feeding in a small, muddy pond in a cow pasture a mile northeast of Francesville, Pulaski County, Indiana. Later in the day, Lehman, Russell R. Hyer, and Harold Grimmett returned and watched the birds, sometimes from a distance of only 20 feet. Lehman saw them again the next morning; that afternoon Hyer, Lehman, Warren S. Rowe, Duane Shroufe, and Mumford visited the site and Mumford collected one. The second bird flew a half mile and alighted at another pond. The specimen is a non-fat, adult female, which weighed 506 grams and contained ova up to 5 mm in diameter. It has been deposited in the United States National Museum (No. 531517), where Roxie C. Laybourne verified the identification. This is the first glossy ibis taken in Indiana, but an adult was observed 20 May 1962 at Indianapolis (Keller, C. E., Indiana Audubon Quarterly, 44:55–86, 1966).

We thank John O. Whitaker, Jr., who identified the contents of the gizzard and proventriculus of the collected specimen as follows: earthworms, 45%; flesh (fish ?), 7%; vegetable matter (mostly tubers of an aquatic plant), 15%; snails, 3%; fairy shrimp, 25%. Considerable bluish-gray mud was also present. Seven mallophaga from the bird were determined by Roger D. Price to be *Colpocephalum leptopygos*; we thank Price for his determination and Nixon A. Wilson for forwarding the parasites to him. —Russell E. Mumford and Larry E. Lehman, *Department of Forestry and Conservation, Purdue University, Lafayette, Indiana, and Department of Natural Resources, Jasper-Pulaski Fish and Game Area, Medaryville, Indiana, 23 October 1968.*

Breeding status of Whistling Swans near Churchill, Manitoba.—Bent (U.S. Natl. Mus. Bull., 130, Part II. 300, 1925) and the AOU Check-list of North American birds (1957) do not list the Whistling Swan (*Olor columbianus*) as a nesting species in the Churchill area. However, Godfrey (The birds of Canada, 1966) reported that nesting occurred but did not give information on the nesting status of the species.

From late May through August 1968, while employed as biologists with the Manitoba Department of Mines and Natural Resources, we noted swan numbers and nests while conducting surveys for nesting Canada Geese (*Branta canadensis*). Aerial surveys by helicopter were conducted 25 and 27 June, and daily from 16 through 20 July. Ground and aerial surveys were also conducted on 20 May, 9 June, 18–22 June, 22 July, and 17 August in the Churchill and Cape Churchill areas.

Twenty-five adult swans summered in the area in 1968. Sixteen, or 65 per cent, of these birds were known to have nested, with eight nests being located. Four of eight nests contained four eggs, while the clutch size of the remaining four was not determined. Seven nests were followed through the study period.

Highest nesting density was from 5 to 10 miles south of Cape Churchill, but nesting pairs ranged from Gordon Point, 12 miles east of Fort Churchill, to 43 miles south of Cape Churchill, near Thompson Point. All nests were within 1 mile of the Hudson Bay coastline. On 11 June, a single low-flying swan was seen 48 miles south of Churchill, near Fletcher Lake. On 22 July, a pair of swans was observed in the same area, but no nests or young were located.

Measurements of two nests and their contents were recorded. Both were in similar habitat and consisted of the following measurements.

Nest 1.—Nest materials consisted of 40 per cent sedge (*Carex* spp.) and 60 per cent unidentified mosses. Measurements were as follows: eggs—109.4 × 68.9, 108.8 × 67.9, 108.2 × 68.6, 106.3 × 68.0 mm; nest base diameter—164.0 × 190.0 cm; nest height—282.5 mm; nest cup depth—142.5 mm; cup base diameter—18.5 cm; nest crown diameter—90.0 × 42.9 cm. This nest was located on a peninsula in a lake of approximately 15 acres. One side of the nest was surrounded by willows (*Salix* spp.), while open water and scattered sedge occurred on the remaining three sides.

Nest 2.—Nest materials consisted of dried mosses, sedges, and unidentified grasses. Measurements are as follows: eggs—108.1 × 69.9, 107.5 × 71.0, 104.4 × 69.5, 101.3 × 67.7 mm; nest base diameter—160.5 × 140.0 cm; nest height—220.0 mm; nest cup depth—140.0 mm; cup diameter—47.6 × 42.9 cm; cup base diameter—20.5 cm; nest crown diameter—80.0 × 84.0 cm. The nest was among 6-inch-tall willows, grasses, and sedges and was located 2 inches from a temporary 8- × 6-foot pool. The nearest permanent water was 35.7 meters northeast of the nest site and consisted of approximately 12 acres.

Vegetation used in nest construction had been pulled from a area 1 to 2 meters around the site.

During incubation, only one pair occupied a lake, pond, or slough. Shortly after hatching the young left the nest, and broods were occasionally seen near other family groups. On 17 August, two pairs, each with three young, were sighted on Norton Lake, approximately 18 miles east-southeast of Fort Churchill. One pair, with their young, apparently had traveled at least 2 miles overland from their nesting site.

Of six broods observed following incubation, five contained three young, while one consisted of four young. One clutch was destroyed by an arctic fox (*Alopex lagopus*), while the fate of the remaining nest was not determined.

Although the number of breeding Whistling Swans located in the Churchill area represents a small percentage of the total North American population, they were common in 1968 where suitable habitat existed. Future studies will have to determine if the local population is decreasing, static, or increasing.

We are indebted to Clait E. Braun and Dr. Ronald A. Ryder, Colorado State University, for help in the preparation of this note.—ALLAN J. PAKULAK AND CARROLL D. LITTLEFIELD, *Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80521, 25 November 1968.*

Eider hatching goose egg.—On 23 June 1967 I found a nest of a Common Eider (*Somateria mollissima*), containing four Eider eggs and one egg of a Blue Goose (*Chen caerulescens*). The incubating Eider appeared to be the sole inhabitant of an island 40 meters in diameter, situated in the South Branch Delta of the McConnell River, N.W.T. (60° 50′ N, 94° 25′ W). Only 11 other Eider nests were located in the 6 sq km delta and six of these were on one island. The Delta represents a peripheral breeding area of the McConnell River Blue Goose colony: not more than 200 Blue Goose nests were located here and none was within one quarter km of the Eider nest described above.

The Eider and her brood left the nest, located in the middle of the island, at noon on 9 July and swam towards an adjacent island 60 m distant, where I was observing from a tower 4 m in height. On land the four young Eiders had difficulty keeping up with the hen. They ran after her, flapping their wings for balance but falling every few meters. As a result they were strung out behind the hen over a distance of two–three meters. The blue-phase Blue gosling, on the other hand, walked beside and sometimes in front of the hen, feeding as it moved. When in the calm water between the two islands the gosling and Eiders experienced no difficulty in keeping up with the hen.

Upon arriving at a pool on the tower island the hen and her young immediately entered the water and began to swim rapidly about while feeding below the surface. The gosling remained out of the water, feeding on sedge (*Carex* sp.). When the family moved to another island on their journey down the Delta they crossed at the bottom of a riffle and swam obliquely up it against the current. Here the gosling was at a disadvantage. The Eiders, when falling far behind the hen, "hydroplaned" back up to her. The gosling, however, was unable to keep up and continually trailed the last Eider.

Later when the family left an island at the top of a very fast, choppy, riffle the gosling did not enter the water. Instead it ran along the bank paralleling the course of the Eiders. Seconds later the hen, followed by her brood, swam back to the island but the gosling did not join them in the water. Eventually the Eiders moved down the riffles staying as close to the bank as possible, and the gosling followed. At the end of the island the gosling jumped off the bank and joined the family in the still water. At this point the gosling appeared to be wet and tired. It trailed the family as they headed to the next series of riffles and disappeared from sight.

The above incident has shown that a newly hatched Blue Goose gosling lacks the swimming ability, in fast water, of newly hatched Common Eiders and is unable to adapt itself to their mode of feeding.—BERNARD C. LIEFF, *Department of Zoology, University of Western Ontario, London, Ontario, 28 October 1968.*

Shell color of eggs laid by yearling, 2-, and 3-year-old Pheasants.—In an earlier paper (Wilson Bull., 78:379, 1966), we reported that the shell color of eggs laid by individual yearling Pheasants (*Phasianus colchicus*) varied noticeably. Further investigation revealed that the shell color of eggs laid by these same hens as 2- and 3-year-olds showed similar seasonal variation.

Mean eggshell color changed with increasing breeding age for some Pheasant hens but not for others (Table 1). The eggs laid by hens 335 and 345 showed considerable variation in mean shell color between successive years whereas those eggs laid by hens 337 and 340 showed no deviation in mean shell color from year to year. The degree of purity in the shell color of eggs laid by individual Pheasants in successive years was a more stable character than was hue (and strength of hue).

Although eggshell color is generally thought to be genetically controlled (Labisky and Jackson, op. cit.), it is obvious that the expression of the genotype in Pheasants is dependent on environmental factors and is subject to modification with age.—RONALD

TABLE 1

MEAN SHELL COLOR OF EGGS LAID BY INDIVIDUAL PHEASANTS AS YEARLING, 2-, AND 3-YEAR-OLD BREEDERS IN 1964, 1965, AND 1966, RESPECTIVELY*

	Age of Hen					
Hen	Yearlings		2-Year-Olds		3-Year-Olds	
335	14-E-6†	(47)‡	15^s-G^s-10^s	(74)	—	
337	13-D-3	(78)	13-D-3	(86)	—	
340	12-C-2	(84)	12-C-2	(98)	12-C-2	(95)
342	13-E-5	(104)	13-F^s-5	(122)	13-F-5	(94)
343	13-E-5	(65)	13-F-5	(82)	—	
344	13-E-5	(88)	13-E-6^s	(84)	—	
345	12-C-2	(43)	13-E^s-3^s	(99)	12-C^s-1^s	(74)

* All hens were maintained individually in outdoor cages at Urbana, Illinois, and were fed a standard ration and water, ad libitum.

† Color values are expressed according to the system of Maerz and Paul (A dictionary of color, 1950). The numerals preceding the letter refer to the plate numbers in the orange to yellow color group, which contains eight plates (Nos. 9–16). The plates progressively designate decreasing degrees of purity (e.g., increasing amount of gray), reflecting 86 (Plate 9), 74, 67, 48, 38, 28, 20, and 10 (Plate 16) per cent light, respectively. Each plate is divided into 12 columns (lettered A–L) and 12 rows (numbered 1–12), and shows 23 analogous hues corresponding to the squares in the far right column (L) and in the bottom row (12). Each hue, at its level of purity, is thus expressed in 12 degrees of strength, grading from full strength at the terminal position (lower right) to no hue (upper left). Thus, the letter and following numeral measures hue and its strength. A numerical system was derived so that the differences for each value of mean color could be compared statistically between successive years. The superscript *s* denotes a significant shift ($P < 0.05$) in color value from the previous year.

‡ The numbers of eggs laid by each hen are in parentheses.

F. Labisky and Gary L. Jackson, *Section of Wildlife Research, Illinois Natural History Survey, and College of Veterinary Medicine, University of Illinois, Urbana, Illinois 61801, 1 November 1968.*

The drowning of Bobwhites in a large reservoir.—Establishment of the causes of natural mortality in animal populations is a vital but perplexing problem. The following observations illustrate a dramatic, but probably not unusual demise of Bobwhite (*Colinus virginianus*) living in proximity to a large reservoir.

A covey of 20 Bobwhites was found drowned in Bull Shoals Reservoir, Arkansas, 11 October 1966, by the writers while engaged in limnological studies. Evidently these birds mistakenly landed in the water when confused by a dense early morning fog. They were first observed at about 09:00 when visibility was poor. Examination of several of the birds showed no rigor mortis, bright clear eyes, but no body heat. The water temperature was 68°F and the air temperature 38°F.

Approximately 10 miles from the location of the covey, a single drowned Bobwhite was observed about 200 yards from shore. This bird was fresh but stiff. The time was then 11:30, the fog had burned off and the air temperature had risen to 75°F. One-half hour later 20 bodies, now stiff, were re-examined floating in the water about 50 yards off a small point. Scavengers at the scene included three Crows and three Turkey Vultures.

Discussion with two fishing guides disclosed that on three occasions over a 10-year period they had rescued groups of four to ten live Bobwhites from the reservoir under similar conditions.

Arkansas-Missouri Ozark impoundments are frequently shrouded in dense morning fogs in the fall, resulting from slow cooling combined with windless nights and bowl-type basins. The surrounding hardwood-covered ridges do not support dense Bobwhite populations, but the scattered coveys are attracted to shoreline areas where annual plants are dominant and tree growth is held in check by infrequent fluctuations in water level. Although the breadth of this area between the top of the flood control pool and the top of the normal power pool is limited, its edge effect is large. At Bull Shoals it amounts to 740 shoreline miles, or to an area about one-half that of the 45,440-acre reservoir itself. Thus it can be seen that the potential for Bobwhite drownings under such circumstances is large whereas the chance of observing such occurrences is small.—James W. Mullan *(Present Address: Bureau of Sport Fisheries, 95 South Vernal Avenue, Vernal, Utah)* and Richard L. Applegate (*Present Address: South Dakota Cooperative Fisheries Unit, South Dakota State University, Brookings, South Dakota*), *South Central Reservoir Investigations, Bureau of Sport Fisheries and Wildlife, Fayetteville, Arkansas, 5 July 1968.*

Renesting by Barn and Great Horned Owls.—In late March 1968, a pair of Barn Owls (*Tyto alba*) was found nesting in a cavity in the side of a 10 m deep irrigation ditch six miles northeast of Fort Collins, Larimer County, Colorado. Activities inside the shallow hole could be observed from the opposite bank. A spring snow storm accompanied by strong north winds partially filled the cavity with snow on 3 April. When I visited the site on 4 April, five eggs were visible half covered with snow. One adult was standing near the clutch in the 3 m × 0.5 m × 0.5 m hole. I returned on 10 April to observe an adult, assumed to be the female, apparently brooding while the original eggs were scattered about the cavity floor. On 20 April, I climbed to the nest for the first time. Both adults were in the hollow with five clean white eggs in a depression of broken pellets. Three of the darkened, cracked eggs from the initial clutch were pushed against the opposite wall. The second clutch contained eight eggs, all of which hatched.

East (Bird Lore, 32:4–7, 1930) observed a Barn Owl that incubated a clutch of infertile eggs three months before starting a new one. The Colorado birds evidently ceased incubating their frozen eggs and within six days began a replacement clutch.

I also observed renesting by Great Horned Owls (*Bubo virginianus*) caused by loss of the male early in incubation. A pair chose a cavity 8 m high in a large cottonwood (*Populus* sp.) located on the lawn of a rural home south of Fort Collins. They seemed relatively indifferent to the frequent human activities near them. On 16 February and subsequently the female sat in the cavity and the male roosted nearby. The male disappeared on 8 March and was not seen again. After four days of incubation following the male's disappearance, the female abandoned the eggs. It is not known if the female fed during this time. (The male supplies food to his mate during incubation, making his presence essential to success at least through that period.) After waiting several days, I examined the four eggs and found them to be fertile. Following 13 days of absence, a pair of owls returned to the nest site. Although the female had no distinguishing marks, she was assumed to be the original by her unconcern for human approach. This male, however, was obviously not the original for he was much more wary of human observers. A second clutch of two eggs was laid in the same cavity and both young fledged.

Renesting, at least in the same nest site, following an interruption of the nesting cycle apparently is unusual in owls. The Barn Owl, however, displays a very adaptable reproductive pattern and this may explain its ability to renest. A number of multiple broods have been reported (Wallace, Michigan Agr. Exp. Sta. Tech. Bull., 208, 1948; Stewart, Auk, 69:227–245, 1952; Morejohn, Auk, 72:298, 1955; Ames, Wilson Bull., 79: 451–452, 1967). Double, overlapping broods were observed in 1967 at this same Colorado nest site (Marti, Colorado Field Ornithol., 3:7–8, 1968). Ames (op. cit.: 452) suggests that this indicates a pair of Barn Owls may retain its breeding capability longer than most large raptors, and this facilitates production of second broods. It would facilitate renesting even more.

The Great Horned Owl seems to be less versatile in its reproduction. In this case, because interruption by loss of the male occurred early in incubation, the female's hormonal control may have had time to recycle, allowing her to find a new mate and start a second time. I know of no reported cases of renesting or of double broods in Great Horned Owls in this type of situation.

I would like to thank Dr. and Mrs. Robert D. Haberstroh for their cooperation in observing the Great Horned Owls noted in this paper.—Carl D. Marti, *Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80521, 20 January 1969.*

Foraging association of Green-barred Flickers and Campo Flickers in Argentina.—Approximately 10 observations were obtained of association in foraging between the more arboreal Green-barred Flicker (*Colaptes* [*Chrysoptilus* auct.] *melanochloros*, including the subspecies *nigroviridis*, *perplexus*, and hybrids between *melanochloros* and the former two races) and the terrestrial Campo Flicker (*Colaptes campestris campestroides*) in Argentina. These observations were made during September to November

1967, and September and October 1968, in the provinces of Formosa, Santa Fé and Corrientes. Both these species are entirely ant-feeding, *melanochloros* (most races) being primarily a tree forager and *campestris* almost exclusively a ground forager. This difference in feeding site is undoubtedly correlated with the widespread sympatry of these species, which approach each other in size. The southern races (regarded by some as comprising a species, *C. melanolaimus*) of *C. melanochloros* are restricted in distribution by the presence of trees, but they are not forest birds. Rather, they occur among scattered trees in open country and along the edges of various types of chaco woodland. Individual southern Green-barred Flickers primarily feed in trees, but they also often fly to the ground to forage.

My observations suggest that the abundance of ants and ant colonies in the areas where I have observed association of *melanochloros* and *campestris* is sufficiently great to render significant the number of observations of such associations. Indeed the figure of 10 given above is minimal because I also occasionally have observed wary individuals of *C. campestris* move from a spot where, on closer approach, I found a foraging individual of *C. melanochloros*; these instances are not included in the 10. I estimate having observed Green-barred Flickers foraging terrestrially about 30 times, in approximately half of which instances they were in association or suspected association with Campo Flickers.

Both flickers feed in the same manner on the ground, probing with their bills and plunging the bill deep into an ant colony in the manner of the North American *Colaptes auratus*. They differ strikingly in locomotion, however, for although Campo Flickers hop when progressing greater distances they walk about a feeding site. On the other hand the Green-barred Flicker progresses exclusively by hopping in the manner of *Colaptes auratus*. There appears to be no difference in food ingested by the two flickers at the mutual foraging sites. Specimens of both species were not obtained together at those sites, but comparison of the stomach contents of terrestrially feeding individuals suggests that both ingest ant eggs, larvae, and adults. Both flickers feed on the same species of ants at the foraging sites where they feed in association, for individuals of both were noted probing, one after another, into the same spot on one ant hill.

Other differences in habits between the two flickers are evident. The Campo Flicker is exceptionally wary and vocal, as well as social; three or even four adult birds may feed together. The Green-barred Flicker is much less vocal, and it seems less wary; at least this species is more often surprised by an approaching observer, and it shows less alarm when approached cautiously. Green-barred Flickers usually were encountered individually, but sometimes they were in pairs. One instance was noted in which four Campo Flickers and a pair of Green-barred Flickers foraged at a single ant hill. When together, interspecific individuals forage in as close proximity (within a foot or even less of each other) as do conspecific individuals.

I suggest that selection has favored this terrestrial foraging association by *Colaptes melanochloros*. This species, more arboreal than is *C. campestris*, probably benefits from association with individuals of the slightly larger, more wary, and certainly more terrestrially adapted Campo Flicker. The selection pressure favoring this association is probably predation selection; individuals of *melanochloros* feeding in the open with Campo Flickers are probably less vulnerable to predators than are individuals feeding alone.

The observations were made while I was engaged in field studies of woodpeckers supported by the National Science Foundation (grant NSF GB-5891), to the authorities of which I am grateful. I also thank my research assistant Mr. John J. Morony, Jr., who made some of these observations and otherwise aided me in the field. The taxonomy

used in this report is that resulting from studies of flickers (see Short, Bull. Amer. Mus. Nat. Hist., 129:307–428, 1965) and is to be used in my forthcoming monograph of the genus *Colaptes*.—LESTER L. SHORT, JR., *American Museum of Natural History, New York 10024, 8 January 1969.*

Red-bellied Woodpecker feeds Tufted Titmouse.—On 24 June, 1968, while watching the activities of a pair of adult Tufted Titmice (*Parus bicolor*) and their 3 recently fledged young in the Oliver's Woods Wildlife Preserve, located ½ mile south of the University of Oklahoma campus, I observed the following encounter between one of the fledglings and an adult Red-bellied Woodpecker (*Centurus carolinus*).

At 20:05, 53 minutes after the young birds had fledged, the family group was perched in a large elm tree 20 yards from the abandoned nest. An adult Red-bellied Woodpecker was foraging nearby and carrying food to a single fledgling of its own species which was perched in a tree adjoining the elm. On one trip back to its fledgling, and carrying what appeared to be a larval insect, the woodpecker landed about 18 inches from one of the fledgling tits. The tit immediately began to beg (wing flutter and call) and ran along the limb toward the woodpecker with his bill opened wide and his head and neck stretched forward. The woodpecker quickly moved backward several steps but the fledgling continued in pursuit, whereupon the woodpecker leaned forward and fed the tit.

The tit family group and the woodpecker were both active in the immediate area for the remainder of the day but no further encounters between the two were observed.—JAMES R. CURRY, *Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069, 26 September 1968.*

A Carolina Wren shadow-boxing.—On 21 August 1968 a Carolina Wren (*Thryothorus ludovicianus*) came to my window feeding-shelf, and soon seemed to notice its image in the pane. It stared toward that for some seconds, then, still staring, gave three bursts of song. Then it moved closer and after singing several more times gave the glass a number of sharp pecks. It flew away, in six minutes returned, stared again at the pane and gave it one peck, then left for good. On 18 October the same wren, presumably, came again and, before I accidentally frightened it away, sang four phrases while gazing at the pane. A few other times in 1968, between 22 June and 24 December, I saw a Carolina Wren on the feeder but it ignored the window. Likewise, the species has visited this feeder in other years, some color-banded birds over periods as long as three months, without ever being seen to shadow-box.

Possibly these comparatively unusual late-summer and fall instances of the behavior are related to the Carolina Wren's occupation of territory throughout the year (Laskey, Bird-Banding, 19:101, 1948), just as I have a number of August to January dates for the Cardinal (*Richmondena cardinalis*) and Mockingbird (*Mimus polyglottos*), which maintain year-round or winter territories—although I also have December dates for the House Sparrow (*Passer domesticus*) and Purple Finch (*Carpodacus purpureus*). No literature available to me records this behavior by any species of wren.—HERVEY BRACKBILL, *2620 Poplar Drive, Baltimore, Maryland, 8 January 1969.*

Robin kills snake.—On the afternoon of 20 June 1968, at a distance of about 25 yards, I saw an adult Robin (*Turdus migratorius*) kill a snake. The encounter took place in the bare wheel-track of a farm lane, which had grass in the center and at both sides. The Robin had apparently caught the snake crossing or sunning itself on the bare area. The snake was about as long as the Robin and was most likely a garter snake (*Thamnophis sirtalis*), which is the common species in the area.

When first seen, the snake was violently and erratically writhing on the ground and several times it abruptly raised the front third or half of its body off the ground. It was apparently having convulsions secondary to brain damage.

The Robin repeatedly pecked at the snake and several times jumped up and back as the snake's forceful movements carried it toward the bird or off the ground. The snake's movements finally ceased completely in response to the persistent attacks, whereupon the Robin gathered the snake up in two coils in its bill and flew away.

Bent, (U.S. Natl. Mus. Bull., 196:30, 1949) cites three reports of Robins killing snakes, and Netting (Wilson Bull., 81:470, 1969) lists three others.—William F. Davis, *423 West 46th Street, Ashtabula, Ohio 44004, 7 November 1968.*

Does the Robin Eat DeKay's snake?—The Robin is a common bird locally and DeKay's snake vies with the garter snake for the credit of being the most common snake within the city limits of Pittsburgh, Pa. It might be expected, therefore, that the interrelations of Robins and DeKay's snakes would be thoroughly known, yet such is far from the case. On 16 March 1935, Allan D. Kirk, of Forest Hills, collected, and subsequently donated to Carnegie Museum, a DeKay's snake (*Storeria d. dekayi*) (CM 8293) which had been seized by a Robin and then dropped after a few shakes. Shortly thereafter, in the hope of adding a new species to the Robin's menu, I caught a small DeKay's snake (as we called it in those days; its official common name now is northern brown snake) and endeavored to feed it to the Robins in my yard. This attempt was unsuccessful, but it bears repetition by persons with more patience, for the Robin is known to carry other small snakes to the nest and it is unlikely that the bird is able to distinguish species of small inoffensive snakes. Guthrie (Wilson Bull., 44:97, 1932) cites two references to Robins killing garter snakes, of 10 and 13 inches, but in one case the young were unable to eat the snake, and in the second instance feeding was not actually witnessed. Friedmann (The cowbirds:259–60, 1929) reports that a Robin fed a very young garter snake to a Cowbird, about 7 days old, which he had previously placed in the nest.—M. Graham Netting, *Carnegie Museum, Pittsburgh, Pennsylvania 15213, 30 December 1968.*

Recurrent use of territories by individual American Redstarts.—Previous studies of the American Redstart (*Setophaga ruticilla*) (cited in Yarrow, MS) have not dealt with banded populations. As a result, little is known about whether this species returns to the same territory in successive years. Using the predator-decoy method (R. Root and R. Yarrow, Auk, 84:423–424, 1967) I banded five adult redstarts during two seasons of field work in Renwick Bird Sanctuary, Ithaca, New York. Both adult males banded in 1965, each with a government band and two color bands, returned to the study area the following spring. They both defended territories adjacent to and somewhat overlapping the territories they had held the previous year. In 1967 and again in 1968, one of these males returned and appeared to defend the same area as in 1965. Redstarts may thus return at least four years in succession to virtually the same territory.—Ruth M. Yarrow, *Section on Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, New York, 14 August 1968.*

Unusual feeding behavior of three species of birds.—On 25 May 1958 I was attracted to a noisy Blue Jay (*Cyanocitta cristata*) outside my window in Irving, Dallas County, Texas. Upon investigation, a jay was seen flying away from an eave of the house where a number of wasps were angrily buzzing around a partially destroyed "live" nest. Although the jay was not seen actually feeding, the fact that it was seen flying away from the wasp nest, of which some of the cells showed the work of a bird's bill and removal of larvae, gave evidence of the jay's predation.

Summer Tanagers (*Piranga rubra*) have been frequently recorded preying on wasps (Hamaker, Auk, 53:220–221, 1936; Rau, Canadian Entomol., 73:196, 1941; Alvarez del Toro, Auk, 67:395, 1950), yet I know of no instances of Blue Jays doing so. Richard M. Bohart, Professor of Entomology at the University of California Agricultural Experiment Station, Davis, California, kindly identified the wasps in question as *Polistes exclamans*.

On 26 January 1959 I observed a number of meadowlarks (*Sturnella* sp.) feeding alongside the highway near the Irving city limits. The birds were confined to the edge of the road because of snow, although it is not unusual for this species to feed in this manner. One meadowlark was seen to walk up to a badly smashed dead striped skunk (*Mephitis mephitis*), peck at the animal and eat the flesh. Terres (Auk, 73:289–290, 1956) and Hubbard and Hubbard (Wilson Bull., 81:107–108, 1969) reported meadowlarks feeding on carrion including its own species.

Bent (U.S. Natl. Mus. Bull., 211, 1958) indicates that several races of the Common Grackle (*Quiscalus quiscala*) soften dry food by soaking it in water, but there apparently are no observations of this behavior cited for the Boat-tailed Grackle (*Cassidix mexicanus*). During the early summer of 1967, female Boat-tailed Grackles came repeatedly to a bird bath at my home and soaked dry dog food. At this time of the year, few grackles feed or water in my yard, so only one bird may have been involved. The observations were made from 9 June to 16 June and again for several days about a week later.

Similar behavior was described in a letter to the editor of the Dallas Times Herald on 3 June 1968. Pertinent parts of the letter are quoted: "I threw some stale bread outside yesterday and immediately a large brownish bird swooped down on it. After pecking at it and turning it over a few times, he picked it up and hopped over to a pan of water and dropped it into the water, turned it over a couple of times, then ate it. He did this until all the bread was gone." Since Boat-tailed Grackles are very common in the Dallas area, this casual observation in all likelihood was of a female or an immature bird of this species.

On 8 July 1968 Rev. Timothy Gollob observed a female Boat-tailed Grackle pick up dry bread and soak it before eating. He indicated that insects and table scraps were likewise treated.

It appears unlikely that soaking is associated with the feeding of young birds since only one date falls within the period (4 May–3 June) in which I banded nestling boat-tails in the Dallas area.

Rand (Wilson Bull., 79:455–456, 1967) raises the question whether or not Common Grackles learn this unique feeding habit. My observations show that the habit may be more common than is realized. It is not a widespread behavior, however, as I have repeatedly put out dry dog food in the winter without obtaining evidence of soaking at this time of the year.—Warren M. Pulich, *Department of Biology, University of Dallas Station, Texas, 75061.* *6 November 1968.*

ORNITHOLOGICAL NEWS

On 13 September 1969 the Cornell Laboratory of Ornithology awarded the third Arthur A. Allen Award to George M. Sutton.

The Bureau of Sport Fisheries and Wildlife dedicated the new quarters of The Migratory Bird Populations Station, to be known as the Gabrielson Laboratory on 11 October 1969. In celebration of the dedication a two-day symposium on Population Ecology of Birds was held.

The Cornell Laboratory of Ornithology sponsored a two-day research planning conference on Peregrines and other birds of prey on 4–5 November 1969. One of the principal goals of the conference was to organize a North American survey of Peregrine nests in 1970.

The dates for the 51st Annual Meeting to be held at Fort Collins, Colorado have been set as Wednesday, 17 June 1970 through Sunday, 21 June 1970. Most members attending the meeting will be housed in dormitories. Full details will be mailed early in 1970.

It is a pleasure to welcome Dr. Douglas A. James of the University of Arkansas as the newest member of the Editorial Board.

The Society's reserve supply of some recent issues of *The Wilson Bulletin* is inadequate. The supply of all issues of Volume 80(1968) is especially critical, but we also need additional copies of the March, 1963 issue. Members who do not keep all back issues will be doing the Society an important service by returning any of the above issues to: The Josselyn Van Tyne Memorial Library, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104.

As the final number of Volume 81 goes to press I again wish to acknowledge with gratitude and pleasure the cooperation of the many people whose assistance contributed to the success of the volume. As usual the members of the Editorial Board, and the Review Editor were unflagging in their services and assistance. The other officers of the Society have been a steady support to the publication. Special thanks this year go to Miss Mildred Stewart who is retiring after five year's service as indexer. This year, too, I want to give special appreciation to all those authors of papers who have been so unfailingly patient, despite the overly long delays in publication of their work.—G.A.H.

FROM THE AOU

At its annual meeting in Fayetteville, Arkansas on 1 September 1969 the AOU elected the following officers:

John W. Aldrich, President
Donald S. Farner, First Vice-President
S. Charles Kendeigh, Second Vice-President
Richard C. Banks, Secretary
Burt L. Monroe, Jr., Treasurer
Oliver L. Austin, Jr., Editor

The University Press of Kentucky has announced The Kentucky Fellowship, a $5,000 grant for the best work in progress on any aspect of ecology or conservation. The competition will run from November 1969 through October 1970. It will be open to any environmental scientist, humanist, social scientist, or anyone writing or researching a book-length study likely to make a valid and important contribution to man's understanding of his relationship to nature. Inquiries should be directed to The University Press of Kentucky, Lexington, Kentucky 40506.

The sum of $988.00 is available in the Josselyn Van Tyne Memorial Fund for research grants in 1970. Of this amount, $185.00 is reserved for research in systematics. Any student of birds is invited to apply for research grants. Young investigators just starting their careers or others not eligible for government grants are encouraged to apply.

Further information may be obtained from and applications should be submitted, not later than 1 April 1970, to Alan H. Brush, Chairman, A.O.U. Research Committee, Biological Sciences Group, University of Connecticut, Storrs, Connecticut, 06268.

LOUIS AGASSIZ FUERTES RESEARCH GRANTS

These grants, established in 1947, are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic organizations. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge.

An anonymous donor gave $500 to found the fund; later donors have provided additional money. The Council of the Wilson Ornithological Society has added funds as necessary to provide at least one $100 grant annually. Two grants have been made in several recent years. In 1970 a single grant of $200 will be made, although on occasion a second award of $100 has been given.

Although grantees are not required to publish their studies in *The Wilson Bulletin*, is is hoped that they will submit their manuscripts to the Editor of the *Bulletin* for consideration.

Since its inception, the Fuertes Research Grant has been awarded to 27 persons, many of whom have continued their research work.

Application forms may be obtained from Harrison B. Tordoff, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Completed applications must be received by 1 March 1970.

THE MARGARET MORSE NICE AWARD

This award, of $100 annually made possible by the generosity of an anonymous donor, is to be made to the candidate, not having any college or university affiliation, whose project is adjudged by the Research Committee to have the best potential of adding to the sum of ornithological knowledge. High school students are eligible. Applications for this award should be made before 1 March 1970 to Harrison B. Tordoff, Chairman of the Research Committee, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

ORNITHOLOGICAL LITERATURE

Birds of Surinam. By François Haverschmidt. Oliver and Boyd, Edinburgh, 1968: 8 × 11 in., xxix + 445 pp., 40 col. pls. and many figs. by Paul Barruel, 30 bl. and wh. photos, map. $37.50 (available in U.S.A. from Livingston Publishing Company, Narberth, Pennsylvania 19072).

This monumental and long-awaited volume represents the culmination of many years of fieldwork by the author, and is based on some 8700 specimens and extensive notes taken on the ecology and natural history of Surinam birds. The book opens with a short discussion of the topography and climatology of the country and is accompanied by ten full-page photographs of selected habitats. This is followed by a detailed historical account of the ornithological exploration of Surinam and the repository for major collections of specimens. This section will be particularly useful to researchers planning future explorations in this country and in the analysis of their results. Following this account are sections on "Bird Migration in Surinam," "Future Ornithological Research in Surinam," and "Conservation in Surinam." The last section includes a description of the present forest reserves and a list of "game" species. In the section on migration a list of "Migrants Visiting Surinam" is presented. It is pretty much of a catch-all list of 61 species (not 60 as stated on p. xxii) which are not known to breed in Surinam. It includes such obvious migrants as the numerous shorebirds which breed in Arctic areas and the several species known to nest in southern South America during the austral summer and which move North of the equator during the months of the southern hemisphere "winter." Strangely, *Chaetura andrei meridionalis* is mentioned in the text (p. 171) as being such a migrant but is omitted from this list. The list of "migrants" also includes several species of casual or rare occurrence in Surinam—e.g., the Green Heron (represented by only two specimens collected during the last century), as well as species which occur during all months of the year and are known to breed both to the north and to the south of Surinam—but for which no evidence presently exists for their actually breeding in Surinam. Thus many of the species on this list are not migrants in the usual sense of the word. The inclusion of other categories for some of these birds (vagrants, wanderers, non-breeding residents, etc.) would have helped to clarify this section.

The bulk of the book is given over to the individual species account, in most cases accompanied by a color or black-and-white illustration. In addition to the name of the subspecies represented in Surinam and the local name of the species, each account provides information under the headings of "Identification," "Soft Parts," "Measurements," "Habitat and Habits," "Nesting," "Recorded Food," and "Range of the Species." (The range of the subspecies is included under the range of the species). In some cases these accounts are abbreviated and some headings are omitted due to a lack of information. This is not to be construed as a failing of the book but rather an indication of a need for further field observation.

In general the book is well planned and laid out and, although its size and weight (5 lbs.) will prevent its being used extensively in the field, it is the most complete and available source of information for the birds of Surinam as well as much of northeastern South America. It is unfortunate that the author chose to limit the scope of his book so strictly to Surinam, particularly in the bibliography, for in so doing he detracts from its usefulness over a wider area. In the species accounts valuable sources of additional life history information on Surinam birds, recorded mostly by the author in Surinam, are frequently cited. To my mind, the inclusion of still more such references to life history studies, including ones done outside Surinam, would have been well worth the time and effort involved, particularly when little information is available for the species in Surinam. This was done in at least one instance—Sick's study of the Palm Swift in Brazil—and could easily have been done for many others. Reference to Schaefer's study in Venezuela (Auk, 70:403–460, 1953) would have been a very useful addition to the otherwise abbreviated account of the Swallow-tanager (*Tersina viridis*) and would have called attention to its seasonal populational movements in other parts of its range. If this should also prove to be true of Surinam populations, the Swallow-tanager could be a possible exception to Haverschmidt's view (p. xxiii) that no species which breeds in Surinam leaves the country when the nesting season is over. Similarly, the increased use of footnotes to explain unusual treatments in the text would certainly have improved the book's usefulness. Readers as yet unfamiliar with the findings of Junge and Voous (1955) may find the lumping of *Sterna sandvicensis* and *S. eurygnatha* puzzling, whereas a simple footnote citation of this paper, which is already listed in the terminal bibliography, would have easily explained this action. On rare occasions such footnotes are used very effectively to clarify some points (see page 19) and it is a shame that they were not used more frequently.

The sections on "Identification" and "Soft Parts" are for the most part brief and usable. The section on measurements is tantalizing at best. When available, the range of wing measurements and body weights are given, sometimes separately for each sex. At no time is the sample size recorded. The extra effort of presenting the sample mean, as well as the range, and also the number of values considered, would have converted this section into a treasure-trove of badly needed data. In its present form it is of limited usefulness at best. This need for a consistent presentation of data in a usable form is even more clearly shown later in the presentation of egg measurements. At least three different forms of presentation are used for these data, none indicating the sample size on which they are based. In many cases it is unclear whether entries—e.g., "Measurements: 35.2 × 25.6 mm" for the Scaled Pigeon (*Columba speciosa*) (p. 128)—are to be considered as the data for a single egg or, as is more likely and sometimes stated for other entries, an average value for an unknown number of eggs.

The sections on "Habitat and Habits" and on "Nesting" are excellent and often include much useful information about the species and its life history and behavior. In some of the species accounts—e.g., the Striped Cuckoo (*Tapera naevia*) and the Barn Owl (*Tyto alba*)—extra information is given on variation in clutch size, the distribution of clutches throughout the year, as well as notes on voice and incubation periods. Even notes on the method of head scratching are included in other species accounts. It is a shame that additional accounts could not have included more of this type of information, even if still anecdotal at the time of writing. Additional published accounts could have simply been cited when space was at a premium.

The section on "Recorded Food" is a welcome addition to a regional work of this sort, and the information it contains represents much hard work for little apparent reward. "Food in Surinam" would have been more appropriate for the heading since no use has been made of analyses made elsewhere. This section does not purport to be a summary of all food items ever recorded for the species and should not be mistaken for such.

The section on species and subspecies ranges is by and large correct and is a useful part of each account. Occasional errors of omission and commission can be found—an almost inevitable failing in a work of this sort, particularly when based on a heretofore poorly studied part of the world where new information seems to appear almost daily. Nonetheless, several errors must be considered rather flagrant and as such they detract from the credibility of the book as a whole. For example, *Chaetura chapmani* (p. 169; "Range of the species: Trinidad, Surinam, French Guiana and Matto Grosso.") has been known to occur also in Panama, Colombia, Venezuela, and Brazil for more than ten years and has been recorded in Guiana since 1966. A more complete version of its range has been given in several major regional works on South American birds dating back to 1958, and at least two are listed in the bibliography of this book. Similarly, the range of *Chaetura spinicauda spinicauda* is still said to include "eastern Venezuela" although the populations of that area were recognized as being particularly distinct (*C. s. latirostris*) as long ago as 1952 and this was so stated in the major work on Venezuelan birds which appeared in 1958. Other errors—e.g., including Tobago as well as Trinidad in the range of *Leistes militaris*, and the frequent omission of Trinidad and/or Tobago from the listed range of species widely distributed on continental South America—are but minor irritations.

Paul Barruel's figures and color plates are a major contributing factor to the great usefulness of this book. Although they are not in every case the equal of the plates of some field guides to the birds of North America or Europe, they far surpass any presently available portrayal of the birds found in northeastern South America. As has been pointed out to me, however, the iris color of many birds shown in the color plates fails to be in strict agreement with the color listed in the text description of the species. In many cases this is simply the minor difference between a brown iris appearing distinctly reddish, a white iris appearing pale yellowish, or a yellow iris appearing quite orange-brown. In other cases it is in sharper disagreement. There seems to be little difference to me between the iris colors of *Myrmeciza ferruginea* and *Formicarius colma* in Plate 25 and yet in the text descriptions the former is said to have a "dark brown" iris and the latter a "reddish" iris. An even more striking error of this sort can be seen in Plate 13. There, the iris color for both *Ciccaba virgata* and *C. huhula* appears to be a distinct dark brown. In the text (p. 161) *C. virgata* is said to have a "yellow" iris while that of *C. huhula* is said to be "brown." The black-and-white figures are in general quite nice but there are a few cases where I would have suggested revisions—e.g., the neck length of the Solitary Sandpiper (p. 132) and the bill size of the Ruddy Turnstone (p. 108) and the Willet (p. 107). It is a shame that it was not possible, in at least a few cases, to show the birds, particularly the raptors, in flight. This would certainly have aided in the separation of such species as the Greater and Lesser Yellow-headed Vultures (not figured at all) and the Rufous-thighed Kite and the Bicolored Hawk which appear extremely similar when perched (Pl. 7). In the case of the vultures, *Cathartes aura*, *C. burrovianus*, and *C. melambrotus*, it would have been helpful to have drawings of even the heads alone, showing the amount and distribution of the yellow on the head (including the yellow nape patch present in *C. a. ruficollis* but not mentioned in the text).

Typographical errors are pleasantly minimal. The color plates are well reproduced although one (Pl. 26) in my copy is quite blurry. Without sounding unduly provincial, I would like to take issue with the editorial(?) changes made in the spelling of some of the common names. I do not feel it is necessary, or even correct, to make such changes in the common names of birds confined to the Neotropical Region simply to conform with contemporary usage in that part of the world where the book is printed. I cite two examples: "Tricoloured Heron" (p. 18) and "Bicoloured Hawk" (p. 54). In the case of the latter species, the name is correctly (?) spelled in the caption for Plate 7 (p. 80).

Despite the several criticisms here offered, this book is clearly a valuable addition to the ornithology of Surinam and South America. The book's array of minor failings will unquestionably chip away at the confidence a reader will have in the mass of information presented. While this is certainly unfortunate, it should only slightly impair the overall usefulness of the book.—CHARLES T. COLLINS

ADAPTATIONS FOR LOCOMOTION AND FEEDING IN THE ANHINGA AND THE DOUBLE-CRESTED CORMORANT. By Oscar T. Owre. Ornithological Monographs No. 6, American Ornithologists' Union, 1967: 138 pp., 56 figs., 26 tables. $3.50.

Based on over 500 hours of field observations and detailed comparisons of feathers, bones, and muscles, Oscar Owre's study of the Anhinga and Double-crested Cormorant describes the anatomical complexes associated with two rather different modes of environmental exploitation.

The book begins with a one-and-a-half-page introduction and ends with an equally short conclusion. The remainder of the text is divided into five main sections: aerodynamics and the wing, the tail, the leg, the head, and the food. Throughout the various sections and subsections, the Anhinga and Double-crested Cormorant are treated together, frequently in the same paragraph. This reduces to a minimum the amount of information which the reader must remember as he peruses the comparisons. The sections dealing with the wing, tail, leg, and head begin with field observations. These are followed by osteological comparisons, myological comparisons, discussion, and conclusions. The osteological comparisons are based on gross observations, measurements, and ratios calculated from the measurements. Approximately half the pages are devoted to the muscles. Comparable muscles in the Anhinga and Double-crested Cormorant are compared in terms of gross structure and per cent volume (volume of a muscle expressed as a percentage of the total volume of the group of which it is a part; the groups delimited include wing muscles, caudal muscles, leg muscles, etc.).

The less labored, frequently soaring flight of the Anhinga is correlated with lighter wing loading, greater slotting of the distal primaries, better development of the alula, and a total volume of wing muscles which is equal to that of the Double-crested Cormorant although the cormorant has a larger total body weight. Presumably the aerodynamic properties of the Anhinga's wing are adaptive to feeding in small ponds and water courses which are closely surrounded by trees. In such situations the vegetation minimizes wind action and prevents long unobstructed take-offs and landings.

Differences in tail structure parallel those seen for the wings. The surface area of the Anhinga's tail is approximately two and one-half times larger than that of the Double-crested Cormorant. Also, it is argued that the Anhinga's tail musculature is capable of producing more intricate and more laterally-directed motions of the tail. Owre concludes that these modifications facilitate soaring and maneuverable flight.

The hindlimb and head anatomy of the Double-crested Cormorant are consistent with its feeding by active pursuit of fish, culminating when the prey is seized between its mandibles. Conversely, the Anhinga is modified for slow, prowling underwater swimming in which the prey is approached with stealth and impaled on the mandibular tips by a rapid, forward thrust of the head.

A striking aspect of Owre's study is that, in spite of extensive field observations, many aspects of the underwater activities of the two species are unclear. Hopefully, it will eventually be possible to observe these birds foraging underwater in large tanks. Until then, uncertainty remains. The anatomical and observational evidence convincingly point to the Anhinga stalking rather than swimming rapidly after its prey. However, the exact manner in which either the Anhinga's or Double-crested Cormorant's legs, neck, and head are used underwater is largely unknown. Until they are known, it seems that correlations between function and form must be tentatively assigned.

Also, the rather distant phylogenetic relationship between cormorants and anhingas raises serious questions regarding the functional interpretation of anatomical differences. Some differences are undoubtedly interpretable on the basis of the two species having evolved into their present niches from different ancestral forms. Owre's attempts to separate phylogenetic differences from those largely adaptive sometimes seem tenuous. For instance, Owre's assertion that the dissimilar proportions of certain skeletal elements are suggestive of phylogenetic separation seems arbitrary in view of the restriction of his study to two species.

By and large, Owre handles well the pitfalls inherent in such a study and must be commended. His work should be recognized as a valuable contribution to the study of morphological adaptations.—LOWELL SPRING.

HUMMINGBIRDS AND THEIR FLOWERS. By Karen A. Grant and Verne Grant. Columbia University Press, New York, 1968. 7¾ × 10¼ in., vii + 115 pp., 30 col. pls. $17.50.

It is normally a worthwhile occasion when two investigators who have been working in a particular scientific field distill their ideas and information into a single book. In producing the present book the Grants have drawn together information from a variety of sources, including much of their own published and unpublished work, to present an account of flowers pollinated by hummingbirds and the potential impact of the birds on the evolution of these specialized flowers. On the whole the book is very readable and highly informative, although there are very few data presented to document many of the ideas. It is unfortunate that lack of information forced them to restrict their analysis to western North America when it is possible, as they suggest, that characteristics of hummingbird flowers in tropical areas will show striking differences from those in temperate areas. On the other hand the book will serve as a useful guideline for analysis of the results from studies of tropical forms.

For people primarily interested in birds this book will be somewhat of a disappointment as the major emphasis (8 of 11 chapters) is on the biology and evolution of the hummingbird flowers. Discussion of the birds is mostly restricted to generalities about morphological features that adapt the birds for flower visitation and to aspects of the biology of the hummingbirds—e.g., migration routes and timing, that might be important to the flowers. Perhaps the book should have been entitled "Adaptations of Flowers for Hummingbird Pollination." However, even this title would be slightly misleading at this time as it appears that the authors are equating pollination with bird visitation to flowers that look as if they are adapted for hummingbird pollination. The Grants probably are generally correct that these flowers are more or less dependent on the hummingbirds, but there is little mention of other possible visitors or of any experiments to show that hummingbirds indeed pollinate the flowers or, in fact, that animal pollinators are essential for reproduction by the flowers.

If we accept their premise that these 129 species of flowers are in fact hummingbird pollinated, then the book has some interesting information on the morphological characteristics of the flowers and their distribution in time and space. Perhaps the most interesting chapter is the final one in which the Grants speculate on the co-evolution of the birds and flowers. It points up potential interactions of an organism and its food source that may influence evolutionary changes occurring in both.

Hopefully this book will be a stimulus for other workers to continue research in this field, at least in part along the lines determined by the Grants. It should be very evident to any serious amateur who reads the book that much of the information could be gathered by bird watchers who are willing to spend the time making detailed observations of individual hummingbirds or an area of flowers. As the Grants point out, they have positive records for visitation for only about one-third of the flowers which they consider to be hummingbird flowers, and these are mostly representatives from the California flora. For persons interested in both birds and flowers, here is an excellent opportunity to combine interests in a productive way.

Perhaps the greatest shortcoming of the book is its price ($17.50). I suspect that this will greatly restrict the audience to those who can afford to pay a rather high price for such a short book. Most of the expense of the book comes from the 30 color plates that appear at the end. In my opinion many of these color photographs could have been chosen with more care or eliminated from the book without detriment to the information content. For example, the habitat pictures would have told as much in black and white, especially since most of the important flowers pictured are shown in more detail in other plates. On the following plates—13, 14, 17, 18, 19, 21, 22, 23, 24, 25—one or more pictures could have been left out and we would still have learned as much from the book. This is especially true of pictures of sitting hummingbirds, of several pictures of the same birds at the same flower, and of pictures in which it is hard to locate and distinguish the bird. Finally, I do not think that compliments are at all in order to Columbia University Press for the quality of the color reproductions, at least in my copy. It is possible that this poor reproduction has reduced the value of some of the figures previously mentioned.—LARRY L. WOLF.

THE LOVELY AND THE WILD. By Louise de Kiriline Lawrence. McGraw-Hill Book Company, New York, 1968: 9¼ × 6¼, 228 pp., drawings by Glen Loates. $6.95.

To those of us who struggle to write clearly in our native tongue, it is humbling to find someone who writes both clearly and gracefully in English as an adopted language. Mrs. Lawrence is a member of that distinguished group.

After a childhood in Sweden and several years as an interpreter and nurse in missions to Russia, she sought out a new life in the wilderness of northern Ontario. Here she served in the outpost nursing service of the Red Cross, married, and settled on a forest homesite in the region of North Bay. This book is mainly about her experiences with birds near her home during the next thirty years.

Those who expect warm enjoyment from nature writing will find it in these pages. And those who are looking for solid information will not be disappointed. A quality that shines through all of Mrs. Lawrence's work is intelligence—the ability to sort out from a myriad of sights and sounds those impressions that are significant. She does not merely exclaim over the beauty of nature; she searches constantly for connections and explanations.

Although the style and format of the book invite recreational reading, students of the birds she discusses will not want to ignore these accounts. They are filled with original observations on many species nesting in the North Woods. A partial list of the birds discussed is as follows (in Check-list order): Ruffed Grouse, Whip-poor-will, Ruby-throated Hummingbird, Yellow-shafted Flicker, Yellow-bellied Sapsucker, Hairy Woodpecker, Downy Woodpecker (in 1967 she published an A.O.U. monograph on these four woodpeckers), Eastern Phoebe, Eastern Kingbird, Least Flycatcher, Black-capped Chickadee, Myrtle Warbler, Ovenbird, American Redstart, Evening Grosbeak, Red Crossbill, White-winged Crossbill, Chipping Sparrow, Slate-colored Junco, and White-throated Sparrow. Although the emphasis is on birds, one chapter deals with the red squirrel, which

Mrs. Lawrence finds not so single-mindedly in search of birds' nests as some people may think.

The pencil sketches by Glen Loates, numbering more than 30, are a pleasing embellishment to the text.

Apparently others also have thought well of this book. It earned for Mrs. Lawrence the 1969 John Burroughs Medal for the year's best book in the field of natural history. Here is a delightful gift for the armchair naturalist, and at the same time it may awaken some bird watchers to the excitement to be found in observation at the scientific level.—Harold F. Mayfield.

PUBLICATION NOTES AND NOTICES

The Preservation of Natural History Specimens. Volume 2. Edited and compiled by Reginald Wagstaffe and J. Havelock Fidler. Philosophical Library, 15 East 40th Street, New York, 1968: 7½ × 10 in., xvi + 404 pp., 150 figs. $17.50.

This volume consists of three parts: Zoology—Vertebrates, Botany, and Geology. The chapter on Aves (pp. 39–74) gives directional information under two main headings: Preservation and Storage—Dry; Preservation and Storage—Wet. Under the first heading are (1) detailed directions with drawings for preparing a study skin of a passerine bird together with methods for measuring, sexing, labelling, wrapping, drying and storing the specimen, (2) brief directions for handling large and very small birds, birds with long necks, long legs, large hoods, etc., and downy young, and (3) special techniques: refrigeration; injecting for temporary or permanent preservation; salting; removing fat, blood, and dirt; and renovating old skins. Under the second heading are directions for blowing eggs both fresh and incubated, preserving ova and embryos, and collecting and storing nests.—O.S.P.

A Dictionary of English and Folk-names of British Birds: With Their History, Meaning and First Usage, and the Folk-lore, Weather-lore, Legends, etc., Relating to the More Familiar Species. By H. Kirke Swann. First published by Witherby and Company, London, in 1913; republished by Gale Research Company, Book Tower, Detroit, 1968: 5½ × 8¼ in., xii + 266 pp. $9.50.

Approximately 5,000 names are listed alphabetically.

Annotated Index to Some Early New Zealand Bird Literature. Compiled by H. C. Oliver. Wildlife Publication No. 106, Department of Internal Affairs, Wellington, 1968: 8 × 10 in., x + 222 pp. No price given.

A bibliographical undertaking that covers ten works published from 1843 to 1900. Included are the Transactions and Proceedings of the New Zealand Institute, vols. 1–33. Besides a general index to every species mentioned, there is an annotated index in four sections: systematic, geographic distribution, subject, and author.

An Extensive Bibliography on Falconry, Eagles, Hawks, Falcons, and Other Diurnal Birds of Prey. Part 1. Falconry and Eagles. By Richard R. Olendorff and Sharon E. Olendorff. Privately printed, 1968: paper covered, 8½ × 11 in., 78 pp. $4.00. Order from senior author, Aggie Village 7-D, Fort Collins, Colorado 80521.

Three other parts to follow, priced at $3.00 each. Total bibliography will include

5,000 entries, all in the English language, from various ornithological and falconry books and journals published through December, 1967.

Birds of the Toledo Area. By Lou Campbell. The Blade, Toledo, Ohio, 1968: 5 × 7¾ in., viii + 330 pp., illus. with bl. and wh. wash drawings by Patricia Eckhart. $4.11 (send order to Blade Bird Book, Box 555, Toledo, Ohio 43601).

This is an updating and considerable expansion of the "Birds of Lucas County," by the same author, published in 1940 as a Toledo Museum of Science Bulletin. The area covered now takes in "all of Lucas County, a strip northward to Monroe lying between Route 25 and Lake Erie and another eastward to Sandusky River and Bay between the Ohio Turnpike and Lake Erie." Introductory information is organized under several headings: Physical Geography of the Area, Bird Habitats, Migration Lanes, General Scope [of the book], Treatment of Species [in the book], Seasonal Changes in Birdlife, History of Birdlife in the Toledo Area, How to Identify Birds. An appendix presents a summary of birds found in winter. The bulk of the book is devoted to a list of 334 species, with extensive annotations that include field identification marks (in boldface type), comments on habits and local distribution, and (if applicable) data on nesting and a table on migration giving earliest and average dates of arrival and average and latest dates of departure.—O.S.P.

Wild Refuge. By George Laycock. Natural History Press, Garden City, New York, 1969: 6¼ × 9½ in., 151 pp., 39 photos. $3.50.

The story of the more important United States National Wildlife Refuges from the Aleutians to Florida and from Maine to California.

PICTORIAL CHECKLIST OF COLORADO BIRDS: With Brief Notes on the Status of Each Species in Neighboring States of Nebraska, Kansas, New Mexico, Utah, and Wyoming. By Alfred M. Bailey and Robert J. Niedrach. Denver Museum of Natural History, 1967: 9 × 12½ in., 168 pp., 23 bl. and wh. photos., 124 col. pls. $10.00.

A condensation of the two-volume "Birds of Colorado" by the same authors, published in 1965 (see review in Wilson Bull., 79:352–353, 1967). Introductory chapters in this edition cover topography, life zones, and migration in the state, followed by 130 pages of new text briefly summarizing recognition marks, general range, and status of each of the species in Colorado and the neighboring states. Included from the original work are *all* the color plates, illustrating "420 (more than 700 individual birds) of the 441 species recorded from Colorado." Priced at $10.00, this book is a remarkable bargain and almost certain to be out of print before long.—O.S.P.

REQUEST FOR INFORMATION

As part of a study of the ecology and population dynamics of the Mississippi Kite, adult and juvenile birds are being color-tagged, banded and released in areas of southwestern Kansas, western Oklahoma, and north central Texas. Marked birds carry a large plastic oval on the humeral area of each wing, and colors used have been white, red, orange, yellow, dark green, dark blue, and light blue. Information desired includes: color of plastic oval on each wing; date, time and location of sighting; activity of the bird; and observer. Please send information to: James W. Parker, Museum of Natural History, University of Kansas, Lawrence, Kansas 66044.

THE WILSON ORNITHOLOGICAL SOCIETY

OFFICERS, 1969

President	William W. H. Gunn
First Vice-President	Pershing B. Hofslund
Second Vice-President	Kenneth C. Parkes
Secretary	Jeff Swinebroad
Treasurer	William A. Klamm
Editor	George A. Hall

ADDITIONAL MEMBERS OF THE EXECUTIVE COUNCIL

Elective Members

Andrew J. Berger
C. Chandler Ross
Ernest P. Edwards

Past Presidents

Albert F. Ganier
Margaret M. Nice
George M. Sutton
S. Charles Kendeigh
Olin Sewall Pettingill, Jr.
Maurice G. Brooks
Walter J. Breckenridge
John T. Emlen, Jr.
Lawrence H. Walkinshaw
Harold F. Mayfield
Phillips B. Street
Roger Tory Peterson
Aaron M. Bagg
H. Lewis Batts, Jr.

Trustees

Phillips B. Street
Edward L. Altemus
Allan Crawford, Jr.

EDITORIAL STAFF OF *THE WILSON BULLETIN*

Editor

George A. Hall

Editorial Advisory Board

William C. Dilger
Douglas A. James
William A. Lunk
Andrew J. Meyerriecks
Robert W. Nero
Kenneth C. Parkes
Glen E. Woolfenden

Ornithological Literature Editor

Olin Sewall Pettingill, Jr.

CHAIRMAN OF COMMITTEES

Annual Meeting	Ronald A. Ryder
Conservation	H. Lewis Batts, Jr.
Endowment	Aaron M. Bagg
Library	William A. Lunk
Membership	David F. Parmalee
Nominating	Phillips B. Street
Research	Harrison B. Tordoff
Student Membership	Douglas A. James

INDEX TO VOLUME 81, 1969

BY MILDRED STEWART AND TANYA HALL

This index includes, in addition to names of genera, species, and authors, references to the following topics: Anatomy, behavior, breeding, distribution, ecology, food habits, habitat, hatching, incubation, measurements, migration, molts and plumages, mortality, nests and nesting, parasitism, pesticides, physiology, populations, predation, taxonomy, territory, voice, weather, and weights. Also included are references of biological significance to reptiles and mammals.

Accipiter cooperii, 60, 61
  gentilis, 340
  striatus, 186, 209
Acrocephalus arundinaceus, 312
  scirpaceus, 276
Aethia cristatella, 213
  pusilla, 213
Agelaius phoeniceus, 220, 221, 222, 275, 276, 301, 336, 456
  tricolor, 316
Aix sponsa, 95
Alauda arvensis, 272, 297
Alca torda, 213
Amazilia tobaci, 462
Anas acuta, 50, 94
  cyanoptera, 95
  discors, 45, 94
  platyrhynchos, 50, 95, 309, 332, 436
  rubripes, 332
  strepera, 44, 94
Anatomy, 50–51, 55–68, 220–223, 270–279, 280–292, 339–340, 342
Andrle, Robert F. and Harold H. Axtell, Mew Gulls in Ontario, 211–213
Ani, Groove-billed, 33
  Smooth-billed, 462
Anous stolidus, 462
Antbird, Bare-eyed, 363–395
  Bicolored, 369, 370, 372, 377, 379, 380, 382, 383, 384, 385, 386, 389, 390
  Crested, 363–395
  Hair-crested, 363–395
  Harlequin, 363–395
  Hoffmann's, 365, 372
  Pale-faced, 369, 382, 383
  Rufous-capped, 381
  Scale-backed, 378, 381
  Spot-backed, 381
  White-breasted, 363–395
  White-cheeked, 369, 381
  White-fronted, 369
  White-plumed, 381
  White-throated, 369, 381
Anthus spragueii, 261
Antshrike, Saturnine, 381
Anumbius acuticaudatus, 15, 135
Aphelocoma ultramarina, 317
Aplonis tabuensis, 222
Applegate, Richard L., see Mullan, James W. and ———
Apus apus, 273
Aquila chrysaetos, 60, 61
Araçari, Collared, 268
Archilochus colubris, 101
Ardea herodias, 94
Arenaria interpres, 142
Artamella viridis, 220, 221, 222
Asio flammeus, 63
Auklet, Crested, 213
  Least, 213
  Parakeet, 213
Austin, George T., A record of the Tufted Duck for Connecticut, 332
Automolus ochrolaemus, 34
Avitabile, Alphonse, Egg transportation by a female Mallard, 331–332
Avocet, 142
Axtell, Harold H., see Andrle, Robert F. and ———
Aythya affinis, 49, 95, 96
  americana, 51, 96
  collaris, 331
  fuligula, 332
  valisineria, 96
Babbler, Jungle, 317
Bailey, Alfred M., and Robert J. Niedrach,

Pictorial checklist of Colorado birds, reviewed, 482
Bananaquit, 132, 463
Baptista, Luis F., An unusual nest site of the Starling, 335–336
Barbtail, Spotted, 27
Bare-eye, Black-spotted, 369, 380, 381, 382
  Rufous-winged, 381
Bartonek, James C., Build-up of grit in three pochard species in Manitoba, 96–97
Bartramia longicauda, 211
Becard, Rose-throated, 13
Behavior, 24–30, 69–74, 79–86, 87–93, 97–99, 101–102, 106–107, 107–108, 122–139, 140–154, 169–183, 196–206, 246–257, 264–269, 330–331, 331–332, 338–339, 363–395, 419–440, 465–466, 468–470, 470
Belrose, Frank C., Waterfowl migration corridors east of the Rocky Mountains in the United States, reviewed, 195
Berger, Andrew J., Appendicular myology of passerine birds, 220–223; The nest, eggs, and young of the Elepaio, 333–335
Berger, Daniel D., see Mueller, Helmut C., and ———
Bird of Paradise, Magnificent, 18
Bittern, Least, 340–341
Bjärvall, Anders, Unusual cases of re-nesting Mallards, 94–96
Blackbird, European, 299, 303, 304, 305, 307, 310
  Red-winged, 301, 302, 307, 336–337, 455, 456
  Tricolored, 316
  Yellow-headed, 262
Bluebird, Azure, 104–105
  Mexican, 105
  Mountain, 105
Bobolink, 259
Bobwhite, 79–86, 338–339, 466
Bock, Walter J. and Allan McEvey, The radius and relationship of owls, 55–68
Bombycilla cedrorum, 275
Bonasa umbellus, 97, 303
Bongiorno, Salvatore F., and Jeff Swinebroad, Increase in Herring Gull colony in Cape May, New Jersey, 99–100
Booby, Brown, 461, 463
  Red-footed, 461, 463
Boonsong Lekagul, Bird guide of Thailand, reviewed, 345
Borror, Donald J. and K. C. Halafoff, Notes on song structure in the Townsend's Solitaire, 163–168
Brackbill, Hervey, A Carolina Wren shadow-boxing, 470
Branta canadensis, 95, 464
Breeding, 30–31, 123–138, 464–465
Brown, Irene L., see Smith, Robert W. and ———
Brown, Jerram L., Territorial behavior and population regulation in birds: a review and re-evaluation, 293–329
Brushrunner, Larklike, 342
Bubo bubo, 160
  virginianus, 58, 155, 332, 468
Bucephala clangula, 383
Budgerigar, 309
Bunting, Lark, 108
  Yellow, 251
Buteo buteo, 298
  jamaicensis, 108, 258
  lagopus, 108
  melanoleucus, 60, 61
  regalis, 108
  swainsoni, 61, 62
Buzzard, 298
Cacicus cela, 13, 135
Cacique, Yellow-rumped, 13, 135
Cade, Tom J., review by, 348–351
Calamospiza melanocorys, 108
Calidris alpina, 141
  bairdii, 143
  fuscicollis, 142, 143
  mauri, 142, 143
  melanotos, 143, 149
  minutilla, 142, 143
  pusillus, 142, 143, 144, 145, 147
Calocitta formosa, 265
Campbell, Lou, Birds of the Toledo area, reviewed, 481–482
Campylorhynchus nuchalis, 137
  zonatus, 40
Canastero, Short-billed, 342
Canvasback, 96–97
Caprimulgus carolinensis, 332
Cardinal, 216, 470
Carpodacus purpureus, 470

Cassidix mexicanus, 472
Catbird, 260, 454, 455, 456, 457, 458
Cathartes aura, 94, 108
Catotrophorus, semipalmatus, 142, 143
Causey, M. Keith and Jerry D. Graves, Insecticide residues in Least Bittern eggs, 340–341
Centurus aurifrons, 264
  carolinus, 274, 470
  rubricapillus, 10
Cepphus columba, 213
  grylle, 213
Chaetura pelagica, 273
Chaffinch, 197, 296, 297, 307
Chamaea fasciata, 436
Charadrius semipalmatus, 142, 143
  vociferus, 143
Chasiempis sandwichensis, 333, 334
  sclateri, 334
Chen caerulescens, 465
Chickadee, Black-capped, 293, 308, 310, 436
Chiroxiphia linearis, 264
  pareola, 18
Chrysoptilus melanochloros, 274
Chuck-will's-widow, 332
Cinclodes antarcticus, 34
Cinclus mexicanus, 275
Circus cyaneus, 108
  c. hudsonius, 60, 61
Clark, George A., Jr. Oral flanges of juvenile birds, 270–279
Cnemotriccus fuscatus, 462
Coccyzus americanus, 273
Coereba flaveola, 132, 463
Colaptes auratus, 170, 214, 274, 332, 469
  campestris campestroides, 468
  campestroides, 342
  melanochloros, 468, 469
Colinus virginianus, 79, 338, 467
Colius indicus, 273
  macrourus, 273
Collins, Charles T., review by, 475–478
Colluricincla harmonica, 275
Columba cayennensis, 462
  livia, 50
Columbina talpacoti, 462
Contopus virens, 260
Coot, 450–453
Coracius garrulus, 273
Coragyps atratus, 461
Corcorax melanorhamphus, 275
Corvus brachyrhynchos, 46, 275, 333
  corax, 108, 275
  cryptoleucus, 108
  monedula, 95, 276
  ossifragus, 275
Coryphistera alaudina, 342
Cowbird, Bay-winged, 135
  Brown-headed, 251, 262, 296, 336–337, 399, 400, 402, 455, 471
  Shiny, 462
Cranioleuca erythrops, 13, 27
Crocethia alba, 142, 143
Crotophaga sulcirostris, 33
Crow, Common, 46, 100–101, 210, 333, 467
Cuckoo, Striped, 137
  Yellow-billed, 259
Cuculus micropterus, 273
Curlew, Eskimo, 296
Curry, James R., Red-bellied Woodpecker feeds Tufted Titmouse, 470
Curtis, Steven G., Spring migration and weather at Madison, Wisconsin, 235–245
Cyanerpes cyaneus, 265
Cyanocitta cristata, 106, 275, 333, 400, 472
Cyanocorax chrysops, 342
Cyclorrhynchus psittacula, 213
Davis, William F., Robin kills snake, 470–471
Davison, Verne E., Attracting birds: from the prairies to the Atlantic, reviewed, 232
Dendragapus obscurus, 412
  o. fuliginosus, 302
Dendrocincla merula, 378, 381
Dendrocolaptes concolor, 381
  hoffmannsi, 378
Dendrocopos major, 274
  pubescens, 271, 274
  villosus, 169, 171, 180, 182, 274
Dendroica auduboni, 185
  coronata, 236
  kirtlandii, 220, 221, 222, 247, 296
  palmarum, 236, 258, 338
  petechia, 275, 454
  striata, 260
  tigrina, 258
  virens, 106

Dickerman, Robert W. and Kenneth C. Parkes, Juvenal plumage of the Spotted Rail, 207–209
Dinsmore, James J., and Richard P. ffrench, Birds of St. Giles Islands, Tobago, 460–463
Diphyllodes magnificus, 18
Distribution, 104–105, 184, 211–213, 215, 219–220, 261–262, 332, 337–338, 363–368, 460–463, 463–464, 464–465
Dove, Rock, 50
  Mourning, 108, 258, 261, 338–339
  White-tipped, 462
  White-winged, 261
Dowitcher, 142
  Long-billed, 338
Dryocopus martius, 271, 274
  pileatus, 181, 271, 274, 332
Duck, Black, 332
  Ring-necked, 95, 331
  Tufted, 332
  Wood, 95, 210
Dulus dominicus, 22
Dumetella carolinensis, 261, 275, 454
Dunlin, 302
Eastwood, Eric, Radar ornithology, reviewed, 344–345
Eckleberry, Don R., review by, 351–352
Ecology, 99–100, 104–105, 140–154, 441–449
Edwards, William R., and Jack A. Ellis, Responses of three avian species to burning, 338–339
Eggs, 102–103, 128, 190, 253
Eider, Common, 465–466
Eira barbara, 378
Eisenmann, E., review by, 345
Elaenia flavogaster, 462
  frantzii, 267
Elaenia, Greenish, 265
  Mountain, 267
  Yellow-bellied, 462
Elepaio, 333–335
Elliot, Bruce G., Life history of the Red Warbler, 184–195
Ellis, Jack A., see Edwards, William R. and ———
Emberiza citrinella, 251
Empidonax traillii, 272, 275
Eremophila alpestris, 108
Ereunetes pusillus, 338
Ergaticus ruber, 184
  r. melanauris, 184, 190
  r. ruber, 184
  versicolor, 184
Erolia acuminata, 337
  alpina, 302
  bairdii, 338
  melanotos, 338
Errington, Paul L., Predation and life, reviewed, 348–351
Estrilda astrild, 22
Euphonia, Scrub, 268
  Thick-billed, 137
Evans, Roger M., Territorial stability in Sharp-tailed Grouse, 75–78
Evans, William F., Communication in the animal world, reviewed, 352
Falco columbarius, 258
  mexicanus, 61
  peregrinus, 340, 461
  sparverius, 61, 62
Falcon, Peregrine, 340, 461
ffrench, Richard P., see Dinsmore, James J. and ———
Ficedula hypoleuca, 302
Ficken, Millicent S. and Robert W. Ficken, Responses of Blue-winged Warblers and Golden-winged Warblers to their own and the other species song, 69–74
Ficken, Robert W., see Ficken, Millicent S. and ———
Fidler, J. Havelock, see Reginald Wagstaffe and ———
Finch, Purple, 470
  Saffron, 136–137
Firewood-gatherer, 15, 27, 135
Fisher, James, editor, Thorburn's birds, reviewed, 351–352
Flatbill, Sulphury, 133
Flicker, Campo, 468, 469
  Field, 342
  Green-barred, 468, 469
  Yellow-shafted, 170, 214–215, 332
Flycatcher, Acadian, 259
  Boat-billed, 264, 266
  Brown-crested, 462
  Fuscous, 462
  Jinete, 134–135
  Mounted, 134
  Kiskadee, 268

Pied, 302, 313, 320
Piratic, 28, 31, 42, 132–134, 264
Social, 264, 266
Streaked, 264, 266, 267
Sulphur-bellied, 264, 266, 267
Traill's, 272, 456
Vermilion-crowned, 10
Food Habits, 7–8, 96–97, 100–101, 107–108, 264–269, 336–337, 468–470, 472
Formicarius colma, 381
Franks, Edwin C., Behavior of a Ruby-throated Hummingbird in a room, 101–102
Franks, Edwin C. and John E. Warnock, Great Horned Owl nesting in a populated area, 332–333
Fratercula arctica, 213
Fredrickson, Leigh H., Mortality of coots during severe spring weather, 450–453
Fregata magnificens, 460, 461
Fregilupus varius, 220, 221, 222
Frigatebird, Magnificent, 460, 461, 463
Fringilla coelebs, 296
Frith, H. J., Waterfowl in Australia, reviewed, 230–231
Fulica americana, 450
Gadwall, 44–53, 94
Gallinula chloropus, 341
Gallinule, Common, 341
Purple, 341
Gallus domesticus, 309
Gavia immer, 331
Geothlypis trichas, 402
Gochfeld, Michael, Status of Lincoln's Sparrow in Jamaica, West Indies, 219–220
Goddard, Stephen V., Fall and winter food habits of Red-winged Blackbirds and Brown-headed Cowbirds in western Oklahoma, 336–337
Godwit, Bar-tailed, 338
Marbled, 142
Goldeneye, American, 383
Goose, Blue, 466
Canada, 95, 464
Goshawk, 340
Grackle, Boat-tailed, 472
Common, 400, 472
Grassquit, Blue-black, 463
Grant, Karen A. and Verne Grant, Hummingbirds and their flowers, reviewed, 479–480
Grant, Verne, see Grant, Karen A. and ———
Graves, Jerry B., see Causey, M. Keith and ———
Greenway, James C., Jr. Extinct and vanishing birds of the world, reviewed, 352; review by, 116–117
Grosbeak, Evening, 441
Rose-breasted, 259
Ground-Dove, Ruddy, 462
Grouse, Blue, 302, 307, 411
Red, 300, 302, 305, 306, 307, 311, 312
Ruffed, 97–99, 303
Sharp-tailed, 75–78
Gull, Bonaparte's, 212
California, 102–103
Herring, 99–100, 105, 211, 212, 342
Laughing, 99, 100, 461, 463
Mew, 211–213
Ring-billed, 102–103, 211, 212
Gymnopithys bicolor, 369, 372, 374, 375, 377
leucaspis, 370, 371, 375, 379, 381
salvini, 369, 371, 376, 381
Gymnorhina dorsalis, 316, 317, 318
tibicen, 304, 305, 307, 317
Habitat, 5–7, 454–459
Halafoff, K. C., see Borror, Donald J. and ———
Hall, George A., review by, 231–232
Hatching, 79–86
Haverschmidt, François, Birds of Surinam, reviewed, 475–478; The migration of the American Golden Plover through Surinam, 210–211
Hawk, Pigeon, 258
Red-tailed, 258
Sharp-shinned, 186, 209–210
Heather, B. D., A biology of birds with particular reference to New Zealand birds, reviewed, 352
Helmitheros vermivorus, 253
Helms, Carl W. and Robert B. Smythe, Variations in major body components of the Tree Sparrow (*Spizella arborea*) sampled within the winter range, 280–292

Helpers, 17–18, 36–37
Heron, Black-crowned Night, 210
  Great Blue, 94
  Whistling, 330–331
  Yellow-crowned Night, 461
Hesperiphona vespertina, 441
Hewitt, Oliver H., editor, The Wild Turkey and its management, reviewed, 111–113
Hirundo rustica, 462
Honeycreeper, Red-legged, 265, 266, 267
Horwich, Robert H., Behavioral ontogeny of the Mockingbird, 87–93
Hubbard, Claudia L., see Hubbard, John P. and ———
Hubbard, John P. and Claudia L. Hubbard, Meadowlarks feeding on road-kills, 107–108
Hummingbird, Allen's, 261
  Copper-rumped, 462
  Ruby-throated, 101–102
  Rufous, 261
Hundley, Margaret H., review by, 347; see Kale, Herbert W. II and ———
Hunt, L. Barrie, Physiological susceptibility of Robins to DDT poisoning, 407–418
Hylocichla fuscescens, 454
  minima, 259
  mustelina, 167, 275, 396, 454
Hylophylax naevia, 381
  poecilonota, 378, 381
Ibis, Glossy, 463–464
  Wood, 12
Icterus galbula, 275
  icterus, 23, 123
  leucopteryx, 124
Incubation, 31–34, 45, 129, 189–191, 253, 254–255
Indicator indicator, 273
  minor, 273
Iridoprocne bicolor, 272, 275
Ixobrychus exilis, 340
Jackdaw, 95
Jackson, Gary L., see Labisky, Ronald F. and ———
Jaeger, Pomarine, 298
Jay, Blue, 106–107, 333, 400, 472
  Magpie, 265, 266, 267
  Plush-crested, 342
Johnsgard, Paul A., review by, 230–231
Johnson, Ned K., review by, 225–230
Johnson, Robert A., Hatching behavior of the Bobwhite, 79–86
Jones, Robert E., see Longcore, Jerry R. and ———
Jynx torquilla, 274
Kale, Herbert W. II, Margaret H. Hundley, and James A. Tucker, Tower-killed birds from Grand Bahama Island, 258–263
Kelley, Alice and Neil Kelley, Porcupine quills found in foot of Sharp-shinned Hawk, 209–210
Kelley, Neil, see Kelley, Alice and ———
Kendeigh, S. Charles, Energy responses of birds to their thermal environments, 441–449
Kilham, Lawrence, Reproductive behavior of Hairy Woodpeckers. III. Agonistic behavior in relation to courtship and territory, 169–183
Kingbird, Tropical, 462
Kinglet, Golden-crowned, 186
Kiskadee, Great, 19, 124, 137
Labisky, Ronald F. and Gary L. Jackson, Shell color of eggs laid by yearling, 2-, and 3-year-old Pheasants, 466–467
Lagopus lagopus scoticus, 300
  mutus, 302
Lancaster, D. A., review by, 345–347
Land, Hugh C., review by, 110–111
Lark, Horned, 108
Larus argentatus, 99, 105, 342
  atricilla, 460, 461
  californicus, 102
  canus, 213
  c. brachyrhynchus, 211, 212
  delawarensis, 102
Lawrence, Louise de Kiriline, The lovely and the wild, reviewed, 480–481
Laycock, George, Wild refuge, reviewed, 482
Leaftosser, Scaly-throated, 9
Leck, Charles F., Observations of birds exploiting a Central American fruit tree, 264–269
Legatus leucophaius, 28, 132, 264
Lehman, Larry E., see Mumford, Russell E. and ———
Lepidocolaptes souleyetii, 264

Leptotila verreauxi, 462
Letters to the Editor, 119–120
Leucopternis albicollis, 378
  kuhli, 378
Lieff, Bernard C., Eider hatching goose egg, 465–466
Ligon, J. David, Factors influencing breeding range expansion of the Azure Bluebird, 104–105
Limnodromus scolopaceus, 338
Limnothlypis swainsonii, 246, 275
Limosa fedoa, 142, 143
  lapponica, 338
Littlefield, Carroll D., see Pakulak, Allan J. and ———
Liversidge, Richard, see Skead, C. J. and ———
Lobipes lobatus, 143
Longcore, Jerry R. and Robert E. Jones, Reproductive success of the Wood Thrush in a Delaware woodlot, 396–406
Loon, Common, 331
McCabe, Robert A., review by, 111–113
McEvey, Allan, see Bock, Walter J. and ———
Machetornis rixosa, 134
Magpie, Australian, 304, 305, 307, 308, 310, 312, 313, 317
Mallard, 50, 94–96, 309, 331–332
Malurus cyaneus, 316, 318
Manacus aurantiacus, 18
  manacus, 215
Manakin, Black-and-white, 18
  Long-tailed, 264, 266
  Orange-collared, 18
Marti, Carl D., Renesting by Barn and Great Horned Owls, 467–468
Martin, Carribean, 462
Mathisen, John E., Use of man-made islands as nesting sites of the Common Loon, 331
Mayfield, Harold F., review by, 480–481
Meadowlark, 107–108
Meanley, Brooke, Pre-nesting and nesting behavior of the Swainson's Warbler, 246–257
Measurements, 102–103, 128, 190, 212, 217, 280–292
Megarhynchus pitangua, 264
Melopsittacus undulatus, 309
Melospiza lincolnii, 219, 262
  melodia, 90, 220, 251, 297, 416, 436
Merops apiaster, 273
Mewaldt, L. Richard, see Smith, Robert W. and ———
Micrastur gilvicollis, 378
Micrathene whitneyi, 105
Micropus caffer, 273
Migration, 119–120, 156–158, 210–211, 235–257, 258–263
Mimus gilvus, 462
  polyglottos, 87, 260, 270, 276, 470
Mniotilta varia, 215, 256, 259
Mockingbird, 87–93, 260, 270, 470
  Tropical, 462
Molothrus ater, 251, 262, 296, 336, 399, 455
  badius, 135
  bonariensis, 462
Molts and Plumages, 47–50, 207–209, 213–214, 388–390, 423–424
Monasa morphoeus, 378
Morse, Douglass H., Distraction display of a pair of Black-throated Green Warblers, 106–107
Mortality, 105–106, 159–161, 193, 258–263, 310–313, 407–418, 450–453, 467
Mueller, Helmut C. and Daniel D. Berger, Letter to the Editor, 120
Mullan, James W. and Richard L. Applegate, The drowning of Bobwhites in a large reservoir, 467
Mumford, Russell E. and Larry E. Lehman, Glossy Ibis in Indiana, 463–464
Murray, Bertram G., Jr., Letter to the Editor, 119–120
Muscivora forficata, 275
Myadestes townsendi, 163, 168
Mycteria americana, 12
Myiagra freycineti, 275
Myiarchus tyrannulus, 462
Myioborus miniatus, 185
Myiodynastes luteiventris, 264
  maculatus, 264
Myiopagis viridicata, 265
Myiopsitta monachus, 22
Myiozetetes similis, 10, 264
Myrmoborus myotherinus, 381
Nesomimus macdonaldi, 317
Nests and Nesting, 11–30, 34–40, 44–47, 94–

96, 103–104, 123–139, 188–194, 203–205, 216, 251–253, 331, 332–333, 333–335, 335–336, 396–406, 454–459, 464–465, 467–468
Netting, M. Graham, Does the Robin eat DeKay's snake?, 471
Nickell, Walter P., Unusual nesting habitats of three bird species in Rondeau Provincial Park, Ontario, 454–459
Niedrach, Robert J., see Bailey, Alfred M. and ———
Ninox novaeseelandiae, 57, 58
  strenua, 55, 56, 57, 58, 61
Niven, Cecily M., see Skead, C. J. and ———
Noddy, Brown, 461
Nucifraga columbiana, 419
Numenius borealis, 296
Nutcracker, Clark, 419
Nuthatch, Pygmy, 436
Nyctanassa violacea, 461
Nyctea scandiaca, 298
Olendorff, Richard B. and Sharon E. Olendorff, An extensive bibliography on falconry, eagles, hawks, falcons, and other diurnal birds of prey, reviewed, 481
Olendorff, Sharon E. see Olendorff, Richard B. and ———
Oliver, H. C., Annotated index to some early New Zealand bird literature, reviewed, 481
Olor columbianus, 464
Ontogeny, 87–93
Onychognathus morio, 312
Oporornis formosus, 256, 402
Oring, Lewis W., Summer biology of the Gadwall at Delta, Manitoba, 44–54
Oriole, Jamaican, 124
Oropendola, Crested, 13, 462
Osprey, 322
Osteology, 55–68
Otogyps calvus, 61
Otus asio, 57, 63, 273
Ovenbird, 248, 256, 259, 261, 298
Owl, Barn, 467, 468
  Barred, 100–101
  Eagle, 160
  Elf, 105
  Great Horned, 155–162, 332–333, 467, 468
  Screech, 57
  Snowy, 298
  Tawny, 305, 308
Owre, Oscar T., Adaptations for locomotion and feeding in the Anhinga and Double-crested Cormorant, reviewed, 478–479
Pakulak, Allan J. and Carroll D. Littlefield, Breeding status of Whistling Swans near Churchill, Manitoba, 464–465
Palm-Chat, 22
Palmer, Walter L., The frequency between successive drumming performances of Ruffed Grouse, 97–99
Panurus biarmicus, 275
Paradisaea rubra, 220, 221, 222
Parakeet, Gray-breasted, 22
Parasitism, 253–254, 455, 456, 457
Parkes, Kenneth C., On abnormally crossed mandibles in birds, 342; see Dickerman, Robert W. and ———
Parmelee, David F., H. A. Stephens, and Richard H. Schmidt, The Birds of Southwestern Victoria Island and adjacent small islands, reviewed, 231–232
Partridge, 305, 307, 309
Parus atricapillus, 293, 436
  atricristatus, 275
  bicolor, 470
  caeruleus, 296, 342
  major, 276, 296, 342
Passer domesticus, 103, 220, 221, 275, 363, 411, 419, 441, 470
Pedioecetes phasianellus, 75
Penny, R. L., review by, 117–118
Perdix perdix, 309
Pesticides, 340–341, 407–418
Petrochelidon pyrrhonota, 103
Pewee, Eastern Wood, 259, 261
Phacellodomus rufifrons, 5, 6, 123
  r. inornatus, 5, 6
Phaethon aethereus, 461
  lepturus, 460
Phasianus colchicus, 303, 411, 466
Pheasant, Ring-necked, 303, 411
Pheucticus ludovicianus, 275
Phileatirus socius, 22
Philohela minor, 333, 411

Phlegopsis erythroptera, 381
  nigromaculata, 369, 380, 381
Physiology, 407–418, 441–449
Picoides arcticus, 274
  tridactylus, 274
Picus canus, 274
  viridis, 274
Pigeon, Pale-vented, 462
Pintail, 50, 94
Pipilo erythrophthalmus, 275, 402
Pipit, Sprague's, 261
Piranga olivacea, 262
  rubra, 471
Pitangus sulphuratus, 19, 137, 268
  s. rufipennis, 124
Pithys albifrons, 369, 377, 381, 391
Platypsaris aglaiae, 13
Plautus alle, 213
Plectropterus, 55
Plegadis falcinellus, 463
Plover, American Golden, 210–211, 338
  Black-bellied, 142
  Semipalmated, 142, 149, 151
  Upland, 211
Pluvialis dominica, 210, 338
Populations, 99–100, 146–148, 158–159, 293–329
Porcupine, 209–210
Porphyrula martinica, 341
Prairie Chicken, Greater, 77
  Lesser, 75
Predation, 40–41, 46, 94, 399, 400, 402
Premnoplex brunnescens, 27
Procnias nudicollis, 220, 223
Progne dominicensis, 462
  subis, 275
Protonotaria citrea, 455
Prunella modularis, 276
Psarocolius decumanus, 13, 462
Ptarmigan, Rock, 302, 305, 307
Pteroglossus torquatus, 268
Publication Notes and Notices, 195, 232, 342, 352, 481–482
Puffinus lherminieri, 460
Pulich, Warren M., Unusual feeding behavior of three species of birds, 472
Pulsatrix perspicillata, 57, 58
Quiscalus quiscala, 400, 472
Raikow, Robert J., Sexual and agonistic behavior of the Common Rhea, 196–206
Rail, Spotted, 207–209
Rallus maculatus insolitus, 208, 209
  m. maculatus, 207, 209
Rand, Austin L., Ornithology: An introduction, reviewed, 345–347; review by, 118–119
Rea, Scott C., Plastic device causes gull mortality, 105–106
Recher, Harry F. and Judy A. Recher, Some aspects of the ecology of migrant shorebirds. II. Aggression, 140–154
Recher, Judy A., see Recher, Harry F. and ———
Recurvirostra americana, 142
Redhead, 51, 96
Redstart, 249
  American, 258, 259, 315, 454, 457, 471
  Red-bellied, 184
  Slate-throated, 185
Regulus satrapa, 186
Rhea americana, 196
Rhea, Common, 196–206
Rhegmatorhina berlepschi, 363–395
  cristata, 363–395
  gymnops, 363–395
  hoffmannsi, 363–395
  melanosticta, 363–395
Rice, Orville O., Record of female Cardinals sharing nest, 216
Richmondena cardinalis, 216, 220, 470
Riparia riparia, 275
Robin, 400, 407–418, 470, 471
  Clay-colored, 265, 268
Samuel, David E., House Sparrow occupancy of Cliff Swallow nests, 103–104
Sanderling, 142, 149
Sandpiper, Baird's, 338
  Least, 142, 143, 152, 153
  Pectoral, 149, 338
  Red-backed, 141, 142
  Semipalmated, 142, 143, 144, 145, 146, 147, 149, 150, 151, 152, 153, 338
  Sharp-tailed, 337–338
  Western, 142, 143, 149, 150, 151, 152, 153
  White-rumped, 142
Sapsucker, Yellow-bellied, 179, 180, 182, 259
Sayornis phoebe, 275

Scaup, Lesser, 49, 95, 96
Schmidt, Richard H., see Parmelee, David F. and ———
Selerurus guatemalensis, 9, 34
Sealy, Spencer G., Color aberrations in some alcids on St. Lawrence Island, Alaska, 213–214
Seedeater, Yellow-bellied, 463
Seiurus aurocapillus, 248, 259, 298
  motacilla, 256, 275
  noveboracensis, 462
Selasphorus rufus, 261
  sasin, 261
Setophaga ruticilla, 249, 258, 315, 454
Shearwater, Audubon's, 460, 463
Short, Lester L., Jr., Relationships among some South American seedeaters (*Sporophila*) with a record of *S. hypochroma* for Argentina, 216–219; An apparent agonistic display of the Whistling Heron (*Syrigma sibilatrix*), 330–331; Foraging association of Green-barred Flickers and Campo Flickers in Argentina, 468–470; Three papers on variation in flickers (Colaptes), reviewed, 225–230
Sialia currucoides, 105
  mexicana, 105
  sialis, 275
  s. fulva, 104
Sicalis flaveola, 136
Simmons, K. E. L., review by, 113–116
Sindelar, Charles R., Barred Owl feeds on Crow, 100–101
Sitta pusilla, 276
  pygmaea, 276, 436
Skead, C. J., Cecily M. Niven, J. M. Winterbottom and Richard Liversidge, The Sunbirds of Southern Africa: also the Sugarbirds, the White-eyes, and the Spotted Creeper, reviewed, 118–119
Skutch, Alexander F., A study of the Rufous-fronted Thornbird, and associated birds. Part I: Life history of the Rufous-fronted Thornbird, 5–43. Part II: Birds which breed in thornbirds' nests, 123–139; Life histories of Central American Highland Birds, reviewed, 110–111
Skutchia borbae, 370, 382
Skylark, 272, 297, 303, 304, 307, 312
Smith, Robert W., Irene L. Brown and L. Richard Mewaldt, Annual activity patterns of caged non-migratory White-crowned Sparrows, 419–440
Smythe, Robert B., see Helms, Carl W. and ———
Snake, DeKays, 471
  Garter, 470
Solitaire, Townsend's, 163–168
Somateria mollissima, 465
Soper, Tony, see Sparks, John and ———
Sparks, John and Tony Soper, Penguins, reviewed, 117–118
Sparrow, Chipping, 338
  Clay-colored, 262
  Grasshopper, 259
  House, 103–104, 363, 411, 419, 441, 442, 443, 445, 446, 447, 448, 470
  Lincoln's, 219–220, 262
  Song, 90, 251, 297, 305, 306, 307, 310, 416, 436
  Tree, 280–292, 296, 306, 441, 448
  White-crowned, 419–440
  White-throated, 236, 423, 444, 445
Sphyrapicus varius, 179
Spinetail, Pale-breasted, 8
  Red-faced, 13, 27
Spizella arborea, 220, 221, 280, 291, 296, 441
  breweri, 108
  pallida, 262
  passerina, 275, 338
Spofford, Sally Hoyt, Flicker incubates pink plastic balls on a lawn for five weeks, 214–215
Sporophila castaneiventris, 217, 218
  cinnamonea, 217, 218
  hypochroma hypochroma, 217, 218
    h. rothi, 218
  minuta, 216, 217, 218
  m. hypoxantha, 216, 218, 219
  m. parva, 216
  nigricollis, 463
  ruficollis, 217, 218, 219
Spring, Lowell, review by, 478–479
Squatarola squatarola, 142
Starling, 169, 174, 335–336
  Red-winged, 312, 316
Stelgidopteryx ruficollis, 275

Stephens, H. A., see Parmelee, David F. and ———

Sterna anaethetus, 460, 462
  dougallii, 460, 461, 462
  fuscata, 462

Stewart, Paul A., Movements, population fluctuations, and mortality among Great Horned Owls, 155–162

Stercorarius pomarinus, 298

Storeria d. dekayi, 471

Strix aluco, 305
  varia, 100

Sturnella magna, 107, 108
  neglecta, 107, 108, 275

Sturnus vulgaris, 169, 222, 275, 276, 335

Sula leucogaster, 461
  sula, 461

Swallow, Barn, 462
  Cliff, 103–104
  Tree, 272

Swan, Whistling, 464–465

Swann, H. Kirke, A dictionary of English and folk-names of British birds, reviewed, 481

Swinebroad, Jeff, review by, 344–345; see Bongiorno, Salvatore, F. and ———

Synalluxis, 19, 21, 23, 34
  albescens, 8
  erythrothorax, 21

Syrigma sibilatrix, 330

Tanager, Blue, 135–136
  Blue-gray, 463
  Sayaca, 136
  Scarlet, 259, 262
  Summer, 472

Tanagra affinis, 268
  laniirostris, 137

Tapera naevia, 137

Taxonomy, 64–66, 216–219

Taylor, Joseph W., Sharp-tailed Sandpiper and Palm Warbler in Alaska, 337–338

Teal, Blue-winged, 45, 46, 94
  Cinnamon, 95

Telmatodytes palustris, 275

Temple, Stanley A., A case of Turkey Vulture piracy on Great Blue Herons, 94

Tern, Bridled, 462, 463
  Roseate, 461, 463
  Sooty, 462, 463

Territory, 10–11, 75–78, 175–177, 187–188, 247–249, 293–329, 471

Thamnomanes saturninus, 381

Thamnophis sirtalis, 471

Thornbird, Rufous-fronted, 5–43, 123–139

Thrasher, Curve-billed, 87, 90, 91, 92

Thraupis episcopus, 135, 463
  sayaca, 136

Thrush, Bare-eyed, 462
  Gray-cheeked, 259, 260, 261, 262
  Song, 305
  Swainson's, 241
  Wood, 167, 396–406, 454

Thryothorus leucotis, 8
  ludovicianus, 470
  rufalbus, 265

Tityra, Masked, 264, 266

Tit, Blue, 296, 307, 308, 342
  Coal, 307, 308, 310, 311
  Great, 296, 298, 305, 306, 308, 309, 310, 342

Titmouse, Tufted, 470

Tityra semifasciata, 264

Todus subulatus, 273

Tolmomyias sulphurescens, 133

Towhee, Rufous-sided, 402

Toxostoma curvirostre, 87
  rufum, 275

Tringa flavipes, 142, 143
  melanoleucus, 142, 143
  solitaria, 143

Tripsurus chrysauchen, 40

Troglodytes aedon, 275, 303, 443, 462
  musculus, 8, 138

Trogon citreolus, 264

Trogon, Citreoline, 264, 266, 267

Tropicbird, Red-billed, 461, 463

Troupial, 23, 27, 34, 41, 123–132

Tucker, James A., see Kale, Herbert W. II and ———

Tudor, Guy, Antbirds of the genus *Rhegmatorhina*, painting by, facing p. 363

Turdoides, striatus, 317

Turdus grayi, 265
  merula, 276, 299
  migratorius, 275, 407, 470
  nudigenis, 462
  philomelos, 305

Turnstone, Ruddy, 142

Tympanuchus cupido, 77
  pallidicinctus, 75
Tyrannus melancholicus, 462
Tyrant, Fire-crowned, 134
  Short-winged, 134
Tyto alba, 57, 58, 60, 467
Upupa epops, 273
Uria aalge, 213, 214
  lomvia, 213, 214
Veery, 454
Vermeer, Kees, Egg measurements of California and Ring-billed Gull eggs at Miquelon Lake, Alberta in 1965, 102–103
Vermivora celata, 338
  chrysoptera, 69
  pinus, 69
  superciliosa, 185
Vireo flavoviridis, 265
  gilvus, 275
  olivaceus, 222, 275, 402
Vireo, Red-eyed, 259, 402
  Yellow-green, 265, 266, 267
Voice, 8–10, 69–74, 124, 163–168, 170, 186–187, 369–373
Volatinia jacarina, 463
Vulture, Black, 461
  Turkey, 94, 108, 467
Wagstaffe, Reginald and J. Havelock Fidler, The preservation of natural history specimens, reviewed, 481
Warbler, Audubon's, 185
  Black-and-white, 215, 256, 259
  Black-throated Blue, 259
  Black-throated Green, 106–107
  Blackpoll, 259, 260, 261, 262
  Blue-winged, 69–74
  Cape May, 258, 259, 262
  Crescent-chested, 185
  Golden-winged, 69–74
  Great Reed, 312, 315
  Hooded, 215, 256
  Kentucky, 256, 402
  Kirtland's, 247, 296, 306
  Magnolia, 259
  Myrtle, 236
  Orange-crowned, 338
  Palm, 236, 258, 259, 261, 262, 338
  Parula, 259
  Pink-headed, 184, 191
  Prothonotary, 455
  Red, 184–194
  Red-faced, 184
  Swainson's, 246–257
  Wilson's, 262
  Worm-eating, 253, 256
  Yellow, 454, 455, 457, 458
Warnock, John E., see Franks, Edwin C. and ———
Waterthrush, Louisiana, 256
  Northern, 215, 259, 462
Watson, George E., Seabirds of the tropical Atlantic Ocean, reviewed, 113–116
Waxbill, Barred, 22
Weather, 235–245, 258, 397, 450–453
Weaver, Social, 22
Weights, 51–52, 211, 413, 414, 415, 416, 422–423, 451
White, Clayton M., Functional gonads in Peregrines, 339–340
Wildash, Philip, Birds of South Vietnam, reviewed, 116–117
Willet, 142, 149
Willis, Edwin O., On the behavior of five species of *Rhegmatorhina*, ant-following antbirds of the Amazon basin, 363–395
Wilson Ornithological Society, Louis Agassit Fuertes Award, 474; Membership, 279, 453, 459; Officers, 483; Ornithological News, 109, 224, 343, 473–474; Proceedings of the Annual Meeting, 353–360
Wilsonia canadensis, 275
  citrina, 215, 256
  pusilla, 262
Winterbottom, J. M., see Skead, C. J., and ———
Wolf, Larry L., review by, 478–480
Wood, Merrill, Birds of Pennsylvania: When and where to find them, reviewed, 342
Woodcock, American, 338–339, 411
Woodcreeper, Buff-throated, 381
  Concolor, 381
  Hoffmann's, 378
  Streak-headed, 264, 268
  White-chinned, 378, 381, 382
Woodpecker, Black, 271
  Downy, 271

  Golden-fronted, 264, 266, 267
  Golden-naped, 40
  Hairy, 169–183
  Pileated, 181, 271, 332
  Red-bellied, 469
  Red-crowned, 10
Worth, C. Brooke, Hooded Warbler in Trinidad, West Indies, 215; A naturalist in Trinidad, reviewed, 347
Wren, Banded-backed, 40
  Buff-breasted, 8
  Carolina, 470
  House, 303, 305, 307, 309, 312, 443, 462
  Long-billed Marsh, 306
  Rufous-and-white, 265, 268
  Southern House, 8, 138
  Striped-backed, 137
  Superb Blue, 316, 317
Wrentit, 436
Xanthocephalus xanthocephalus, 262
Xenops minutus, 27, 34, 268
Xenops, Plain, 27, 268
Xiphorhynchus guttatus, 381
Yarrow, Ruth M., Recurrent use of territories by individual American Redstarts, 471
Yellowlegs, Greater, 142
  Lesser, 142
Yellowthroat, Common, 259, 402
Zenaida asiatica, 261
Zenaidura macroura, 108, 258, 338
Zonotrichia albicollis, 220, 236, 423, 444
  atricapilla, 419
  leucophrys, 108
  l. gambelli, 419, 432, 438
  l. leucophrys, 425
  l. nuttalli, 419–438
  l. pugetensis, 435, 437
  querula, 419

This issue of the Wilson Bulletin was published on 14 January, 1970.

SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the AOU Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subsequently identified. Summaries of major papers should be brief but quotable. Where fewer than five 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 "Style Manual for Biological Journals" (1964. AIBS). Photographs for illustrations should be sharp, 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. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

The permanent mailing address of the Wilson Ornithological Society is: c/o The MUSEUM of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

WILSON ORNITHOLOGICAL SOCIETY

ANNUAL MEETINGS

1st	1914	Chicago, Illinois
2nd	1914	Chicago, Illinois
3rd	1915	Columbus, Ohio
4th	1916	Chicago, Illinois
5th	1917	Pittsburgh, Pennsylvania
6th	1919	St. Louis, Missouri
7th	1920	Chicago, Illinois
8th	1921	Chicago, Illinois
9th	1922	Chicago, Illinois
10th	1923	Cincinnati, Ohio
11th	1924	Nashville, Tennessee
12th	1925	Kansas City, Missouri
13th	1926	Chicago, Illinois
14th	1927	Nashville, Tennessee
15th	1928	Ann Arbor, Michigan
16th	1929	Des Moines, Iowa
17th	1930	Cleveland, Ohio
18th	1931	New Orleans, Louisiana
19th	1932	Columbus, Ohio
20th	1934	Pittsburgh, Pennsylvania
21st	1935	St. Louis, Missouri
22nd	1936	Chicago, Illinois
23rd	1937	Indianapolis, Indiana
24th	1938	Ann Arbor, Michigan
25th	1939	Louisville, Kentucky
26th	1940	Minneapolis, Minnesota
27th	1941	Urbana, Illinois
28th	1946	Omaha, Nebraska
29th	1947	Columbus, Ohio
30th	1949	Madison, Wisconsin
31st	1950	Jackson's Mill, West Virginia
32nd	1951	Davenport, Iowa
33rd	1952	Gatlinburg, Tennessee
34th	1953	Cheboygan, Michigan
35th	1954	Cape May, New Jersey
36th	1955	Stillwater, Oklahoma
37th	1956	Buffalo, New York
38th	1957	Duluth, Minnesota
39th	1958	Wheeling, West Virginia
40th	1959	Rockland, Maine
41st	1960	Gatlinburg, Tennessee
42nd	1961	Huntsville, Ontario, Canada
43rd	1962	Lafayette, Indiana
44th	1963	Charleston, South Carolina
45th	1964	Kalamazoo, Michigan
46th	1965	Sylvan Lake, South Dakota
47th	1966	University Park, Pennsylvania
48th	1967	Crawford Notch, N. Hampshire
49th	1968	Carbondale, Illinois
50th	1969	Williamsburg, Virginia
51st	1970	Fort Collins, Colorado
52nd	1971	Dauphin Island, Alabama