PROCEEDINGS
XIII INTERNATIONAL
ORNITHOLOGICAL CONGRESS

Augastes scutatus, life size

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HUMMINGBIRDS FROM THE BRAZILIAN PLATEAU

Photographs by CRAWFORD H. GREENEWALT
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PROCEEDINGS
XIII INTERNATIONAL ORNITHOLOGICAL CONGRESS

Ithaca 17-24 June 1962

VOLUME I

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1963

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THE INTERNATIONAL ORNITHOLOGICAL CONGRESSES 1884–1962[1]

	Place	*Year*	*President*	*Secretary-General*
I	Vienna	1884	Dr. G. F. R. Radde	Dr. Gustav von Hayek
II	Budapest	1891	Prof. Victor Fatio and Otto Herman	—
III	Paris	1900	Dr. Émile Oustalet	Jean de Claybrooke
IV	London	1905	R. Bowdler Sharpe	Dr. E. J. O. Hartert J. Lewis Bonhote
V	Berlin	1910	Prof. Dr. Anton Reichenow	Herman Schalow
VI	Copenhagen	1926	Dr. E. J. O. Hartert	E. Lehn Schiøler
VII	Amsterdam	1930	Prof. Dr. A. J. E. Lönnberg	Prof. Dr. L. F. de Beaufort
VIII	Oxford	1934	Prof. Dr. Erwin Stresemann	Rev. F. C. R. Jourdain
IX	Rouen	1938	Prof. Alessandro Ghigi	Jean Delacour
X	Uppsala	1950	Dr. Alexander Wetmore	Prof. Dr. Sven Hörstadius
XI	Basel	1954	Sir Landsborough Thomson	Prof. Dr. Adolf Portmann
XII	Helsinki	1958	Prof. J. Berlioz	Dr. Lars von Haartman
XIII	Ithaca	1962	Dr. Ernst Mayr	Dr. Charles G. Sibley

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[1] A history of the early International Congresses is given in the Presidential address of Erwin Stresemann, Proc. Eighth Intern. Ornithol. Congr., Oxford: 6–23.

PREVIOUS REPORTS

OF THE

INTERNATIONAL ORNITHOLOGICAL CONGRESSES

I. Sitzungs-protokolle des ersten Internationaler Ornithologen-Congresses. . . . vom 7. bis 11. April 1884 in Wien abgehalten wurde. Wien, Verlag des Ornithologischen Vereines in Wien, 1884. vi + [90] p.

Mitteilungen des Ornithologischen Vereins Wien, Band viii–x, 1884–86.

II. Bericht . . . Zweiter Internationaler Ornithologischer Congress, Budapest, 1892. (Blasius) [n.p., 1891] 58 p.

III. III^{e} Congrès Ornithologique international, Paris/26–30 juin 1900. Compte rendu des séances publié par É. Oustalet . . . et J. de Claybrooke . . . . Masson et Cie, Paris. xii + 503 p. 1901. [= Ornis, vol. 11]

IV. Proceedings of the Fourth International Ornithological Congress, London/June 1905. Edited by R. B. Sharpe, E. J. O. Hartert, and J. L. Bonhote. Dulau & Co., London. 696 p. 1907. [= Ornis, vol. 14]

V. Verhandlungen des V. Internationaler Ornithologen-Kongresses, Berlin 30. Mai bis 4. Juni 1910. Herausgegeben von Herman Schalow . . . . Deutsche Ornithologische Gesellschaft, Berlin. x + 1186 p. 1911.

VI. Verhandlungen des VI. Internationalen Ornithologen-Kongresses in Kopenhagen, 1926. Herausgegeben von Dr. F. Steinbacher. Berlin. vi + 641 p. 1929.

VII. Proceedings of the VIIth International Ornithological Congress at Amsterdam. Amsterdam. vii + 527 p. 1931.

VIII. Proceedings of the Eighth International Ornithological Congress/Oxford/July 1934. Edited by F. C. R. Jourdain. Oxford University Press, Oxford. x + 761 p. 1938.

IX. IX^{e} Congrès Ornithologique International/Rouen—9 Au 13 Mai 1938. Compte Rendu publié par Jean Delacour . . . . Rouen. 543 p. 1938.

X. Proceedings of the Xth International Ornithological Congress/Uppsala/June 1950. Edited by Sven Hörstadius. Almqvist & Wiksells, Uppsala. 662 p. 1951.

XI. Acta XI Congressus Internationalis Ornithologici/Basel 29.V.–5.VI. 1954. Herausgegeben von Adolf Portmann und Ernst Sutter. Berhäuser Verlag, Basel und Stuttgart. 680 p. 1955.

XII. Proceedings/XII International Ornithological Congress/Helsinki. 5.–12. VI. 1958. Edited by G. Bergman, K. O. Donner, L. v. Haartman. Tilgmannin Kirjapaino, Helsinki. 2 v. 820 p. 1960.

OFFICERS
OF THE
XIIIth INTERNATIONAL ORNITHOLOGICAL CONGRESS

President: Ernst Mayr

Secretary-General: Charles G. Sibley

Permanent Executive Committee 1958–62

Sálim Ali
G. P. Dementiev
R.-D. Etchécopar
Gustav Kramer (deceased)
Lars von Haartman
G. C. A. Junge (deceased)
Ernst Mayr
Alden H. Miller
W. H. Thorpe

Preface

The fragmentation of biology into specialized disciplines during the present century has threatened to overshadow the traditional studies of zoology and its component parts. Subjects like physiology have received far more attention than ornithology in recent years, and these in turn have been divided into lively offspring, including endocrinology and neurophysiology.

The present volumes are witness, however, to the fact that ornithology is by no means dead. Indeed it seems to be more vigorous than ever. The *Proceedings* of the XIIIth Congress contain about 75 percent more pages than the average for the last ten Congresses, and they are about 45 percent longer than the report on the last Congress at Helsinki. Of the 152 papers and films that were presented or read by title at Ithaca, 110 are published here, usually in their entirety. Those that do not appear in these volumes include papers that authors intended to publish elsewhere, often at greater length, and sometimes with differing titles. The titles of these additional papers are listed near the end of Volume II as a part of the permanent records of the Congress.

Something of the growth of our science can be seen in the following tabulation of the enrollments and publications of the ten most recent International Ornithological Congresses.

Year Held	*Where Held*	*Members Enrolled*	*Papers Published*	*Pages in Proceedings*
1905	London	349	40	696
1910	Berlin	240	57	1,186
1926	Copenhagen	198	42	641
1930	Amsterdam	291	48	527
1934	Oxford	347	65	761
1938	Rouen	300+	53	543
1950	Uppsala	377	84	662
1954	Basel	527	107	680
1958	Helsinki	511	98	820
1962	Ithaca	879	110	1,217 (plus index)

The New Ornithology is no wordier than its predecessors—it simply covers more ground and more research activity. It is characterized by the new need for comprehensive reviews which the reader will find scattered throughout the present volumes. It is also distinguished by an increasing interest in bridging the gaps between studies like taxonomy and psychology, between ecology and physiology, and the like.

This straddling of specialized disciplines was particularly evident to the editors when—in response to a directive from our officers—we attempted to group papers into simple categories within the present two volumes. Modern ornithological research no longer can be so rigidly classified, and the 13 categories that we have used in these volumes must be regarded as very loose ones. The subject index at the end of Volume II will, we hope, more accurately classify and cross-index the papers.

In stylizing the XIIIth *Proceedings*, the editors have endeavored as far as possible to follow the *Style Manual of the American Institute of Biological Sciences* in such matters as abbreviations and literature citations. A few periodicals have been abbreviated according to the third edition of Oxford's older *World List of Scientific Periodicals Published in the Years 1900–1950.*

As a general rule we have accepted the authors' designations of scientific names. Our own lack of time prevented us from adding in the Index more commonly accepted generic names for some of those used in these volumes.

The editors are especially indebted to Crawford H. Greenewalt and to the National Geographic Society for printing the handsome frontispiece that adds so much to Volume I. In addition to the members of our editorial committee, the following colleagues assisted us in a variety of much appreciated ways: Frank C. Bellrose, Jean Delacour, Virginia M. Emlen, Klaus Gerdes, Richard F. Johnston, J. Allen Keast, J. Anthony Keith, Harland W. Mossman, Robert Cushman Murphy, Douglass Payne, Victor Rabinowitch, Ernst Schüz, Donald D. Stamm, Erwin Stresemann, Melvin A. Traylor, Jan Vansina, Doreen M. Wallace, and Albert Wolfson. Dr. and Mrs. Ernst Mayr read proof of the papers printed in German. The editorial work on these volumes involved approximately 2,000 hours, about half of which had to come on nights and weekends when we were free from normal teaching and research responsibilities. We are indeed grateful to our authors for their patience and understanding in helping us to publish this report of the XIIIth International Ornithological Congress, and to the officers and council of the American Ornithologists' Union for their continuous encouragement. A very special vote of thanks goes to the staff of The Allen Press for their patience, efficiency, and constant cooperation.

The support of the National Science Foundation contributed importantly to all aspects of the Congress, including the publication of these *Proceedings*.

Looking back on the work of our editorial predecessors, we are impressed with the difficulties that they must have faced with the surface mails of a now-departed era. In 1963, modern airmail service made it routine for proofs to leave Madison, Wisconsin, and return from Europe in 6 days, from Japan in 10, and from Australia and South Africa in 11. Lest our successors become overly optimistic, we can also add that, while rocket mail service may in the future reduce these time intervals even to hours, some ornithologists can always be counted on to be sitting in distant bogs or on mountain tops, bemused by wonderful birds, miles away from post offices and telephones, and happily oblivious to the time schedules of harassed editors and busy printers. Come to think of it, we hope it will always be that way.

THE EDITORS

October 1963

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BEHAVIOR: PHYLOGENY AND EVOLUTION

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XIII INTERNATIONAL ORNITHOLOGICAL CONGRESS

The XIIIth International Ornithological Congress
Ithaca, New York, 17-24 June 1962

Report of the Secretary-General

Charles G. Sibley

At the Eighth Congress, in 1938, the invitation of the United States delegation to hold the Ninth Congress in the United States in 1942 was accepted. World War II intervened and postwar conditions made it inadvisable to extend a second invitation for a Congress in the New World until 1958, in Helsinki. The invitation was accepted, and Professor Ernst Mayr of Harvard University, was elected President. The invitation was extended jointly by the American Ornithologists' Union, the Cooper Ornithological Society, and the Wilson Ornithological Society. The U.S. and Canadian members of the International Ornithological Committee formed a General Committee to organize the Thirteenth Congress. The author was elected as Secretary-General, and the members of this committee were as follows:

Dean Amadon
James P. Chapin
Herbert G. Deignan
Jean Delacour
Herbert Friedmann
Hoyes Lloyd
George H. Lowery, Jr.
Ernst Mayr
Alden H. Miller
Roger T. Peterson
Austin L. Rand
S. Dillon Ripley
Charles G. Sibley
Lester L. Snyder
Robert W. Storer
Alexander Wetmore

The Secretary-General was concurrently the Treasurer of the American Ornithologists' Union, and the Congress finances were handled through this office.

The scientific program of the Congress was planned by the Program Committee consisting of the Secretary-General, Dean Amadon, Donald S. Farner, George H. Lowery, Jr., and Alden H. Miller. This committee screened the abstracts of the papers that were offered for presentation.

A Travel Grants Committee, consisting of the President, the Secretary-General, Dean Amadon, and S. Dillon Ripley was responsible for the awarding of 46 travel grants to applicants from outside North America. In addition, the International Union of Biological Sciences supported two travel grants as a subvention for the Congress. Additional travel assistance was awarded directly to foreign ornithologists by the American Museum of Natural History through the Frank M. Chapman Memorial Fund and by the International Council for Bird Preservation.

The Congress Committee on Student Participation (S. Charles Kendeigh, William H. Behle, Robert T. Orr) awarded ten travel grants ($1,225) to

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graduate students in North American universities and the Frank M. Chapman Fund awarded eight such grants ($1,399).

Travel support, from all sources, was $57,553, of which $24,406 was provided by or through the Congress, $28,277 through the Frank M. Chapman Memorial Fund and $4,870 through the International Council for Bird Preservation.

The excursions were planned and carried out by a committee of 22 members under the direction of O. S. Pettingill, Jr. The other members were:

Alfred M. Bailey
Irston R. Barnes
Donald L. Bleitz
Shirley A. Briggs
Roland C. Clement
William H. Drury
Dr. and Mrs. Robert T. Gammell
Mr. and Mrs. James Gates
J. T. Marshall, Jr.
Allen H. Morgan
Robert J. Niedrach
William B. Robertson, Jr.
Margaret S. Rusk
Mr. and Mrs. Arnold Small
Walter R. Spofford
Arthur Stupka
Prof. and Mrs. G. A. Swanson

Two long excursions, by air, were arranged. The first, 3–16 June, was to the Great Smoky Mountains and to Florida. The second, 25 June–7 July, was to the Great Plains (North Dakota), the Rocky Mountains near Denver, Colorado, the Arizona desert, and southern California.

Shorter excursions, each of 1-week's duration, were planned to the Boston area of eastern Massachusetts, northern New York State (Oneida Lake, Adirondack Mountains), the New York City region, and the Washington, D.C., region. These excursions were scheduled for the 2 weeks preceding and following the week of the Congress. Relatively few persons participated in the excursions. The New York City excursions and most of the Boston area excursions were canceled.

The Local Committee of 70 persons assisted the Secretary-General with the exhibits, local field trips, registration, transportation, ladies' program, and the many other aspects of the meetings in Ithaca. The members of the Local Committee were:

Philip F. Allan
Arthur A. Allen
David G. Allen
Elsa G. Allen
Rosemary E. Almendinger
Robert Angstadt
Mrs. M. C. Bond
Mary F. Boynton
Mrs. Harlan B. Brumstead
Paul A. Buckley
Carl A. Carlozzi
Mrs. Carl A. Carlozzi
Jane Corbin
Kendall W. Corbin
Martha Dilger
William C. Dilger
Olan W. Dillon
W. Robert Eadie
Elizabeth A. Ferguson
Millicent Ficken
Robert W. Ficken
Richard B. Fischer
Neal Robert Foster
Douglas J. Futuyma
Marie A. Gast
Joan H. Haavie
W. J. Hamilton, Jr.
James M. Hartshorne
Mrs. Walter Heasley
Herbert T. Hendrickson
Jean Hewitt
Oliver H. Hewitt
Sally F. Hoyt
Byrl Kellogg

Peter Paul Kellogg
Paul Kelsey
Ethel Little
Randolph S. Little
Charles D. MacInnes
Paul Mundinger
James R. Nolan
Marta Nolan
Mrs. Paul O'Leary
Douglass Payne
Lewis F. Pearsall
Mrs. A. H. Peterson
Eleanor Pettingill
O. S. Pettingill, Jr.
Edward C. Raney
Richard Reynolds
G. F. Shepherd, Jr.
Mrs. G. F. Shepherd, Jr.
Lester L. Short, Jr.
Charles G. Sibley
Frances Sibley
Fred C. Sibley
Richard A. Sloss
Neal G. Smith
Alice Stein
Robert C. Stein
J. Bolling Sullivan, III
Evadene Swanson
Gustav A. Swanson
Katharine Thorp
Grace Tilger
Doreen M. Wallace
A. Richard Weisbrod
Mrs. A. Richard Weisbrod
John W. Wells
John S. Weske

An Editorial Office under the direction of J. J. Hickey was open daily to assist authors with the final stages of their manuscripts. An Editorial Committee of 24 persons was appointed to assist the editorial staff in the screening and editing of submitted papers. The committee was as follows:

John Davis
Keith L. Dixon
Eugene Eisenmann
John T. Emlen, Jr.
Donald S. Farner
Harvey I. Fisher
Oliver H. Hewitt
Thomas R. Howell
E. W. Jameson, Jr.
Paul A. Johnsgard
James R. King
Wesley E. Lanyon
George H. Lowery, Jr.
Robert A. McCabe
Harold F. Mayfield
Ernst Mayr
Alden H. Miller
Kenneth C. Parkes
Austin L. Rand
Lester L. Short, Jr.
Gustav A. Swanson
Harrison B. Tordoff
Charles Vaurie
Alexander Wetmore

In accordance with tradition, the Secretary-General accepted appointment as Editor, but the actual work was carried out by the Associate Editors, J. J. Hickey and Mrs. Margaret B. Hickey.

The Congress was opened officially at 8:00 PM on Sunday, 17 June, in the Alice Statler Auditorium of Cornell University. The President of Cornell University, Deane W. Malott, welcomed the members of the Congress, and the President of the Congress, Ernst Mayr, presented his presidential address. Following the opening ceremonies, members of the Congress were the guests of Cornell University at a reception in the ballroom of Statler Hall. The President of the University and Mrs. Malott were host and hostess.

The sessions for the presentation of scientific papers occupied the mornings (9–12 AM) and the afternoons (2–4:30 PM) of Monday, 18 June; Tuesday, 19 June; Thursday, 21 June; Friday, 22 June; and the morning only of Saturday, 23 June. Films were shown during the evenings of Monday, Tuesday, Thursday, and Friday. A special film on the birds of the Galapagos by Heinz Sielmann was shown on both Monday evening and Thursday evening.

Special meetings on "problem" birds, bird banding, and game-bird biology were also scheduled for evening sessions.

During the five days and evenings, 152 papers and films were presented. The scientific papers were organized into related groups, and three sessions were run concurrently at all times. The groups of papers included the following headings: Visual and Radar Migration Studies; Life-history Studies; Behavior; Breeding Seasons and Desert Adaptations; Systematics and Protein Studies; Nesting Studies; Ecology; Fossil Birds; Orientation and Migration; Avian Anatomy; Zoogeography; Population Studies; Bioenergetics; Molt; Physiology of Migration; Endocrinology; Biology of Penguins and Albatrosses; Evolution of Isolating Mechanisms; Conservation and Management; Vocalization. A special symposium on Birds and Arthropod-borne Viruses was arranged by Telford S. Work of the U.S. Public Health Service.

On Wednesday, 20 June, an all-day excursion, by bus, was enjoyed by the members. Various scenic places in the Finger Lakes region were visited, including Montezuma National Wildlife Refuge and several state parks. A barbecue supper at Taughannock State Park concluded the day of field excursions.

Special exhibits of photographs, paintings, and books were arranged. A. A. Allen was in charge of the photographic exhibit, and Mrs. A. A. Allen arranged the book exhibit. The White Art Museum of Cornell University cooperated in the organization of the exhibit of paintings. An exhibit of banding and trapping equipment was arranged by Olan W. Dillon and John S. Weske at the aviary of the Department of Conservation. A special exhibit of stereo photographs of hummingbirds was provided by Crawford H. Greenewalt.

A women's program, under the direction of Mrs. Sally F. Hoyt and Mrs. Evadene Swanson, arranged campus tours and other activities for the ladies.

The banquet was held in the ballroom of Statler Hall on Saturday, 23 June. The Ithaca High School Concert Choir sang several numbers which were well received. The President and the Secretary-General also contributed to this closing session.

The members of the International Ornithological Committee and their wives were entertained at a banquet preceding the official opening of the Congress on Sunday, 17 June. At this time, a short meeting of the Committee was held, and the members present were asked to submit nominations for vacancies on the Committee.

A second meeting of the International Ornithological Committee was held on Friday, 22 June, and the Committee for 1962–66 was elected, as follows:

Argentina: Jorge R. Navas, C. C. Olrog
Australia: H. J. Frith, A. J. Marshall, D. L. Serventy
Austria: K. M. Bauer, G. von Rokitansky
Brazil: H. Sick
Canada: W. E. Godfrey, H. Lloyd
Chile: R. A. Philippi B.
Colombia: Jose I. Borrero H.
Czechoslovakia: W. Černý
Denmark: B. Løppenthin, K. Paludan, F. Salomonsen
Finland: L. von Haartman, P. Palmgren
France: J. Berlioz, F. Bourlière, J. P. Dorst, R.-D. Etchécopar, H. Heim de Balzac, F. Hue, C. Jouanin, J. Prevost, F. Roux
Germany: J. Aschoff, R. Drost, F. W. Goethe, O. Koehler, R. Kuhk, H. Löhrl, W. Meise, G. Niethammer, E. Schüz, E. Stresemann
Great Britain: Phyllis Barclay-Smith, J. Fisher, D. Lack, J. D. Macdonald, R. E. Moreau, G. Mountfort, E. M. Nicholson, P. Scott, A. L. Thomson, W. H. Thorpe, V. C. Wynne-Edwards
Hungary: A. Keve
Iceland: F. Gudmundsson
India: H. Abdulali, S. Ali, B. Biswas
Italy: S. Frugis, E. Moltoni
Japan: Nagahisa Kuroda, Nagamichi Kuroda, Y. Yamashina
Kenya: J. G. Williams
Malaya: Loke Wan-Tho
Netherlands: G. A. Brouwer, W. H. Bierman, H. N. Kluyver, K. Voous
New Zealand: R. A. Falla, J. Gibb
Norway: Y. Hagen, H. Holgersen
Peru: Maria Koepcke
Philippines: D. S. Rabor
Rhodesia: R. H. N. Smithers
South Africa: J. Vincent, Cecily Niven
Spain: F. Bernis, J. A. Valverde
Sweden: K. Curry-Lindahl, S. Horstadius, G. E. Rudebeck
Switzerland: P. Geroudet, L. Hoffmann, A. Portmann, A. Schifferli
U.S.A.: D. Amadon, J. P. Chapin, H. G. Deignan, J. Delacour, H. Friedmann, G. H. Lowery, Jr., E. Mayr, A. H. Miller, R. T. Peterson, A. L. Rand, S. D. Ripley, C. G. Sibley, R. W. Storer, A. Wetmore
U.S.S.R.: G. P. Dementiev, N. Gladkov, A. Ivanov
Venezuela: W. H. Phelps, Jr.

The Permanent Executive Committee met twice. The following persons were elected for 1962–66: Georges Dementiev, Jean Dorst, Lars von Haartman, Gunther Niethammer, Finn Salomonsen, Charles Sibley, William H. Thorpe, and Yoshimaro Yamashina.

David Lack was elected President of the XIVth International Ornithological Congress to be held in England in 1966.

The Standing Committee on Ornithological Nomenclature for 1962–66 consists of the following: Charles Vaurie, Chairman, Jean P. Dorst, Eugene Eisenmann, Finn Salomonsen, and K. H. Voous.

The finances of the Congress.—The principal support for the Congress was a special grant of $36,100 from the National Science Foundation of the United States. Private donations and donations from organizations amounted to $6,522.50, and membership fees $8,990.20. The membership fee for U.S. members was $20; for non-U.S. and student members, $10; and for associate members, $5. These classes of membership enjoyed identical privileges except that associate members will not receive the *Proceedings* without charge.

The various excursions, banquet, etc. were mainly self-supporting.

Total income, from all sources, came to $54,402.73. Up to 1 August 1962, the total expenses, including travel grants, came to $37,056.08. The remainder, $17,346.65, was transferred to the Special Publication Fund of the American Ornithologists' Union to pay for the publication and distribution of the *Proceedings*. A more complete financial report will be published in *The Auk* as part of the A.O.U. Treasurer's Report for 1961–62.

The Thirteenth International Ornithological Congress is especially indebted to the National Science Foundation, the American Ornithologists' Union, the Cooper Ornithological Society, and to the many private donors who supported the Congress. The International Union of Biological Sciences provided a special subvention of $1,000, which was allocated to the Travel Grant Fund. Without these grants and gifts, the Congress could not have been held, for the membership fees paid for only a small percentage of the costs.

Members of the Congress.—A total of 879 persons were members of the Thirteenth Congress. Of these, 717 were regular members, 109 were associate members, and 53 were honorary members. The honorary members were mostly members of the Cornell faculty and administration and officials of the National Science Foundation. The total attendance at the Ithaca meeting was approximately 770 persons. Of these, 614 were regular members.

The following 37 countries or areas were represented at the Ithaca meeting: Argentina, Australia, Austria, Brazil, Canada, Canal Zone (Panama), Chile, Colombia, Curaçao, Czechoslovakia, Denmark, Finland, Germany, Great Britain, Guatemala, Iceland, India, Ireland, Israel, Italy, Japan, Korea, Malaya, Netherlands, New Zealand, Norway, Peru, Philippines, Poland, Puerto Rico, Rhodesia, South Africa, Spain, Sweden, Switzerland, United States, and Venezuela.

Members of the XIIIth International Ornithological Congress

H—Designates Honorary Member
A—Designates Associate Member
*—Member not present at the Ithaca meeting

Abs, Michael, Meckenheimerstr. 44, Bonn, Germany
Acland, Clemence M., 2 Orchard Close, Banstead, Surrey, England
Adams, Donald K., Duke Univ., Durham, N.C., U.S.A.
Adelholt, Ella, Skydebanegade 23, Copenhagen, Denmark
H Adelmann, Howard B., Dept. of Zool., Cornell Univ., Ithaca, N.Y., U.S.A.
Aldrich, John W., U.S. Bur. of Sport Fisheries and Wildlife, Washington 25, D.C., U.S.A.
A Aldrich, Louise K. (Mrs. John W.), 7725 Lakeview Dr., Falls Church, Va., U.S.A.
* Alexander, Gordon, Univ. of Colorado, Boulder, Colo., U.S.A.
Alexander, Horace G., 26 Bon Accord Rd., Swanage, Dorset, England
Alexander, Rebecca B. (Mrs. Horace G.), 26 Bon Accord Rd., Swanage, Dorset, England
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Allen, A. A., Ornithol. Lab., Cornell Univ., Ithaca, N.Y., U.S.A.
Allen, David G., Ornithol. Lab., Cornell Univ., Ithaca, N.Y., U.S.A.
Allen, Elsa G. (Mrs. A. A.), Ornithol. Lab., Cornell Univ., Ithaca, N.Y., U.S.A.
*H Allen, J Frances, Natl. Sci. Fdn., Washington 25, D.C., U.S.A.
Allen, Ted T., Jacksonville Univ., Jacksonville 11, Fla., U.S.A.
Almendinger, Rosemary E., 642 Donlon, Cornell Univ., Ithaca, N.Y., U.S.A.
Amadon, Dean, Am. Mus. Nat. Hist., New York 24, N.Y., U.S.A.
Ames, Peter L., Peabody Mus., Yale Univ., New Haven, Conn., U.S.A.
H Anderson, John M., Dept. of Zool., Cornell Univ., Ithaca, N.Y., U.S.A.
Angstadt, Robert, Ornithol. Lab., Cornell Univ., Ithaca, N.Y., U.S.A.
A Annan, Betty D. (Mrs. Ormsby), Dept. of Biol., Stephen F. Austin State Coll., Nacogdoches, Texas, U.S.A.
Annan, Ormsby, Dept. of Biol., Stephen F. Austin State Coll., Nacogdoches, Texas, U.S.A.
Arbib, Robert S., Jr., 226 Guion Dr., Mamaroneck, N.Y., U.S.A.
Armstrong, Rev. Edward A., St. Mark's Vicarage, 13 Barton Rd., Cambridge, England
H Atwood, Sanford S., 300 Day Hall, Cornell Univ., Ithaca, N.Y., U.S.A.
A Austin, Elizabeth S. (Mrs. Oliver L.), 205 S.E. 7th St., Gainesville, Fla., U.S.A.
Austin, Enid K., 1116 Mandana Blvd., Oakland 10, Calif., U.S.A.
Austin, Oliver L., Jr., Florida State Mus., Gainesville, Fla., U.S.A.
Aveledo H., Ramón, c/o W. H. Phelps, Apartado 2009, Caracas, Venezuela
de Ávila-Pires, Fernando D., Mus. Nacional, Rio de Janeiro, Estado da Guanabara, Brazil

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The Role of Ornithological Research in Biology

Address of the President

Ernst Mayr, Harvard University, Cambridge 38, Mass., U.S.A.

According to a long-standing tradition, the President in his address is to review the advances of ornithological science during the past 4 years. Remembering that about 2,500 ornithological titles are now annually listed in the *Zoological Record*, in other words 10,000 in a 4-year period, it becomes evident how futile it would be to try to review or summarize such an avalanche of literature. My recent predecessors in this office came to the same conclusion, and each of them selected some special aspect of ornithological science for special treatment. The topic of *my* choice is to review in what respect ornithological research differs from or resembles research in other branches of biology.

Ornithology is often referred to as the *scientia amabilis*, and indeed there are only few branches of science, for instance the study of orchids and of butterflies, that combine a similar appeal to our aesthetic senses and our scientific mind. The ten thousands who enjoy bird watching and the hundreds who enjoy bird keeping do so primarily for aesthetic reasons. Yet, nearly all of them also have a lesser or greater amount of interest in scientific ornithology.

There is perhaps no other branch of biology, indeed of science as a whole, to which the amateur has made so many and such important contributions as ornithology. In a way, I do not like the word "amateur" because it suggests something dilettante, and this would surely be a misleading description of the work of so many of our leading ornithologists. The precision of their observations, the imaginative and highly original posing of problems, and the lucid and informative recording of their researches, which characterize the work of many nonprofessional ornithologists, would dispel any notion of their work being that of dilettantes. Let me mention merely a few leaders, such as the late Gottfried Schiermann who worked on bird populations, Harold Mayfield on the Kirtland's Warbler, Larry Walkinshaw, François Haverschmidt, and Keith Hindwood; or to go back to an earlier generation, Admiral Lynes, Claude Ticehurst, Eliot Howard, and the great Seebohm, to convince you what splendid scientists these nonprofessionals are and were. They differ or differed from professionals only in one respect, by earning their living as doctors, lawyers, or businessmen and receiving no pay for their ornithological labors.

Large areas of ornithology owe their major progress to the devotion of such nonprofessionals. The study of bird migration, the study of avian life histories, and the systematic search for undiscovered birds in Africa, Asia, and South America, to quote just a few examples, have largely been in the

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hands of ornithologists who were businessmen, government officials, or doctors by profession. The number of professional ornithologists only a generation ago was extremely small, most countries being able to support only one or two of them, and even the most prosperous countries less than ten.

There has been a subtle but steady change within recent decades. To be sure, the importance of the nonprofessional continues undiminished, as can be seen by a glance at any of our ornithological journals. Yet throughout the world there has been a dramatic increase in the number of professionals. It would lead too far to investigate the reasons for this development; indeed there are presumably numerous reasons, one of the most important surely being the general rise in the prestige of science as such. Equally important is the shift of the position of ornithology from being merely a hobby, to being a legitimate branch of zoology. Erwin Stresemann has perhaps done more than anyone else to bring about this recognition. The numerous young ornithologists whom he trained, as zoologists, at the University of Berlin, formed the first school of genuine scientific ornithologists. The *Journal für Ornithologie*, during that same period, set an entirely new style which has been adopted to a lesser or greater degree by most major ornithological journals.

Since that time, there has been an active development of centers of scientific ornithology at many universities. To single out just a few of the many names that I could list here, I shall merely mention Joseph Grinnell and Alden H. Miller at the University of California, the group here at Cornell, David Lack and the Edward Grey Institute at Oxford, and Pontus Palmgren and his associates at Helsinki. How insufficient these few names are to indicate the spread of ornithological research at the universities throughout the world may be illustrated by a few figures from American universities. There are at least 50 colleges or universities in the United States in which graduate students are working at the present time for a higher degree and are in the process of doing a thesis dealing with birds. In all, there are now more than 160 graduate students in the United States working on an ornithological thesis. Obviously they will not all become ornithologists, in fact most of them will eventually specialize in physiology, comparative anatomy, animal behavior or ecology, and some of them will go into applied biology, such as wildlife management. Nevertheless, these figures document an unprecedented increase in professional training. The breadth of scientific interest in ornithology is further illustrated by the contents of scientific journals. For instance, if we look at some of the recent volumes of *Behaviour* or the *Zeitschrift für Tierpsychologie*, we find that about a quarter of these journals is devoted to publications on birds.

Their evident success in contributing to basic biological theory has encouraged ornithologists to go deeper and to establish contact with other branches of biology. Let me cite as illustrations only a few examples, such as Tinbergen's work on behavior, Lack's work on animal populations, Grinnell's and Miller's work on ecological problems, and my own studies of speciation. The significance of these contributions attracted in each case new students to these areas and encouraged closer contact with other areas of biology. Literally dozens of other ornithologists have done the same for still other biological problems.

As a result, in ornithology we are now in the happy situation of having not only a large, keen, and dedicated army of nonprofessionals, but also an increasing troupe of highly trained professional leaders. There has never been a period when the future of scientific ornithology was more promising than it is now.

THE SUITABILITY OF BIRDS FOR BIOLOGICAL RESEARCH

When one looks back over the last 30 years, it almost seems as if it had been suddenly discovered that birds are specially suitable material for scientific studies. This is indeed part of the explanation of the current boom of ornithological research. The answer is, however, not quite so simple. Without question, birds are specially suitable material for certain types of researches, yet they are far less favorable material for others. There are two properties of birds that make them exceptionally favorable material. One is that they are conspicuous and unique in being easily observed. The dominant sense organs of birds, sight and hearing, are the same ones that are dominant in man. The intraspecific signals of birds, such as plumage displays, songs, and calls are as easily perceived by man as by fellow members of the various bird species. As a result, the biology of birds can be studied without any elaborate apparatus. Birds are furthermore mostly diurnal and of convenient size and numerical frequency. Finally, being aerial animals, they are usually above the ground and outside water, which adds to their ease of observation. Anyone who has been trying to observe mammals, fish, or insects appreciates these manifold advantages of birds.

A second scientific advantage of birds is a direct consequence of this first advantage. Birds are more completely known than any other group of organisms. Wherever it is important to make generalizations and to arrive at statistically valid results, one is much safer with birds than with other kinds of organisms. This is particularly true in all sorts of comparative studies and in faunistic–zoogeographic research.

The inventory of the species of birds throughout the world is nearly completed. The last new species of North American birds was described in 1889, the last new species of Australian birds in 1910, and the last new species of Palaearctic birds in 1937. The same completeness is true for avifaunistic exploration. The number of islands or isolated mountain areas that have not yet been explored ornithologically has become extremely small. Among the most recent gaps to be filled are some mountain areas in the Philippines explored by D. S. Rabor and others, the mountains of New Britain explored by E. Thomas Gilliard, some isolated forests in Angola explored by Gerd Heinrich, and some isolated forests on the western slopes of the Peruvian Andes explored by Maria Koepcke. The zoogeographer who wants to find white spots on the map, in order to explore them, finds it harder and harder to come up with promising areas. Birds are surely unique in the entire organic world as far as the completeness of the inventory-taking is concerned.

Let us now survey some of the branches of biology where ornithology has made unique contributions or has displayed leadership owing to the unique advantages of birds.

Systematics.—Much in the development of modern systematic concepts is due to the work of ornithologists. They have made major contributions to the development of the biological species concept, to the theory and practice of recognizing polytypic species, to the critical evaluation of the meaning of subspecies, and to other methods and concepts of the new systematics. Nearly all of these major contributions are from the area of what might be called "population systematics." This is where the completeness of the knowledge of birds has been particularly useful. Indeed, this completeness is so great that most bird species are not merely known but also abundantly sampled from throughout their range. Even most of the more striking subspecies are already known and well described. I shall say nothing more about population systematics (a field that I have recently discussed in more detail, Mayr, 1959), except for calling attention to Allen Keast's (1961) remarkable application of population systematics to a reconstruction of the pathways of speciation among the birds of Australia.

The contribution of ornithology to systematics has been almost entirely in the area of population systematics. Ornithology has made virtually no contributions to the theory of the higher systematics and to the general theory of classification. Indeed, paradoxically, there are perhaps few groups of organisms the higher classification of which is shrouded in so much uncertainty as that of birds, as various authors have pointed out (Stresemann, 1959; Mayr, 1959).

Evolutionary Research.—Ornithologists have played a leading role in recent and current evolutionary research. This can be documented by mentioning B. Rensch, E. Stresemann, D. Lack, E. Mayr, A. H. Miller, H. Friedmann, J. Huxley, and L. v. Haartman, to single out just a few names among many others that might be cited with equal justification. Geographic variation and the causal factors involved, the determination of the pathway of speciation, the meaning and functioning of isolating mechanisms, the evolutionary effects of the interaction of sympatric species, and adaptive trends are some of the subjects on which the study of birds has shed light particularly.

The Study of Behavior.—There is perhaps no other branch of biology in which ornithologists have so consistently displayed leadership as in the study of animal behavior. Such names as Whitman, Heinroth, and Craig in former generations, and Lorenz, Tinbergen, and Lack, as well as their students and associates more recently, characterize this leadership. The outstanding achievements, as well as the shortcomings, of ethology are too well known to require further discussion before this audience. How rapidly this field is developing becomes obvious when one compares the leading journals in the field at 5-year intervals. The originally rather typological treatment of species-specific behavior has been broadened increasingly by a study of individual variation, of the role of various kinds of learning, of the contribution of maturation, and of other physiological factors in the facilitation and evoking of behavior. Names like Thorpe, Hinde, Marler, Fabricius, Moynihan, and Lehrman come to one's mind; it would not be difficult to triple or quadruple the length of this list before running out of names of authors who have made significant contributions.

Zoogeography.—The completeness with which the faunistics of birds is known makes them specially suitable material for zoogeographic analysis. Two areas where ornithologists have made particularly important contributions are the problem of the colonization of islands and that of the mixing of faunas. In the case of the colonization of islands, it has been possible, time after time, to determine the place of origin of the different faunal elements. This is true not only for oceanic islands but also for such ecological islands as the table mountains along the border of Guiana, Venezuela, and Brazil. The generalizations emerging from these analytical studies are of the broadest significance for all biogeographers. The same is true for the problem of the mixing of faunas. For this type of study, we have two specially favored areas, the East Indies where the tropical Asiatic and the Australo-Papuan faunas intermingle, and tropical America where the tropical North American and the tropical South American faunas have mingled during the closing of the Central American water gaps toward the end of the Tertiary. The analysis of this particular faunal mixture has only begun.

Population Biology.—Birds offer a number of obvious advantages for the student of populations. These include the possibility of marking each individual in such a way that it can be observed without the need for recapturing; the fact that population size is sufficiently small so that the total number of individuals of a local population can be studied simultaneously and the survivors identified in consecutive years; the fact that food items are sufficiently large and well marked in most cases so that food can be determined qualitatively and quantitatively; and finally, that there are sufficient differences between juveniles and adults and between males and females so that in many species the composition of the population according to sex and age can be determined by visual inspection. Particularly suitable for such studies are species that nest in well-confined and often widely separated breeding colonies. The work of Burkitt, Nice, Lack, von Haartman, and many other contemporary ornithologists shows how productive population biology is, but the large number of unsolved problems, as well as the contradictory conclusions at which certain authors have arrived, shows how much more work needs to be done in this area.

The Problem of Adaptation.—The problem of adaptation is sometimes described as the central problem of biology. Birds are indeed exceptionally favorable material for the study of adaptation to many components of the environment. Since we devoted a special symposium at Helsinki to the problem of adaptation, I will at this time call attention only to the extraordinary morphological, physiological, and behavioral reconstruction that birds had to undergo to make these feathered reptiles well suited for the occupation of the air niche. Our ornithological textbooks contain detailed descriptions of the changes in the avian morphology that make birds more efficient flying machines. The physiology of birds is affected perhaps even more drastically. Let us just remember their high body temperature, the total reconstruction of the lungs, the increased efficiency of the water metabolism, and the superb vision and hearing with which these rapidly moving organisms are endowed. Every aspect of growth, development, and behavior is affected by this need for adaptation to the air niche. In order to keep body weight as constant as possible, one egg is laid at a time, instead of an entire clutch simultaneously as in reptiles. To shorten the highly vulnerable egg and nestling stage, development is speeded up tremendously as is juvenile growth, in order to reach as quickly as possible the ideal ratio between body weight and a constant wing surface. As a result, birds may reach fully adult size within about 1 percent of their total life span, indeed a remarkable achievement. Studies of these adaptations are now being pursued actively at literally scores of institutions. I, for one, am looking forward to a comprehensive treatment of this subject. Alas, this is perhaps impossible if, as seems likely, every specialization of birds is somehow an adaptation for life in the air niche.

The Annual Cycle.—There is probably no other kind of organism in which an annual cycle is as pronounced and as easily studied as among birds. A correlation between larval stages, adulthood, breeding season, and seasonal cycle of the environment is, of course, taken for granted in organisms such as insects, in which the annual cycle coincides with the life cycle. Man, in his almost complete independence of the seasons, stands near the other extreme of the spectrum. Birds are somewhere between these extremes; but it is safe to say that, except for a few tropical areas, they are subject to a greater amount of seasonal variation than almost any other kind of animal that has a life span of more than a single year.

Many phenomena are involved in this annual cycle, in addition to the breeding season. There are no other organisms, except for a few species of fish, migratory locusts, butterflies, and mammals in which migrations are as conspicuous as in birds. Indeed, there are some species of birds in which a greater part of the year seems to be devoted to migration than to breeding.

The study of the molt cycle is very important not only because of its great energy demands, but also because the adaptive significance of various molt patterns is not yet fully understood.

The great interest in seasonal phenomena which ornithologists have displayed for many decades has had a considerable influence in stimulating similar studies in other types of organisms. Ornithologists, and zoologists working with birds, have been pioneers in many areas of biology to an extent that is not always fully appreciated. Let me mention, for instance, the study of hormones in which ornithologists, beginning with the pioneering studies of Berthold in 1849, have greatly contributed to the development of the important field of endocrinology.

For the sake of contrast, let us now look at some branches of biology where birds are unfavorable study material.

Genetics.—Birds are poor material for genetic researches, owing to the small number of offspring per brood and the slow sequence of generations. Anyone interested in the elucidation of the basic principles of genetics will turn to Drosophila, to Neurospora, to Escherichia, or to bacteriophage as more suitable material. This does not mean, however, that it would be useless to study avian genetics. On the contrary, a great deal has been learned about methods of breeding and selection by a study of the genetics of the domestic fowl. Also, wherever a specific answer is needed on some problem of variation, an *ad hoc* genetic analysis will be indispensable. The polymorphism of the Blue Goose and Snow Goose and a number of other similar cases are apt illustrations for this situation.

Paleontology.—The study of fossil birds encounters exceptional technical difficulties, as correctly stressed by Wetmore (1950): "Bones of most kinds of birds are fragile so that they are easily destroyed, and there are in the skeleton no strongly made structures like the teeth of mammals that easily become fossilized, which at the same time offer clear-cut diagnostic characters. Our reliance in the identification of extinct birds is placed mainly on single bones, often on fragments, with only occasional specimens that show several parts of the skeleton of a single individual." There is no equivalent among fossil birds for the rich sample of dinosaurs or the splendid evolutionary sequences of horses, proboscidians and many other ungulates, or carnivores. Nevertheless, all that we know on rates and trends of evolution in birds is based on the evaluation of the fossil record. This record, as far as the Tertiary is concerned, is becoming increasingly complete. A. Wetmore, Hildegarde Howard, and a number of other paleornithologists have acquainted us with a growing number of extinct genera and families, including the immediate ancestors of many Recent types. Alas, as a result of these studies it has become evident that the major radiation of birds took place as early as the Cretaceous. Up to now, it is unhappily true that not a single fossil bird has led to an improvement of the avian classification. No missing link has so far been found, to my knowledge, between any of the orders and superorders of birds.

NEW TECHNIQUES

It is sometimes claimed that all major advances in science are the result of the introduction of new techniques. This claim, I feel, is even more erroneous for ornithology than for most other branches of biology, and yet there is no doubt that the application of new techniques has often led to notable advances in science. One hundred years ago, the accurate labeling of specimens and the collecting of whole series from a single locality were new techniques which greatly facilitated our understanding of geographic variation and geographic speciation. The introduction of bird banding, or bird ringing, was a technique that has added tremendously to our understanding of bird migration.

The four new techniques that have perhaps been most productive in recent ornithology are the following. First, the introduction of radar by Sutter (1957) for the analysis of bird migration, the enormous consequences of which will be discussed by numerous speakers at this Congress. Second, the "Kramer cage," the invention of which has resulted in numerous discoveries in the field of avian orientation. Indeed, variants of this cage are now used by investigators in many countries and with ever-new findings. Third, electronic devices for sound recording and sound analysis. Again I will say nothing about the importance of this development, because we will hear abundantly about it during this Congress. My own feeling is that we have merely begun to tap this rich source of information and that the analysis of acoustic signals transmitted by birds may well lead to major additions to our existing theories of communication and behavioral motivation. Fourth, protein analysis by refined methods of electrophoresis and other techniques. We all know how successful (Sibley, 1960) this new tool of research has been in the hands of our Secretary-General. The use of radio-isotopes in metabolic research and the development of small radio transmitters to permit the tracking of individuals are other techniques that are already in use in biology and will surely become increasingly important in the near future also in ornithology.

FASHIONABLE AND CLASSICAL FIELDS

A look at recent issues of our ornithological journals tells us that new fields of research are being developed every year. The lure of the new is almost irresistible to the young investigator, and yet one cannot help but regret that such jumping on bandwagons often leads to the abandonment of still-productive lines of research. Berlioz pointed out quite rightly in his presidential address at Helsinki that the so-called "old" fields are virtually never exhausted. Sooner or later they experience a renaissance such as we have witnessed in recent years for comparative anatomy, for systematics, and for classical physiology. Let me illustrate this by a few examples.

In comparative anatomy, the classical search for homologies is increasingly supplemented by research into the causes of differences between taxa.

This new Fragestellung parallels similar developments in the study of the evolution of phylogenetic lines. A revival is occurring also in other classical fields. Classical physiology has displayed new vigor in connection with the study of special and unique properties of birds. The discovery of the salt glands by Schmidt-Nielsen, the problem of thermoregulation in birds, particularly in species subject to torpidity like poor-wills, hummingbirds, and swifts, and the study of the physiology of molt and of fat metabolism are examples of such activity. The internal clocks of organisms were discovered by Gustav Kramer during a study of orientation in birds, independently of the same discovery by von Frisch in bees. The great current activity in the field of sensory physiology (including orientation) is part of this same renaissance. We will hear much during this Congress about research in orientation, yet it seems to me that we are still faced by a mystery. It is almost certain that we are making certain basic assumptions that are not valid, assumptions that blind us to the truth.

Other classical areas that will still yield rich rewards are the study of the phylogeny of birds and ornitho-geography. The lines for productive research in these areas are already quite apparent.

GAPS IN OUR KNOWLEDGE

In spite of the enormous amount of literature on birds that is being published every year, even a quick look at the pages of one of our new handbooks will reveal some curious gaps in our knowledge of birds. Let me single out a few of them for a short discussion.

There is a great deal of scattered information on the diseases of birds, but we lack altogether a "Natural History of Avian Diseases." We know that birds play an important role as vectors or reservoirs of diseases that may be important for man, such as encephalitis and various kinds of ornithoses. We know that birds occasionally succumb to epidemics of various sorts, such as ornithoses and coccidioses, but in most cases we have no idea whether the infection was really the primary cause of the mortality or whether some other environmental factor, such as a food shortage or an inclemency of the weather, had previously weakened the birds to the extent that they had become vulnerable to the disease. We suspect that disease has played a great role in the extinction of island birds, but again our knowledge is fragmentary. Here is, surely, a vast area for fruitful research and for integration.

The role of food in the adaptive radiation of birds is another subject almost entirely neglected. Huxley's (1960) paper on the specializations of mollusk-eating birds is a notable exception. We know that preference for the same kinds of food may lead to convergent evolution, as in the case of the various so-called finches, flycatchers, and warblers, but no one has so far followed up these questions in detail.

Let me mention some other gaps in our knowledge in the hope of stimulating future research.

Many of the pigments that are responsible for the coloration of bird feathers are still unanalyzed chemically, for instance, two of the pigments of parrots that were discovered by Völker (1937). On the other hand, the riddle of the iridescence of bird feathers was finally elucidated by Greenewalt et al. (1960).

The dynamics of bird flight and the question of energy consumption during flapping flight are still areas of rather profound ignorance, in spite of important recent contributions (Greenewalt, 1960; King and Farner, 1960).

The physiology of the avian molt is not at all understood. Most investigations so far have concentrated on the growth of newly regenerating feathers, but very few have dealt with the factors and mechanisms responsible for the dropping of feathers from follicles. The problem of why the modes of molt in different genera and families of birds are so different is also still largely an unsolved question. What part of this variation is random and what part of it is adaptive? The most informative studies of the Stresemanns (1961*a*, 1961*b*) are beginning to give us a far better insight than we have had before. Yet such researches always provide not only new answers but also new puzzles, new questions. Even though molt pattern, for instance, is sometimes a valuable clue to relationship, in other cases closely related species differ from each other drastically and, I might say, almost capriciously. There is no conceivable reason, for instance, why the Spotted Flycatcher (*Muscicapa striata*) should have an ascending wing molt (Diesselhorst, 1961) when not only all of its close relatives in the genus *Muscicapa* but indeed all other passerine birds have a regular descending molt. This may serve as one more warning not to trust a single character when trying to establish classifications.

It would be an easy matter to point out innumerable other gaps in our knowledge of birds and in our understanding of their biology. Let us rejoice in the enormous opportunities left for future generations.

CONCEPTUAL CONTRIBUTIONS BY ORNITHOLOGY

Before closing, I want to call attention to one aspect of ornithological research that is frequently neglected. Ornithologists have not only added greatly to the body of fact and theory in biology, but more importantly they have made fundamental contributions to the basic conceptual framework of biological science. Let me single out four conceptual areas where ornithology has made major contributions.

Population Thinking.—No one has worked as vigorously in replacing typological thinking by population thinking than the ornithologists. As far back as the first half of the 19th century, ornithologists such as Schlegel and Baird stressed variation, samples, series, and populations. Variability and the differences among individuals loomed larger and larger in the ornithological literature in the latter half of the century, and have contributed to the ultimate victory of population thinking in the first half of this century.

This kind of thinking is now becoming increasingly prevalent even in the study of animal behavior, where not so many years ago it was customary to say *the* Black-headed Gull does such and such, while *the* Mallard does so and so. We now emphasize the uniqueness of the individual both morphologically, physiologically, and behaviorally, and describe "typical" characters in statistical rather than in absolute terms. This does not deny, of course, that there is much species-specific behavior.

The Discrimination between Proximate and Ultimate Causes.—The students of breeding seasons and seasonal cycles, as well as those of bird migration, have been pioneers in making a distinction between these two kinds of causes (Mayr, 1961). This distinction has led to a great clarification in the interpretation of phenomena that have both an ultimate evolutionary and genetic causation, as well as a proximate physiological one.

The Recognition of Observation as a Significant Scientific Method.—Under the impact of the splendid achievements of chemistry and physics, there has been a regrettable tendency in science to consider the experiment the only legitimate scientific method. We ornithologists have perhaps supplied the best body of evidence in refutation of this one-sided claim. In virtually all areas in which ornithology has made major contributions to scientific biology, the advance has been due to the careful evaluation of observations. Ethology, evolutionary biology, and population biology, all three have supplied abundant proof for the validity of this assertion. To be sure, it is often possible to confirm the conclusions by experiment, but the basis of the original discovery was in each case a set of carefully controlled observations.

The Bridging of the Gap between the "Two Cultures."—It is often claimed that in the modern world there is a complete gap in the thinking of the "two cultures," as Sir Charles Snow has expressed it. This claim is most frequently made by representatives of the physical sciences. It seems to me that biology in general, and ornithology in particular, serves as an admirable bridge between the physical sciences on one hand and the humanities on the other. The preoccupation with the individual, the study of communication among individuals, the pathways of adaptation, the appreciation of the aesthetic aspects of avian colors, of courtship movements, and of song, and many other of the preoccupations of the ornithologist actually provide for closer contact with the humanities than with the physical sciences. Many artists, musicians, writers, and students in all sorts of other human endeavors find birds not only a suitable hobby but indeed a subject for serious study. This further substantiates my claim of the usefulness of birds and their study as a bridge between the two so-called cultures.

Our *scientia amabilis*, then, offers unique advantages. It not only provides for the most pleasant study of nature and contributes significantly to our body of knowledge of the scientific world and to the basic understanding of the workings of nature, but it also helps to bring about the spiritual unity of man. Long live our favorite science, ornithology!

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The Cranial Evidence for Ratite Affinities

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The affinities of the ratites to one another and to other birds have caused more controversy among ornithologists and anatomists than any other problem in avian classification. Much evidence has been marshaled to support opposing stands of whether or not these birds comprise a natural group within the class Aves and even whether or not they are related to other birds. One can wonder with great justification, as does Stresemann (1958), if final solutions to these problems can ever be reached. Extensive morphological comparisons of known features, no matter how detailed or statistical, whether weighted or not, and search for new characters will provide much new information, but it is doubtful whether these methods can resolve the ratite problem. Tremendous amounts of morphological and other data have been available for years; these are more than sufficient for the application of the classical and even the newer methods of morphological–taxonomical comparison. Yet, these methods have never provided a definite answer. In this paper, I wish to inquire into the ratite problem using the method of comparative functional anatomy and analysis of the probable evolution of the taxonomic characters. None of the anatomical features to be discussed are new; all of them have been known for at least 50 years. All that is "new" are the interpretations permitted by an inquiry of the functional significances of these features, and by the following application of evolutionary principles.

Since the early days of avian classification, the ratites, or flightless birds, have been considered together because of their obvious similarity resulting from loss of flight and subsequent increase in size. Originally, these birds were placed in the same taxonomic group on the basis of their unkeeled sternum, as contrasted to the keeled sternum of the flying birds. Soon, however, the question of the true affinities between the groups of flightless birds was raised when ornithologists realized that structural features associated with loss of flight could easily become similar through convergent evolution. From his study of the bony palate, T. H. Huxley (1867) provided new evidence to support a close relationship between the ratites. He showed that the dromaeognathous (=palaeognathous of later authors) palate is characteristic of the ratite birds and serves to distinguish them sharply from all other Recent birds. The dromaeognathous palate became the hallmark of the group and hence the focal point about which the controversy on their affinities turned. One group of workers, including Huxley, Parker, Pycraft, Beddard, and Gadow, believed the ratites to be a monophyletic assemblage, while others, notably Fürbringer, argued that the similarity in palatal structure is the result of convergence, and that the ratites are a heterogeneous

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group of unrelated birds, as shown by other anatomical features. Discussion of this problem waned as interest in avian anatomy descreased, but ornithologists became more and more skeptical of the naturalness of the Palaeognathae, the superorder containing only the ratites.

McDowell (1948) reopened the debate with his study on the bony palate of birds. He concluded that the palaeognathous palate could not be defined morphologically, and that it actually is composed of a heterogeneous assemblage of four distinct morphological conditions. Thus, he argued, the ratite birds do not form a monophyletic group, and the distinction between the superorders Palaeognathae and Neognathae should be abolished. Believing the morphological evidence supporting the Palaeognathae to be refuted, ornithologists pointed to the disjunct distribution of these flightless birds as final proof that they could not be related. All recent classifications (Mayr and Amadon, 1951; Wetmore, 1951 and 1960; and Storer, 1960) list the ratites as a series of unrelated orders, whose affinities to other avian groups are still uncertain. However, students of comparative vertebrate anatomy, less concerned with problems of distribution, were not fully convinced that the palaeognathous palate is a heterogeneous structure. Both Hofer (1945, 1954) and Simonetta (1960) regard this palate type as a uniform morphological condition, although they are cautious about drawing definite taxonomic conclusions from their data. Most anatomists still accept the belief that the ratites are closely related, and a few have maintained the extreme position that the ratites are not only a monophyletic group, but that they evolved from the reptiles independently of other birds, and are thus convergent to flying birds (Lowe, 1935, 1942, 1944; Glutz von Blotzheim, 1958; and personal conversations with workers since 1959). This extreme view has made ornithologists suspicious of the arguments advanced by anatomists for the naturalness of the ratites. Solution of the ratite problem has halted here with both ornithologists and anatomists knowing only part of the entire picture and each not understanding the arguments presented by the other. While investigating the palate in all groups of birds, I have examined the ratite palate as well as the structure of the entire skull. The data from the entire cranial anatomy suggested that a different interpretation of the palaeognathous palate could be reached, and that the "ratite problem" could profitably be reopened.

The ratites consist of the Recent and subfossil families: Struthionidae (ostriches), Aepyornithidae (elephantbirds), Rheidae (rheas), Tinamidae (tinamous), Casuariidae (cassowaries), Dromiceidae (emus), Dinornithidae (including the Anomalopterygidae, moas), and Apterygidae (kiwis), the superorder Palaeognathae of Wetmore prior to 1951. These birds, whether or not they form a monophyletic group, are all typically avian (=primarily adapted for flying, and subsequently modified) in their entire morphology, in spite of their flightlessness, and there can be no doubt that they have descended from flying ancestors (de Beer, 1956). All birds, flying and non-flying, are monophyletic. Every feature in the morphology of the ratites points to this conclusion, which shall serve as the basic assumption for the present study. Those workers who still believe that the ratites evolved from flightless ancestors and represent a group convergent to typical birds, base their arguments upon selected characters that support their conclusions while avoiding other features. They now are obliged to prove that the huge mass of evidence supporting the theory that all birds are monophyletic is incorrect by demonstrating how these features became similar in flying and non-flying birds through convergent evolution. It is not sufficient for them to present only data supporting the hypothesis that ratites have evolved from the reptiles independently of other birds.

DESCRIPTION OF THE RATITE SKULL

Description of the ratite skull will be brief and restricted to the characters of importance to this study. Those readers interested in more complete details are referred to the papers cited above. I shall base my description on the rhea skull, as it is fairly typical for the entire group (see Fig. 1–7).

The palate, the most complicated structure to be considered, is really a complex of characters, not a single one. The vomer is long, extending from the premaxillae to the pterygoids. Only in the ostrich does the short vomer fail to reach the pterygoids, although in some adults it is longer, almost touching the pterygoids (Webb, 1957:86–87). (The short vomer of the ostrich appears to be a specialization derived from the typical ratite condition.) The anterior end of the vomer contacts the premaxillae and/or the maxillo-palatines in a tight suture, or it may fuse with these bones. At its posterior end, the vomer rests on the basitemporal rostrum and articulates with the anterior ends of the pterygoids (except in the ostrich, as mentioned), which also rest on the rostrum. The articulation between the vomer and the pterygoid is characteristically a long suture. In some ratites, the contact between the vomer and the pterygoid may not be visible from below (see figures) and can only be seen in the dorsal view (see McDowell, 1948,

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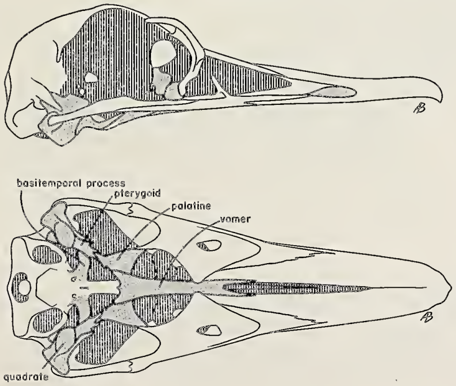

Fig. 1. Skull of *Rhea* seen from the side (upper figure) and from below (lower figure). In the upper figure, the orbital and nasal septa are indicated by vertical stripes. In the lower figure, the bones of the palate and of the basitemporal articulation are shown in gray.

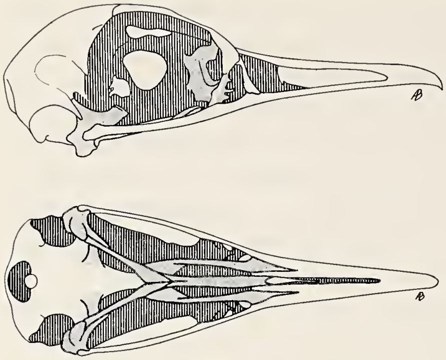

Fig. 2. Skull of *Tinamus* seen from the side (upper figure) and from below (lower figure).

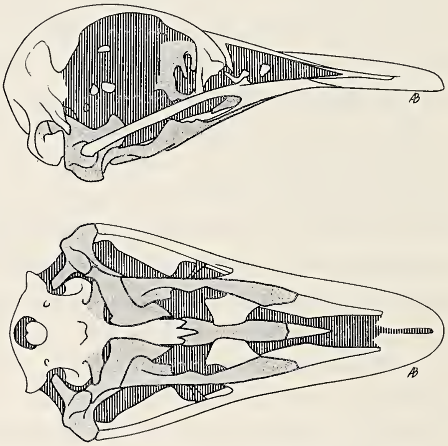

Fig. 3. Skull of *Struthio* seen from the side (upper figure) and from below (lower figure).

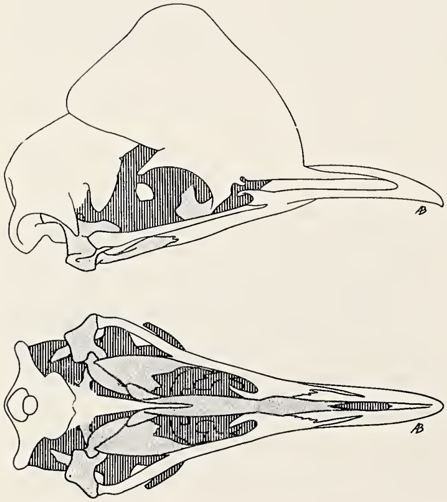

Fig. 4. Skull of *Casuarius* seen from the side (upper figure) and from below (lower figure).

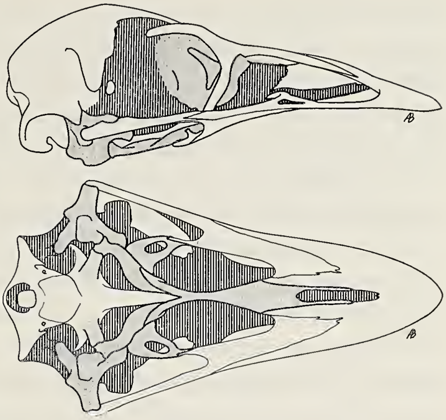

Fig. 5. Skull of *Dromiceius* seen from the side (upper figure) and from below (lower figure).

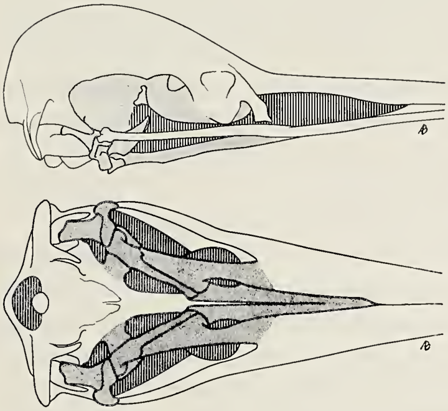

Fig. 6. Skull of *Apteryx* seen from the side (upper figure) and from below (lower figure).

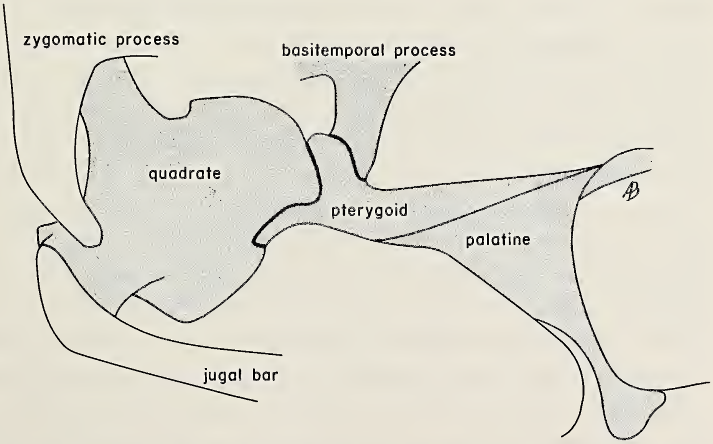

Fig. 7. Oblique view showing the pterygoid–quadrate articulation and the basitemporal articulation of *Rhea*. The articulations are indicated by heavy lines. Note that the pterygoid is wedged between the quadrate and the basitemporal process.

which included dorsal views of the palates as well as the usual ventral views). The palatines are displaced laterally by the pterygoids; they run from the maxillae to the pterygoids, to which they articulate by a suture. McDowell (1948:528 and fig. 4) claimed that the palatines do not contact the pterygoids in the emu, but Simonetta (1960:fig. 3) correctly points out that the palatine does articulate with the pterygoid in most specimens; those in which no such contact exists represent individual variants or, more likely, younger individuals in which ossification is not complete. The pterygoids lie between the quadrates and the basisphenoid rostrum. They have a complex articulation with the quadrate, abutting against the base of the orbital process as well as against the main body of that bone. The stout basitemporal process lies far back on the basisphenoid rostrum and articulates with the pterygoid near its posterior end, so that the pterygoid is held in place between the quadrate and the basitemporal process (Fig. 7).

Basically, the ratite palate consists of a pair of stout pterygoids lying between the quadrates and the basisphenoid rostrum, with three bars of bone—the two lateral palatines and the medial vomer—connecting the pterygoids to the upper jaw. The entire palatal structure is one of strength and rigidity, with the individual parts fused to one another or articulating by long sutures, and with some bones held in place between several others, e.g. the pterygoid between the quadrate and the basitemporal process.

The palate of all other Recent birds, the so-called neognathous palate, is characterized by a shorter vomer, which typically does not have a direct connection with the pterygoids, and usually is small to vestigial, or may be lost. The palatines of adults extend medially to rest on the basisphenoid rostrum, and thereby separate the vomer from the pterygoids. Actually, in most forms a short portion of the anterior end of the pterygoid splits off and fuses with the palatine during embryonic development. The articulation between the palatine and the pterygoid in the adult is located somewhere in the anterior third of the embryonic pterygoid. In some neognathous birds, however, the pterygoid does not split, so that the vomer still contacts the pterygoids in the adult (McDowell, 1948; Simonetta, 1960; and others). The vomer may or may not articulate or fuse with the maxillo-palatines, but it rarely if ever abuts against the premaxillae. The basitemporal articulation may or may not be present, but when present, it is near the anterior end of the pterygoid. In general, the articulations between the bones of the neognathous palate are "ball and socket" joints, not sutures as in the ratite palate. Basically, the neognathous palate is one of lighter construction with more flexibility. The pterygoids converge from the quadrates to the basisphenoid rostrum where they meet the palatines. The palatines diverge from the basisphenoid rostrum to the lateral part of the upper jaw where they contact the premaxillae along its palatine process. Thus, the connection between the quadrate and the upper jaw is effected by a single pair of palatal bars—the pterygoids and the palatines, which meet at a common point on the basisphenoid rostrum. I do not distinguish between the condition in which the two sides of the paired pterygoid–palatine strut actually contact one another at their common articulation from that in which the rostrum separates the two sides (see Hofer, 1954:106). (The jugal bars also connect the quadrates with the upper jaw, but these may be disregarded for the purposes of the present study.) The palatal bars converge to a point, and then diverge again when traced from the quadrates to the upper jaw. This is in sharp contrast to the condition found in ratite birds, and appears to be of great functional importance, as will be shown below.

The maxillary process of the nasal does not meet or fuse with the maxilla. Instead, a gap exists between the two bones; hence, there is a continuous opening from the orbit to the external naris. In life, the tips of the maxillary process of the nasal and of the short dorsal process of the maxilla probably are connected by a ligament. The tinamous exhibit the most primitive stage in the development of this condition. The maxillary process of the nasal is long and reaches the maxilla, but does not fuse with it. The two bones are separated by a loose suture allowing movement of one bone past the other. All other living birds are uniform in having the nasal and maxillary bones fused together to form a solid bar of bone bordering the posterior edge of the external naris and hence separating this area from the orbital space.

The orbital septum is well ossified and is continuous anteriorly with the nasal septum—there is no break between the orbital and nasal septum at the base of the upper jaw. The nasal–frontal hinge is, thus, obliterated. Most, but not all, other Recent birds have a break between the orbital and nasal septa at the base of the upper jaw, below the nasal–frontal hinge. Some neognathous birds also have a continuous orbital and nasal septum; these birds lack a nasal–frontal hinge, as in the ratites.

The zygomatic process lies along the lateral side of the quadrate and is closely applied to it. This latter feature cannot be seen completely from a lateral view of the skull, but is evident readily when viewed from an oblique angle. In other birds, the zygomatic process lies more dorsally on the side of the skull and projects forward, with the quadrate being ventral to the base of the zygomatic process.

FUNCTIONAL ASPECTS OF THE RATITE SKULL

The several cranial characters described above appear to form a single character complex (=functional unit of characters), but one of uncertain function and evolution. Unfortunately, I have not been able to examine the jaw muscles, which may supply additional information, or to observe living birds which would provide the best possible data. Nevertheless, much information about the possible function of the individual cranial features, and of the skull as a unit, can be extrapolated from the morphology and from what we know about the skull in other birds. I emphasize that the conclusions reached in this analysis are only deductions, and should be treated as such.

All ratite birds appear to be kinetic and to have a "rhynchokinetic skull" (Hofer, 1954). Simonetta (1960:210–213) disagrees in part with this conclusion and states that some ratite birds have an akinetic skull. Unfortunately, his discussion on this point is not completely clear, as he does not always state exactly which groups he believes to be akinetic, nor are reasons for his conclusions always given. In some forms, e.g. the Aepyornithidae, he argues that the bar of bone forming the dorsal rim of the upper jaw is too thick; hence, the upper jaw could not be flexible. This point is debatable. Direct observations are needed before we can say definitely whether the several groups of ratites are or are not kinetic, but as the available morphological evidence suggests that all ratites possess a kinetic skull, I shall accept this hypothesis for the present purposes. The continuity of the orbital and nasal septa have necessitated a shift in the hinge of the kinetic skull from the nasal–frontal region at the base of the upper jaw to some point within the upper jaw along the dorsal bar of bone formed by the nasal process of the premaxilla and the nasal bones. This bar appears to be flexible in all ratites. In some, notably the kiwi, it is especially so, suggesting a highly kinetic bill.

Rhynchokinesis, in the sense of Hofer, means that bending occurs within the upper jaw. Only the anterior part of the upper jaw moves upward—the base of the dorsal rim remains stationary. In birds having a functional nasal–frontal hinge, bending occurs at the hinge, so that the entire upper jaw swings upward as a unit. The problem in rhynchokinetic birds is that the ventral part of the upper jaw moves forward, thereby forcing only the anterior portion upward, while the posterior part of the dorsal rim behind the region of bending remains stationary. Clearly, the stationary part must be isolated from the movable part (Fig. 8). In prokinetic birds (those with a functional nasal–frontal hinge), the entire upper jaw moves; hence, no part of the upper jaw needs to be isolated from other parts. In those neognathous birds having a rhynchokinetic skull (e.g. Gruiformes, Charadriiformes), separation of the movable ventral part from the stationary base of the dorsal rim is effected by the schizorhinal condition of the external naris. The long nasal cleft between the lateral bar (formed by the maxillary process of the nasal fused to the maxillae) and the medial dorsal rim extends backward beyond the base of the upper jaw—beyond the connection of the dorsal rim and the lateral bars to the brain case. Thus, the lateral bars are free to move with the ventral part of the upper jaw, while the base of the medial dorsal rim remains stationary (see Hofer, 1954:113 for a more complete discussion of this point). Hofer showed that rhynchokinesis is correlated with a schizorhinal nostril, while prokinesis is correlated usually with a holorhinal nostril (but it should be noted that some prokinetic birds have a schizorhinal nostril).

The ratite birds probably evolved from birds having a holorhinal nostril. When this group became rhynchokinetic, separation between the stationary base of the dorsal rim and the ventral part was essential. This was effected by an actual break in the lateral bar between the maxillary process of the nasal and the maxilla, not by the development of the schizorhinal nostril. Such a split in the lateral bar can develop by a simple suppression of the fusion between the nasal and the maxilla during embryological development.

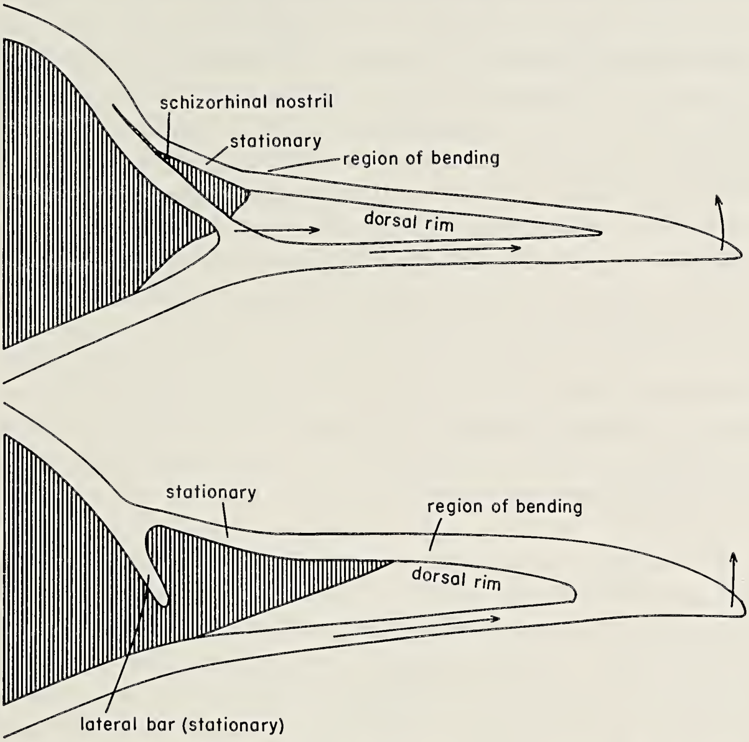

Fig. 8. Schematic drawings of a schizorhinal bird (upper figure) and a ratite bird (lower figure) illustrating the relationships between the stationary base of the dorsal rim and the movable ventral part of the upper jaw. In the schizorhinal birds the backward elongated cleft of the schizorhinal nostril separates the stationary base of the dorsal rim and the movable lateral bar. In the ratites, these parts of the jaw are separated by a break in the lateral bar.

In the tinamous, these bones are separated from one another by a suture—probably a sliding articulation which allows the ventral part of the upper jaw to move past the stationary lateral bars. In the other ratites, a wide gap separates the maxilla and the nasal, with at most a ligament connecting them. Thus, the schizorhinal nostril and the gap in the lateral bar are two ways of solving the same functional problem—by allowing the ventral part to move while the base of the dorsal rim remains stationary.

The jaw structures in the ratites indicate that much force is needed to bend the dorsal rim, and that the palate must carry these stresses. The stout bones of the palatal complex, the three bars of bone connecting the paired pterygoids to the base of the upper jaw (except in the ostrich, of course), the strong sutural articulations between the bones, and the tight suture or actual fusion between the vomer and upper jaw all indicate this. The direct connection between the quadrate and the upper jaw formed by the palatine articulating near the middle of the pterygoid, and thus being more in a straight line between the quadrates and the lateral edge of the upper jaw, also suggests that the force transmitted by the palate is great. The position of the zygomatic process along the lateral edge of the quadrate, the location of the basitemporal articulation near the posterior end of the pterygoid, and the complex articulation between the quadrate and the pterygoid indicate that the movement of the quadrate and of the pterygoid is restricted to one plane of motion. All lateral movement seems to be eliminated. The entire arrangement of the palaeognathous palate appears to be more effective than that of the neognathous condition in transmitting great forces. As the bones of the ratite palate are oriented closer to a straight line between the quadrate and the upper jaw, less of the force carried by the palate would be lost. All of the force used to raise the upper jaw is produced by muscles acting on the quadrate, or on the pterygoid at its quadrate articulation (which can be regarded as part of the quadrate for this discussion). This force must be transmitted to the base of the upper jaw, either through the jugal bars or through the palate. The jugal bars may be disregarded because they are thin, and probably would bend if a pushing stress was applied on them. In neognathous birds, the force is transmitted through the pterygoid–palatine bar, which is relatively inefficient because of the sharp angles between the pterygoid and the basisphenoid rostrum, and between the pterygoid and the palatine at their articulation. At this point, much of the force carried by the pterygoid would be lost as a medially directed component; only the anteriorly directed component is transmitted by the palatine. In the ratites, the palatine has a more lateral position on the pterygoid, one that is more in line with the movement of the quadrate; hence, a smaller amount of force would be lost. Whatever force is not transmitted from the pterygoids by the palatines would be carried by the pterygoid-vomer–upper jaw system. This system would gain additional efficiency, since all of the bones are tightly bound or fused together and would move as a unit. It is quite possible that the basic functional reason for the evolution of the ratite palate was associated with the need to have a more efficient means of transmitting greater forces from the quadrate to the upper jaw.

The possible functional significance of the ratite palate has been discussed in terms of raising the upper jaw. Its depression appears to have the same functional demands, although the muscles that act to lower it have a different attachment on the palate. The M. pterygoideus, which is the largest of these muscles, originates directly from the palate. This muscle would have a rather efficient action because of its attachment to the palatine, which is in direct line with the pull of the muscle. The part attaching to the pterygoid would have more effect because the pterygoid and vomer move as a unit. None of the force is lost through a lateral component at the pterygoid–palatine articulation, as in neognathous birds.

The continuous orbital and nasal septa and the gap between the nasal and maxillary bones are directly associated with the rhynchokinetic upper jaw of the ratites, while the palaeognathous palate and the condition of the zygomatic process are associated only indirectly with it. A major problem remains as to why rhynchokinesis evolved in the ratites—whether it was a primary functional change associated with a new feeding method, or whether it was secondary, the result of some still-unknown primary demand. It is also necessary to determine whether the four cranial features characteristic of the ratites are associated primarily in the same character complex, or whether smaller combinations of these features have their main associations with different functional demands, and perhaps share only a secondary affiliation. The continuous orbital and nasal septa and the gap in the lateral bar of the upper jaw appear to be closely related functionally, while the palaeognathous palate and zygomatic process seem to be tightly bound together. But whether these two sets of characters are closely correlated must still be proven. Even if all of the above functional deductions are correct, the largest unsolved problem is the evolution of the palaeognathous palate and associated structures, together with its functional significance as correlated to feeding methods.

MORPHOLOGICAL AND SYSTEMATIC IMPLICATIONS

The material gathered on the structure and function of the ratite skull allows inquiry into two separate, but related, problems: (1) whether or not the palaeognathous palate is a homologous structure; and (2) whether or not the ratites form a monophyletic group. Solution of the second problem depends greatly upon resolution of the first, but these do not have a single absolute relationship to one another. To conclude that the palaeognathous palate is a homologous structure does not mean that the ratites must be related to one another, nor does an assumption that the palaeognathous palate may be a heterogeneous feature mean that the ratites are not so related.

As stated above, McDowell (1948:536–537) concluded that it is impossible to define the palaeognathous palate morphologically, and hence that this palate type included a heterogeneous assemblage of unrelated forms. Hofer (1954) and Simonetta (1960) concluded that the palate in all ratites corresponded to the same morphological pattern, but did not say whether this palate type was homologous, or whether the ratites formed a monophyletic group. May I ask, then, if the ratite, or the palaeognathous, palate can be defined morphologically? The answer is definitely yes, but the definition cannot be given simply in one or a few sentences. This is where the problem lies. Most workers believe that the morphological definition had to be simple, and that such definition had to separate it absolutely from the palate of all other living birds. This is not necessary. A definition does not have to be simple—a very complex one may be more correct than a simple one. There is no need to reduce the complex structure under discussion to a single feature—such as how the pterygoid and palatine articulate, or whether or not the vomer and pterygoid articulate in the adult in a manner different from that seen in all other birds. Nor is there any need for this palate type to be absolutely uniform within the group. McDowell (1948:537–539) was preoccupied in showing that the palate in the different ratites is very diverse in several features, and indeed, it does vary greatly within the group. But this does not prove that the basic palatal condition is heterogeneous. The real issue is whether or not the palaeognathous condition of the palate is homologous. By homology I mean whether or not a feature in different groups can be traced back to the same feature in the common ancestor of these forms, i.e. whether or not the most recent common ancestor of the different ratite orders had a palaeognathous palate. It is my belief that the palaeognathous palate is homologous (in the strictest sense) in all ratites, hence that the palate in these birds can be traced back to one in the common ancestor that possessed all the basic features found in the existing forms under discussion. The palate in all ratites agrees in all or most of the following features: (a) The vomer is relatively large, and articulates with the premaxillae and the maxillo-palatines anteriorly and (except for the ostrich) with the pterygoids posteriorly; (b) the pterygoid prevents the palatine from articulating with the basisphenoid rostrum; (c) the palatine articulates with the pterygoid along a suture; (d) the basitemporal articulation is large, and is found near the posterior end of the pterygoid; (e) the articulation between the pterygoid and the quadrate is complex, and includes part of the orbital process of the quadrate; and (f) the palaeognathous palate as a whole presents a general configuration similar in all birds possessing it, and sharply distinct from the condition found in all other birds.

The features characterizing the palate in all groups of ratites are so numerous that a conclusion other than common ancestry is scarcely conceivable. If the palate in these birds became similar through convergent evolution, then one must explain the similarity of each of these features through the action of one or more selection forces. This to me appears impossible for the following reasons. The palaeognathous palate includes several features which appear to have been "semi-independent" in their evolution, so that the appearance of one does not mean the automatic appearance of the others. If a single selection force had acted on several different ancestral bird groups to produce a palate having the function suggested for the palaeognathous condition, the end result probably would not be exactly the same. It would seem more likely that the form of this feature in these different birds would be different in some manner because of the principle of multiple pathways of evolution. There are several alternate morphological structures for each functional subunit of the palaeognathous palate, rather than a single solution for each function. It is most probable that if the same selection force acted on different groups, some of these alternates would have appeared, resulting in basically different palates in the several ratite groups. This is not the case, since, as indicated, the palate in each of the ratite groups is basically the same. Even in cases in which the palate does not agree in one of the above-cited features, the observed condition is clearly derived from the typical condition. For example, the ostrich does not agree with the other ratites in structure of the vomer; this element is short and does not articulate with the pterygoid. But in some individuals, in which the vomer is somewhat longer, it almost reaches the pterygoid, indicating that the abbreviated bone in the present-day ostriches evolved from the typical ratite condition. Nonratite birds may possess one or more of the palatal characteristics described, but in these cases it is clear that the feature evolved independently, that is, we can easily explain the similarity in the ratites and these other birds through convergent evolution. There is no reason to suppose, as does McDowell (1948) that, because some characteristic of the ratite palate is found in some other birds, this feature must be excluded from the definition of the palaeognathous palate. What is important is that no bird outside of the ratite complex possesses a majority of these palatal features. Lastly, there are no features seen in any of the ratite birds that suggest the palate of this form is not homologous to that found in the other ratites. The features listed by McDowell in his discussion of "the diversity of the palaeognathous palate" (1948:537–539) do not in any way argue against the homology of the ratite palate. And finally, it should be noted that the homology of the ratite palate was deduced independently of the conclusion that the ratites may be related and independently of the probable homology of other cranial features.

The second and more difficult question is whether or not the ratite birds form a monophyletic group within the Aves. Most ornithologists, following McDowell, have concluded that these birds are not related to one another because the palate was believed to include a heterogeneous grouping of different types.

Since I have shown that the palaeognathous palate is, in all probability, homologous in all ratite birds, the entire question of their interrelationships is reopened. To summarize, I have shown that these birds all possess a homologous palatal condition, lack a connection between the nasal and maxillary bones, have a continuous orbital and nasal septum, and have the zygomatic process lying along the lateral edge of the quadrate. These features appear to form a definite character complex. While some are found in other avian groups, they appear sporadically, and, as far as I have been able to determine, no nonratite bird possesses more than one of these features. The occurrence of any in a nonratite bird usually can be explained on functional grounds. For example, those birds possessing a continuous orbital and nasal septum also have a rhynchokinetic upper jaw. I conclude, then, from the fact that all ratites possess all of these cranial characters, that they are closely related, and that they form a monophyletic group within birds in the strictest sense of the term. If these birds were not all related—the only other possibility—then I would expect that some of these characters would be absent in one or another ratite groups. It would be possible to have a similar palate in these groups through convergence, but to have all of the elements in this character complex identical through convergent evolution appears most improbable, again because of the principle of multiple pathways of evolution. Moreover, if the palate and skull of the ratites were similar through convergence, then the function of their jaw apparatus should be similar. Hence, the feeding mechanism in all should be similar in some way. There is little in the literature on the exact feeding methods used by these birds, but from the general information available I venture to say that the kiwi, the cassowaries, and the tinamous differ in feeding habits, while the rheas, emus, and ostriches appear rather similar to one another. If these groups were not related, since their feeding habits are at least somewhat dissimilar, then one could expect the skull and palatal structures to be different.

This argument is especially powerful in the case of the kiwi, which is so markedly different from the others. Its upper jaw is very long and flexible. It feeds largely on earthworms by probing into the ground. The mechanism used by the kiwi in this process appears to be exactly the same as that used by woodcocks (*Scolopax*). The kiwi probes with its long bill until it locates a worm, possibly aided by an olfactory sense, and catches it by raising the tip of the upper jaw and grasping the worm between the very tips of the jaws (Beecher, 1962). The mechanism in the kiwi and woodcock by which this is accomplished is identical, except that in the kiwi, modification is from the standard form of the ratite skull, and in the woodcock, from the usual shorebird condition. Even in this remarkable case of convergence, the basic cranial features—those of the ratite in the kiwi and those of the shorebird in the woodcock—can be seen clearly and separated from those that have become similar through convergence because of the similar feeding method used by these unrelated birds.

The argument has been advanced that the ratite palate is correlated either genetically or developmentally in some way with flightlessness and large size. The foundation for this suggestion was the misconception that the palaeognathous palate was different only in the pterygoid–vomer junction. Some workers have tried to explain the theory of independent appearance of this feature by its correlation with obvious convergence found in the different ratites. This argument is not reasonable since the palaeognathous palate is more complex in structure, and the ratites as a whole agree in several other cranial features. In addition, the tinamous can fly and are of medium size, yet have all the basic ratite palatal and cranial features.

Some workers have argued that the ratite palate is a neotenic feature, others believe it to be a reversal to the primitive condition of the avian palate, and still others hold that it represents an original primitive condition, and that the neognathous palate has evolved from it (see de Beer, 1956). There is little evidence to support these suggestions. The argument for neoteny is based mainly upon retention of the vomer–pterygoid articulation in the adult but, as this is only one of the many features characterizing the ratite palate, I doubt that it is reasonable to regard the entire palatal condition as neotenic. The main mass of available evidence suggests that the palaeognathous palate evolved from the neognathous palate as an adaptation for some new, but still unknown, method of feeding. It is not primitive for birds, nor does it appear to represent a secondary primitive condition. The structure of the palate and of the skull as a whole, as seen in the tinamous, appears to be primitive for the ratites. This conclusion is not based primarily upon the fact that the tinamous can still fly, but upon a comparison between the cranial structure in all ratites and a sampling of other birds. The ostrich and the kiwi appear to be the most specialized forms, each being, however, quite different from the other.

The cranial evidence suggests that the ratites should be united once again into the same taxonomic group. The only assumption required for this conclusion is that the cranial characteristics had appeared, and that the ratites had reached the limits of their present-day distribution, before they became completely flightless. They could have been poor fliers, as the rails are at present, and still have been able to spread and colonize their known area of distribution. This assumption is reasonable as the tinamous possess a typical ratite skull and can still fly, which proves that the skull features evolved before the related forms became flightless. The loss of flight doubtless occurred independently in the different lines of ratites.

The ratites do not appear to be primitive among birds (Cobb and Edinger, 1962), nor do they have to be any older than other typical avian orders. They are specialized, but I doubt that they are any more specialized than other avian groups (orders). It seems likely that the cranial features concerned may have evolved first, associated with some new method of feeding, and that this new method permitted this group to become large, ground dwelling, and finally flightless. While the structure of the palate and correlated cranial features are very different from those seen in other birds, their evolutionary potential was not great, as only a small group of flightless birds resulted from this innovation. Members of this group may appear very distinct morphologically, but in terms of diversification this group is only average compared to all avian orders. If the ratites are reunited into the same taxonomic group, what rank should be given to them—superordinal, as previously done, or ordinal? This is an open question and one that I do not care to answer definitively now, since more study of this problem is needed. The rank to be assigned is really of little importance at this time. Of far greater importance are additional studies of other characters—anatomical, behavioral, and so forth—through which we can verify or reject the conclusion that the ratites are monophyletic. The cranial evidence supporting this conclusion is, I believe, convincing, but this should be accepted as tentative until we have other independent supporting data.

SUMMARY

The ratites possess a palaeognathous palate, a continuous orbital and nasal septum, a gap between the maxillary process of the nasal and the maxilla, and a zygomatic process lying along the lateral side of the quadrate. These structures form a character complex associated with rhynchokinesis; however, their correlation with feeding habits in the ratites is not known. This palatal configuration is thought to be homologous within the group, which is believed to form a monophyletic group within birds. It is suggested that the ratites be reunited as a single taxonomic unit, but the rank to be assigned left as an open question for further study.

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Birds from the Upper Cretaceous of Wyoming

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Paleornithology has been criticized on several occasions for having contributed little to our knowledge of avian phylogeny. Like most sweeping pronouncements, this generalization has some factual basis, but appears exaggerated upon careful scrutiny.

The many valuable studies of living birds, in the fields of morphology, physiology, zoogeography, and behavior, allow us to draw tentative conclusions as to the interrelationships of various living groups, but without paleontological support these remain but tantalizing hypotheses. It is only through study of the fossil record that we may eventually know what has in fact happened.

Almost all (97 percent) of the 840 known species of extinct fossil birds are from the Pleistocene and Tertiary. The careful studies of Wetmore, the Millers, Howard, Lambrecht, Lydekker, Milne-Edwards, and many others give us an insight into the great zoogeographical and ecological changes of the past. From the standpoint of phylogeny they demonstrate that the living species of birds arose in the Pleistocene, or immediately prior thereto, and that the now-living genera and families became established during the Tertiary. On a larger scale, they tell us that the adaptive radiation of many orders took place near the Cretaceous-Tertiary boundary.

If paleornithology has not contributed as much as we should like to the clarification of interordinal relationships, it is only because our knowledge of the earliest, Mesozoic, birds is still so miserably poor. From the latest Jurassic, only *Archaeopteryx* is known, and this is possibly a sideline in avian evolution. From the Cretaceous, the 70-million-year span of which exceeds all subsequent time, only 22 valid species of birds are known. No additions to the list of Mesozoic birds have been made in more than 30 years.

Recently William A. Clemens and Richard Estes have made extensive collections of small vertebrates in the Upper Cretaceous of Wyoming for the University of California Museum of Paleontology. Dr. Clemens is studying the mammals, Dr. Estes the reptiles and amphibians, and they have kindly asked me to report upon the birds.

I am greatly indebted to these gentlemen for the opportunity to study this most interesting material. In addition, I should like to thank the National Science Foundation for financial assistance, through grant number G-19595, and Philip E. Humphrey and Elwyn L. Simons of Yale University for the privilege of examination of Marsh's types of *Cimolopteryx.* The photographs of the fossils are by Robert W. McFarlane.

Proc. XIII Intern. Ornithol. Congr.: 55–70. 1963

DESCRIPTION OF LOCALITIES

The material reported herein is from the type locality of the Lance formation, along Lance Creek, a tributary of the Cheyenne River, in Niobrara County, Wyoming. This area was once included in Converse County and is so listed in earlier reports.

The Lance formation underlies Paleocene deposits and overlies the Fox Hills sandstone of the Upper Cretaceous. Cobban and Reeside (1952) correlate the Lance with the Danian and upper part of the Maestrichtian stages in the European chronology, but Clemens (1960) and Estes (*in litt.*) suggest that it is entirely of Maestrichtian age.

The bird bones come from four localities in the upper half of the formation and are located within a few miles of each other along Lance Creek. They will be described shortly in detail by Clemens.

University of California locality V-5620 is about 2,100 ft above the base of the section, in the SW ¼, Section 10, Township 36 North, Range 64 West. The birds from this locality include two loon-like divers, a flamingo-like wader, and three species of shorebirds. Indeterminate material includes fragments of a vertebra and shafts of a tibiotarsus and tarsometatarsus.

Locality V-5711 is in the SW ¼, Sec. 20, T 37 N, R 64 W. The two avian species determined, a diver and a shorebird, also occur in the preceding locality. Undetermined material includes fragments of vertebra, humerus, and coracoids.

Locality V-5003 lies in the south half of Section 20. It is represented by a fourth species of shorebird.

Locality V-5817 lies in the center of Sec. 16, T 37 N, R 64 W. The single avian element, a cervical vertebra, is indeterminate.

AVIFAUNA OF THE LANCE FORMATION

Order Gaviiformes

Genus **Lonchodytes**, new genus

Type of Genus. *Lonchodytes estesi,* new species.

Diagnosis. Differs from *Gavia* Forster in having the shaft of the tarsometatarsus less compressed, with edges rounded, and tendinal grooves less sharp; intertrochlear space wider; middle trochlea without swollen area on medial face; outer trochlea shorter, falling decidedly short of middle trochlea, its plantar face shorter, and its shaft with a deep, wide groove leading from distal foramen; inner trochlea less deflected, wider, and extending farther mediad, with intertrochlear space distinct, and its shaft and acrotarsial face rounded; no separate infratendinal shelf extending proximad from below opening for extensor brevis digiti quarti; depression on plantar surface of shaft at base of inner trochlea located proximo-mediad (rather than slightly disto-mediad) to distal foramen; facet for first metatarsal more distinct.

The above differences are so pronounced that they prevent reference of *Lonchodytes* to the Gaviidae. The genus is therefore made the type of a new family, to be known as **Lonchodytidae.**

ETYMOLOGY. From Greek *logche* (a lance) and *dutes* (masculine, a diver).

Lonchodytes estesi, new species

HOLOTYPE. Distal portion of right tarsometatarsus (Fig. 1), University of California Museum of Paleontology No. 53954. From upper portion of Lance formation, along Lance Creek, Wyoming, at locality V-5620.

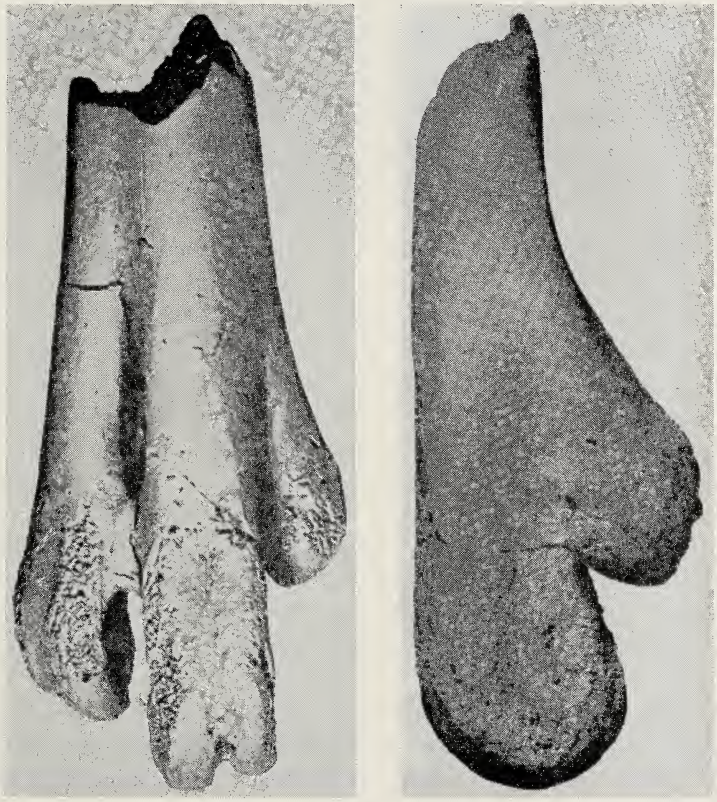

Fig. 1. *Lonchodytes estesi.* UCMP 53954, holotype tarsometatarsus.

Trochleae lengthened, compressed.

Middle trochlea longest; its tendinal groove moderately developed, and continuous along plantar and acrotarsial faces, apparently deepest at distal end (eroded in part of groove), and with slight deepening at upper acrotarsial end; no shelf bounding proximal end of plantar surface; outer rim extending somewhat farther distad than inner rim; borders parallel; lateral face deeply excavated in plantar half; medial face moderately excavated, without the swollen area characteristic of loons and grebes.

Outer trochlea about as wide as middle trochlea, falling short of end of middle trochlea by one-third distance from tip of latter to distal end of fusion between the two; medial rim with distal end at angle of about 45° to shaft; outer rim eroded; acrotarsial surface sloping laterad at angle of about 45°, with tendinal groove faint; lateral face rounded (abrasion at external distal corner prevents detailed description of this area); plantar face of shaft of trochlea with rather deep, wide, oblique groove, extending from distal foramen; medial face strongly concave; medial rim nearly parallel with middle trochlea on anterior face, slightly divergent distally; intertrochlear space one-third width of middle trochlea, slighty expanded proximally.

Inner trochlea deflected 30° from middle trochlea, its acrotarsial surface nearly at level of plantar surface of shaft of middle trochlea; trochlea elevated on shaft, with its distal end extending slightly beyond level of distal end of fusion between middle and outer trochleae; acrotarsial face rounded, without depressed area at root of shaft (distal and plantar surfaces abraded, preventing description); lateral face strongly concave; intertrochlear space narrow.

Shaft with lower end moderately compressed; acrotarsial face with a groove separating adnate portion of first and second metatarsals, extending somewhat above level of distal foramen, but without proximal deepening. Distal foramen an elongate oval, with its acrotarsial opening continued proximally as a deep gorge for a distance greater than length of trochleae; its plantar opening entirely visible in acrotarsial view. Supratendinal shelf (forming distal boundary of distal foramen) long, equal to three-fourths width of middle trochlea. Foramen for tendon of extensor brevis digiti quarti seated deep in anterior wall of distal foramen, without infratendinal shelf over opening for tibialis anticus artery. Plantar surface of shaft with short but deep depression (for sesamoids of toe flexors?) proximal and medial to distal foramen, its proximal wall steep. Facet for first metatarsal large but shallow, located just above base of inner trochlea and well within plantar area.

Width through trochlea, 12.5; width of middle trochlea, 4.2; length of inner intertrochlear notch, 8.6; length of outer intertrochlear notch, 7.5; length of middle trochlea, 7.4; width of shaft at first metatarsal scar, 7.1 mm.

Lonchodytes pterygius, new species

HOLOTYPE. Distal portion of left carpometacarpus (Fig. 2), University of California Museum of Paleontology No. 53961. From locality V-5620.

Metacarpal II extending somewhat farther distad than metacarpal III, its medial face swollen and rounded distally; a round pit on medial face near end of distal fornix; distal fornix short (compared with loons or grebes), with distal end of intermetacarpal space relatively wide and rounded; a triangular notch proximal to facet for digit III, extending from below facet onto medial face of bone.

In distal view, facet for digit II swollen at base; interdigital groove deep, transverse, with slight medial ridge running through its length; facet for digit III large, subtriangular, sloping ventromedially, its upper border at angle of about 20° to face of shaft, its outer border slightly convex but nearly parallel to shaft, its inner border parallel dorsally for dorsal fourth, then deflected at about 30° to outer border.

Length of distal fornix, 6.6; height through facets for digits II and III, 4.6 mm.

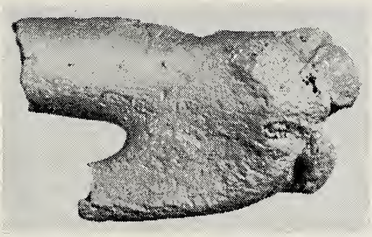

Fig. 2. *Lonchodytes pterygius.* UCMP 53961, holotype carpometacarpus.

Diagnosis. Differs from *Gavia* in having the metacarpals less extensively fused, metacarpal II longer (instead of shorter) than metacarpal III, a pit (rather than a convex scar) near tip of metacarpal II, and in having the facet for digit III large, subtriangular, and sloping ventromedially (instead of narrow, transverse, and horizontal).

The disparity in size between the tarsometatarsus described as *L. estesi* and the carpometacarpus described as *L. pterygius* appears too great for reference of the elements to the same species. The tarsometatarsus of *L. estesi* is somewhat larger than in modern *Gavia immer*, but the carpometacarpus of *L. pterygius* is only about the size of *G. arctica.* The well-developed facets for the fingers in *L. pterygius* indicate that the wings were quite functional, without any reduction in proportional size.

Tentatively Referred Material. The distal portion of the shaft of a right tarsometatarsus, No. 53971, from locality V-5711, is referred to *L. pterygius* with considerable reservation. It agrees with *L. estesi* in position and conformation of the scar for metacarpal I and in the strongly deflected base of the inner trochlea. It differs markedly from that species in having the shaft more rounded, with a deep but narrow groove separating the bases of the inner and middle trochleae, and in being smaller. Width of shaft at scar of first metatarsal, 5.7 mm. Although the size is about right for *L. pterygius*, it may possibly represent some other type of diver.

Etymology. Adjective formed from Greek *pterugion* (a little wing).

Position of the Enaliornithidae. The family Enaliornithidae includes two divers from the Lower Cretaceous Albian stage of England, *Enaliornis barretti* and *E. sedgwicki* Seeley. Although currently placed in the order Hesperornithiformes, these birds are only slightly less specialized than modern loons of the family Gaviidae and should be transferred to the order Gaviiformes.

In *Enaliornis* the distal portion of the tarsometatarsus is almost identical with that of *Gavia*, differing only in having the outer trochlea slightly the longest (middle trochlea slightly the longest in *Gavia*), in having the posterior surfaces of the trochleae not extending as far proximally, in having the profile of the inner trochlea angular (rounded in *Gavia*), and in lacking a deep depression above the trochleae on the posterior aspect (present in *Gavia*). The condition of the distal foramen of the tarsometatarsus is not apparent in the illustrations of *Enaliornis*, and the proximal end of the bone is known only in juveniles.

The tibiotarsus of *Enaliornis* is similar to that of *Gavia*, and differs in only minor respects. The procnemial process is less produced proximally. The distal portion of the bone is parallel with the shaft, whereas the area is inflected in *Gavia*. The condyles extend an equal distance distad, but in the *Gavia* the internal condyle extends farther distad.

In the femur the trochanter of *Enaliornis* is apparently lower than in the loons. The intertrochanteric area is wider in distal view, and the shaft is said to be less curved.

Order Ciconiiformes

Suborder PHOENICOPTERI

Genus **Torotix**, new genus

Type of Genus. *Torotix clemensi*, new species.

Diagnosis. Humerus similar to that of Phoenicopteridae, but external condyle unhooked; origin of anconal branch of extensor metacarpi radialis a rounded pit on ectepicondylar process palmar to origin of tensor patagii brevis; pit of anconal branch of flexor carpi ulnaris confined to side of bone and barely visible in palmar view.

In external view, with a transverse ridge continuous with longitudinal ridge on ectepicondylar process and bounding proximally common pit for origins of anconaeus and flexor metacarpi radialis and common pit for origins of flexor digitorum communis and supinator brevis; shaft strongly depressed proximal and anconal to ridges.

In anconal view, with olecranal fossa rather deep, with edges rounded.

In internal view, origin of pronator brevis a deep, oval depression above apex of supracondylar tubercle (well distal to and confluent with apex in

Phoenicopterus); facet for anterior articular ligament somewhat shorter than proximal leg of supracondylar tubercle (much longer than proximal leg in *Phoenicopterus*); lower portion of shaft straight, compressed in area opposite brachial depression, and strongly depressed distal and anconal to origin of pronator brevis; origin of pronator longus a small depression at foot of distal leg of supracondylar triangle; entepicondyle entirely proximal to internal condyle, with its apex rounded; origin of anconal branch of flexor carpi ulnaris a round, shallow depression slightly distal to apex of entepicondyle; origin of palmar branch of flexor carpi ulnaris a lengthened groove, parallel with shaft and forming palmar boundary of entepicondyle.

These characters require separation of *Torotix* as the type of a new family, to be known as **Torotigidae.**

The humeri of other phoenicopterine families differ as follows. In the Scaniornithidae, from the Lower Paleocene, the external condyle is longer than the internal condyle, the ectepicondylar process is laterally produced, and the brachial depression is short, wide, and shallow. In the Telmabatidae, from the Lower Eocene, the internal condyle is longer than the external condyle, the ectepicondylar process is obsolete, and the brachial depression is short. In the Palaelodidae, from the Miocene and Pliocene, the external condyle is hooked, the ectepicondylar process is laterally swollen, and the brachial depression is short and round.

Torotix clemensi, new species

HOLOTYPE. Distal portion of right humerus (Fig. 3), University of California Museum of Paleontology No. 53958. From upper part of Lance formation, along Lance Creek, Wyoming, at locality V-5620.

In internal view, with lower portion of shaft straight, compressed in area opposite brachial depression; supracondylar tubercle rising to a sharply pointed triangle with apex of 100°, the proximal leg 3 mm long, the distal leg (edge of attachment for anterior articular ligament) 2.8 mm long; origin of pronator brevis a deep, oval depression on medial face of shaft above apex of triangle; medial surface of shaft strongly depressed distal and anconal to origin of pronator brevis; origin of pronator longus a small depression at foot of distal leg of triangle; entepicondyle entirely proximal to internal condyle, with its apex rounded; origin of anconal branch of flexor carpi ulnaris a round, shallow depression slightly distal to apex of entepicondyle; origin of palmar branch of flexor carpi ulnaris a lengthened groove, parallel with shaft and forming palmar boundary of entepicondyle.

In palmar view, with entepicondyle well medial and proximal to internal condyle, with entepicondylar prominence medially produced; internal condyle transversely flattened; intercondylar groove rather deep, both distally and palmarly; external condyle extending distally as far as internal condyle, its axis at angle of 55° to shaft, apparently straight throughout (tip missing); ectepicondyle slightly produced laterally beyond external condyle; ectepicondylar process long, extending well proximal to level of anterior articular ligament and condyles, but process only slightly produced laterally, its edge straight and parallel with edge of shaft, furrowed along latero-palmar edge, its tip rounded and unproduced; scar of insertion of tensor patagii brevis extending from lateral edge of tip of ectepicondylar process onto its anconal surface; origin of anconal branch of extensor metacarpi radialis a rounded pit on ectepicondylar process palmar to origin of tensor patagii brevis; a tendinal groove along edge of ectepicondylar process beginning on palmar surface just distal to origin of anconal branch of extensor metacarpi radialis and extending distally along nearly entire external edge of process; scar of origin of palmar branch of extensor metacarpi radialis a deep, circular pit, located on shaft just medial and partly proximal to tip of ectepicondylar process, and proximal to and larger than origin of anconal branch; brachial depression large and distally very deep, extending up shaft for distance about twice length of external condyle; attachment of anterior articular ligament short, about as wide as long; pit of origin of pronator

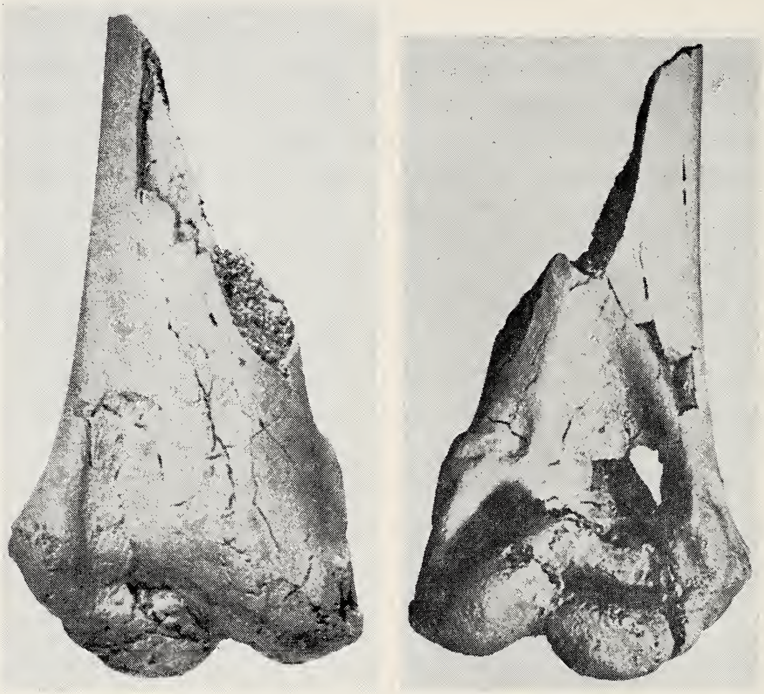

Fig. 3. *Torotix clemensi.* UCMP 53958, holotype humerus.

brevis proximal and medial to attachment of anterior articular ligament; origin of pronator longus medial to distal corner of anterior articular ligament; pit of origin of palmar branch of flexor carpi ulnaris distal to origin of pronator longus; pit of origin of anconal branch barely visible in palmar view.

In external view, with ectepicondyle falling slightly short of external condyle, its distal end unproduced and rounded off; common pit for origins of anconeus and flexor metacarpi radialis deep, entirely separated by a high oblique shelf from common pit for origins of flexor digitorum communis and supinator brevis; the latter pit located more palmad and slightly more proximad than the former pit, but nearly as deep; a transverse ridge bounding proximally both pits and continuous with longitudinal ridge on ectepicondylar process; shaft strongly depressed proximal and anconal to ridges.

In anconal view, with entepicondyle straight, short, thin, and entirely proximal to internal condyle, with edges rounded; olecranal fossa rather deep, with edges rounded; tricipital grooves obsolete.

Distal width, 12.3; width of shaft above ectepicondylar process, 8.5; depth through external condyle, 6.8; depth through entepicondylar prominence, 6.0; length of ectepicondylar process, 7.5; distance from distal end of external condyle to proximal end of brachial depression, 13.5; length of brachial depression, 11.6; width of brachial depression, 4.8; depth of brachial depression near upper end, about 2.0; depth of brachial depression below internal condyle, about 3.3; depth of brachial depression below peak of anterior articular ligament, about 3.5 mm.

Etymology. From Greek *torotix*, imitation of a bird's cry, attributed to the flamingo by Aristophanes. The gender is not given in lexicons but may be assumed to be feminine.

Position of *Gallornis*. *Gallornis straeleni* Lambrecht, from the Neocomian stage of the Lower Cretaceous of France, is only slightly younger than *Archaeopteryx*. Lambrecht (1931) based it on the proximal portion of a femur and a scrap of the humerus, the latter of no comparative value. He referred it to the Anatidae, although he remarked that it must have been a very weak swimmer.

The femur shows no agreement with the Anatidae, but its characters are those that appear or are even exaggerated in the suborder Phoenicopteri. The head of the femur lacks proximal reflection, and the neck is without the restriction characteristic of ducks and geese. The trochanter is too high for the Anatidae. The iliac facet is excavated instead of convex, and in proximal view it makes a more triangular figure with the head, compared with the Anatidae. Since the femur is unknown in other Cretaceous phoenicopterans, *Gallornis* may be tentatively placed in the oldest allied family, the Scaniornithidae.

Order CHARADRIIFORMES

Suborder CHARADRII

Family **CIMOLOPTERYGIDAE**, new family

Genus *Cimolopteryx* Marsh

Cimolopteryx Marsh, 1889, Am. J. Sci., ser. 3, vol. 38, p. 83, footnote (nomen nudum).

Marsh, 1892, Am. J. Sci., ser. 3, vol. 44, p. 175 (type *Cimolopteryx rarus*, designated by Hay, 1902, Bull. U.S. Geol. Surv., no. 179, p. 537).

Timolopteryx Ogilvie-Grant, 1912, General Index to Hand-list Gen. Sp. Birds, pp. 153, 154, 184 (misreading of *Cimolopteryx*, printed in antique type in Sharpe).

The genus *Cimolopteryx* is currently considered of Incertae Sedis, but examination of the types of Marsh's two species indicates that they belong in separate families.

Marsh erroneously applied masculine endings to the specific names, but words ending with the Greek noun *pteryx* (wing) are feminine, the correction having been made previously by Sharpe (1899).

Cimolopteryx rara Marsh

Cimolopteryx rarus Marsh, 1889, Am. J. Sci., ser. 3, vol. 38, p. 83, footnote (nomen nudum).

Marsh, 1892, Am. J. Sci., ser. 3, vol. 44, p. 175, pl. 3, fig. 2.

HOLOTYPE. Left coracoid, lacking head and hyposternal process, and with damage to internal distal angle and middle of sternal facet, Yale Peabody Museum No. 1805. From "Converse" [=Niobrara] County, collected by J. B. Hatcher, June 1889.

REFERRED CORACOIDS. University of California No. 53962 and 53963 (Fig. 4), upper portion of right and left coracoids, both from locality V-5620.

Marsh's figure is accurate, except that the distal view shows the sternal facet too thick. Certain measurements of the three coracoids are given in Table 1. Other measurements of the type are as follows: length to internal sternal angle, as preserved, 26.0; length to external distal angle, 30.8; length to middle of sternal facet, 30.5; width of sternal end, as preserved, 11.6; maximum thickness of sternal facet, 1.8; internal distal angle to anterior intermuscular line, 10.0 mm.

The coracoid resembles that of members of the suborder Charadrii, particularly the Recurvirostridae, Burhinidae, and Glareolidae. The resemblance seems closest to the Recurvirostridae, from which *Cimolopteryx* differs in having the head with much less medial thrust, the furcular facet and the brachial tuberosity poorly developed, the procoracoid process short and not curved toward the furcular facet, and the external distal edge of the glenoid facet at the level of the proximal edge of the scapular cup (at level of middle of cup in *Recurvirostra*), swinging thence at a steeper angle to join distal border of cup. These differences require the separation of *Cimolopteryx* as the type of a new family.

Fig. 4. *Cimolopteryx rara*. UCMP 53963, referred coracoid.

TABLE 1.—MEASUREMENTS (in mm) OF CORACOID OF *Cimolopteryx* AND ALLIED GENERA

Species and Catalog Number	Length Scapular Facet	Width Scapular Facet	Length Glenoid Facet	Width Glenoid Facet	Scapular Facet to Procoracoid Foramen	Least Width Shaft	Width Below Brachial Tuberosity
Cimolopteryx minima							
UCMP 53976[a]	1.5	1.6	3.0	1.8	0.8	2.1	2.9
Cimolopteryx rara							
YPM 1805[a]	2.0	2.3	5.5	3.2	1.3	2.6	—
UCMP 53963	2.0	2.3	5.4	3.3	1.7	2.8	4.3
UCMP 53962	2.0	2.2	4.6	3.0	1.5	2.6	—
Cimolopteryx maxima							
UCMP 53973[a]	3.7	3.7	8.7±	4.7	2.6	—	—
UCMP 53957	3.7	4.2	8.9	5.0	—	—	—
Ceramornis major							
UCMP 53959[a]	3.0	3.2	7.9	4.4	1.8	—	6.0
Apatornis retusus							
YPM 513[a]	2.6	2.5	6.4	4.2±	—	4.0	3.9+
Apatornis celer							
YPM 1734 (ex Marsh)	—	—	5.5	3.8	—	3.0	—

[a] Type.

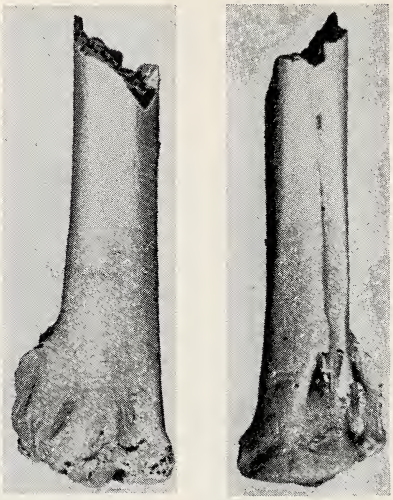

Fig. 5. *Cimolopteryx rara.* UCMP 53964, referred carpometacarpus.

Carpometacarpus. No. 53964, left side, distal portion (Fig. 5) from locality V-5620. Length of distal fornix, 4.1; height through facets for digits II and III, 4.7; width of facet for digit II, 3.5; width of shaft of metacarpal II, 2.3 mm.

Resembles *Recurvirostra* in having distal fornix short; distal portion of metacarpal II swollen on internal face, with concave area near base of tuberosity; external face with deep, oblique fossa at end of tendinal groove; facet for digit III decidedly shorter than facet for digit II.

Differs from *Recurvirostra americana* in being slightly smaller, and thus of the right size for the present species; tuberosity of metacarpal II much less elevated; facet for metacarpal II with median groove very deep (as in Phoenicopteridae); oblique fossa deeper; tendinal groove between facets for digits II and III roofed.

Fig. 6. *Cimolopteryx rara.* UCMP 53969, referred quadrate.

Quadrate. No. 53969, left side (Fig. 6), from locality V-5620. Length, 6.0; depth through heads, 2.2; pterygoid process to quadratojugal socket, 3.1; length of quadratojugal socket, 2.0 mm.

Quadrate double-headed, with squamosal head large and rounded, pro-otic head compressed; mandibular process short, with quadratojugal articulation a well-formed socket; pterygoid process flat, unswollen, two-pronged; orbital process present (largely broken off in specimen); a large pneumatic foramen medial to base of orbital process; shaft with a fossa on external face opposite orbital process.

Closest to Recurvirostridae, from which it differs in having otic process lengthened and in lacking an extra articular facet between the quadratojugal and pterygoid processes.

Cimolopteryx minima, new species

Holotype. Upper two-thirds of right coracoid (Fig. 7), University of California Museum of Paleontology No. 53976. From locality V-5003.

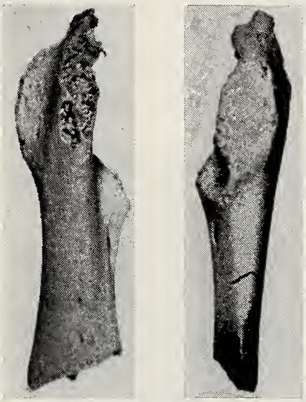

Fig. 7. *Cimolopteryx minima.* UCMP 53976, holotype coracoid.

Diagnosis. Agrees with *C. rara* in having scapular facet a deep cup and and posterior opening of procoracoid foramen well below level of scapular facet, but size much smaller (Table 1).

Cimolopteryx maxima, new species

Holotype. Upper portion of left coracoid (Fig. 8), University of California Museum of Paleontology No. 53973. From locality V-5711.

Referred Specimen. Upper portion of left coracoid, No. 53957 (Fig. 9), from locality V-5620.

Diagnosis. Agrees with *C. rara* in having scapular facet a deep cup and procoracoid foramen located well below level of scapular facet, but glenoid facet narrow and size much larger (Table 1).

Fig. 8. *Cimolopteryx maxima.* UCMP 53973, holotype coracoid.

Fig. 9. *Cimolopteryx maxima.* UCMP 53957, referred coracoid.

Fig. 10. *Ceramornis major.* UCMP 53959, holotype coracoid.

Genus **Ceramornis**, new genus

Type of Genus. *Ceramornis major*, new species.

Diagnosis. Coracoid similar to that of *Cimolopteryx*, but glenoid facet relatively shorter; scapular cup somewhat less deep; procoracoid foramen high, approaching level of scapular cup.

Etymology. From Greek *keramos* (potter's clay) and *ornis* (masculine, bird).

Ceramornis major, new species

Holotype. Upper portion of right coracoid (Fig. 10), University of California No. 53959, from locality V-5620.

Diagnosis. Smaller than *Cimolopteryx maxima*, larger than other species of that genus (Table 1).

Order ICHTHYORNITHIFORMES

Family APATORNITHIDAE

Genus *Apatornis* Marsh

Apatornis Marsh, 1873, Am. J. Sci., ser. 3, vol. 5, p. 162 (type by original designation *Ichthyornis celer* Marsh).

Apatornis retusus (Marsh)

Cimolopteryx retusus Marsh, 1892, Am. J. Sci., ser. 3, vol. 44, p. 175.

Holotype. Upper fragment of left coracoid, lacking head, Yale Peabody Museum No. 513. From "Converse" [=Niobrara] County; collected April 13, 1890, by J. B. Hatcher.

Glenoid facet greatly extended laterally, strongly recurved, with surface thus somewhat concave; scapular facet a shallow cup; posterior face with a wide, deep, irregular groove, running from opposite second fourth of glenoid facet to level of middle of scapular facet; no procoracoid process in part preserved; a deep, wide groove on posterior face of shaft below scapular facet; a narrower and shallower groove running near internal edge of bone from below area of brachial tuberosity to broken lower end of specimen; anterior face of shaft with a deep concave area along glenoid facet. Measurements are given in Table 1.

Resemblances to the Phalacrocoracidae include the recurved glenoid facet, the shape and plane of the posterior face of the shaft below the furcular facet, and the apparent absence of a procoracoid process. The main differences are the presence of a scapular cup (absent in Phalacrocoracidae) and the grooves on the shaft of the fossil. The grooves could represent concavities on either side of a procoracoid process, possibly broken off in the type.

The fossil agrees with *Apatornis* in the recurved glenoid facet and cuplike scapular facet. In the absence of better material it may be referred to that genus.

SUMMARY

The Lance formation in the Upper Cretaceous (Maestrichtian) of Wyoming includes eight species of birds, which gives this locality the largest Mesozoic avifauna with the exception of the Niobrara formation of Kansas. Two of the birds, *Cimolopteryx rara* and *C. retusa*, were previously described by Marsh; the others represent new genera or species. The family Cimolopterygidae is proposed as new in the suborder Charadrii, for *C. rara* Marsh and the new forms *C. minima*, *C. maxima*, and *Ceramornis major*. *Cimolopteryx retusa* Marsh is transferred to the genus *Apatornis* Marsh in the order Ichthyornithiformes. The family Lonchodytidae is proposed in the order Gaviiformes for two divers, *Lonchodytes estesi* and *L. pterygius*. The family Torotigidae is erected in the suborder Phoenicopteri, with *Torotix clemensi* as the only included member. The material indicates that the characters of the orders are merging, with the phylogenetic lines little separated in the Upper Cretaceous.

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Some Osteological Adaptations in Parulidae

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This is a study of some osteological characters in the family Parulidae designed to show adaptive trends occurring in the fore- and hindlimbs and in the size of the sclerotic eye-ring. The work was done at St. Bonaventure University from 1958 to 1961, and breeding males from New York and Michigan were used as subjects. We hope that this work will help in a fuller understanding of parulid ecology and behavior.

To study as broad a spectrum of variation as feasible, five general functional categories of warblers were chosen. Each category was represented by a single species—the canopy gleaners by *Dendroica virens*, the trunk foragers by *Mniotilta varia*, the shrub foragers by *Geothlypis trichas*, the aerial feeders by *Setophaga ruticilla*, and the ground feeders by *Seiurus aurocapillus*.

The work reported on here does not emphasize comprehensive comparative anatomy, such as that advocated by Fisher (1955) and Jollie (1958), or anatomical work to discover hidden relationships, like that of Beecher (1950, 1953) and Tordoff (1954). Instead, it attempts to show osteological adaptation to microhabitat. With this as the major objective, sexual, seasonal, and geographic variation have been avoided by using breeding male birds from New York and Michigan.

NATURAL HISTORY OF REPRESENTATIVE SPECIES

Mniotilta varia breeds in various types of deciduous and coniferous forests, especially where there is a somewhat open canopy, such as is typical of oak woods (Stewart and Robbins, 1958:270). Although typically a tree-trunk and large-limb forager (Skutch, 1954:383), it nests on the ground, usually at tree bases, using the tree trunk to approach the nest. In the Northeastern States it arrives on its breeding grounds second only to the aquatic-feeding *Seiurus motacilla*. Its long slightly decurved bill is used to pick up insect larvae lodged in bark, at least early in the spring.

Dendroica virens inhabits intermediate levels of coniferous or deciduous forest canopies. MacArthur (1958) has said that it moves in a tangential direction, hopping through the dense parts of the branches and new buds. It usually forages and nests at midelevations in the trees, 10–17 m from the ground.

Seiurus aurocapillus is a typical ground warbler, foraging on the forest

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floor and seeking cover in the lower forest canopy, where it utters its territorial song. It nests on the ground and often makes long flights under the canopy from one end of its territory to the other. It is a distinct, deliberate walker, the only walker of the group.

Geothlypis trichas is a shrub specialist. Hofslund (1959) has stated that brushy thickets are of great importance in the nesting cycle. These serve as feeding stations, singing perches, and as protection for the young. This species nests on the ground.

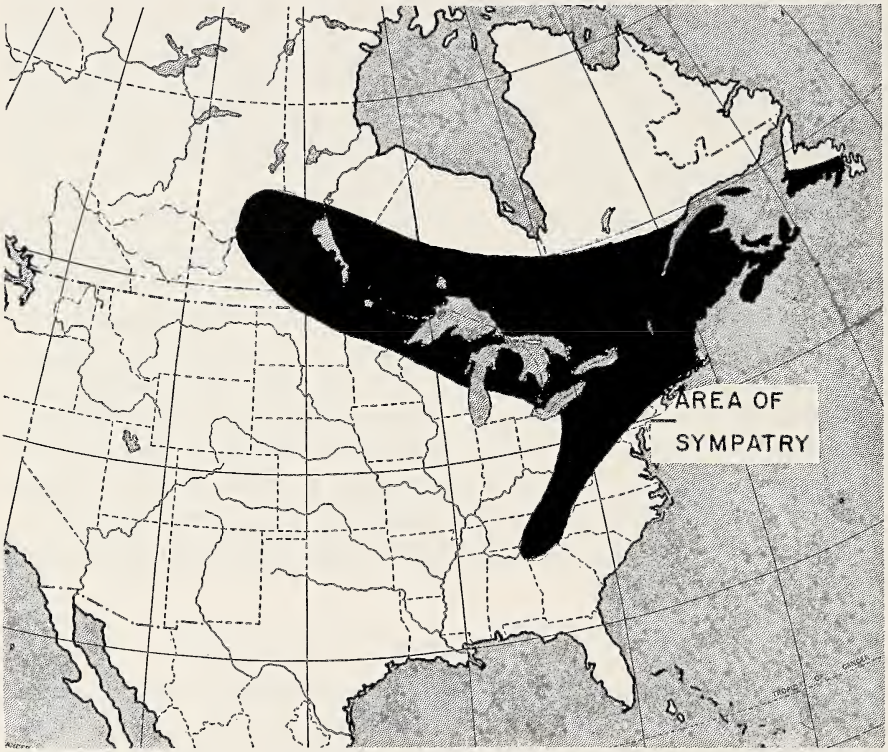

Fig. 1. Large black area is where the five species treated in the text are sympatric in the breeding season.

Setophaga ruticilla is an arboreal species of deciduous woodlands where canopies are usually closed and there is a good growth of shrubs and saplings beneath. The bird is essentially an aerial forager and nests 2–7 m above the ground in upright, forked branches.

All five species are sympatric in the eastern parts of North America (Fig. 1) and, except for *Geothlypis*, avoid, in the nesting season, the southern Atlantic and Gulf coastal plains, as well as the open prairies of the West. All five are what MacArthur (1959) called migrant Nearctic species. They have all invaded various seral stages of the taiga, but none reach maximum population densities there. *Dendroica virens* has been the most successful of this selected group in colonizing the coniferous forests (Purcell and Eaton, 1959).

Dendroica virens was selected as a standard for comparison in these studies because it was considered to be the most generalized of the five species for the following reasons: (1) It is a member of a rather distinct superspecies (*artenkreis*) which circles the tall- and short-grass prairies (*Dendroica virens, D. chrysoparia, D. occidentalis, D. townsendi*); (2) the intermembral lengths of bones of fore- and hindlimbs are least modified (Fig. 2, 3, and 4); (3) the shape of the wing feathers is typical of the general warbler type, being neither particularly rounded or pointed; (4) the sclerotic eye-ring diameter is close to the mean of 32 warbler species measured (Fig. 5).

METHODS AND RESULTS

To reduce measurements to a reasonably comparative figure, we followed the method used by Amadon (1943) where measurements (longest measurements of limb members, longest inside diameter of the sclerotic ring) were equated to the cube root of the breeding males' weight. Certain weaknesses of this method have been pointed out by Fisher (1955). The pioneering work of Böker (1927) and Palmgren (1932) has influenced this study, as has work by Miller (1937), Engels (1940), Richardson (1942), Fisher (1946), and Dilger (1956).

Forelimb Studies.—Data on the three principal wing segments were compiled by O'Connor (1961). The warbler forelimb has a moderately stout humerus, a slender, somewhat extended forearm, and a manus not markedly elongate. Structurally, the warbler pectoral appendage appears well adapted for flapping flight rather than for soaring or gliding, and for quickness and maneuverability rather than for speed.

Linear measurements of the three wing segments were made with dial calipers accurate to 0.1 mm. These were taken as follows: (1) *humerus*—greatest length from the most proximal point of the head to the most distal curvature of the external condyle; (2) *ulna*—the greatest length from the most proximal tip of the olecranon process to the most distal tip of the external condyle; (3) *manus*—the greatest length from the tip of the proximal curvature of metacarpal 1 to the tip of phalanx 2 of digit II. Where possible, the wing complex was left articulated; when disarticulated, the separate segments were measured and the sum taken. When measured in this disarticulated manner, precautions were taken to make the measurements comparable. *Total limb length* was the sum of the various segments (humerus, ulna, manus). The length of the humerus was considered to be least subject to instrumental error (Engels, 1940:367). In Table 1, linear proportions of the five species are equated following Amadon (1943). *Dendroica virens,* considered here as generalized, appears in the right-hand column as 100 percent. The other species are compared with *D. virens* in percentage differences.

TABLE 1.—STATISTICS OF THE SKELETAL ELEMENTS OF THE PECTORAL APPENDAGE

Species (and Mean Body Weight)	Sample Size	Range in Length (mm)	Mean (mm)	SD	Coeff. Var.	Equated Value	Percent of *D. virens*
HUMERUS							
D. virens	10	13.15–13.98	13.41	0.31	2.31	6.49	100.0
M. varia	6	13.65–14.97	14.06	0.55	3.92	6.56	101.07
S. ruticilla	11	12.35–13.42	12.70	0.35	2.75	6.27	96.6
S. aurocapillus	12	16.75–19.43	17.90	0.70	3.91	6.81	104.9
G. trichas	6	13.04–14.35	13.68	0.45	3.28	6.26	96.4
ULNA							
D. virens	10	17.25–17.96	17.45	0.48	2.75	8.33	100.0
M. varia	6	18.05–19.01	18.55	0.42	2.26	8.69	104.3
S. ruticilla	11	16.12–18.15	17.04	0.71	4.16	8.42	101.8
S. aurocapillus	12	20.17–24.85	22.15	1.08	4.87	8.43	101.2
G. trichas	7	15.29–16.50	15.84	0.46	2.90	7.26	87.1
MANUS							
D. virens	9	14.75–15.95	15.15	0.35	2.31	7.23	100.0
M. varia	6	13.95–15.65	14.85	0.66	4.44	6.96	96.2
S. ruticilla	12	13.44–15.34	14.77	0.68	4.60	7.48	103.4
S. aurocapillus	12	17.81–22.50	18.86	1.32	6.99	7.18	99.4
G. trichas	7	12.92–14.70	13.86	0.67	4.83	6.35	87.8
TOTAL LIMB LENGTHS							
D. virens (9.2 g)	10		46.01			21.96	100.0
M. varia (9.7 g)	6		47.46			22.26	101.3
S. ruticilla (8.3 g)	11		44.51			21.99	100.1
S. aurocapillus (18.1 g)	12		58.91			22.44	102.1
G. trichas (10.4 g)	6		43.38			19.42	88.4

Hindlimb Studies.—These data were compiled by Osterhaus (1962). Linear measurements were made with the same dial calipers. The lengths of the various segments were taken as follows: (1) *femur*—from the most proximal part of the greater trochanter to the most distal part of the external condyle; (2) *tibiotarsus*—from the most proximal part of the cnemial crest to the most distal part of the outer condyle; (3) *tarsometatarsus*—from the most proximal point of the intercondylar tubercle to the most distal point of the third trochlea; (4) *hallux*—the proximal phalanx and the ungual phalanx with horn claw were measured separately and summed to obtain the total length; the cord length of the ungual phalanx (with claw) was taken from its proximal articulation to its attenuated tip; (5) *third digit*—the three proximal phalanges were measured in linear arrangement between two microscope slides; if articulated, they were moistened to facilitate extension; if disarticulated, a small amount of water-soluble, herbarium glue was used to facilitate alignment; distal phalanx with claw was measured separately and the cord measurement added to that of other phalanges; (6) *total limb length*—sum of femur, tibiotarsus, and tarsometatarsus. Results of these measurements are given in Table 2.

Table 2.—Measurements of Hindlimb

Species (and Mean Body Weight)	Sample Size	Range in Length (mm)	Mean (mm)	SD	Coeff. Var.	Equated Value	Percent of *D. virens*
			FEMUR				
D. virens	8	12.02–13.35	12.51	0.39	3.12	6.04	100.0
G. trichas	6	14.19–15.20	14.72	0.30	2.04	6.81	112.7
M. varia	6	12.50–13.45	13.00	0.29	2.19	6.08	100.7
S. ruticilla	13	11.29–13.10	12.33	0.47	3.81	6.12	101.3
S. aurocapillus	14	15.75–19.00	16.79	0.74	4.41	6.25	103.5
			TIBIOTARSUS				
D. virens	8	23.30–24.05	23.62	0.27	1.14	11.41	100.0
G. trichas	4	27.49–28.21	27.48	0.53	1.92	12.71	111.4
M. varia	5	22.86–24.20	23.67	0.58	2.43	11.06	96.9
S. ruticilla	13	21.91–23.50	22.74	0.53	2.34	11.30	99.1
S. aurocapillus	12	27.69–30.95	29.41	0.82	2.78	10.95	95.9
			TARSOMETATARSUS				
D. virens	8	17.00–17.62	17.29	0.23	1.30	8.35	100.0
G. trichas	4	20.84–21.37	20.85	0.37	1.77	9.65	115.6
M. varia	5	16.91–17.84	17.44	0.38	2.18	8.15	97.6
S. ruticilla	14	15.92–17.94	16.95	0.46	1.69	8.42	100.8
S. aurocapillus	14	20.94–25.01	22.30	1.03	4.65	8.30	99.4
			HALLUX				
D. virens	5		10.55			5.10	100.0
G. trichas	1		13.10			6.06	118.8
M. varia	4		15.30			7.15	140.3
S. ruticilla	8		10.17			5.06	99.2
S. aurocapillus	7		13.04			4.85	95.1
			THIRD DIGIT				
D. virens	3		14.20			6.86	100.0
G. trichas	1		17.52			8.11	118.2
M. varia	4		14.27			6.67	97.2
S. ruticilla	4		14.45			7.18	104.7
S. aurocapillus	4		18.17			6.76	98.5
			TOTAL LIMB LENGTHS				
D. virens (8.9 g)	9		53.54			25.85	100.0
G. trichas (10.1 g)	5		63.21			29.24	113.1
M. varia (9.8 g)	5		54.13			25.29	97.8
S. ruticilla (8.2 g)	12		52.06			25.86	100.0
S. aurocapillus (19.4 g)	13		67.91			25.27	97.7

Sclerotic Ring Studies.—The sclerotic rings in this study were obtained from dermestid-cleaned specimens because in such small birds macerated preparations usually lack this material. Measurements were taken of the greatest inside diameter of the ring, because this was assumed to be the maximum opening for the entrance of light to the eye. Dial calipers accurate to 0.1 mm were used (Anicete, 1960). The results obtained for these warblers are shown in Table 3.

Table 3.—Measurements of Inner Diameter Sclerotic Ring

Species Studied	No. of Individual Rings[a]	Mean Body Weight (g)	Mean Ring Diameter (mm)	Equated Value[b]	Habitat
D. virens	10	9.1	3.8	1.82	Closed canopy
M. varia	8	10.1	3.6	1.67	Open canopy
S. aurocapillus	10	19.1	4.7	1.76	Open canopy
G. trichas	7	10.0	3.8	1.77	Shrubs
S. ruticilla	6	8.2	3.9	1.93	Closed canopy, aerial feeder

[a] Number of sclerotic rings from different individuals. When both left and right rings were present, the average of the two was used.

[b] Mean diameter of the sclerotic ring (in mm) divided by the cube root of the bird's mean weight (in g).

DISCUSSION

These three areas of the skeleton (forelimb, hindlimb, and sclerotic eyering) of the five species of wood warblers studied show some interesting adaptive trends. Migratory distances are quite similar and were assumed not to be responsible for the variation shown (Averill, 1925). Other environmental selective factors influencing variation in birds, such as temperature, length of foraging day, humidity, and aridity, which have been summarized particularly for the wing by Hamilton (1961) and for other areas of the bird by Mayr and Vaurie (1948), can largely be discounted. It seems reasonable to conclude, then, that the variation shown is mainly of a functionally adaptive type for better use of microhabitat or niche (Friederichs, 1958:156), during the nesting season and probably on the wintering grounds.

The data on the forelimb lengths showed that there has been slightly less

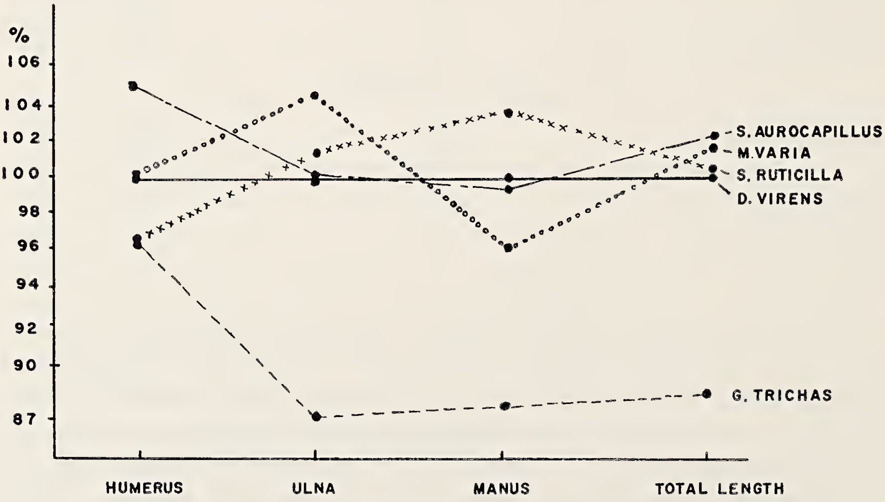

Fig. 2. Equated forelimb segments with *Dendroica virens* at 100 percent.

Table 4.—Percentage Differences in Total Limb Length Compared with *D. virens*

Species	Forelimb	Hindlimb
M. varia	+1.3	–2.2
S. ruticilla	0.1	0.0
S. aurocapillus	+2.1	–2.3
G. trichas	–11.6	+13.1
Maximum percentage spread (shortest–longest)	13.7	15.4

modification here than in the hindlimb (Table 4). The range of variation in the total forelimb lengths (humerus, ulna, and manus) amounted to 13.7 percent, while in the hindlimb (femur, tibiotarsus, tarsometatarsus) it amounted to about 15.4 percent. This seems reasonable in that demands of flight within the microhabitat and on migration leave less room for change.

The humeri of the shrub forager (*Geothlypis*) and the aerial feeder (*Setophaga*) are the shortest (Fig. 2). There is a slight increase in length of the humerus in the trunk creeper (*Mniotilta*) and a substantial increase in length of the humerus of the walking, ground-foraging *Seiurus aurocapillus.*

In the forelimb, the ulna of *Mniotilta* is the longest, while the shortest occurred in *Geothlypis.* This segment is quite similar in length in *Dendroica virens, Setophaga ruticilla,* and *Seiurus aurocapillus.*

The longest manus occurred in *Setophaga* and the shortest in *Mniotilta. Seiurus aurocapillus, Mniotilta varia,* and *Setaphaga ruticilla* have maintained the length of the wing by increases in three different segments: *Seiurus* by increasing the humerus, *Mniotilta* by increasing the ulna, and *Setophaga* by increasing the manus. The significance of this variation cannot be solved by mere wing-length-ratio studies, but this does point out some interesting possibilities for future study.

Adaptation in wing length has taken place in all segments; the least change in length is found in the humerus, with a spread among the five species of 8.6 percent (Table 5), the greatest in the ulna (17.5 percent) with slightly less in the manus (15.6 percent).

Table 5.—Amount of Variation Expressed as Percentage Spread in Various Equated Limb Segments of Migratory Thrushes and Warblers

Limb Segment	Thrushes[a]	Warblers[b]
Humerus	3.27%	8.6%
Ulna	6.34	17.5
Manus	6.47	15.6
Femur	5.5	12.7
Tibiotarsus	12.8	15.5
Tarsometatarsus	19.3	18.0

[a] From Dilger (1956) with *Catharus occidentalis* excluded because it is nonmigratory; 3 genera and 6 species.

[b] From Tables 1 and 2 in the present study; 5 genera and 5 species.

In the hindlimb the femur is least modified in length, with a spread among the five species of 12.7 percent, the tibiotarsus next, modified with a spread of 15.5 percent, and the tarsometatarsus most modified, with a spread of 18.0 percent (Fig. 3, Table 5). The long femur of *Geothlypis* is exceptional; the rest have femora that are only slightly greater in relative length than that of *Dendroica virens* (Fig. 3). The tibiotarsus, on the other hand, is short in *Seiurus aurocapillus, Mniotilta varia,* and *Setophaga ruticilla.* The tarsometatarsus is short in *Seiurus* and *Mniotilta,* but longer in *Setophaga.* The length of the hallux in *Mniotilta* is greatest, followed by *Geothlypis.*

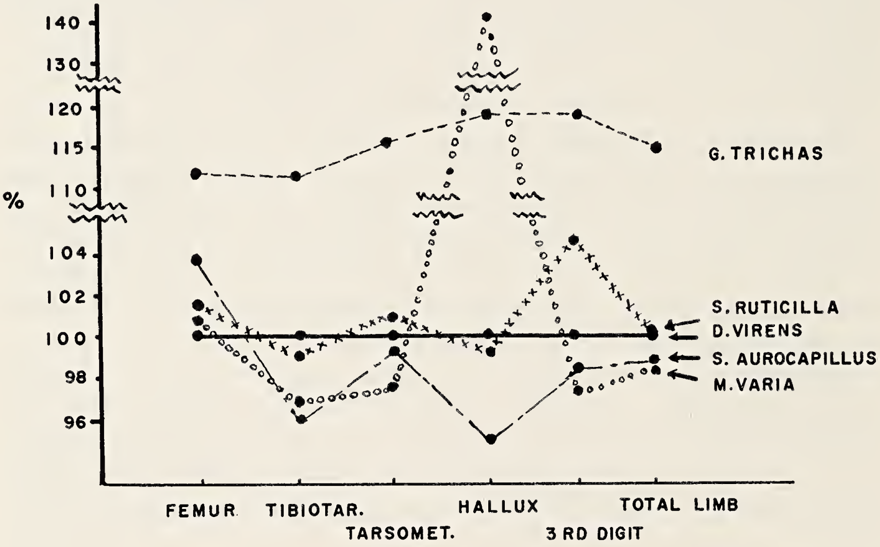

Fig. 3. Equated hindlimb segments with *Dendroica virens* at 100 percent.

In *Setophaga* and *Seiurus* the hallux is less than in *D. virens.* The third digit is longest in the shrub-foraging *Geothlypis,* and quite long in the aerial-foraging *Setophaga.* This third digit is definitely short in the walking *Seiurus,* and shortest in the tree-creeping *Mniotilta.*

Seiurus aurocapillus, the only walker of the group, might be expected to show general lengthening of the hindlimb. Instead, it is short. Dilger (1956: 187) has said that, everything else being equal, a larger bird will tend to have a relatively shorter tarsometatarsus than will a smaller one. This is, he said, merely a reflection of the greater weight of the bird and the need for proportionally greater support. This he used, with additional factors, to explain the relatively short leg of the relatively heavy *Hylocichla mustelina.* Others have found a similar situation with corvids (Dilger, 1956, cites Gustav Kramer, pers. comm.). *Seiurus aurocapillus* is the heaviest of the five warblers by about 90 percent.

The hindlimb of *Mniotilta varia* appears to be adapted in a similar manner as *Sitta* (Richardson, 1942). This wood warbler shows shortening of the tibiotarsus and, as pointed out by Stolpe (1932:212), the weight of the body of the climbing bird continually acts through the leg to pull the bird outward and down and to extend the joint. The leverage of this force of gravity, acting to extend the intertarsal joint during tree-trunk climbing, is decreased with a shortening of the tibiotarsus. It also brings the feet farther anteriorly to an apparently more advantageous climbing position. The extreme lengthening of the hallux is also similar to that found in *Sitta.*

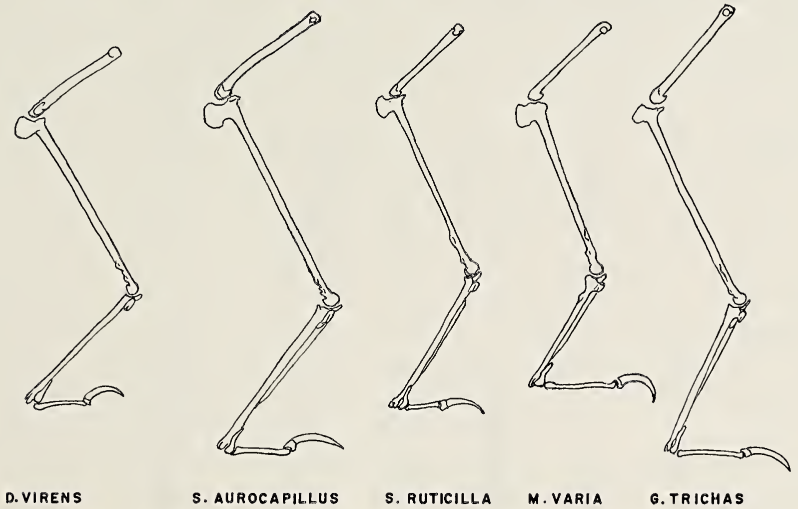

Fig. 4. Mesal view of hindlimbs of the five warblers treated in the text. Original drawings of single specimens all natural size.

The degree of lengthening of the hindlimb in *Geothlypis,* and the similar shortening of the forelimb, is reminiscent of the Troglodytidae and their general adaptation to shrub foraging. Skutch (1960:202) has said that, whatever their habitat, wrens prefer low, dense vegetation and rarely take long flights. *Geothlypis trichas* shows convergence in form toward the wrens in response to this same shrub-foraging habit.

In these small wood warblers, it appears that variation occurs in both forelimb and hindlimb in response to selective pressures centered around most efficient use of microhabitat, but this must stay within certain limits, of course, because of their lengthy migrations. Weight of appendicular bones may also be a complicating factor. In order to keep the species weight, particularly peripheral weight, within certain limits either lengthening of the forelimb is accompanied by shortening of the hindlimb or lengthening of this hindlimb by a shortening of the forelimb (Table 4 and Fig. 4).

Although, to our knowledge, no measurements of light intensities in the specific microhabitats of these birds have been taken, it appears from general impression that light intensity in the microhabitat and diameter of the sclerotic eye-ring are related (Fig. 5). The species occupying habitats of greater light intensities (*Mniotilta varia, Seiurus aurocapillus,* and *Geothlypis trichas*) have a smaller diameter of the sclerotic eye-ring than those occupying habitats with closed canopies and assumed less light intensities (*Dendroica virens* and *Setophaga ruticilla*). Light intensity of the microhabitat seems important here, but feeding behavior also appears to be related to the size of the eye opening. The aerial-foraging *Setophaga ruticilla,* with the largest eye opening, confirms this.

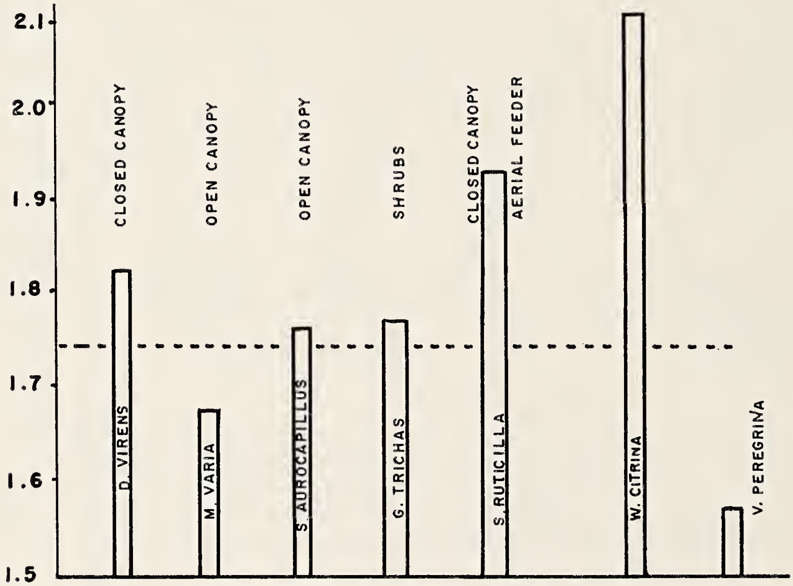

Fig. 5. Histograms to show average equated sclerotic-ring diameters in the five genera treated, and the largest (*Wilsonia citrina*) and the smallest (*Vermivora peregrina*) of 32 species of Parulidae measured, the mean of which is shown by the broken line.

The close correlation of eye-ring diameter to breeding microhabitat may lead to a greater appreciation of light in the life of birds beyond photoperiod-type studies. Light intensity, along with physical "layout" of vegetation, may be of great importance in "habitat selection" by birds. In Fig. 5, *Wilsonia citrina,* an inhabitant of densely shaded habitats, has the greatest diameter of the 32 species measured by Anicete (1960), and *Vermivora peregrina,* a northern-breeding species of rather open habitat, has the smallest. The average for the 32 species of warblers is 1.74, close to the generalized warbler *Dendroica virens.*

To appreciate more fully the amount of variation in wood warblers, we have compared them with another group of woodland birds, the seven species of thrushes of the genera *Hylocichla*, *Catharus*, and *Turdus* studied by Dilger (1956). One, *Catharus occidentalis*, which is a sedentary Mexican species, we excluded from Table 5 because this species is not under the selective forces of migration as are the others.

There is relatively more variation in the limb segments of the migrating wood warblers than in the migrating thrushes, except in the tarsometatarsus. This is interpreted to indicate that variation in wood-warbler limbs is for more efficient use of tree and shrub microhabitats. Thrush variability in limb lengths centers more around the ground as a feeding substrate, although Dilger has shown some species to be somewhat arboreally adapted.

Bock and Miller (1959), in discussing the foot of woodpeckers and the perching foot in general, showed that there are nonadaptive and adaptive elements to explain present structural features. Most of the variation shown in the wood warblers studied we feel to be of the narrower, adaptive type. The small size of the group (weight 8–18 g), and their range in foraging on tree trunks, on the forest floor, on branches, and in the air have acted to select these changes rapidly, perhaps aided by competition in sympatry. In the thrushes studied by Dilger, a group of birds of larger size (26–76 g), breeding in eastern North American forests, and essentially sympatric in species-pairs from north to south, there has been less adaptive modification in limb lengths than in the wood warblers. Of importance also in comparing thrushes and wood warblers are nonadaptive elements inherent in both families, as thrushes generally are considered to be Old World in origin, and wood warblers New World (Darlington, 1957).

Our results show a rather remarkable amount of variation in limb lengths in the five categories of migrating wood warblers examined, a variation that appears to be functionally adaptive and of benefit to the species in their microhabitats.

Perhaps the rather rapid adaptive radiation indicated in both hindlimb and forelimb is due to their small size, the greater number of microhabitats with sufficient small foods, and their ability to migrate and to utilize the varied microhabitats of the northern summer. The rather lengthened scratching foot of sparrows may reduce chances of variability, particularly in their forelimbs.

Further studies on topography of bones, action of joints, and myology would certainly bring out many more interesting functional adaptations only hinted at here. Such studies are needed before a full appreciation of wood-warbler ecology and behavior can be realized.

ACKNOWLEDGMENTS

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SUMMARY

For this study, five species representing five general functional categories of parulid warblers were selected. *Dendroica virens* was considered a typical member of the family for comparison.

The wings of *Seiurus aurocapillus, Mniotilta varia,* and *Setophaga ruticilla* were all quite similar in equated total lengths, but different elements of the wing were long or short to produce the similarity. The wing of *Geothlypis* was shortest. Variation in the hindlimb showed great lengthening in *Geothlypis,* shortening in *Seiurus aurocapillus* and *Mniotilta varia,* and little change in *Setophaga ruticilla.* Where lengthening of the hindlimb occurred, there was also a shortening of the forelimb. Where lengthening of the forelimb occurred, there was also a shortening of the hindlimb. The diameter of the sclerotic eye-ring was found to be smaller in wood warblers frequenting microhabitats of presumably higher light intensities, and larger in wood warblers found in lower light intensities. The degree of variation in the five genera of Parulidae was compared with variation in three genera of Turdidae and found to be greater, except in the tarsometatarsus.

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Plumages and Systematics of the Whistling Heron (*Syrigma sibilatrix*)

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The little known Whistling Heron (*Syrigma sibilatrix*) of South America has long been thought to be closely allied to the night herons (*Nycticorax*). Gray (1847:558) apparently was the first to include *Syrigma* in the genus *Nycticorax,* in which he also put *Gorsachius* and *Pilherodius.* Most subsequent authors have preferred to recognize these genera and usually have placed *Syrigma* and *Nycticorax* next to one another in the taxonomic sequence (Peters, 1931:114; Hellmayr and Conover, 1948:205). Bock (1956), in his interesting preliminary review of the heron family, has merged *Syrigma* with *Nycticorax,* in which he also includes *Nyctanassa* and *Philherodius.*

During a recent trip to northeastern Argentina (April–July, 1961), we saw many and collected several Whistling Herons; they impressed us as neither looking nor acting like night herons. Upon returning to the United States, we initiated an investigation of the relationships of the genus *Syrigma.*

AFFINITIES OF *SYRIGMA*

Syrigma is a slender, small-headed bird with relatively small eyes and moderately slender bill. In normal resting posture the "S" curve of the neck is always visible. In contrast, *Nycticorax* (sensu stricto) is a heavy, chunky, large-headed bird with large eyes and a relatively short, heavy bill. In normal resting posture the head is pulled down to the body, so that the bird appears to have no neck.

Whistling Herons are predominantly diurnal in habit, assembling in large arboreal roosts well before dusk. Although we saw them often in marshy situations, we also found them commonly in much drier habitats than frequented by night herons. In northern Misiones (northeasternmost Argentina), predominantly a region of dense subtropical forest, we saw *Syrigma* only in open upland fields, except when roosting. Wetmore (1926:57) has seen Whistling Herons in Uruguay "walking about in dry fields in search of the abundant grasshoppers." Foster Smith (Friedmann and Smith, 1950:434) saw them in Venezuela "only at savanna ponds." The note of the Whistling Heron is a long-drawn-out mournful whistle, which has great carrying power and is given only in flight. Two other calls have been described: a harsh alarm note (Wetmore, 1926), and a high, rapidly repeated call note (Friedmann and Smith, 1950).

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Outside the breeding season, *Nycticorax* is predominantly crepuscular and nocturnal in habit. It roosts by day and makes early evening flights to the marshlands or other generally aquatic situations where it feeds. It is almost never seen in dry open-field habitats. The call of the Black-crowned Night Heron (*N. nycticorax*) is a hoarse croak, which is uttered both during flight and while the bird is perched. As far as is known, *Nycticorax* makes no note that in any way resembles the whistle of *Syrigma.*

We have examined 83 study skins of *Syrigma* from many localities and times of year. The limited number of specimens prevented us from making a detailed analysis of the molts and sequence of plumages of the Whistling Heron, a tropical and subtropical species that is quite variable in timing and extent of molt, especially during the first year of life. The evidence suggests that the molts of *Syrigma* are as follows: The first prebasic molt (nomenclature of Humphrey and Parkes, 1959) begins before the juvenal remiges and rectrices have completed their growth; it involves most of the body feathers and most of the upper wing coverts but not the remiges. There appears to be a first prealternate molt involving feathers of the crown, crest, and neck, and perhaps others. The definitive prebasic molt is complete; the prealternate molt (for which there is not conclusive evidence) apparently involves crown, crest, and neck.

The first basic plumage of *Syrigma* differs from the definitive basic only in extent; we have been unable to distinguish birds in first basic plumage from those in either of the two definitive plumages in any way except by accompanying retained juvenal feathers. *Nycticorax,* on the other hand, does not attain definitive basic plumage until its third prebasic molt.

Nycticorax has a very extensive prealternate molt which, according to Witherby (*in* Witherby et al., 1939:151), is complete in the Old World race. In *Syrigma* the prealternate molt, if it exists, is confined to the head and neck.

The appearance of a young Whistling Heron in fresh juvenal plumage is like that of the adult except that colors are duller and feathers of the neck are streaked. The fresh juvenal plumage of *Nycticorax* and *Nyctanassa* is completely unlike that of the adult; it is brown, spotted with white on back and wings, and streaked on head, neck, and underparts.

A preliminary examination of the cervical vertebrae of representatives of several genera of herons (*Ardea, Botaurus, Butorides, Cochlearius, Egretta, Nyctanassa, Nycticorax, Pilherodius, Syrigma*) reveals that in structure and proportions of cervical vertebrae *Syrigma* has more in common with *Egretta, Butorides,* and *Ardea* than it does with the night herons and *Cochlearius.* The cervical vertebrae of *Syrigma* resemble those of *Egretta* and *Butorides* not only in general proportions but also in many minute details. *Syrigma* differs sharply from *Nycticorax, Nyctanassa,* and *Cochlearius* in these features of the cervical vertebrae.

Nycticorax, Nyctanassa, and *Cochlearius* have relatively very short, stout cervical vertebrae. *Syrigma* has long cervical vertebrae and a relatively longer, more slender neck than *Butorides*.

Syrigma also differs markedly from *Nycticorax* in form of the axis (Fig. 1). This difference is probably related to the attitude in which the head can be held in relation to the anteriormost vertebrae. In *Nycticorax*, *Nyctanassa*, and *Cochlearius* the articular surfaces of the postzygapophyses are 2 mm or more anterior to the caudal margins of the postzygapophyses. In addition, the posterior articular surface of the body of the axis is vertical and is not produced caudally; correlated with this, the caudal intervertebral notch is very shallow. This condition may allow the arc of movement between the axis and the third cervical vertebra to proceed to a more acute angle than is possible in the other herons examined, including *Syrigma*.

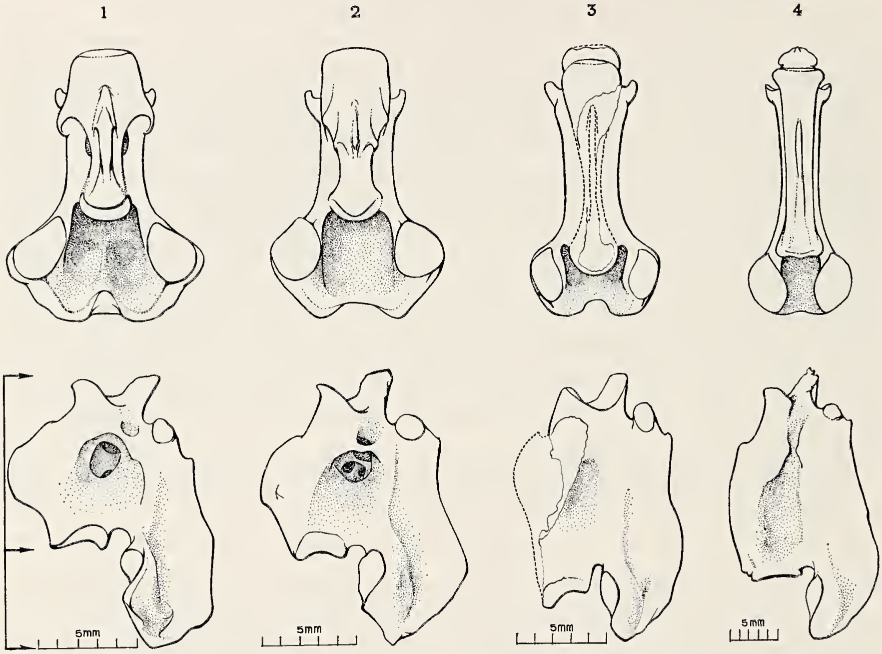

Fig. 1. Axis of the Whistling Heron compared to those of other genera.

(1) *Cochlearius cochlearius zeledoni* (U.S.N.M. 18,386)
(2) *Nycticorax nycticorax hoactli* (U.S.N.M. 18,799)
(3) *Syrigma s. sibilatrix* (U.S.N.M. 227,360)
(4) *Ardea h. herodias* (U.S.N.M. 292,925)

Upper row: ventral view; lower row: left lateral view. Arrows indicate measurements discussed in the text.

On the basis of what is known of the posture, behavior, molts, juvenal plumage, and proportions and structure of the cervical vertebrae, there seems to be little justification for submerging the genus *Syrigma* in *Nycticorax* or even considering the two to be closely related. Without a much more detailed analysis of the whole family Ardeidae, it is impractical to speculate on the close affinities of the Whistling Heron.

COLOR CHANGES OF FEATHERS OF *SYRIGMA*

During our study of the molts and plumages of the Whistling Heron, we discovered that some of its feathers undergo striking color changes of two kinds.

A freshly collected adult Whistling Heron has light yellow rump, sides, breast, belly, flanks, and thighs. After several months to a year, the yellow disappears from study skins of this species, leaving the rump and underparts of the body white. Hudson (1920:104) noted that in museum specimens of *Syrigma* "the primrose yellow fades to white. . . ."

The streaked juvenal neck feathers of flightless nestlings are grayish in general tone—not yellowish—and these feathers retain their pristine unyellowed aspect in museum specimens. Juvenal middle and lesser upper wing coverts at this age also lack the yellowed, buffy orange aspect of older juvenal birds. By the time juvenal Whistling Herons have left the nest, the middle and lesser upper wing coverts and the streaked feathers of the neck have become yellowish buffy orange *without an intervening molt.* In adult birds, growing neck feathers are uniform medium gray; fully grown feathers of the neck are buffy orange distally and medium gray basally. There is a similar color difference between growing and fully grown medium and lesser upper wing coverts.

The evanescent yellow suffusion on the white area of the underparts and rump of adult Whistling Herons vanishes after skinned specimens have been in a museum for a few months, whereas the acquired buffy orange of the neck feathers and middle and lesser upper wing coverts remains little changed or not at all. It seems to us possible that certain groups of feathers are structurally susceptible to permanent staining from a source of color that does not become available until the juvenal Whistling Heron is about ready to leave the nest. We think that the color source may be the oil gland or—more probably—the powder down patches. The evanescent yellow color, which fades from the white feathers of the Whistling Heron, presumably comes from the same source but fades from the white feathers because they are not structurally modified to hold it.

The Cattle Egret (*Bubulcus ibis*) has elongate specialized buffy to tawny plumes which are white when they first break from their sheaths. These plumes appear to be stained in the same way as are the neck feathers of the Whistling Heron.

GEOGRAPHIC VARIATION

The Whistling Heron has a disjunct distribution. The northern population is restricted to the upper Orinoco region of Colombia and Venezuela; the southern one occurs in Bolivia, Paraguay, northeastern Argentina (south to

Buenos Aires), and southeasternmost Brazil. In the southern population, there is no consistent geographical trend in color or pattern, but there is a tendency for Bolivian birds to be larger, particularly in bill length.

Friedmann (1949) described the Orinoco population as *fostersmithi* on the basis of longer bill, yellower upper wing coverts with narrower dark streaks, yellower neck and breast, and paler crown. We have been able to examine only three specimens of *fostersmithi*: a male (the type) and a female from Venezuela, and a first-year bird from Colombia.

The bill length of the type of *fostersmithi* can be matched by extreme specimens from Bolivia but the other Venezuelan specimen, a female, has a slightly longer bill than any southern specimens measured. Similarly, the black lines on the upper wing coverts are narrower on the type than in any specimens of the southern population, but those of the female can be matched by extreme southern specimens.

Crown color shows variation that may be related to age of bird, museum age of specimen, degree of wear, and amount of bloom, and is consequently untrustworthy as a taxonomic character. The crown of the type of *fostersmithi* is exactly matched by various specimens in our series of nominate specimens.

The buffy orange color of the neck and upper wing coverts presents a special problem of interpretation since, as discussed earlier, this color appears to be at least in part of adventitious origin. Hence, apparent geographic variation of this character may result from other than genetic causes. Nonetheless, both Venezuelan specimens are somewhat warmer and tawnier in color of the upper breast than are any southern specimens, and the wing coverts of the male (but not the female) are also yellower than in southern birds. Thus, although the yellow color of the neck and upper wing coverts of *Syrigma* is acquired *after* the feathers have developed and may be subject to nongenetic variation, it is possible that either (1) the structural modification of the feathers themselves, or (2) the source of this adventitious yellow stain may be geographically variable.

On the basis of the few specimens available, *Syrigma s. fostersmithi* appears to be separable from the nominate population.

ACKNOWLEDGMENTS

We thank the following people and institutions for allowing us to study specimens in their care: Dean Amadon (American Museum of Natural History), Emmet R. Blake (Chicago Natural History Museum), S. Dillon Ripley (Yale Peabody Museum of Natural History), Kenneth E. Stager (Los Angeles County Museum), and Robert W. Storer and Harrison B. Tordoff (University of Michigan Museum of Zoology).

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Alexander Wetmore and Andrew J. Meyerriecks gave us several helpful suggestions; Mrs. Carolyn Lutz drew the figure.

SUMMARY

The yellow or yellowish components of the coloration of *Syrigma* are acquired after the feathers have developed. On some parts of the bird, the yellow is evanescent and is ultimately lost from museum specimens. The acquired yellow of the upper wing coverts and neck feathers is a permanent acquisition.

Juvenal neck feathers of the Whistling Heron change from grayish to yellow or buffy orange without a molt. This color change may be caused by the development of a source of color in the powder downs, oil gland, or both, at about the time the young Whistling Heron leaves the nest. Similarly, growing definitive neck feathers of the Whistling Heron are medium gray when they break from their sheaths. They subsequently acquire a buffy orange stain which probably originates from the same source. The buffy color of the "nuptial" plumes of the Cattle Egret is also acquired some time after these feathers have broken from their sheaths.

Geographic variation of *Syrigma sibilatrix* is discussed and the validity of the northern population *fostersmithi* is tentatively upheld.

Finally, what is known of the behavior, voice, molts, juvenal plumage, and structure of the cervical vertebrae of *Syrigma* is evidence that it should not be merged with the genus *Nycticorax* or even placed in the same tribe. The Whistling Heron belongs in the tribe Ardeini as defined by Bock, but at present we cannot say where in that tribe it should be placed.

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The Taxonomic Significance of Avian Sperm

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Knowledge of the remarkable differences in size, form, and structure of animal sperm has existed for many years, but no attempt has been made to undertake a comparative survey of the sperm of an entire class. The extensive works of Ballowitz (1886) and of Retzius (1909) showed the tremendous morphological diversity that exists among vertebrate and invertebrate groups. Wilson (1925) has suggested that the variation might be sufficient to identify the species from the sperm alone. Friend (1936), Bishop and Austin (1957), and Hirth (1960) have demonstrated the specific distinctness of certain mammalian sperm. The present study was undertaken to determine the possible phylogenetic or taxonomic significance of the sperm of birds.

Most of our knowledge of the sperm of avian species goes back to Ballowitz (1886, 1888, 1913) and Retzius (1909, 1911, 1912). Grigg and Hodge (1949) and Grigg (1951, 1952) studied the structure of fowl spermatozoa by various means, including electron microscopy. Spermatogenesis has been described for several other species (Guyer, 1909*a*, 1909*b*; Smith, 1912; Zlotnik, 1947; Mehrota, 1951*a*, 1951*b*; Gupta, 1955; and Sharma et al., 1956), but these reports relate little regarding the actual size and variation of the spermatozoa for the respective species.

In the present study, morphological variation is investigated at various taxonomic levels, from the order to the species.

METHODS

The vas deferens and the seminal glomerule, if present, were excised and fixed in 10 percent formalin. Alcohol has a disintegrating effect upon the sperm and should be avoided. Sperm undergo the final stages of maturation, a reduction in head size and increase in tail length, while traversing the vas deferens. This necessitates securing sperm from the distal portion of the duct. Slides are prepared by placing a 1- to 2-mm section of duct in a small drop of distilled water upon the slide. The duct is then gently teased apart with needles to allow the sperm to float free in the water. After removal of the larger particles of tissue, the drop is smeared and air-dried.

The refractive index of avian sperm is such that normal mounting media (balsam, Permount, etc.) are unsuitable. All observations, including oil immersion, were conducted without cover slips.

In the present study a phase-contrast microscope was used to minimize the introduction of artifacts. It was hoped that phase-contrast microscopy

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would eliminate the necessity of staining procedures. Subsequent experience has shown that the limitations and boundaries of the various spermatozoan components can be extremely difficult to determine. It will henceforth be desirable to incorporate differential staining techniques to permit precise measuring.

Recently, the electron microscope has been utilized in this investigation. Several electron micrographs have been included here because of the detail they reveal. However, techniques are very tentative at present.

STRUCTURE OF SPERM

Several subdivisions of the head and tail of a spermatozoan are of significance in comparative studies. The head consists of the greatly condensed *nucleus* of the spermatid, and the *acrosome,* a derivative of the Golgi bodies. The acrosome is the most anterior portion of the sperm and, except in the passerines, is considerably smaller than the nucleus. Grigg and Hodge (1949) discuss the apical cap and spine, which compose the acrosome. The spine may occasionally be observed when the cap becomes detached during preparation. The tail, which attaches directly to the nucleus, consists of an *axial filament* and a *mid-piece* surrounding the axial filament anteriorly. The axial filament is enclosed within a protein sheath for most of its length, this portion being known as the *principal piece.* The distal segment, however, extends beyond this sheath and is referred to as the *end-piece.* The axial filament is derived from the centrioles of the spermatid, and the mid-piece is considered a product of the mitochondria. The mitochondrial enzymes of the mid-piece are believed to be the powerhouse of the sperm, converting chemical energy into the motile activity expressed by the axial filament. Many of the passerines possess a *helical membrane* which extends posteriorly from the mid-piece, winding around the principal piece for varying distances.

The size of avian sperm is highly variable, ranging from 30 to 300 microns. There is no correlation between the size of a bird and its sperm, some of the smaller finches and wood warblers exhibiting extremely elongated sperm. Measurements of total length are difficult to obtain because of breakage of the tail, and reliable figures can be obtained only when the end-piece is visible.

The spermatozoa of birds are of two general types, the simpler one being common to most birds and showing a remarkable resemblance to that found among the reptiles. This resemblance encouraged Ballowitz and Retzius to designate this the "sauropsid" type, as opposed to the second and more complex form found among the passerines. The first type is generally rather plain and elongated. The passerine type has a pronounced spiral to the head region, approaching a conic helix in some forms, and an enormous acrosome, often 3–4 times the length of the nucleus. Frequently a helical membrane extends some distance along the axial filament.

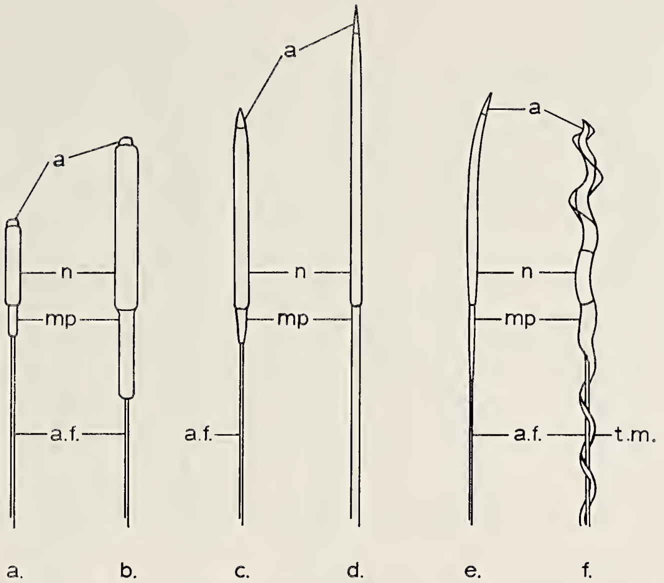

Fig. 1. Some basic designs of avian sperm. All approximately same scale.

a—Trogoniformes, *Trogon collaris*
b—Charadriiformes, *Larus marinus*
c—Anseriformes, *Somateria mollissima*
d—Columbiformes, *Claravis pretiosa*
e—Galliformes, *Gallus gallus* (dom.)
f—Passeriformes, *Dendroica coronata*

a—acrosome
a.f.—axial filament
mp—mid-piece
n—nucleus
t.m.—tail membrane

TAXONOMIC VARIATION

Orders.—As might well be expected, the differences between sperm are greatest at higher taxonomic levels. At the ordinal level this variation involves structural differences in the major components of the sperm. The head may be cylindrical with the acrosome appearing as a small knob or projection, or the head may be tapering with the acrosome continuing as a conical tip. The mid-piece may assume a cylindrical shape, of equal or lesser diameter than the nucleus, or it may taper posteriorly. It may be relatively smaller, of equal length, or considerably longer than the head, extending far down the tail in some instances. The tail itself is of highly variable length. Fig. 1 illustrates the extreme diversity in the relative proportions of the sperm as found among various orders. The trogons (Trogoniformes, Fig. 1*a*) and the Charadriiformes (Fig. 1*b*) have somewhat similar cylindrical mid-pieces and nuclei with button-like acrosomes. The ducks (Anseriformes, Fig. 1*c*) have a conical mid-piece. In the doves (Columbiformes, Fig. 1*d*), the mid-piece extends far down the tail. The sperm of the domestic chicken (Galliformes, Fig. 1*e*) has a slightly curved head. The helical nature of the passerine sperm (Passeriformes, Fig. 1*f*) makes it the most distinctive of the 15 orders examined.

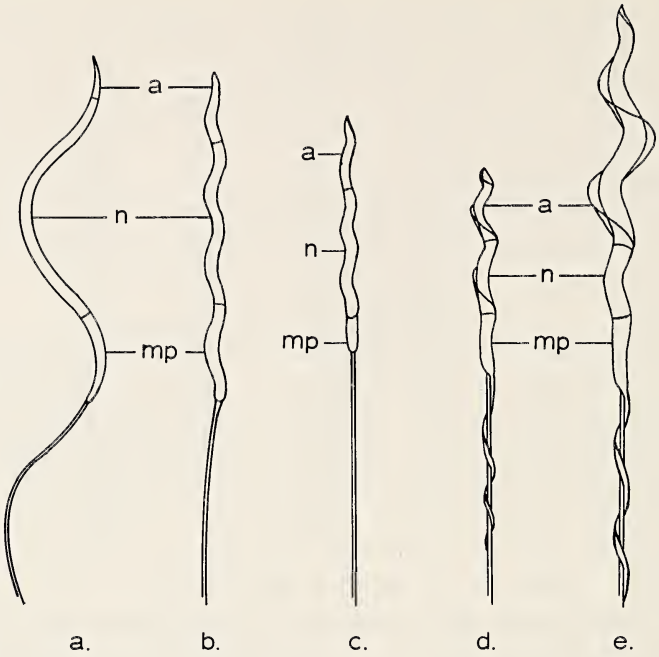

Fig. 2. Some variations of passerine sperm. *a*—acrosome; *mp*—mid-piece; *n*—nucleus.
a—Dendrocolaptidae, *Deconychura typica* *c*—Corvidae, *Corvus brachyrhynchos*
b—Tyrannidae, *Tyrannus tyrannus* *d*—Vireonidae, *Vireo olivaceus*
e—Fringillidae, *Spinus pinus*

Families.—Fig. 2 illustrates some of the more striking differences found among the families of the Passeriformes. The woodhewers (Dendrocolaptidae, Fig. 2*a*) and ovenbirds (Furnariidae) have a very simple sperm, which, while appearing to lie in a single plane, is actually a spiral that completes one revolution from the acrosome to the mid-piece. A more highly coiled form occurs in the ant-thrushes (Formicariidae), cotingas (Cotingidae), manakins (Pipridae), and tyrant flycatchers (Tyrannidae, Fig. 2*b*). A very similar pattern is found among the corvids (Corvidae, Fig. 2*c*) and the shrikes (Laniidae), but the mid-piece is not included in the spiral portion. In vireos (Vireonidae, Fig. 2*d*), a ribbon-like membrane extends from the nucleus to the acrosome, and another helical membrane extends a short distance down the tail. In finches (Fringillidae, Fig. 2*e*), the helical membrane extends to the distal end of the principal piece of the tail.

Genera.—A study of several genera of Hirundinidae demonstrates that qualitative differences still are present (Fig. 3), but quantitative differences assume a new importance. While some overlap occurs in comparative lengths of the head and mid-piece (their combined length in this instance), the total lengths of the four are completely distinct.

Species.—Morphological differences between species of a single genus are

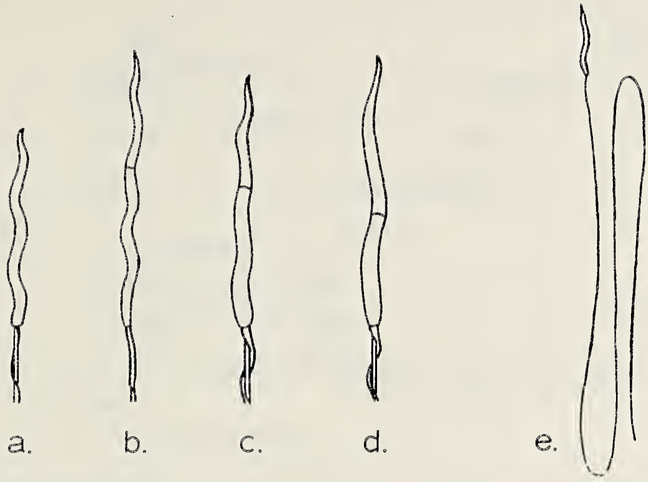

Fig. 3. Variation of sperm in the family Hirundinidae.

	Total length (microns)	Head and mid-piece length (microns)
a—Petrochelidon pyrrhonota	81 (76–82)	10.3 (9.7–10.7)
b—Hirundo rustica	89 (87–94)	13.0(12.2–12.8)
c—Riparia riparia	119(117–123)	11.7(10.7–12.7)
d—Iridoprocne bicolor	233(230–240)	12.6(12.2–13.8)

e—Full view (reduced scale) of *Iridoprocne bicolor* (a helical tail membrane, not apparent in drawing, extends to within 6 microns of the end of the tail).

apparently only quantitative. Fig. 4 compares the total length and head length of seven species of wood warblers of the genus *Dendroica.* These closely related forms would seem to provide an ideal test for the effectiveness of specific distinction as indicated by spermatozoa. There is considerable overlap of both total length and head length, although a slightly greater distinction is apparent when both measurements of two overlapping species are compared. For example, the diagrams for head length of *D. caerulescens* (*c*) and *D. coronata* (*f*) overlap in all respects, yet the observed ranges of total length are completely separated. The total length diagram for *D. coronata* is almost identical to that of *D. fusca* (*g*), but the means of the head lengths are separated from each other by 2 standard errors. Comparisons within genera composed of fewer species have tended to show a greater distinction between the species.

Fig. 7–12 provide more graphic evidence of several of the morphological characters considered above.

INDIVIDUAL VARIATION

In order to determine the effectiveness of a single specimen as a sample of the species, head lengths of 20 sperm of each of 10 individuals of the Red-

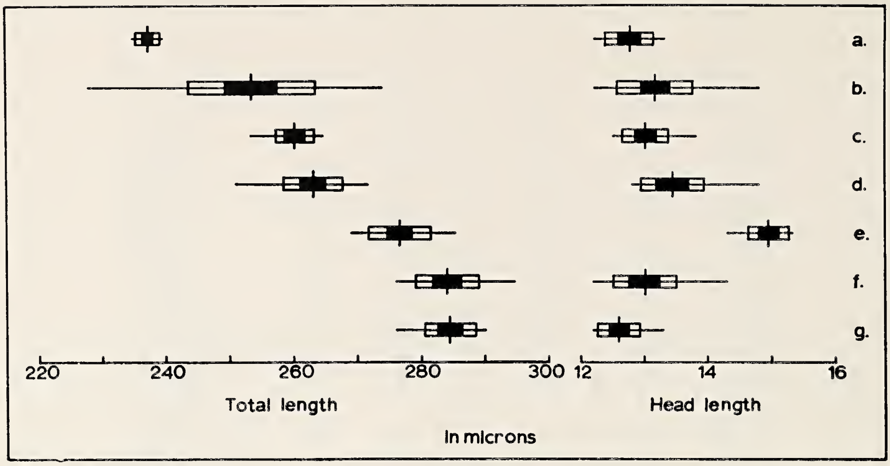

Fig. 4. Variation of sperm among wood warblers of the genus *Dendroica*.

a—D. discolor
b—D. dominica
c—D. caerulescens
d—D. cerulea
e—D. castanea
f—D. coronata
g—D. fusca

Diagrams *a–g* represent measurements of total length and head length of the sperm of a single bird, with 20 sperm measured for each. The observed range is indicated by the horizontal line; a vertical line marks the mean; the rectangle shows 1 standard deviation, with solid black indicating 2 standard errors, on each side of mean.

winged Blackbird, *Agelaius phoeniceus*, are compared (Fig. 5). Statistics for the combined sample are as follows: range, 12.8–15.8 microns; mean, 14.2; standard deviation, 0.64; coefficient of variation, 4.6 percent. The coefficients of variation for the 10 individuals range from 2.8 to 4.6 percent. Of the 10 individual samples, 6 show overlap within 1 standard deviation and all within 2.

No geographic variation is apparent within the samples taken from Maine to Florida. Three subspecies are included (*A. p. phoeniceus, A. p. mearnsi, A. p. floridanus*), but no subspecific distinction is demonstrable. Although morphological differences exist between strains of the laboratory mouse (Braden, 1959), subspecific differences in avian sperm remain unproven.

IMPLICATIONS

Intriguing glimpses of the possible implications of this study are already apparent. The 25 families of the passerines examined thus far seem to indicate what possibly may be an evolutionary trend within that order. The sperm of the two suborders examined, Tyranni and Passeres, are separable. There are apparently no spiral head membranes or helical tail membranes among the Tyranni. The ratio between the head length and the tail length of Tyranni is conspicuously lower (1.3–3) than in all the Passeres examined (5.5–22) except the Corvidae and Laniidae (2.2–3). Among the Dendrocolaptidae, Furnariidae, and Formicariidae, placed in the superfamily Furnari-

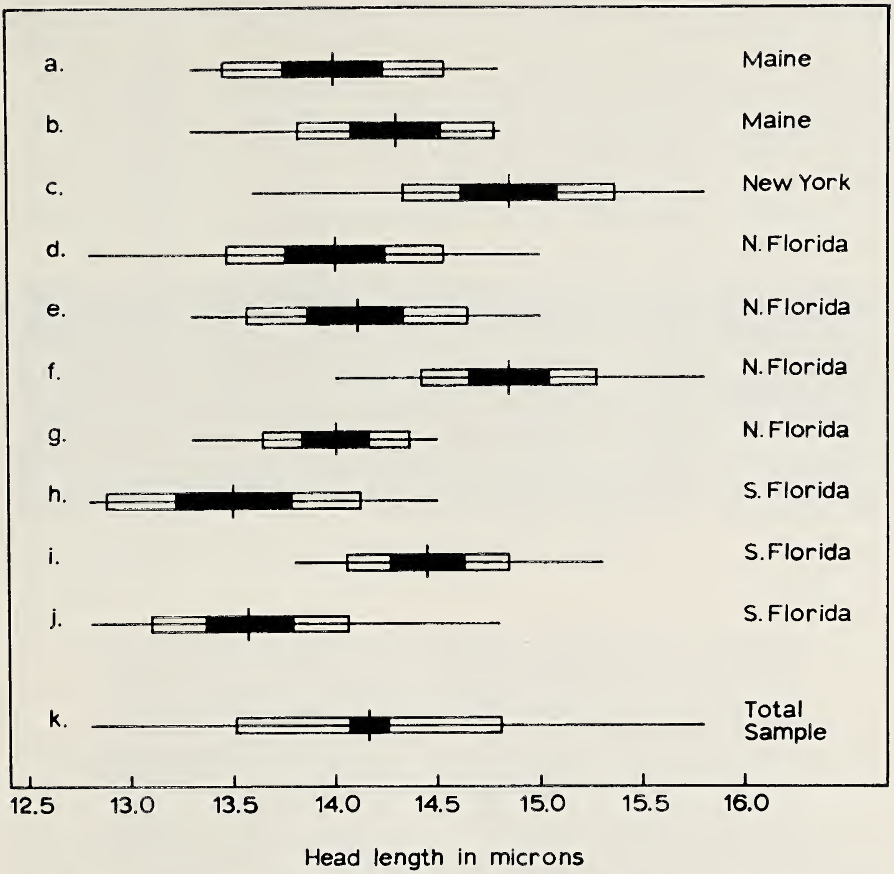

Fig. 5. Comparative head lengths of sperm of *Agelaius phoeniceus*. *a–f*, *A. p. phoeniceus*; *g–i*, *A. p. mearnsi*; *j*, *A. p. floridanus*. Diagrams *a–j* each represent a single bird, with 20 sperm measured for each. Diagram *k* represents the total for all the specimens. The observed ranges are indicated by the horizontal lines; vertical lines mark the mean; rectangles show 1 standard deviation, with solid black indicating 2 standard errors, on each side of mean.

oidea by Wetmore (1960), the first two families have sperm that describe a single revolution, whereas the Formicariidae resemble the superfamily Tyrannoidea, in which the sperm are highly coiled.

Among the families of the suborder Passeres thus far examined, only the Corvidae and Laniidae lack the helical filament so conspicuous among the remainder of the group. In addition, the sperm of both these families are very short in contrast to the extreme elongation that occurs among the higher passerines. Preliminary examination seems to indicate an evolutionary trend toward spiralization of the head, elongation of the tail, and development and elongation of a helical membrane around the tail.

The significance of the spiralization of the head warrants further investi-

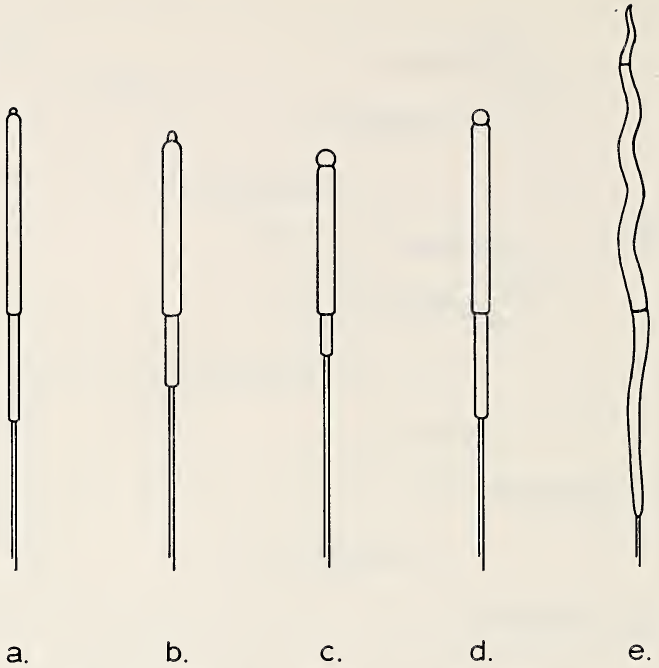

Fig. 6. Variation of sperm among the Charadriiformes.

a—Alcidae, *Fratercula arctica*
b—Laridae, *Gelochelidon nilotica*
c—Recurvirostridae, *Himantopus mexicanus*
d—Charadriidae, *Charadrius wilsonius*
e—Scolopacidae, *Actitus macularia*

gation, especially since it appears to have developed more than once, as will be mentioned later. Its function is unknown, but it would certainly seem to intensify the rotary forward motion of the spermatozoan that has been demonstrated in a number of animals (Rothschild, 1953).

Electron microscope studies of the helical tail membrane (Masuda, 1958; Yasuzumi, 1956) indicate a fibrous character similar to the mid-piece mitochondria. Its function is unknown, but it may be instrumental in energy transfer to distal portions of the axial filament, comparable to Columbiform

Fig. 7. Gull-billed Tern (*Gelochelidon nilotica*). Phase-contrast. Note button-like acrosome and mid-piece of smaller diameter than nucleus.

sperm, also greatly elongated, in which the mid-piece is extended far down the tail.

The simplicity and small size of the nonpasserine sperm require more critical examination. However, an interesting comparison has been observed among the Charadriiformes. The underlying feature of this order is apparently a cylindrical shape with a mid-piece of slightly smaller diameter. Representatives of four families (Recurvirostridae, Charadriidae, Laridae, Alcidae) indicate only minor variations of this pattern, but specimens of the Scolopacidae exhibit a remarkable contrast. In this instance (Fig. 6), the spermatozoan has an elongate, spiral form very reminiscent of the passerines. This shape has been observed by the author in *Actitis* and *Catoptrophorus* and has been illustrated by Retzius (1909) in *Tringa*, *Totanus*, and *Scolopax*. If the evidence suggested by the passerines is indicative of spiralization being a recent evolutionary trend, this second occurrence may well be an example of convergence and may perhaps indicate that the Scolopacidae are of a more recent origin than the remainder of the Charadriiformes.

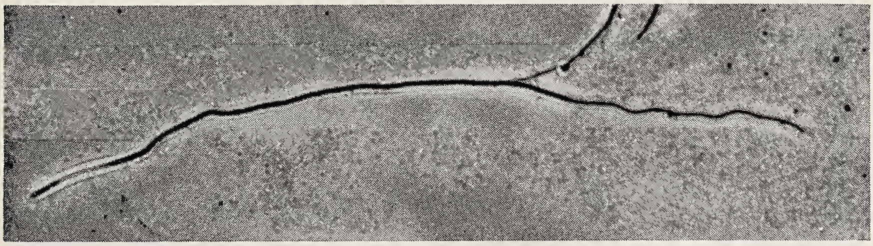

Fig. 8. Short-billed Pigeon (*Columba nigrirostris*). Phase-contrast. Mid-piece extends two-thirds of tail length.

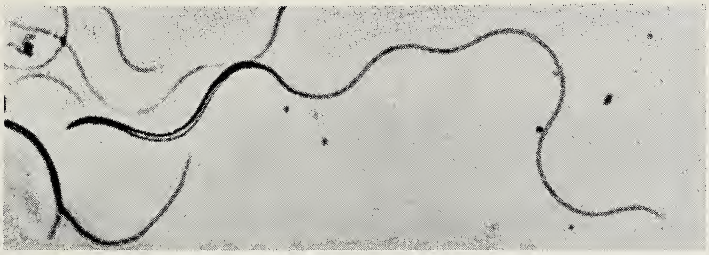

Fig. 9. Long-tailed Woodcreeper (*Deconychura typica*). Phase-contrast. Note helical head and mid-piece, and low tail: head length ratio.

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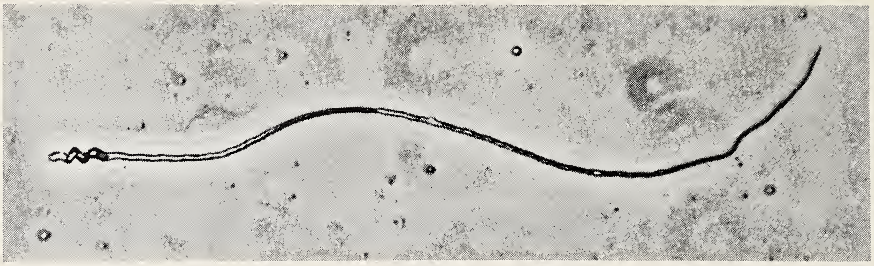

Fig. 10. Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Phase-contrast. Note large tail: head length ratio. Helical tail membrane extends three-fourths of tail length.

Fig. 11. Seaside Sparrow (*Ammospiza maritima*). Electron micrograph. Head and mid-piece, illustrating spiral head membrane.

Fig. 12. Clay-colored Robin (*Turdus grayi*). Electron micrograph. Note short, narrow head membrane and wide helical tail membrane.

for numerous suggestions concerning techniques and for the use of optical equipment. The extent of the present collection has been made possible only through the cooperation of Charles E. Huntington of the Bowdoin Scientific Station and of Paul Slud. This research has been supported by grants-in-aid from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and from the Society of the Sigma Xi and RESA Research Fund.

SUMMARY

Avian sperm exhibit considerable variation from the simple basic design of a cylindrical head and mid-piece that are propelled by a filamentous tail. The magnitude of difference corresponds to the magnitude of the taxon

involved, and is based upon the occurrence, shape, and relative size of the acrosome, head, mid-piece, tail, and helical tail membrane. Differentiating morphology can be extended to the specific level.

Preliminary investigation indicates that the comparative morphology may be of phylogenetic value. Within the order Passeriformes there is apparently an evolutionary trend toward spiralization, elongation of the tail, and development and elongation of a helical tail membrane around the tail. The sperm of the Corvidae and Laniidae are relatively simple and quite distinct from that of other songbirds. Spiralization of the head, the outstanding character of the Passeriformes, has thus far been found in only one additional order. The sperm of the Scolopacidae exhibit a spiral head in contrast to the cylindrical form of four other families of the Charadriiformes examined. This second occurrence may well be an example of convergence and perhaps indicate that the Scolopacidae are of more recent origin than the remainder of the Charadriiformes.

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APPENDIX

List of orders and families with number of genera and species examined indicated.

- Procellariiformes
  - Hydrobatidae (1 gen., 1 sp.)
- Ciconiiformes
  - Ardeidae (2 gen., 2 spp.)
- Anseriformes
  - Anatidae (1 gen., 1 sp.)
- Falconiformes
  - Accipitridae (1 gen., 1 sp.)
- Galliformes
  - Tetraonidae (1 gen., 1 sp.)
  - Phasianidae (1 gen., 1 sp.)
- Gruiformes
  - Rallidae (1 gen., 1 sp.)
- Charadriiformes
  - Charadriidae (1 gen., 1 sp.)
  - Scolopacidae (2 gen., 2 spp.)
  - Recurvirostridae (1 gen., 1 sp.)
  - Laridae (3 gen., 7 spp.)
  - Rynchopidae (1 gen., 1 sp.)
  - Alcidae (1 gen., 1 sp.)
- Columbiformes
  - Columbidae (5 gen., 6 spp.)
- Cuculiformes
  - Cuculidae (1 gen., 1 sp.)
- Strigiformes
  - Strigidae (1 gen., 1 sp.)
- Caprimulgiformes
  - Caprimulgidae (1 gen., 1 sp.)
- Apodiformes
  - Apodidae (1 gen., 1 sp.)
  - Trochilidae (5 gen., 5 spp.)
- Trogoniformes
  - Trogonidae (1 gen., 1 sp.)
- Piciformes
  - Picidae (1 gen., 1 sp.)
  - Ramphastidae (1 gen., 1 sp.)
- Passeriformes
  - Suborder Tyranni
    - Dendrocolaptidae (2 gen., 3 spp.)
    - Furnariidae (1 gen., 1 sp.)
    - Formicariidae (2 gen., 2 spp.)
    - Cotingidae (4 gen., 4 spp.)
    - Pipridae (2 gen., 3 spp.)
    - Tyrannidae (12 gen., 14 spp.)
  - Suborder Passeres
    - Alaudidae (1 gen., 1 sp.)
    - Hirundinidae (4 gen., 4 spp.)
    - Corvidae (2 gen., 2 spp.)
    - Paridae (1 gen., 4 spp.)
    - Sittidae (1 gen., 2 spp.)
    - Troglodytidae (2 gen., 2 spp.)
    - Mimidae (3 gen., 3 spp.)
    - Turdidae (3 gen., 7 spp.)
    - Sylviidae (2 gen., 2 spp.)
    - Bombycillidae (1 gen., 1 sp.)
    - Laniidae (1 gen., 1 sp.)
    - Sturnidae (1 gen., 1 sp.)
    - Vireonidae (2 gen., 4 spp.)
    - Coerebidae (1 gen., 1 sp.)
    - Parulidae (13 gen., 27 spp.)
    - Ploceidae (1 gen., 1 sp.)
    - Icteridae (8 gen., 8 spp.)
    - Thraupidae (7 gen., 8 spp.)
    - Fringillidae (17 gen., 23 spp.)

Immunological Distances and Phylogenetic Relationships in Birds

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Erythrocyte antigens are conservative characters at a high systematic level, as we sometimes find common antigens even between species belonging to different orders. In addition, there is a noteworthy mass of data on their genetic determination, with analyses made not only on mammals but also on many species of birds. An ample bibliography on the subject may be found in the summarizing works of Irwin (1951), Dujarric de la Riviere and Eyquem (1953), and Mainardi (1961). From the combination of these studies, it is clear that the genetic rule for erythrocyte antigens is that each antigenic property is determined by a gene. The exceptions are very rare. A particularly interesting one is the so-called "hybrid antigen," which is found in some hybrids (Miller, 1956), and it is very probably determined by the interaction of several genes coming from the two parental forms.

On the basis of the above rule, that is, one gene to one antigen, by analyzing the sets of kindred species it may be affirmed that from the ratio between common antigens and specific antigens one may obtain, regarding the portion of the genotype that determines erythrocyte antigens, a clear idea of the ratio between common genes and specific genes.

The way in which the antigenic sets vary in the course of speciation has been very carefully studied by Irwin and his coworkers in the genera *Columba* and *Streptopelia*, and can be clearly seen in their latest publications (Stimpfling and Irwin, 1960*a*, 1960*b*; Irwin and Miller, 1961).

In view of this, it seems logical to consider the erythrocyte antigens common to two species as substances derived from a common progenitor, and those (specific) antigens differing in the two species as a sign of the evolutionary progress covered. Consequently, the larger the number of common antigens, the closer to one another, in a phylogenetic sense, will the two species be.

An index of the relations between common antigens and specific antigens between two species may be obtained from the titers with homologous and heterologous red cells, using immune sera against the red cells of the two species. Utilizing the ratios between the titers with homologous and heterologous cells with sera against the two species under examination, a formula was obtained (Mainardi, 1957) which gives values that increase with the diminution of immunological affinity (i.e. the higher the value, the fewer the antigens held in common). Hence, this may be used as an index to the degree of relationship between the species examined. The formula, named "immunological distance," is as follows:

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$$I.D. = \frac{1}{\sqrt{\frac{Oa}{Ea} \cdot \frac{Ob}{Eb}}}$$

where Oa and Ob are the titers with homologous cells and Ea and Eb the titers with heterologous cells, using sera against the species a and b, respectively.

This value gives an indication of the sum total of a series of characters, each of identical genetic weight. It can therefore be regarded as an ideal polygenic character, since the genes that determine it are all appreciable and distributed over nearly all the chromosomes, and since it has no environmental variability. Besides, in contrast with other characters, it does not seem to run the risk of false interpretation due to evolutionary convergence.

So taxonomic weight of immunological distances appears to be appreciable, understood in the sense of defining phylogenetic parentage, because of the large amount of genetic information which it affords.

In addition, if, by studying the evolution in various species of one single well-defined protein, one can in certain cases expect to have good information about the evolutionary stages and the degrees of parentage of the species, there remains the risk, which is anything but a slight one, of running into a period of evolutionary stasis; this interests only the protein in question, while the rest of the organism has gone on evolving, giving origin to new forms, of which it will therefore be impossible to find out the reciprocal degrees of parentage on the basis of this protein alone. On the contrary it is clear that this danger is removed by immunological distances because of their accumulative and summarizing character.

Several avian groups have been studied by the method of immunological distances. Here, two exemplifying problems are examined: the relationships in the order Galliformes, and the relationships of flamingos with Ciconiiformes and Anseriformes.

RELATIONSHIPS IN THE ORDER GALLIFORMES

According to the classification of Wetmore (1960), 6 species of Phasianidae, 1 species of Numididae, 1 species of Meleagrididae (Mainardi, 1958, 1959*a*, 1959*b*, 1960), 4 species of Cracidae, and 1 species of Megapodiidae (Mainardi and Taibel, 1962*a*) have been studied (see Table 1). In Fig. 1 the immunological distances among *Chrysolophus pictus*, *Coturnix coturnix*, *Gallus domesticus*, *Gennaeus nychtemerus*, *Pavo cristatus*, *Phasianus colchicus*, *Numida meleagris*, and *Meleagris gallopavo* are used to construct immunological charts (left) which suggest phylogenetic relationships among the species (right). According to this analysis, *Numida* and *Meleagris* are to be considered true phasianids, having with the other phasianids nearly the same percentage of common antigens as that which the other phasianids have among themselves. *Meleagris* is closely related to pheasants (*Phasianus*,

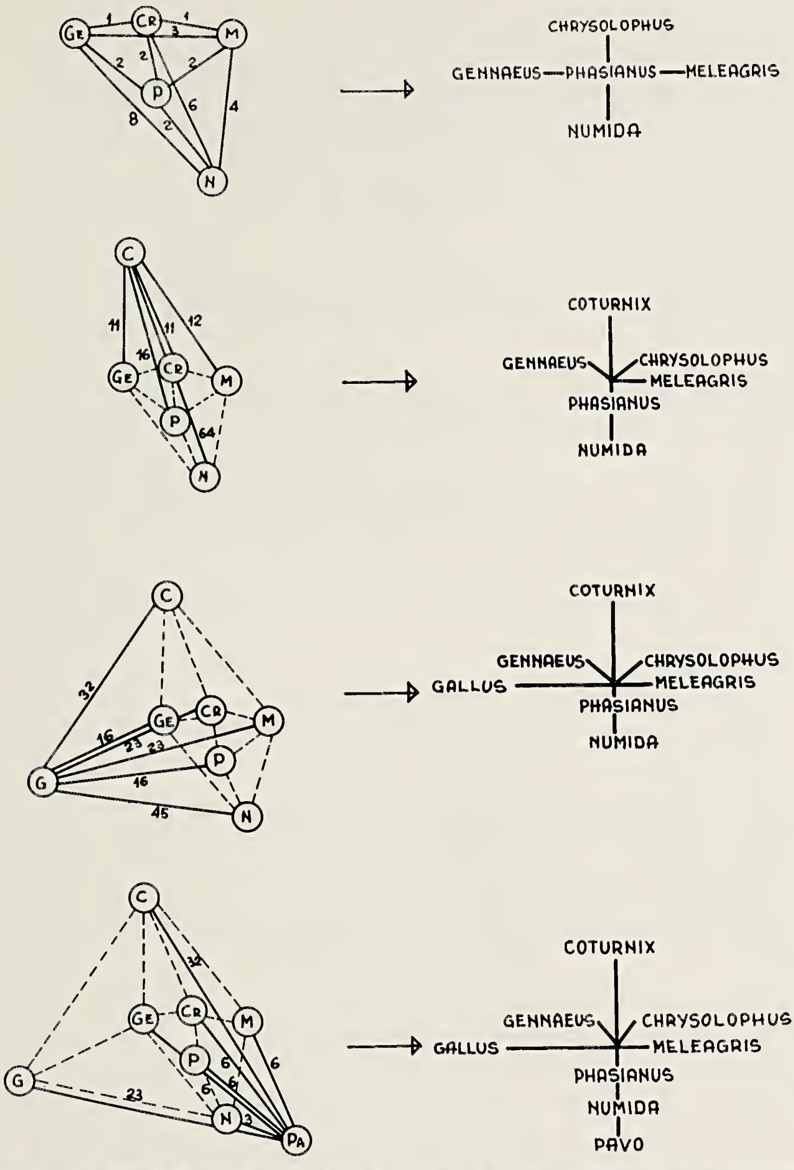


Fig. 1. On the left are immunological maps of some phasianid genera (including *Numida* and *Meleagris*). On the right are the phylogenetic relationships that spring from these maps (from Mainardi and Taibel, 1962*a*, slightly modified).

Gennaeus, Chrysolophus). *Pavo* is more closely related to *Numida* than to any other phasianid. *Gallus* and *Coturnix,* although well differentiated by many specific antigens, show the greatest affinity to pheasants.

Four species of four different genera of Cracidae have been studied: *Crax globicera*, *Mitu mitu*, *Penelope purpurascens*, and *Pipile cumanensis*. These genera appeared to be very closely related to each other (Table 1 and Fig.

Table 1.—Titers Obtained Using Antigens from, and Antibodies against, Representative Genera of Galliform Birds[a]

Red Cells	Anti-sera											
	Pavo	*Numida*	*Gallus*	*Phasianus*	*Gennaeus*	*Chrysolophus*	*Meleagris*	*Coturnix*	*Crax*	*Mitu*	*Penelope*	*Pipile*
Pavo	1/20,480	1/2,560	1/640	1/1,280	1/640	1/640	1/1,280	1/1,280	1/320	1/640	1/320	1/2,560
Numida	1/5,120	1/5,120	1/80	1/1,280	1/160	1/320	1/1,280	1/1,280	1/1,280	1/1,280	1/640	1/2,560
Gallus	1/80	1/40	1/1,280	1/80	1/40	1/40	1/640	1/40	1/10	1/80	1/20	1/20
Phasianus	1/640	1/1,280	1/80	1/1,280	1/640	1/640	1/1,280	1/320	1/320	1/1,280	1/80	1/1,280
Gennaeus	1/640	1/320	1/320	1/320	1/640	1/320	1/640	1/320	1/80	1/2,560	1/160	1/1,280
Chrysolophus	1/640	1/320	1/40	1/320	1/640	1/640	1/640	1/640	1/160	1/320	1/160	1/640
Meleagris	1/640	1/320	1/40	1/320	1/160	1/640	1/1,280	1/320	1/320	1/320	1/160	1/640
Coturnix	1/320	1/20	1/640	1/320	1/320	1/640	1/80	1/20,480	1/640	1/640	1/640	1/640
Crax	1/320	1/320	1/40	1/160	1/80	1/320	1/640	1/320	1/10,240	1/10,240	1/1,280	1/10,240
Mitu	1/320	1/640	1/80	1/160	1/80	1/320	1/320	1/320	1/10,240	1/10,240	1/1,280	1/5,120
Penelope	1/320	1/320	1/80	1/160	1/80	1/160	1/320	1/320	1/10,240	1/10,240	1/1,280	1/10,240
Pipile	1/320	1/320	1/40	1/160	1/80	1/80	1/320	1/320	1/10,240	1/10,240	1/1,280	1/10,240
Alectura	1/320	1/320	1/80	1/160	1/80	1/320	1/320	1/320	1/320	1/1,280	1/320	1/640

[a] To avoid individual differences due to blood groups modifying the results because of variations of the titers, mixtures of red cells of various individuals have been used in the preparations of the anti-sera and in titrations. This appeared to be indispensable in *Gallus*.

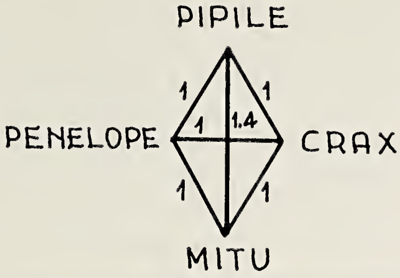


Fig. 2. Immunological map of four genera of cracids (from Mainardi and Taibel, 1962*a*).

2). The strict relationship between *Crax* and *Mitu* is confirmed by data on hybridization (in fact, the hybrids *Crax* × *Mitu* were completely fertile according to Taibel, 1961*a*, 1961*b*).

Immunological distances between cracids and phasianids (Table 2) suggest that these two groups are closely related. Among the phasianids, the nearest to the cracids are the guinea-fowls and the pheasants. Fig. 3 shows the phylogenetic relationships between cracids and phasianids, as suggested by this analysis.

The rather strict affinity between these two groups was first noted by Sibley (1960) in his electrophoretic study of egg-white proteins (other evidence was also cited by him). Believing in the positive reality of the supposed hybrid between *Numida meleagris* and *Penelope superciliaris* described by Ruschi and Amadon in 1959, Sibley also suggested placing the cracids as a subfamily (Cracinae) of the Phasianidae. (The presumed hybrid has since died and been presented as a specimen to the American Museum of Natural History. Dr. Amadon now writes me that, although no exhaustive study has been made, he is very much afraid—with specimen in hand—that it is only a *Numida* × *Gallus* hybrid.)

The nonexistence of hybrids produced under controlled conditions between cracids and phasianids, and the knowledge of the immunological relationships that these two groups have with megapodes suggested to us (Mainardi and Taibel, 1962*b*) the natural existence of the three families Cracidae, Mega-

TABLE 2.—IMMUNOLOGICAL DISTANCES BETWEEN CRACIDS AND PHASIANIDS

	Mitu (*a*)	*Crax* (*b*)	*Pipile* (*c*)	*Penelope* (*d*)	$\frac{a+b+c+d}{4}$
Numida	8	11	8	6	8.25
Chrysolophus	8	11	8	8	8.75
Meleagris	11	11	8	6	9.00
Phasianus	8	16	8	11	10.75
Gennaeus	6	32	8	8	13.50
Coturnix	32	32	32	11	26.75
Pavo	32	45	16	16	27.25
Gallus	45	181	128	32	96.50

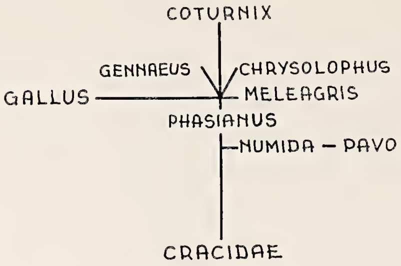


Fig. 3. Phylogenetic relationships between cracids and phasianids (including *Numida* and *Meleagris*), as suggested by immunological distances.

podiidae, and Phasianidae, and the suppression of the two superfamilies Cracoidea and Phasianoidea. In fact, if we consider the titers (Table 1) with the erythrocyte of the megapode *Alectura lathami* and the immune sera against the erythrocytes of cracids and phasianids (unfortunately at present it has not been possible to prepare any immune serum against the red cells of a megapode), we see clearly that *Alectura* is approximately as distant from the cracids as are phasianids, and that it is approximately as distant from phasianids (including *Numida* and *Meleagris*) as are cracids. Immunological data suggest that the Cracidae, Phasianidae, and Megapodiidae are rather strictly related, and that they are nearly phylogenetically equidistant, that is, that these three groups probably evolved at about the same time from a common stock.

A combining of immunological results with the other available data made it possible to propose a phylogeny of galliform birds (Mainardi and Taibel, 1962*b*), as shown in Fig. 4.

Summarizing, the most important information from which this phylogeny has been constructed is as follows. There is some evidence from morphological (Mainardi and Taibel, 1962*b*) and paleontological (Tordoff and Mac-

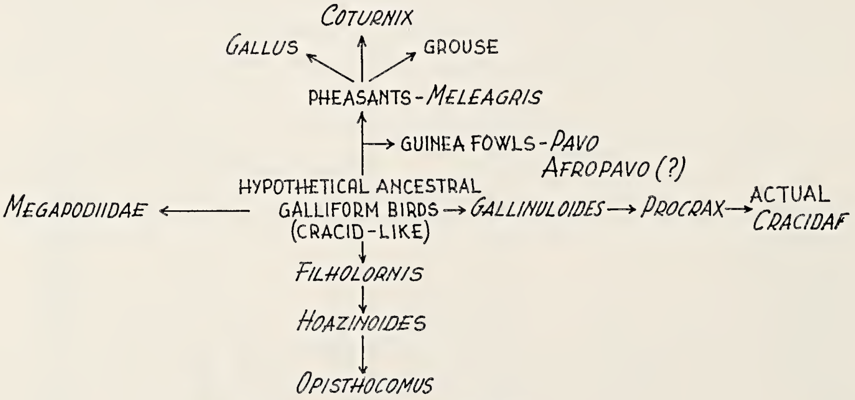


Fig. 4. Phylogeny of galliform birds.

donald, 1957) data that all the actual groups of gallinaceous birds have descended from an ancestral stock of cracid-like birds. From this primitive group, four independent branches radiated: Cracidae, Opisthocomidae, Megapodiidae, and Phasianidae.

The actual Cracidae are the direct descendents of the primitive cracid-like galliforms, important intermediate steps being *Gallinuloides* of the Eocene and *Procrax* of the Oligocene (Tordoff and Macdonald, 1957).

In the evolutionary pathway from the hypothetical, primitive, cracid-like birds to the actual *Opisthocomus*, we find as intermediate forms the fossils *Filholornis* of the Eocene (Howard, 1950) and *Hoazinoides* of the Miocene (Miller, 1953).

A vestigial egg tooth in embryos of megapodes and vestiges of down feathers in the newly hatched birds clearly suggest that megapodes evolved from normal gallinaceous birds (Clark, 1960). Immunological data on red-cell antigens, and the sharing of primitive characters with the fossil cracids *Gallinuloides* and *Procrax* support the idea that the Megapodiidae also derived from the hypothetical group of cracid-like birds.

Of the phasianids, the nearest to cracids are guinea-fowls, which share with actual cracids many red-cell antigens, and with *Gallinuloides* and *Procrax* several primitive osteological characters. Closely related to guinea-fowls are peacocks (*Pavo*). In fact, these two groups share many erythrocyte antigens, hybridize easily (Gray, 1958), have quite similar karyotypes (Yamashina, 1952), and have a centrifugal molt of the rectrices (Ghigi, 1958). *Afropavo congensis* can tentatively be placed near the guinea-fowls and peacocks, as a species rather related to the cracids, because of several morphological (Mainardi and Taibel, 1962*b*) and physio-ethological (Taibel, 1961*c*) characters that suggest this relationship. Related to guinea-fowls and to cracids are pheasants (*Phasianus*, *Gennaeus*, *Chrysolophus*, etc.); this relationship is particularly supported by the large number of red-cell antigens common to these groups. Pheasants are placed very near turkeys, because: (1) their karyotypes are very similar (Yamashina and Udagawa, 1954); (2) they exhibit the same electrophoretic patterns of egg-white proteins (Sibley, 1960); (3) they have many red-cell antigens in common; (4) they hybridize (Asmundson and Lorenz, 1957); and, (5) they show many morphological similarities (Verheyen, 1956; Hudson et al., 1959).

Other groups have been derived from the pheasants. The grouse are among these, as suggested by karyological data (Yamashina, 1950), egg-white protein analysis (Sibley, 1960), and data on hybridization between several genera of grouse and *Phasianus* (Sibley, 1957, 1960). Analysis of red-cell antigens also suggests *Coturnix* as another such group. *Gallus*, too, appears to have evolved from pheasants. This genus differs from pheasants in having many specific red-cell antigens, but pheasants are nevertheless immunologically nearest to chickens. Evolution of *Gallus* from the primordial *Phasianus* stem was also suggested on the basis of hybridization results ob-

TABLE 3.—TITERS OBTAINED USING ANTIGENS FROM, AND ANTIBODIES AGAINST, REPRESENTATIVE GENERA OF WATERFOWL, FLAMINGOS, AND CICONIIFORM BIRDS

Anti-sera	Red Cells						
	Anas	*Cairina*	*Anser*	*Ciconia*	*Ardea*	*Threskiornis*	*Phoenicopt.*
Anseriformes	1/5,120	1/2,560	1/1,280	1/320	1/80	1/320	1/160
Ciconia	1/160	1/80	1/160	1/2,560	1/640	1/2,560	1/160
Ardea	1/20	1/20	1/40	1/160	1/320	1/160	1/40
Threskiornis	1/80	1/80	1/80	1/320	1/1,280	1/1,280	1/80
Phoenicopterus	1/40	1/80	1/80	1/40	1/80	1/80	1/640

tained by Taibel (1949) and Sandnes (1957). In regard to genera discussed herein, hybrids of both sexes between *Gallus* and *Phasianus*, *Gallus* and *Gennaeus*, and *Gallus* and *Chrysolophus* are sterile, while hybrid males of *Phasianus* × *Chrysolophus*, *Phasianus* × *Gennaeus*, and *Gennaeus* × *Chrysolophus* are fertile (Taibel, 1949). Differentiation of *Gallus* from pheasants studied here is also shown by analysis of the chromosome sets. Karyotypes of *Phasianus*, *Gennaeus*, and *Chrysolophus* have been found to be very similar, while *Gallus* differs from these in chromosome morphology (Sandnes, 1954; Yamashina and Udagawa, 1954).

RELATIONSHIPS OF FLAMINGOS WITH ANSERIFORMES AND CICONIIFORMES

Flamingos are placed by taxonomists either in a separate order, the Phoenicopteriformes (e.g. by Storer, 1960), or in the orders Anseriformes (e.g. by Delacour, 1961) or Ciconiiformes (e.g. by Wetmore, 1960). Actually, although flamingos differ from these groups in a number of characters, they share several characters with both anseriform and ciconiiform birds (see Mainardi, 1962).

The red-cell antigens of the Greater Flamingo (*Phoenicopterus ruber*) were studied (Mainardi, 1962) in comparison with those of species representative

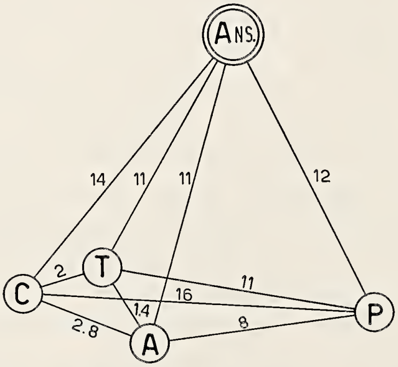


Fig. 5. Diagram showing the immunological distances between the three species of waterfowl (*Ans.*), *Phoenicopterus* (*P*), *Ardea* (*A*), *Ciconia* (*C*), and *Threskiornis* (*T*) (from Mainardi, 1962).

of Anseriformes (*Anas platyrhynchos, Cairina moschata, Anser anser*) and Ciconiiformes (*Ciconia ciconia, Ardea cinerea, Threskiornis aethiopica*).

Immune sera against the red-cell antigens of the ciconiiform birds and of the flamingo were normally prepared, that is, independently of each other; for studying the relationships with the Anseriformes, however, a polyvalent anti-serum against the red cells of the three waterfowl species was used. This anti-serum had been prepared for a previous experiment in which the relationships among these three species were studied (Mainardi, 1959*c*). The three species appeared to be closely related. In the actual study, for calculating the immunological distances between the three waterfowl and the other species, the mean values of the titers of the three waterfowl species were used. Titers are given in Table 3, and the diagram obtained from immunological distances is presented in Fig. 5.

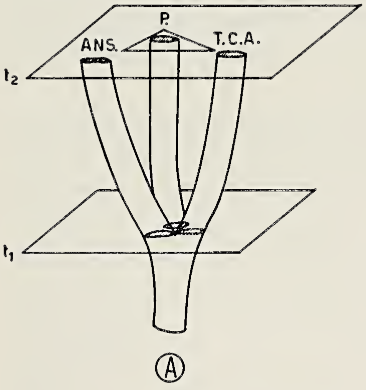
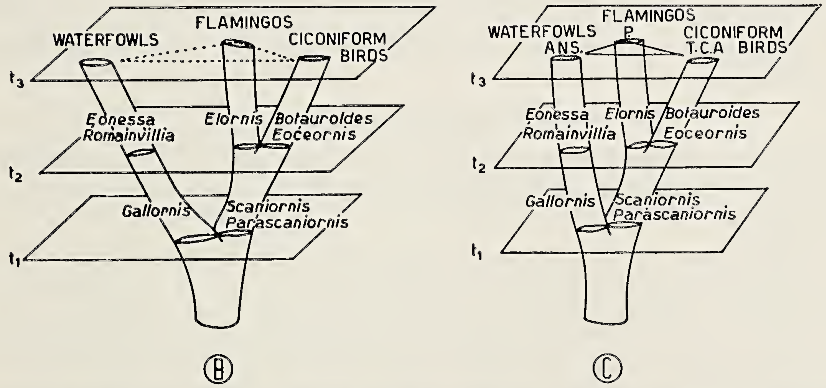


Fig. 6. (*A*): Phylogenetic tree of Anseriformes, Ciconiiformes, and flamingos, according to immunological data; (*B*): The same phylogenetic tree according to paleontological data; (*C*): The same phylogenetic tree obtained by combining the suggestions of both immunological and paleontological data (see text).



Immunological data show mainly that flamingos are related both to Anseriformes and to Ciconiiformes, proving that their resemblance to these two groups is not due to convergence. The same data show that Anseriformes and Ciconiiformes are related to each other. As these three groups have the same proportion of common antigens, the most likely hypothesis concerning their evolution is that, at a certain time t_1 (see Fig. 6*a*), they evolved roughly contemporaneously from a common stem. This hypothesis is not supported by paleontological data. The most ancient records of these groups go back to the Cretaceous. Two species, *Scaniornis lundgreni* and *Parascaniornis stensiöi* (Scaniornithidae), which, according to Howard (1950), show relationships to both herons and flamingos, belong to the Cretaceous, and so does *Gallornis*, a waterfowl which stands between ducks and swans. According to Howard, it was not until Eocene time that ciconiiforms were separable from flamingos. The paleontological data suggest a phylogenetic tree for these birds (see Fig. 6*b*), with first (t_1) the waterfowl branch diverging from the common stem, then later (t_2) the two branches of flamingos and ciconiiforms diverging.

When one combines the suggestions from both immunological and paleontological data, the most likely hypothesis on the evolution of these birds is that waterfowl emerged (t_1, Fig. 6*c*) from the common stem before the bifurcation (t_2, Fig. 6*c*) of the ciconiiforms and flamingos, but that the velocities of differentiation among these three groups were not equal. The result is that waterfowl, ciconiiforms, and flamingos are at the present equidistantly related (t_3), as suggested by the percentages of common genes among them. This seems rather likely from a general viewpoint, if we consider the frequency with which examples showing periods of evolutionary stasis are encountered in animal evolution. This indicates that factors other than the length of time since divergence are important in defining degrees of relationship.

CONCLUDING REMARKS

Few general remarks can be made, because the method of immunological distances is at present not sufficiently mature and needs many further experiments.

Theoretically, the phylogenetic weight of immunological distances comes from the two following points: (a) that they concern, for a portion of the genotype, the ratio between common and specific genes (this being, at any taxonomic level, the unique direct measure of relationship); (b) that they completely avoid the risk of false interpretations due to evolutionary convergence.

Technically, the method is probably far from perfect. Nevertheless, it is clearly evident from studies so far completed that study of the relations between common and specific red-cell antigens can offer important contributions to problems of phylogeny. In fact, the agreement between results drawn from investigations of immunological distances and from other data normally considered of great taxonomic value leads to this conclusion.

SUMMARY

On the basis of their genetic determination, the red-cell antigens common to two species can be considered as substances derived directly from a common progenitor and specific antigens as a track of past evolutionary history.

Consequently, the larger the number of common antigens, the closer, in a phylogenetic sense, will the two species be.

Utilizing the ratios between the titers with homologous and heterologous cells with the sera against the species under examination, a formula was obtained which gives values that increase with diminution of immunological affinity (that is, of common antigens) and which consequently may be utilized as an index of the degree of parentage between the species examined.

The relationship among the families of gallinaceous birds, and the relationships of flamingos with Ciconiiformes and Anseriformes have been studied.

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Verhalten der Straussartigen Vögel und Monophylie der Ratitae

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Seit Merrem 1813 Strauss, Nandu, Kasuar, und Emu (der Kiwi war noch unbekannt) von den Hühnervögeln und deren Verwandtschaft loslöste und als Ratitae zusammenfasste, wird über diese systematische Einheit gearbeitet, nun fast 150 Jahre lang. Trotzdem hat die Ratitenforschung, die nur 5 nicht ausgestorbene Gattungen und 10 Arten von Vögeln betrifft, noch zu keinem allgemein angenommenen Ergebnis geführt. Wir bemühen uns noch immer zu entscheiden, ob die Natur der Straussartigen am besten mit dem Begriff der Monophylie (dazu neigt z.B. Hofer 1950, noch mehr 1955) oder der Polyphylie, mit Primitivität, Pseudoprimitivität, Spezialisation, Adaptation oder gar Paedogenese erfasst wird. Der extremste Polyphyletist (Verheyen, 1960*a*) hat bei der konsequenten Anwendung einer quantitierenden Methode typologische Beziehungen (ich würde sagen Analogien) nicht nur zwischen Rhea und Tinamidae, sondern auch zwischen seinen Struthiones und Otididae, zwischen Casuarii und Anhimidae und gar zwischen Apteryges und Sphenisciformes errechnet. Bei ihm stehen schliesslich (Verheyen, 1961) die Ratitae weit voneinander getrennt in zwei Superordines, bei Stresemann (1959) nebeneinander in 5, bei Wetmore (1960) nebeneinander in 6 Ordnungen. Soviel ich weiss, hat aber noch niemand die Untergruppen alphabetisch angeordnet oder gar in ein alphabetisches Gesamtsystem aller Vögel eingegliedert. Unter den Monophyletisten gibt es solche, die die Ratiten (manchmal mit Ausnahme der Apterygidae) von flugfähigen Vorfahren (Carinatae oder Protocarinatae) ableiten, wogegen andere sie direkt aus Reptilien entspringen lassen (zuletzt wohl Holmgren, 1955, und Glutz von Blotzheim, 1958).

ART DER ZU VERGLEICHENDEN SYSTEME

Meine Aufgabe ist es, nach dem bisher sehr lückenhaft bekannten Verhalten der Ratitae festzustellen, ob ihr Verhaltenssystem mit dem morphologisch-anatomisch-embryologisch-tiergeographisch erarbeiteten System zusammenfällt. Es gilt, das Verhaltenssystem als eins der vielen möglichen typologischen Systeme dem phylogenetischen System gegenüber zu stellen. Da dieses in wenigstens zwei Punkten (Rheae-Struthiones, Crypturi-Ratitae) unsicher ist, können wir das Ergebnis unseres Vergleichs mit Spannung erwarten. Selbstverständlich muss das phylogenetische oder das dafür gehaltene System bestätigt werden, sobald wir nur solche Verhaltungsweisen heranziehen, die unmittelbar auch aus Ergebnissen der vergleichenden Morphologie und Anatomie abzuleiten sind und daher nur Wiederholungen (mit anderen Worten) darstellen. Zum Beispiel weiss der Morphologe längst,

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dass die Flügel der Ratitae verkümmert, die Beine aber stark entwickelt sind. Die an diese und die meisten der von Gadow (1893) und Beddard (1898) zusammengestellten Körperstrukturen geknüpften Verhaltensweisen entfernen wir für den heutigen Zweck aus dem Verhaltenssystem, da sie den Anforderungen an ein neues, unabhängiges Hilfsmittel nicht erfüllen. Dadurch verlieren wir aber Homologien und geraten umso mehr in die Gefahr, unter den herangezogenen, restlichen Verhaltungsweisen analoge bzw. konvergente nicht zu erkennen, wovor Mayr (1958) und Hinde (1958) gewarnt haben. Wir benutzen möglichst Verhaltungsweisen, die andere Hilfswissenschaften der Ornithologie noch nicht "für das System verbraucht" haben, z.B. solche, die bei demselben (oder scheinbar demselben?) Körperbau verschieden sind.

VERGLEICHE

a) Die Methodik veranschauliche ich am besten an dem (zuletzt wohl nach Starck, 1955, und Oliver, 1955) zweifelsfrei zusammengehörigen Familienpaar Dinornithidae und Apterygidae. Von diesen sind die Apterygidae so weit aus der Entwicklungslinie der Ur-Moa-Kiwis und der übrigen Raritae abgewichen, dass sie als apomorph[1] (Hennig, 1950) bezeichnet werden müssen im Vergleich zu den ursprünglicheren, weniger differenzierten, darum als plesiomorph bezeichneten Moas. Dementsprechend zeichne ich die Stammbaumlinie der Moas weniger von der Senkrechten abweichend als die der Kiwis. Als apomorphes Verhalten (da auch ethologische Züge an die Holomorphe gebunden sind, wollen wir dieses Verhalten nicht neu als apobiont, sondern weiter als apomorph bezeichnen) möchte ich das schnüffelnde (und tastende) Suchen nach Bodentieren und anderer Nahrung auffassen und überhaupt die Aufnahme von Würmern und Insektenlarven als Nahrungsmittel (1 im Stammbaumschema, Abb. 1). Schnüffeln und Nahrungswahl sind aus der Anatomie nicht abzulesen, also wichtige Bestätigungen für die Abweichungen der Kiwis vom übrigen Neuseeland-Stamm der Ratitae. Dazu gehört auch das relativ grosse Ei (siehe Anhang) und vielleicht das Brüten in Erdhöhlen, obwohl man (nach einer Diskussionsbemerkung von R. A. Falla) weiss, dass wenigstens Anomalopteryx unter Felsüberhängen nistete (siehe Golson, 1957). Ich habe vergebens versucht, bei den Moas apomorphes Verhalten im Vergleich mit den Kiwis zu finden. Der völlige Verlust der Flügel ist ein solches, aber der Morphologie entnommenes Merkmal. Wir unterdrücken es hier; denn wir müssen uns auf das Verhalten be-

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[1] Die Aufgabelung einer systematischen Einheit ergibt in der Regel zwei neue Einheiten. Beim Vergleich dieser Schwestergruppen gebrauchen wir mit Hennig (1950, 1957) einige Bezeichnungen, die wir kurz definieren wollen: plesiomorph ist die Einheit, die der (verschwundenen) Muttereinheit am ähnlichsten ist, oder der Teil ihrer Merkmale, der den Merkmalen der Stammeinheit am ähnlichsten ist; apomorph dagegen die Einheit bzw. die Merkmale, die sich gegenüber der Stammeinheit stärker verändert haben; symplesiomorph sind Einheiten, die dieselben plesiomorphen Züge aufweisen; synapomorph die Einheiten, die dieselben apomorphen Züge aufweisen.

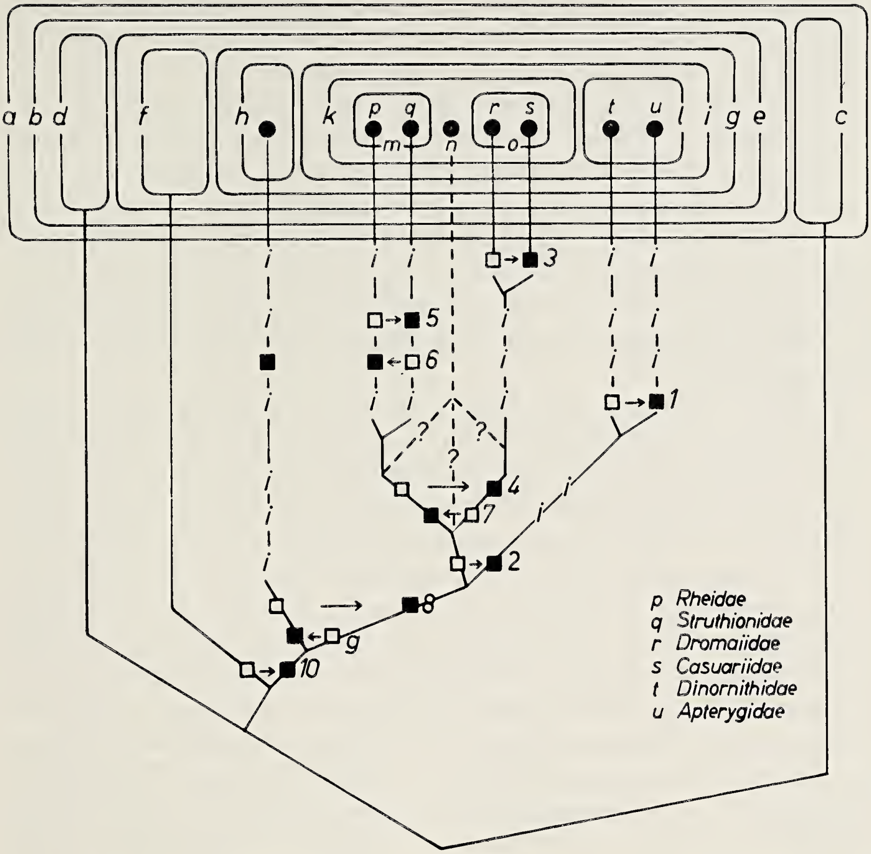

Abb. 1. Argumentationsschema zur Nachprüfung des phylogenetischen Systems der Ratitae mit Hilfe der Ethologie.

Weisse Kästchen: Ursprünglichere (plesiomorphe) Ausprägungsstufe eines Merkmals.
Schwarze Kästchen: Abgeleitetere (apomorphe) Ausprägungsstufe eines Merkmals.
i (im Verlauf der Stammbaumäste): indifferent für die Ausprägungsstufe des Merkmals.
Rechtecke oben: andersartige Wiederholung der Stammbaumdarstellung unten.

Dargestellt ist die Teilung von *a* (Aves) in *b* und *c* (2 Ordnungsgruppen), *b* in *d* und *e* (2 Ordnungsgruppen), *e* in *f* (Galli, Grues, Limicolae-Lari) und *g* (Palaeognathae), *g* in *h* (Crypturi) und *i* (Ratitae), *i* in *k* (Ratitae ausser Neuseeland-Familien) und *l* (= *t* und *u*), *k* in *m* (= *p* und *q*), *n* (Aepyornithidae) und *o* (= *r* und *s*). *p* bis *u* im Schema erläutert. 1–10 im Text erläutert.

schränken. Alle drei Kiwi-Arten verfügen über das obengenannte apomorphe Verhalten. Die daher synapomorph zu nennenden Apterygidae sind als monophyletisch aufzufassen (zur genaueren Begründung vergleiche Hennig, 1957), da die Symplesiomorphien der Moas dem vergleichsweise ursprünglicheren Zustand entsprechen, bei Nachbargruppen vorkommen und aus beiden Gründen nicht als Hinweise auf Monophylien dienen können.

Interessant sind auch übereinstimmende Verhaltensweisen beider Familien, besonders solche, die gegenüber im System benachbarten Stämmen als apomorph gelten müssen. Ich habe nur das Graben im Boden (2 im Stammbaumschema) gefunden, das wenigstens bei wurzelfressenden Moas wie bei allen Kiwis festzustellen ist, dagegen in der Ratiten-Reihe sonst nicht; ferner nach dem Diskussionsbeitrag von Falla (Golson, 1957) Brüten in Erdbezw. Felshöhlen und niedrige Eierzahl im Gelege (ein oder zwei Eier).

b) Bei dem Familienpaar Dromaiidae (1 Art) und Casuariidae (3 Arten) (wohl besser Dromaiinae und Casuariinae, siehe Meise, 1960) sind die Kasuare apomorph, da sie unverträglich sind, Früchte, Beeren und Samen (vor allem) fressen und wenige Eier legen (3 im Schema). Beiden gemein ist das Fehlen von Sandbädern (4 im Schema) (siehe Schneider, 1955), das hier als apomorph gelten muss, da es sich um Abkömmlinge von Graslandtieren handelt. (Diese Feststellung wäre wichtiger, wenn wir über das Baden der Moas etwas wüssten.)

c) Bei der Trennung der Rheidae (2 Arten) und Struthionidae (1 Art) ist das Ergebnis vergleichender Verhaltensforschung nicht sehr überzeugend, weil es in beiden Familien apomorphe Züge gibt. Bei den Struthionidae, die morphologisch eindeutig apomorph sind, finde ich als Verhaltenszug, der das unterstreicht, nur die Sprengung der Eischale durch besondere Nackenmuskeln der Jungen (5 im Schema) (Brinkmann und Haefelfinger, 1954), was aber als Anpassung an die Dicke der Eischale aufzufassen und stammesgeschichtlich kaum auszuwerten ist. Vielleicht könnte man die Aufnahme auch von sukkulenten Pflanzen und das Ansammeln von Nahrung im Rachen vor dem Schlucken auf die Waagschale der Apomorphien werfen. Andererseits verhalten sich Nandus spezialisierter in der völligen Übernahme von Nestbau und Brut sowie der Jungenfürsorge durch das Männchen (6 im Schema) (Steinbacher, 1951; Veselovsky, 1956). Beim Strauss, bei dem einseitige männliche Brutaktivität auch vorkommt (Schneider, 1949:235–236), ist das Männchen oder sind die Männchen meist beteiligt (Schreiner, 1895). Sollte das ein sekundäres Verhalten sein, so wären die Strausse auch in dieser Beziehung apomorph. Ferner verleitet der männliche Strauss (Sauer und Sauer, 1960; Kittenberger, 1959), was ich von keinem anderen Ratiten kenne. (Ich bezweifle aber, dass Kiwi, Emu und Kasuar draussen genügend beobachtet worden sind; das Verleiten wird daher hier nicht verwertet.) Das Nandu-Männchen nimmt zusätzlich fremde Junge in seine Vaterfamilie auf (Faust, 1961); das Straussen-Männchen jagt sie fort, was ich, wenn in der freien Natur üblich, für plesiomorph halte (6 im Stammbaumschema). Beiden Familien gemeinsame synapomorphe Verhaltensweisen habe ich nicht gefunden.

Hier muss ein Vergleich Crypturi-Rheidae-Struthionidae eingeschoben werden. Ich finde für die Ratitae nur dann ein apomorphes Merkmal, wenn ich, wie zum Beispiel beim sogenannten "Tanzen," wenigstens die Emus noch hinzunehme (Brinkmann und Haefelfinger, 1954); aber vielleicht genügt die Regulation des Wärmehaushalts durch Heben der Flügel und Sträuben der Federn (l.c.), um eine 7 am Stammbaumschema niederschreiben zu dürfen, da der Emu nur hechelt. Die Übereinstimmung der Crypturi mit den Rheidae andererseits ist zum Beispiel mit der alleinigen Übernahme der Brutfürsorge für die Jungen durch das Männchen (Nestbau, Brüten, Führung, siehe zum Beispiel Beebe, 1925; Pearson, 1955; Simpson, 1958; Verheyen, 1960*b*) zu belegen (6 im Schema); doch bestehen gewisse Bedenken wegen der möglichen Rückentwicklung der Strausse in dieser Hinsicht (siehe oben unter *c* bei 6). Jedenfalls möchte ich nicht den Schluss ziehen, dass die Tinamidae die Schwestergruppe der Rheidae sind, sondern zu diesen an dieser Stelle wenigstens noch die Struthionidae hinzufügen.

d) Sehr wesentlich wäre es, wenn wir nach der Bewertung der interfamiliären Beziehungen der drei Familienpaare von Ratiten (und der Steisshühner) (siehe *a*, *b*, *c*) für die vier notogaeischen Familien Apomorphie, das heisst Synapomorphie gegenüber den Straussen und Nandus, feststellen könnten. Das gelang mir nicht, obwohl ich noch immer den Verdacht habe (siehe Meise, 1960), dass die Kiwis polyandrisch sind (Henry, siehe Ogilvie-Grant, 1905, fand bei einem brütenden Männchen ein junges Tier und ein frisches Ei, das vielleicht einem anderen Männchen zugedacht war, wenn nicht Jungenfürsorge vom brütenden Männchen aus möglich ist). Der längere Legeabstand bei den notogaeischen Familien ist wohl nicht so wesentlich, und das Errichten von Männchen-Revieren beim Emu (Fleay, 1936; Schneider, 1929) wäre bei Kasuaren nachzuprüfen. Nach dem Verhalten wäre also ausser mit dem Sträuben der Federn (siehe oben, 7 unter *c*) kaum nachzuweisen, dass Nandus und Strausse eine synapomorphe Gruppe bilden, was für Kasuare und Emus (4 im Schema) leicht gelingt. Tatsächlich fassen wir jene ja auch meist nicht zu einer Unterordnung oder Ordnung zusammen. Damit ist einer der erwähnten strittigen Punkte des Systems nicht viel klarer geworden.

e) Wir haben schon oben gezeigt, dass die Neuseeland-Familien synapomorph gegenüber den vier übrigen Familien sind (2 im Schema), für die ich kein synapomorphes Verhalten finde. Dagegen haben sie symplesiomorphe Charakteristika, zum Beispiel die Bevorzugung des Augensinnes. Diese aber darf man nicht heranziehen (siehe *a*).

f) Damit kommen wir zum gemeinsamen Verhalten aller Ratitae, das hier zunächst einfach katalogisiert sei: hohe Geschwindigkeit beim Laufen, Unfähigkeit zu fliegen, Aufnahme von Steinchen in den Magen, weittragendes, meist dröhnendes Rufen (Syrinx des Nandus abweichend), Erreichung der Geschlechtsreife erst mit 2–5 Jahren, Kämpfe mit Fusshieben, Nestbau, oder Herstellung der Nestmulde durch das Männchen, ausschliessliche oder weit überwiegende Durchführung der Bebrütung durch das Männchen, Sehfähigkeit der schlüpfenden Jungen, frühes Verlassen des Nestes durch die (nestflüchtenden) Jungen, selbständige Ernährung der Jungen nach dem Verbrauch der Dottersackreserven, kein zusätzliches Vorhalten von Futter durch den Altvogel, Führung der Jungen meistens nur durch das Männchen und langsames Wachstum der Jungen.

Davon fassen wir als synapomorph gegenüber den Crypturi das Kämpfen mit Fusshieben, das langsame Heranwachsen und die grosse Laufgeschwindigkeit auf (8 im Schema). Die Tinamidae ihrerseits weisen in den glänzenden, bunten Eiern auch ein apomorphes, sie zu einem Taxon (von 43 Arten) stempelndes Merkmal auf (9 im Schema).

g) Beim Vergleich der bisher erwähnten Vogelgruppen, der Palaeognathae, mit den Galli ergeben sich die Hühner als apomorph im Scharren und ausschliesslichen Staubbaden. Es ist aber wohl nicht berechtigt, die Galli für sich allein den Palaeognathae gegenüberzustellen, sondern wahrscheinlich sind sie erst gemeinsam mit den Ordnungen der Grues und der Limicolae-Lari zusammen die Schwestergruppe der (Ratitae und Crypturi) Palaeognathae. Das Scharren spielt dann nur innerhalb jener Ordnungsgruppe eine Rolle, da es in ihr nur den Hühnern zukommt. Dort (bei Galli, Grues, und Limicolae-Lari) fehlt die bei Palaeognathen feststellbare Kombination von schnellem Laufen und männlicher Brutaktivität. (Für Apteryx siehe Anonymous, 1947, und Robson, 1947; für die Crypturi Beebe, 1925, und Pearson, 1955) (10 im Schema). Ob dieses (plesiomorphe) Fehlen durchgängig ist? Wir wissen über die Lebensweise von Phororhacos und Diatryma, also Verwandten der Rallen-Kranich-Gruppe, nichts; ausserdem stimmt die Kombination für die Crypturi nur bedingt, da diese meist schwach laufen. Für ein eigentliches Flugtier wie den Vogel sind wohl beide Verhaltensweisen (Laufen, männliche Brutaktivität) apomorph. Ethologisch scheint daher die auch von mir angenommene Primitivität der Palaeognathae nicht beweisbar zu sein.

ERGEBNIS DER VERGLEICHE

Wir sind damit über die Ratitae schon dreimal hinausgegangen (*c, f, g*), was zur Bestätigung der Monophylie mit Hilfe von Synapomorphien notwendig war. Nun wollen wir zu ihnen zurückkehren. Mit ziemlicher Sicherheit können wir behaupten, dass Kämpfen mit den Füssen und Brutflege nur oder hauptsächlich durch das Männchen spezialisiertere, sekundäre Verhaltensweisen im Vergleich mit Schnabel- und Flügelkämpfen sowie mit Brutpflege durch das Weibchen (oder durch beide Geschlechter mit Überwiegen des Weibchens) sind. Wie wichtig das Kämpfen mit Beinhieben gerade für die Eingliederung der Kiwis ist, möchte ich hier noch näher ausführen. Auch die Rallen Neuseelands haben zum Teil starke Beine, aber wenigstens von der gut beobachteten Wekaralle, Gallirallus, weiss man, dass sie nicht mit den Beinen schlägt (höchstens mit ihnen kratzt, Reischek, 1902), sondern mit dem Schnabel und den Flügeln auf den Feind losgeht. Hier spricht also ein Verhaltensmerkmal eindeutig gegen die von Fürbringer betonten Beziehungen zu Rallen, wenn auch der Oologe Schönwetter (1960) nach dem Ei die Rallenverwandtschaft der Kiwis für möglich hält (siehe Anhang).

Im ganzen ergibt sich, dass die Verhaltenslehre die Ratitenzugehörigkeit der Kiwis erheblich stützt. Aber die Menge der erforschten Verhaltenszüge tritt doch gegenüber den Materialien aus anderen Disziplinen zurück, obwohl es sich um so wenige Arten handelt. Immerhin bestätigt sich wieder, dass die Verhaltenslehre für die Systematik eine Hilfswissenschaft sein kann, deren Bedeutung mit genauerer Kenntnis des Verhaltens der besprochenen Arten steigen wird. Die grossen Unterschiede im Verhalten der Ratiten, die sich in Auswahl der Umwelt (Habitat), Form der Vergesellschaftung, Zeit des Aktivseins (Tag oder Nacht), Auswahl der Nahrung, Balzweise, Eizahl im Gelege, relativer Eigrösse und Brutdauer sowie anderem äussert, sind nicht grösser als die zum Beispiel innerhalb der Ordnung Hühnervögel, abgesehen von der relativen Eigrösse.

Demnach steht wohl auch von der Verhaltenslehre her nichts mehr der Zusammenfassung der Ratitae im Sinne des beigefügten Stammbaumes im Wege. Sie sind in gewissem Widerspruch zu der sonstigen Sonderstellung Südamerikas gegliedert in die vier ausserneuseeländischen und die beiden abweichenderen neuseeländischen Familien, die ersteren weiter in drei gleichwertige Gruppen (Rheidae, Struthionidae, Casuariidae-Dromaiidae) und die letzteren in zwei gleichwertige Gruppen (Dinornithidae, Apterygidae). Über die Aepyornithidae kann wegen des Fehlens von Verhaltenskennzeichen hier nichts gesagt werden. Alle eben genannten Gruppen sind als monophyletisch aufzufassen, ebenso die Ratitae (siehe Stammbaum).

NACHTRÄGE

Als Nachträge möchte ich zwei intraratitische Fragen (a, b) und eine den ganzen Vogelstammbaum betreffende (c) behandeln.

a) *Kriterien für Apomorphie der Apterygidae. Struktur des Ur-Ratiten.*— Beim Vergleich von Verhalten und System gibt es manchmal Widersprüche. So sind die Kiwis nach Würmer- und Insektennahrung sehr verschieden von den Moas. Trotzdem nehmen sie wie diese Magensteine auf und verfügen über lange Blinddärme wie wohl Moas auch. Ist das Verhalten von zwei Gruppen in einem bestimmten Punkt verschieden und deutet die mit diesem Verhalten zusammenhängende körperliche Struktur mehr auf die Struktur für eine der beiden Verhaltensweisen (hier Ernährung mit pflanzlichen Stoffen), dann ist die Verhaltensweise der anderen Einheit und dieses Taxon selbst in seinem monophyletischen Bereich apomorph, also mehr abgeleitet, gleichgültig, ob man das aus dem Verhalten unmittelbar ablesen kann oder nicht. Wir können diesen Satz wohl auf den Gaumenbau erweitert anwenden, indem wir fragen, ob nicht Blinddärme, Magensteine und Aufnahme fast immer zellulosereicher Nahrung gerade diesen Gaumenbau als Anpassung an eine solche Lebensweise erscheinen lassen. Damit würde man sich den Ur-Ratiten als einen Gras- und Sukkulenten-Fresser mit langen Blinddärmen und mit Magensteinen vorstellen. An einer Stelle (Papua) ist er zur Fruchtnahrung, an einer anderen zur Würmernahrung übergegangen. Kann man in beiden Fällen sagen: Magensteine sind eigentlich überflüssig geworden? Wenn ja, dann wären hier Verhaltensweisen neu, die anatomischen Verhältnisse aber stabil geblieben, was ich auch so ausdrücken kann: Die Anpassung ist nicht (synchron) erfolgt, und die notwendige (?) Postadaption ist (bisher) ausgeblieben.

Wie lange sind die verschiedenen Ratiten voneinander getrennt? Ich möchte sagen, zwischen 30 und 80 Millionen Jahren. Jedenfalls kennt man keine Bastarde zwischen den verschiedenen Gruppen.

b) *Eier der Apterygidae.*—Die Eier der Ratitae sind ausser denen der Apterygidae von einheitlichem Charakter, gekennzeichnet durch das Vorkommen gegabelter Porenkanäle, durch das Fehlen einer durchgehenden Schleimauflagerung und durch Eigenschaften, die wohl mit der Eigrösse zusammenhängen (relativ grosse Schalendicke, rundliche Form). Auch die kleinen Moa-Eier stehen allen anderen Eiern gegenüber, obwohl sie kürzer und leichter als die grössten Apteryx-Eier sind (Schönwetter, 1960:29). An dieser Überschneidungsstelle der Grössenkurve zeigt sich, dass Apteryx nicht nur relativ länglicher gestreckte, sondern auch viel dünnschaligere Eier hat. Das relative Schalengewicht beträgt für das schwerste Apteryx-Ei 7,5 Prozent (Schönwetter, 1960:37), für das etwa ebenso schwere Moa-Ei aber 10,8 Prozent. Überhaupt findet Schönwetter die glatte Oberfläche der Apteryx-Eier, auf der man kaum Poren sieht, am ähnlichsten der von einfarbig weissen Ralleneiern und von grossen weissen Enteneiern. Mit weissschaligen Ralleneiern stimmen Apteryx-Eier auch im durchscheinenden Farbton (gelborange) und in der erwähnten Dünnschaligkeit überein; ersterer ist vielleicht durch letztere bedingt. Obwohl sich die relativen Schalengewichte, maximal 8,5 Prozent beim Kiwi und minimal 10 Prozent beim Moa, ziemlich nahekommen, bedarf es doch der Überlegung, wie man den "Makel" der Ralleneier aus dem Ratitensystem hinausbringt. Man muss wohl von der relativen Grösse des Eies zum Vogelkörper ausgehen, die beim Kiwi um 20 Prozent, bei den kleinen Moas mit 15 kg Körpergewicht jedoch höchstens 3–10 Prozent beträgt. Es ist wohl verständlich, dass in derselben Verwandtschaft in dem Masse, in dem das Ei während der vermuteten Grössenabnahme des Vogels langsam kleiner, aber relativ grösser wurde, seine Schale an Substanz und Dicke verlor. Dagegen kann der Unterschied in der Schalenoberflächenstruktur nicht so einfach erklärt werden; doch dürfte er eben mit der geringeren Schalendicke zusammenhängen, die weder weitlumige Poren noch Sammelgruben für mehrere Poren an der Schalenoberfläche verlangt, sondern den Gasaustausch durch enge, kaum sichtbare Porengänge, wie bei den meisten dünnschaligen Eiern, erlaubt. Damit würden einige Eischalenunterschiede zwischen Moa und Kiwi als Anpassungen an das Dünnerwerden der Eischale "erklärt" werden.

c) *Die Schwestergruppe der Ratitae.*—Nach ihrem Verhalten sind die Ratitae, wie wir sahen (8 im Schema), weiter abgeleitet von ihren vermutlichen Vorfahren als die Crypturi. Beide sind Schwestergruppen, die man zusammen durchaus Palaeognathae nennen könnte, vor allem, wenn man sie allen anderen Carinatae gegenüberstellt. Ich glaube aber, dass die Palaeognathae als Schwestergruppe von nur drei Ordnungen (siehe oben g) aufzufassen sind, nicht als Schwestergruppe auch der übrigen, wenigstens 19 Ordnungen. Alle 24 Ordnungen habe ich in 2 Oberordnungen gegliedert, so dass die Ratitae mit den übrigen 12 Ordnungen der 1. Oberordnung zusammen die Schwestergruppe der übrigen Vögel, der Baumvögel, bilden, die allein 11 Ordnungen umfassen. Eine andere Möglichkeit ist die Gegenüberstellung der Ratitae und aller übrigen rezenten Vögel in Schwestergruppen, wobei an der Wurzel dieses Stammbaumes die Gabelung (1. Ordnungsgabelung) in den Vorfahren der Ratitae und in den aller übrigen rezenten Vögel erfolgt wäre. Diesem Extrem des Stammbaumes rezenter Vögel stellen wir, ebenfalls als Extrem, einen anderen gegnüber. Nach unserer Auffassung ist die Gabelung des Stammes des Ur-Carinaten (= Ur-Neornithes), die 1. Ordnungsgabelung, in die beiden Vorfahren der Oberordnungen Boden- und Wasservögel (Geornithes) sowie Baumvögel (Dendrornithes) erfolgt, worauf die (2.) Gabelung bei ersteren zu Ur-Boden- und zu Ur-Wasser-Vögeln führte. Die Bodenvögel gabelten sich dann (3.) weiter in Ur-Palaeognathae und in Ur-Hühner-Kranich-Watvögel. Erst bei der 4. Gabelung des Stammes erfolgte die Teilung im Niveau der eigentlichen Ordnungskategorie; es teilten sich die Ratitae von den Crypturi ab. Das Suchen nach der Schwestergruppe der Ratitae, zu dem Günther (1962) so optimistisch aufforderte, nötigt uns zu einer Entscheidung zwischen diesen beiden Extremen und wenigstens drei dazwischen liegenden Möglichkeiten, und nicht alle Ornithologen werden mit meiner Entscheidung (Meise, 1960: zugunsten der Crypturi als Schwestergruppe der Ratitae) einverstanden sein, vor allem nicht die, die auf das "neueste" Merkmal, die durch Elektrophorese erfassbaren Eigenschaften des Eiereiweisses, eingestellt sind, das die Crypturi den Hühnern näher bringt als den Ratitae (Sibley, 1960).

SUMMARY

Ethology of Struthiform Birds and Monophylety of the Ratitae

It is the purpose of this paper to present evidence based on ethological data indicating the probable monophyletic origin of the Ratitae. The ethology of these birds, as far as known, may be used to determine (after Hennig) apomorphy or plesiomorphy, synapomorphy or symplesiomorphy. Apomorph are groups of organisms that are more deviated from the supposed common ancestor than other ones, which are called plesiomorph. Synapomorphy (several units are apomorph) is indicative for monophylety, whereas symplesiomorphy is not (uniting more "primitive" taxa, not necessarily containing all living taxa sprung from one common ancestor).

The black squares in the scheme for arguments (Abb.1) show the Apterygidae and Casuariidae to be apomorph in comparison with their sister groups, Dinornithidae and Dromaiidae, respectively. The Ratitae of New

Zealand are considered apomorph (and monophyletic) in comparison with their sister taxon (Rheidae through Casuariidae). The Ratitae as a whole are shown as apomorph, and monophyletic with the Crypturi as their sister taxon.

The magnitude of differences in ethology between these flightless birds is not greater than that within the Galli. Ethological similarities are discussed. Some of the behavior similarities are the result of aptery; however, it is emphasized that certain aspects of behavior (method of fighting, role of male in incubation and care of young, and, finally, the slow rate of growth) appear to have developed independently.

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Comments on the Classification of Swifts of the Subfamily Chaeturinae

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As a family, members of the Apodidae are remarkably uniform in a great many respects. With few exceptions the plumage is sooty or black, occasionally with some iridescence, with or without varying amounts of white. This may be present on the ventral part of the body, on the rump, in the form of a circle or semicircle around the neck, or on the tips of certain feathers so as to produce a frosted effect. A few species have chestnut on the head, neck, and occasionally the upper breast. All have a dark, slightly recessed patch of feathers immediately anterior to the eye which may aid in reducing reflection from the sun much as patches of soot do below the eyes of American football players. The colors, therefore, tend to be rather somber and the differences between species not very great.

Swifts do not vary greatly in size. The largest species has a wing length somewhat less than 250 mm and the smallest a wing length slightly less than 100 mm. Only minor differences are apparent in the shape of the bill. This tendency toward relative uniformity, combined with the rarity of some species, especially in museum collections, and the habit of many kinds of swifts of nesting in remote and inaccessible situations have contributed to make comparative studies difficult.

In searching for generic distinctions, taxonomists have made use of such characters as the degree of feathering of the tarsus, the ratio of the length of the hallux to the inner toe, the structure of the tendons of the feet, whether or not the tail is furcate, the presence or absence of spines on the tips of the rectrices as well as the degree of rigidity of the shafts of these feathers, and the location and type of nest. Little emphasis has been placed on skeletal characters, especially the skull and the shape of the palate. This, however, has largely been the result of scarcity or lack of adequate study material.

I wish to comment on some of the previously mentioned characters with reference to certain members of the subfamily Chaeturinae, especially the White-naped Swift variously referred to in recent years by avian taxonomists as *Streptoprocne semicollaris*, *Aërornis semicollaris*, and *Cypseloides semicollaris*. First, however, let me briefly review some of the major opinions presented during the last 60 years relating to the classification of this species.

Hartert (1892:479) placed the White-naped Swift in the genus *Chaetura* along with other species of swifts having very stiff rectrices with perceptibly prominent spinous points. Two other genera in the subfamily Chaeturinae were recognized: *Cypseloides*, in which the shafts of the rectrices are not so

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stiff and in which prominent spines are perceptibly lacking, and *Collocalia*, in which the shafts of the rectrices are "ordinary" and without spinous points.

Oberholser (1906:69) proposed the genus *Streptoprocne* for the Collared Swift, then known as *Hemiprocne zonaris*, on the basis of the deep plantar tendons of the foot and the presence of an emarginate tail. Lucas (1899:78) had previously pointed out that in the Collared Swift the *flexor perforans*, which ordinarily serves the three front toes, has no separate tendon but is attached to the muscle of the first digit, which is the *flexor longus hallucis*. According to Lucas, both muscles connect with the tendon of the latter, which sends a single slip to each of the digits. Whether the *flexor perforans* lacks a tendon or whether its tendon has fused with that of the *flexor longus hallucis* would seem to be a matter of interpretation. Hudson (1937:38) has summarized our knowledge of the deep plantar tendons and points out that these two are fused near the middle of the tarsometatarsus in all groups of birds with the exception of the Passeriformes and the hoopoe (*Upupa*), one of the Coraciiformes. He mentions only one swift, *Chaetura pelagica*, and states that in that species the common tendon divides below into four slips or branches, one for each toe. It would appear possible that in the Collared Swift there is merely a greater fusion of the upper part of the tendons of these two muscles rather than the complete loss of one of them.

Oberholser (1906) also placed *semicollaris* and *biscutata* in the genus *Streptoprocne*, even though the arrangement of the deep plantar tendons was unknown in these species. I have not had a preserved specimen of the White-naped Swift to dissect but have been able to observe the four slips arising from a common tendinous mass near the lower part of the tarsometatarsus and going to each of the four toes on a skeleton to which these structures were still attached, and in the leg of a dissected study skin.

The inclusion of *zonaris, semicollaris,* and *biscutata* in *Streptoprocne* was followed by Ridgway (1911:697, 702) and Cory (1918:144–145). Peters (1940:235), however, decided that *semicollaris*, since it lacked an emarginate tail and feathering on the proximal anterior part of the tarsus, could not be kept in the genus *Streptoprocne* with *zonaris* and *biscutata*. He, therefore, placed it with *senex* in the genus *Aërornis*. Actually, the only specimen of *biscutata* that I have examined (Am. Mus. Nat. Hist. No. 43615) does not have an emarginate tail.

Zimmer (1945:589–591) later concluded that *Aërornis* could not be distinguished satisfactorily from *Cypseloides* and placed *senex* in that genus, making no mention whatsoever of *semicollaris*. He similarly concluded that *Nephoecetes* was not generically separable from *Cypseloides* and included *niger* in the latter genus. In 1950 (p. 158), Friedmann, Griscom, and Moore tentatively placed *semicollaris* back in the genus *Streptoprocne* but stated in a footnote that it is "probably not congeneric with *Streptoprocne* but certainly does not belong in *Cypseloides*." This, however, is exactly where

Lack (1956:3–4) placed it in his review of the swifts. Apart from a few changes, such as the inclusion of *semicollaris*, *zonaris*, and *biscutata* in the genus *Cypseloides* instead of *Chaetura*, his arrangement is essentially like that proposed by Hartert in 1892.

THE SUBFAMILY CHAETURINAE

In Lack's classification, three genera are recognized in the subfamily Chaeturinae. These are *Collocalia*, *Chaetura*, and *Cypseloides*. *Collocalia* comprises the swiftlets, a group of small-sized, mostly dull-colored species with rectrices that have not unduly stiffened shafts and that lack spiny tips. The swiftlets are widespread over the Indo-Australian region and the islands of the western Pacific.

Chaetura, as used to include *Hirund-apus*, *Zoonavena*, and *Mearnsia*, is more widely distributed, occurring in North and South America, Asia, Africa, Australia, and on many islands of the western Pacific area. The various species exhibit considerable range in size from a minimum wing length of about 100 mm to a maximum wing length of about 200 mm. While all members of this genus possess rectrices with prominent spines, there are marked differences between groups found in widely separated geographical parts of the world. Although combined into the genus *Chaetura* by Lack (1956), he points out the possibility of breaking this up into four genera.

THE GENUS *CYPSELOIDES*

Color and Size.—It is with the genus *Cypseloides*, used in a broad sense to include *Streptoprocne*, *Nephoecetes*, and *Aërornis*, that this paper is concerned. As presently understood, it comprises the following nine species, which are confined to the New World and occur principally in tropical America: *semicollaris*, *zonaris*, *biscutatus*, *niger*, *senex*, *fumigatus*, *cryptus*, *cherriei*, and *rutilus*. As far as size and color are concerned, it almost covers the extremes found in the family Apodidae. In body size and wing length *semicollaris* is the largest known member of the family Apodidae, while *rutilus* is about the size of smaller members of the genus *Collocalia* and *Chaetura*. The color may be essentially black, occasionally with white or whitish tips to some of the feathers of the head or ventral parts, in *cryptus*, *niger*, *cherriei*, and *fumigatus*; black with a white nape in *semicollaris*; black with a white collar in *zonaris*; black with a white nape and a white breast in *biscutatus*; or black with chestnut on most of the head, neck, and breast, at least in the male, in *rutilus*.

Ratio of Length of Hallux to Inner Toe.—The ratio of the length of the hallux to the inner toe has occasionally been stressed as a character separating certain genera of swifts. Ridgway (1911) described *Chaetura* as having a hallux that is no more and usually less than half the length of the inner toe and *Cypseloides* as having a hallux more than half the length of the inner toe. The latter was also true of *Streptoprocne* and *Nephoecetes*. When

Peters (1940) removed *rutilus* and *brunnitorques*, which he considered to be conspecific, from *Cypseloides* to *Chaetura*, this made *Chaetura* a genus in which the hallux might be more than half or less than half the length of the middle toe. This confusion seemed to be eliminated when the *rutilus–brunnitorques* group was returned to the genus *Cypseloides*. However, on checking the various members of the genus *Cypseloides*, I have found that all of the specimens of *zonaris* measured have a hallux that is less than half as long as the inner toe.

Shape of Tail.—As has been noted, certain taxonomists have placed considerable emphasis on the shape of the tail, whether forked or truncate, as indication of various degrees of relationship among swifts. I agree with Lack (1956) that this is a character subject to so much modification that it is of little generic value. By way of example, it was pointed out by Zimmer (1945:591) that, while *niger* is a species that is considered to have a forked tail, some specimens have the tail truncate or even slightly rounded. In this instance, it is not even a reliable specific character.

Of considerably greater importance than the relative length of the rectrices, in my opinion, is their basic shape. Among the Chaeturinae one finds the rectrices of members of the genus *Collocalia* to possess shafts that are not unusually stiff and to have the vane of these feathers extending to the tip of the rachis. In *Chaetura* (Fig. 1*f*) the rachis is very stiff and extends considerably beyond the end of the vane. In *Cypseloides* the species *niger* possesses rectrices (Fig. 1*a*) that are essentially like those of *Collocalia*. On the other hand, *semicollaris* possesses rectrices with unusually stiffened shafts. Furthermore, the vane at the distal end of the shaft is very attenuated in newly grown feathers (Fig. 1*c*). Subsequently, the terminal barbs are progressively lost (Fig. 1*d*, 1*e*), possibly as a result of wear, leaving the end of the rachis exposed as a spine, essentially like that in *Chaetura*. These ontogenetic changes suggest possible evolutionary stages that may have taken place in the development of spines on the tails of swifts. In *zonaris* (Fig. 1*b*), we see a somewhat similar condition, although the shafts are neither as heavy, proportionately, nor are the terminal spines as well developed as in *semicollaris*. Somewhat similar rectrices are present in *biscutatus* and *senex*. In *cryptus*, *cherriei*, *fumigatus*, and *rutilus*, the shafts of the rectrices are less rigid, although the tips tend to develop into slender spines, at least with wear.

Skull.—A study of available skulls of various kinds of swifts has revealed some marked variation in the shape of the posterolateral part of the palate (Fig. 2). Complete skeletons of 16 species, representing both families of the suborder Apodi and both subfamilies of the Apodidae, were examined.

In *Hemiprocne longipennis* the posterolateral border of the palate is angular and lacks any wing-like process. Although no skulls of the other two members of the family Hemiprocnidae, *H. mystacea* and *H. comata*, were examined, the close similarity between these three species in general

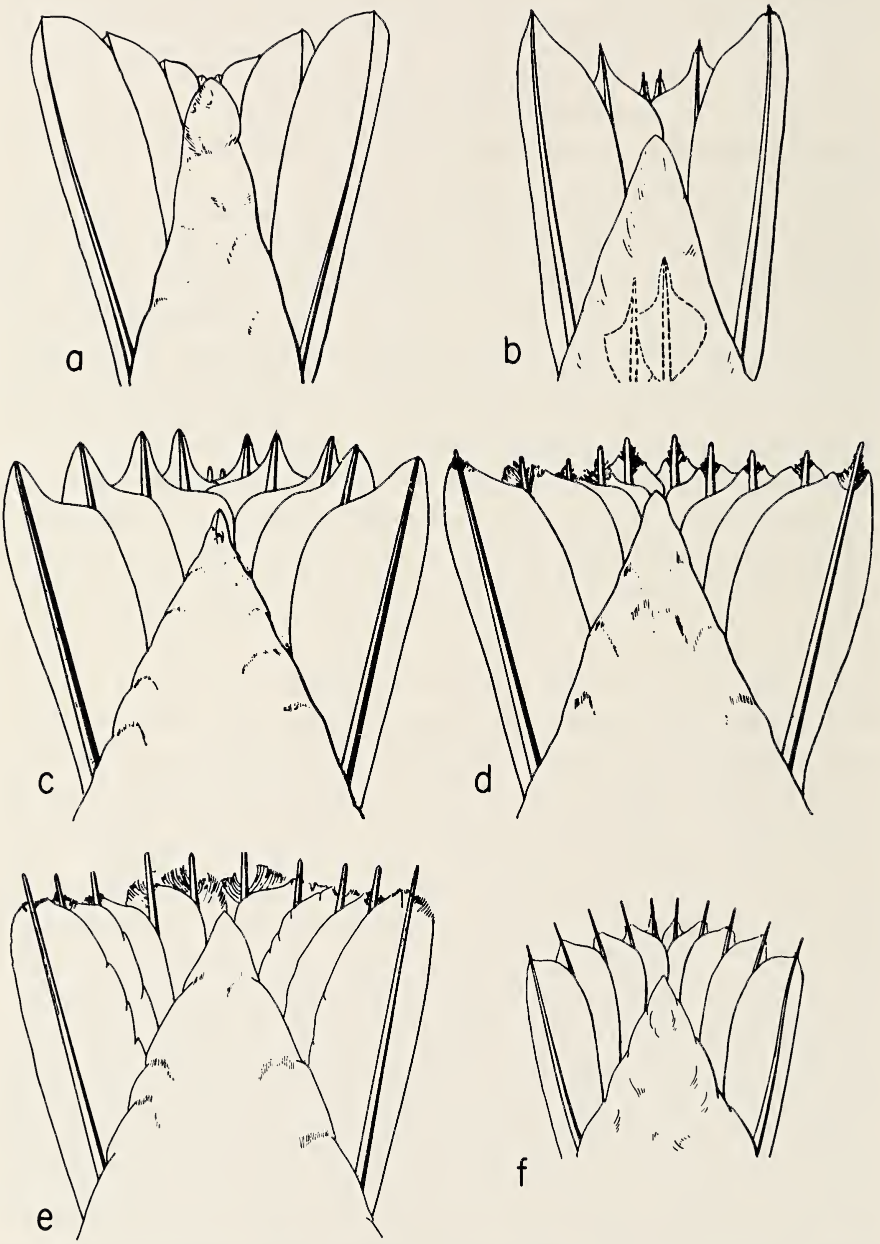

Fig. 1. Rectrices, in ventral view, of (*a*) *Cypseloides niger*; (*b*) *C. zonaris*; (*c*), (*d*), and (*e*) *C. semicollaris* in fresh, slightly worn and moderately worn plumage; (*f*) *Chaetura pelagica*. Drawings 5/6 natural size.

appearance and habits would suggest possible agreement in cranial characters.

Five species, representing four genera of the subfamily Apodinae, agree in possessing posterolateral, wing-like transpalatine processes. These processes are most pronounced in *Cypsiurus, Aëronautes,* and *Apus,* somewhat less so in *Tachornis* (*Reinarda*) *squamata.* In each of these, there is a marked constriction anterior to the transpalatine process.

Fig. 2. Ventral view of the skulls of swifts, as follows: first row, *Hemiprocne longipennis* (family Hemiprocnidae); second row (left to right), *Cypseloides zonaris, C. semicollaris, Chaetura vauxi, Collocalia troglodytes* (subfamily Chaeturinae); third row (left to right), *Apus melba, Cypsiurus parvus, Aëronautes saxatilis, Tachornis* (*Reinarda*) *squamata* (subfamily Apodinae).

In the Chaeturinae three species of *Chaetura* (*pelagica, vauxi,* and *cinereiventris*) and four species of *Collocalia* (*troglodytes, esculenta, inexpectata,* and *spodiopygia*) were examined. Each was found to possess transpalatine processes. These are more pronounced in the genus *Chaetura* than in *Collocalia.* The skulls of only three species in the so-called *Cypseloides* complex were available. These, however, show very marked differences. In *zonaris* (Fig. 3*a*), the structure of the palate is essentially as in *Hemiprocne* with transpalatine processes lacking. The same is essentially true of *niger*. The third, *semicollaris*, has proportionately short but well-marked processes with deep lateral constrictions immediately anterior (Fig. 3*b*). In some respects, this palatal structure appears intermediate between what might be considered the more primitive *zonaris–niger* type, which resembles *Hemiprocne*, and the more specialized *Chaetura* form of palate with very prominent wing-like processes (Fig. 3*c*).

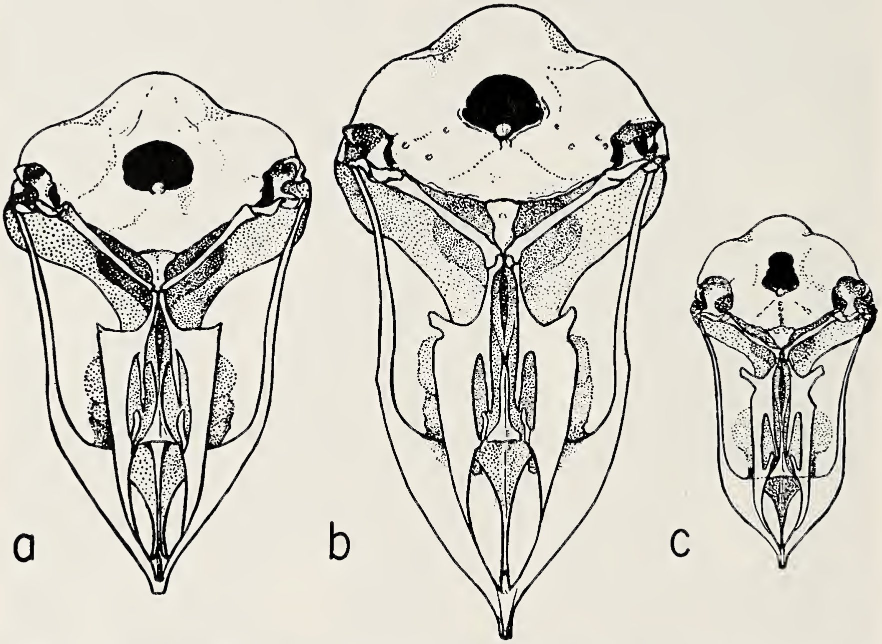

Fig. 3. Ventral views of skulls of (*a*) *Cypseloides zonaris* (Mus. Zool., Univ. Mich., 133752); (*b*) *C. semicollaris* (Calif. Acad. Sci., 62883); (*c*) *Chaetura vauxi* (Calif. Acad. Sci., 42764). Figures 1.8 × natural size.

In regard to the shape of the supraoccipital region of the skull, *niger* differs from all other swifts examined in lacking a prominent posterior bulge. Although only two skulls of this species were available for study, both agreed in this character.

Nesting Habits.—Lack (1956) summarized our knowledge of the nesting habits of swifts and stressed the importance of this in a better understanding of the relationships in this group of birds. At that time, the nests of only 5 of the 9 species that he placed in the genus *Cypseloides* had been described. These were *niger, zonaris, fumigatus, senex,* and *rutilus*. Except for *niger*, whose nesting habits are rather well known, our knowledge of the reproductive habits of these species is extremely limited. Recently, the nest of *semicollaris* was discovered in central Mexico (Rowley and Orr, 1962) and found to differ from that of all other species of swifts in that the eggs, two in number, are deposited in a shallow cavity hollowed out in dry sand on a ledge in a cave. No nesting material is used, and the nest site is quite dry. This is very different from the cone- or cup-shaped nests made of vegetation and mud that are reportedly made by some of the previously mentioned species of *Cypseloides.*

CONCLUSIONS

If the most recently proposed taxonomic arrangement for the subfamily Chaeturinae is accepted, only three genera are recognized, *Cypseloides, Chaetura,* and *Collocalia.* The genus *Cypseloides* accordingly would consist of nine species, including all of those formerly in the genera *Streptoprocne, Nephoecetes,* and *Aërornis,* as well as one species that was considered by Peters (1940) to belong in *Chaetura.* These nine species exhibit considerable diversity in body size, color of plumage, shape of rectrices, and structure of the palate, and even differ considerably in nesting habits. The Black Swift (*C. niger*) not only has rectrices that lack a stiffened rachis as well as a terminal spine, essentially as in the genus *Collocalia,* but possesses a palate somewhat like that of the crested swiftlets of the family Hemiprocnidae. In regard to the shape of the occipital portion of the skull it appears to differ from all other swifts. The White-collared Swift (*C. zonaris*) likewise possesses a simple palate essentially like that of *Hemiprocne* but has rectrices that are somewhat modified, with a stiffened rachis, and the appearance of short spines. The White-naped Swift (*C. semicollaris*) is the largest known species of swift. It has rectrices that are remarkably stiff and have terminal spines, although not as highly developed as in *Chaetura.* In palatal structure it is more or less midway between the *zonaris* type and that seen in *Chaetura, Collocalia,* and all members of the Apodinae examined. Furthermore, it is unique among swifts in that its eggs are deposited in a shallow cavity in dry sand.

In view of the fact that swifts are a relatively uniform and conservative group of birds, these differences assume greater importance than they might in other avian families or suborders. To consider such species as *niger, zonaris,* and *semicollaris* as congeneric seems unrealistic and, in my opinion, tends to confuse our understanding of their true relationships. Nevertheless, while I strongly favor the recognition of the genera *Nephoecetes, Streptoprocne,* and *Aërornis,* I feel that further conclusions regarding their relationship must wait until we have adequate skeletal material representing *biscutatus, senex, fumigatus, cryptus, cherriei,* and *rutilus.*

It is highly probable that Friedmann, Griscom, and Moore (1950:158) were correct in suggesting that, while *semicollaris* certainly does not belong in *Cypseloides,* it probably is distinct from *Streptoprocne.* However, until we know more about the skeletal anatomy of *senex,* for which the genus *Streptoprocne* was named, description of a new genus for *semicollaris* does not seem justified, although I suspect that ultimately this will be necessary.

ACKNOWLEDGMENTS

I wish to express my appreciation to the following persons and institutions for the loan of material pertinent to this study: Dean Amadon, American Museum of Natural History; Kenneth E. Stager, Los Angeles County Museum; Robert W. Storer, Museum of Zoology, University of Michigan; Ned K. Johnson, Museum of Vertebrate Zoology, University of California; Herbert Deignan, U. S. National Museum.

I am deeply grateful to J. Stuart Rowley for securing for me the first museum skeleton of the White-naped Swift, as well as for collecting an excellent series of skins of this heretofore relatively little-known species. The drawings of the rectrices and skulls of selected specimens of swifts were carefully prepared by Mrs. Jacqueline Schonewald.

SUMMARY

A review is given of the several systems of classification of swifts of the subfamily Chaeturinae proposed during the past 70 years as well as a summary of the major characters used in their taxonomic treatment. A recently proposed classification in which species previously placed in the genera *Nephoecetes, Streptoprocne,* and *Aërornis* are grouped under the genus *Cypseloides* is questioned. The inclusion of the White-naped Swift (heretofore known as *Streptoprocne semicollaris*) seems particularly inappropriate inasmuch as it differs basically from other swifts in certain nesting habits as well as in certain morphological characters. With regard to the structure of the palate and shape of the rectrices, it is intermediate between *Chaetura* and *Cypseloides.*

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Egg-white Proteins as an Aid to Avian Systematics

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The fundamental philosophy of biochemical taxonomy is that the chemical makeup of a species varies from species to species, family to family, etc., in the same general way as does gross morphology. Although there are not, in any group of animals, as comprehensive studies on biochemical composition as there are on morphology, there is enough evidence to show that the same type of relatedness exists. This paper is a preliminary study of the relationship of amino acid composition of egg-white proteins to systematics.

There is a rapidly accumulating amount of information on the composition of a wide variety of proteins throughout the animal kingdom. A good deal of this information comes as a by-product of the vast effort that is being made to understand the mechanism of protein synthesis. However, some studies have been undertaken with taxonomic goals in mind. Recent papers include the study of the selective partial hydrolysis of myoglobin by Stockwell (1961) of several classes of animals, including birds. The hemoglobins of a number of mammals, with special reference to the primates, have been studied by Zuckerkandl et al. (1960). Lucas et al. (1961) have made a study of the amino acid composition of the webs of a number of species of spiders. Silva et al. (1960) have examined the amino acid composition of tissue extracts of a number of species of rodents. The amino acid composition of protozoa has been investigated by Loefer and Scherbaum (1961). The fact that all these papers have been published within the last two years, and that the above list is by no means comprehensive, indicates the wide interest in the field of biochemical systematics.

In the field of avian taxonomy, the biochemical work has been reviewed in detail by Sibley (1960). Since then, an account of trypsin and chymotrypsin inhibitors from egg white of a number of species has been published (Feeney et al., 1960). This work includes analysis of two amino acids, tyrosine and tryptophane.

Much of the recent work in this field has been carried out by electrophoretic separation. Since this method is now fairly well known to students of systematics, no description of it will be given here. However, a brief comparison of electrophoresis and amino acid composition analysis will be made. Electrophoresis is a delicate expression of the net charge of the molecule. The change of a single charge can be detected using the boundary method. This net charge, at pH values normally used, is due to a balance between the negative charge carried by the free aspartic and glutamic residues and the positive charges carried by lysine and arginine. There

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are also contributions from the bound phosphorus and the free terminal groups. Electrophoresis does not give any information as to what combination of amino acids makes up the net charge, nor does it give any information on the 14 uncharged amino acids. On the other hand, amino acid analysis is not accurate enough to detect readily the change of a single residue which, if it carries a charge, can be detected by electrophoresis. Neither method gives any indication of the sequence of the amino acids in the protein.

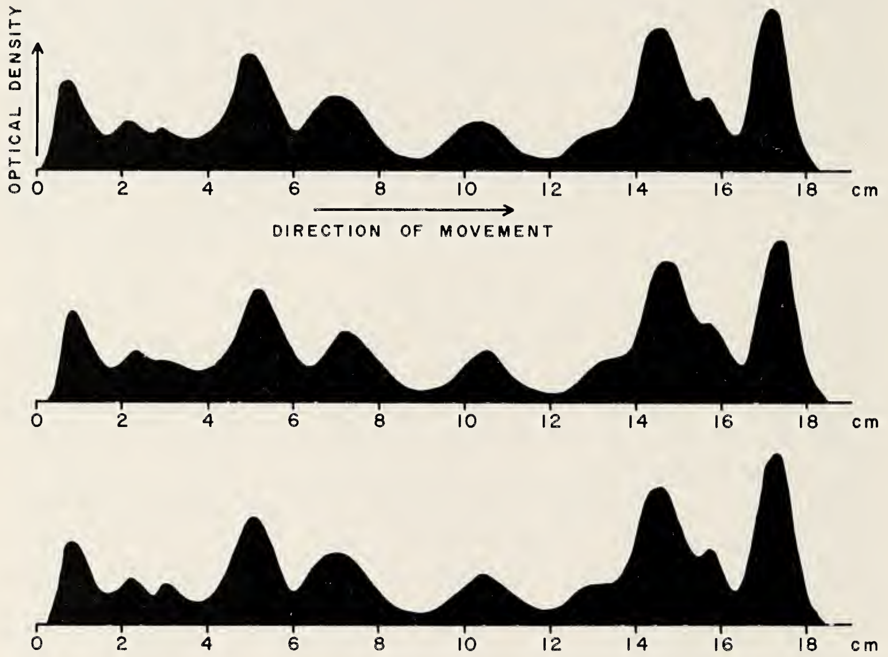

Fig. 1. Three amino acid separations of the main albumin fraction of three different samples from different nests of *Corvus brachyrhynchos.*

The experimental procedure for the work described in this paper was as follows. The egg white was dialyzed for 16 hours to a pH of 3.8, and then fractionated on a carboxyl methyl cellulose column (Rhodes et al., 1958). The main albumin fraction was then collected and hydrolyzed by boiling under reflux with 6N hydrochloric acid for 16 hours. The resulting solution of amino acids was evaporated to dryness and then desalted with an electric desalter. This desalted solution was evaporated to dryness, and the residue was then dissolved in 10 percent aqueous isopropyl alcohol. The amino acid solution was then ready for analysis.

To elucidate completely the amino acid composition, several different sets of chromatographic conditions must be used. For initial comparative purposes, a single method can be used. Ascending chromatography was carried out on Whatmann No. 1 filter paper. Solvents were n-butyl alcohol : water :

acetic acid (9 : 2 : 1) followed by methylethylketone : t-butyl alcohol : water : pyridine (40 : 40 : 20 : 1) in the same direction. The paper was then dried and dyed with ninhydrin. The plots of optical density against distance are shown in the figures presented below.

Under these conditions the presence or absence of all but two amino acids can be shown. These two are tryptophane, which is destroyed by acid hydrolysis, and proline, which does not react with ninhydrin. Tryptophane must be assayed after alkaline hydrolysis, and proline can be readily detected by the use of isatin as the dye.

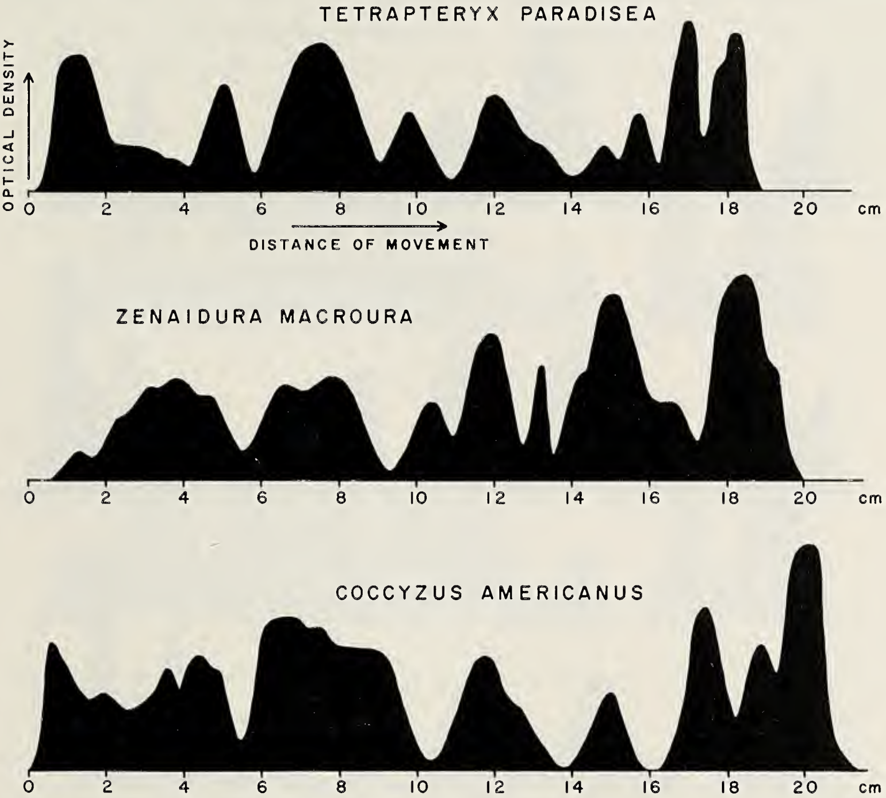

Fig. 2. Amino acid separations of the main albumin fraction of *Tetrapteryx paradisea, Zenaidura macroura,* and *Coccyzus americanus.*

The degree of reproducibility of the method is shown in Fig. 1. It will be seen that the patterns are almost identical.

It was found, as would be expected from electrophoretic studies, that there is considerable variation in the amino acid composition of the main albumin fraction from different avian orders. This is illustrated in Fig. 2 by analysis of single species from three different orders, the Gruiformes, Columbiformes, and Cuculiformes. There is wide variation. Thus, the variation or "information content" of egg-white albumin is wide enough for it to be a useful protein to study for taxonomic purposes. Some proteins are so vital to the animal that little or no variation is possible. A good example of this is insulin, one of the few proteins for which the structure is completely known (Sanger and Tuppy, 1951*a*, 1951*b*). Insulin from whale and pig is identical and that from the horse varies by only a single amino acid residue (Harris et al., 1956). Thus, we find that this protein, which controls the sugar level in the blood, is too vital to the animal to allow for appreciable variation to occur during the course of evolution. Egg white is a less vital protein, and therefore a much greater variation has occurred. Because of this, it is a more useful protein for the study of biochemical taxonomy.

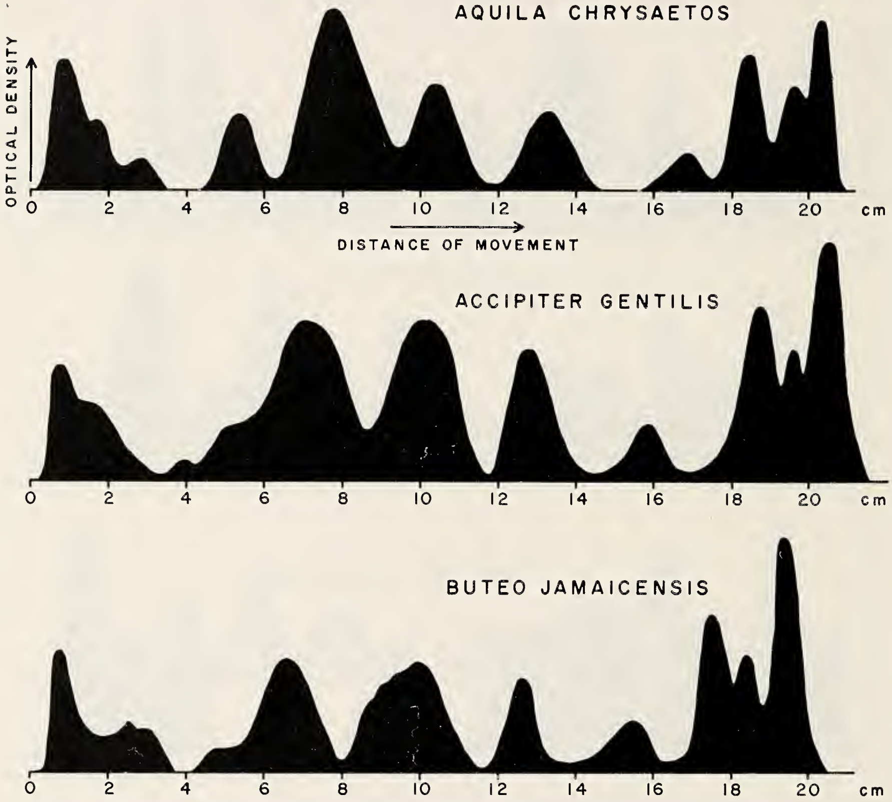

Fig. 3. Amino acid separations of the main albumin fraction of *Aquila chrysaetos, Accipiter gentilis,* and *Buteo jamaicensis.*

The reproducibility is good enough and the information content high enough to indicate that amino acid analysis is a useful tool in biochemical taxonomy. Before any broad systematic use can be made of the method, a large number of species will have to be examined. A single systematic point will be considered here, the relationship of the Cathartidae to the Accipitridae. The patterns of three species of the Accipitridae (Fig. 3) are fairly closely related to each other, showing relationship to be expected within a family. The patterns of the two common North American species of the Cathartidae, shown in Fig. 4, are similar. This is in agreement with the fact that hybridization has been reported (Gray, 1958) and with the similarity of the electrophoretic patterns (Sibley, 1960). However, these patterns are not similar to those species of the Accipitridae that have been examined. Sibley considers, on the basis of electrophoretic separation, that the Cathartidae are closely related to the Accipitridae. That conclusion is not supported by the present investigation which, however, covers too few species of Accipitridae to be conclusive. Rather, it supports the conclusion of Jollie (1953) that this family is not closely related to the other members of the Falconiformes. No investigation has been made of Jollie's suggestion that the Cathartidae are related to the Pelecaniformes and Procellariiformes.

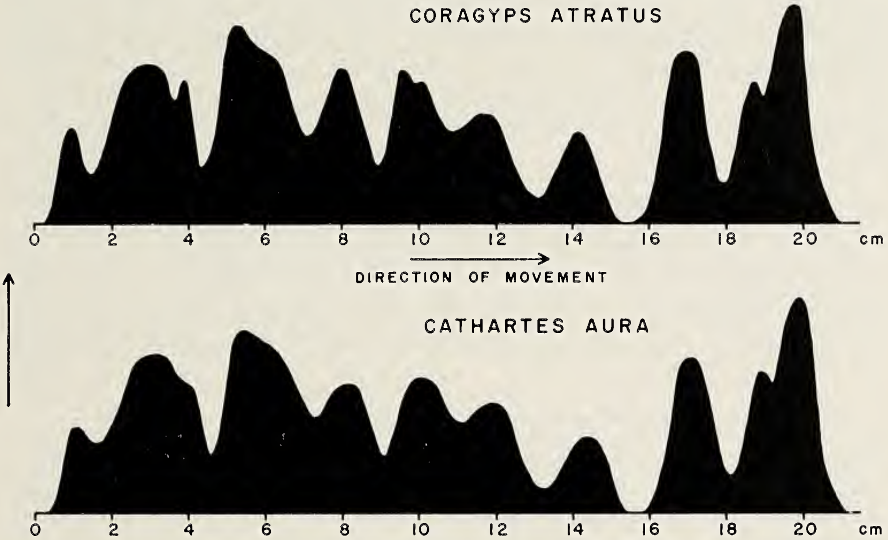

Fig. 4. Amino acid separations of the main albumin fraction of *Coragyps atratus* and *Cathartes aura.*

In conclusion, it appears that amino acid analysis is a useful additional tool in biochemical taxonomy. No single method, nor for that matter any single set of proteins, will form a complete basis for classification. But, the sum of information obtained by comparing many properties, physiological as well as biochemical, of many proteins should add a great deal to our knowledge of evolutionary relationships.

The author is grateful to the National Science Foundation for financial support of this work.

SUMMARY

The methods of separating egg white into individual proteins and subsequent hydrolysis to free amino acids are given. The separation of individ-

ual amino acids by paper chromatography is described. The reproducibility of the method is demonstrated by analysis of three different samples of *Corvus brachyrhynchos*. Wide differences occur in the amino acid composition of the main albumin fraction of species from different orders. Family resemblances are found within the Accipitridae, but two species of the Cathartidae are not similar to those species of the Accipitridae so far studied.

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Notes on Trochilidae: The Genus *Augastes*

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This paper is concerned with the morphology, geographical distribution, habitat, and biology of the species *Schistes g. geoffroyi* (Bourcier), *Augastes scútatus* (Temminck), and *A. lumachellus* (Lesson), which for some years have been the object of my attention, in their natural habitat as well as in captivity and in the examination of skin collections in American museums in New York, Washington, and the Professor Mello Leitão Museum of Biology at Santa Teresa in Brazil. These studies produced results sufficient to group the above-mentioned species in a single genus.

I wish to express my sincere thanks to Crawford H. Greenewalt for his valued help in furnishing me not only with slides and the beautiful color photographs, which form the frontispiece of this volume, but also the opportunity of visiting Equador and Venezuela in pursuit of these studies. I also tender my sincerely felt appreciation to Dean Amadon, Alexander Wetmore, and Herbert Friedmann, and the Directors of the American Museum of Natural History and the U.S. National Museum, who generously gave me access to their valuable collections.

MORPHOLOGY

The trochilid genus *Augastes*, as listed by Peters (1945) and others, contains two species, both monotypic, *A. scutatus* and *A. lumachellus*. The latter, until I rediscovered it in 1960, was known only from a few ancient trade skins, and the noted student of hummingbirds, J. Berlioz, had suggested (1950) that it might be extinct. From 9–16 May 1928, E. Kaempfer collected four specimens for the American Museum of Natural History, but these records have not been published. Recently I have also studied in the field the Andean species *Schistes g. geoffroyi* and concluded that both in habits and also, as shown by specimens, in morphology, this species is so similar to *scutatus* and *lumachellus* that Gould in 1861 might well have refrained from placing it in a separate genus *Schistes*. The latter I herewith propose be regarded as a synonym of *Augastes*, Gould, 1849, type *A. scutatus* (Temminck).

Gould (1861) describes the characters of these species as follows:

> *Schistes g. geoffroyi* (Bourcier).—Across the forehead a faint line luminous green; crown of the head, upper surface and wing-coverts bronzy green, deepening into rich bronze on the rump and upper-tail-coverts; wings purplish brown; tail green, crossed near the tip by a broad chalybeate band, beyond which the feathers are of a paler green than at the base, and the four outer feathers on each side are fringed with white at the tip; throat luminous green; behind the eye a small tuft of white; ear-coverts dark brown; on each side the breast a tuft of lilac-blue; feathers margined posteriorly with green; under surface glossy green; tuft behind the thigh white; vent feathers grey at the base and tip, olive green in the middle; bill and feet blackish brown.

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Augastes scutatus (Temminck).—The male has the face and throat clothed with small scale-like feathers of the richest and most luminous emerald green, the feathers lengthened into a pendent point on the chest; band across the crown and ear coverts deep velvety black; immediately behind the eye a small oblong spot of white; on each side of the neck a lengthened tuft of feathers of a rich indigo blue, separated from the equally rich indigo blue of the abdomen by two crescent-shaped marks of deep buff, one on either side of the chest; all the upper surface, upper and under wing-coverts rich bronzy green; wings purplish brown; vent white; under-tail-coverts white spotted with shining green; tail shining metallic green; tarsi clothed with brown feathers; bill black; feet brown. Total length, 4 inches; bill ¾; wing 2¼; tail 1½; tarsus 3/16. In general colouring the female is very similar to the male, but the face is much less brilliant; the blue tufts on the sides of the neck are much less developed; the crescent-shaped marks on the chest are white instead of buff; the abdomen is green, with only a tinge of the rich blue; the under tail-coverts are pure white; and the outer tail-feather on each side is tipped with white. Total length, 3¾ inches; bill ⅝; wing 2⅛; tail 1⅜; tarsus 3/14.

Augastes lumachellus (Lesson).—The male has the face and throat rich lustrous golden green, bounded below by a narrow line of bluish green, and terminating in a few pointed feathers of rich shining iridescent crimson-red, head deep velvety black, which colouring extends over the side of the neck, and is continued in a narrow line behind the luminous colouring of the throat; plumage of the body, both above and beneath, shining bronzy green; on either side of the chest a crescent-shaped mark of white; wings purplish brown; tail golden bronzy red, except the apical three-fourths of the two central feathers which are pure bronzy, and the outer margins of the two next feathers on each side which are washed with green; under surface of the tail rich deep luminous bronzy crimson; across the vent an irregular line of white; bill black. Total length, 4¼ inches; bill ⅞; wing 2⅜; tail 1½; tarsus ¼. The female has the upper and under surface of a more bronzy hue; the head green instead of velvety black; the ear-coverts dull blackish brown; the green of the throat less lustrous, not extending to the forehead; the greenish blue feathers at its base more apparent, and the locket-like mark less conspicuous; the upper surface of the tail of a uniform bronzy copper hue, and the under surface similar to, but less brilliant than, that of the male. Total length, 4⅛ inches; bill ¾; wing 2¼; tail 1⅜; tarsus ¼. The young birds of the year have upper surface bronzy green; the throat white, each feather tipped with shining green; only a trace of the locket-like mark so conspicuous in the adult; the under surface brown, glossed with bronzy; the upper surface of the tail bronzy copper, except the two middle tail-feathers, which assume a crimson hue, and are narrowly edged with purple; and the under surface of the tail similar in colour, but less brilliant than in the adult.

Gould does not describe the female and young of *Schistes g. geoffroyi*. Simon (1921) describes the female and male as similar, but does not ascribe to them tufts of lilac-blue and black at the side of the neck, nor does he describe the young. Hartert (1900) describes the female and the young, stating that the lilac-blue of their lateral tufts is less intense and that the black band is absent, the ventral parts lighter, and the wings shorter, 47–48 mm, the young being similar to the female. In my observation of specimens in captivity, I was able to determine that the young have less brilliant coloring; the ventral parts are ash-white, with no iridescent plates on the head or throat, and without the lilac-blue and black on the sides of the neck. As the male matures, the iridescent green of the forehead and throat begins to appear; the lateral parts of the neck begin to turn lilac-blue with black bands, and the white band becomes reduced in area until it is quite narrow. The female does not have the brilliance of the male; she displays the lilac-blue tufts and rarely, when fully adult, she shows traces of a blackish band next to the tufts.

Gould, Simon, and Hartert, in their cited works, describe the female of *Augastes scutatus*, but only Hartert describes the young as being similar to the female. In my observations of specimens maintained in captivity, I was able to determine that the young have less brilliant coloration; the ventral parts are also ash-white, without iridescent plates on forehead and throat, and without indigo-blue and black on the sides of the throat. As the male grows older, the forehead and throat turn iridescent; the lateral tufts of the throat become more and more black and indigo-blue, and the white band turns pinkish white.

Gould, Simon, and Hartert, in the cited works, describe the female of *A. lumachellus*, but only Simon uses the same description for female and young male. In my observations of captive specimens, I found that these young also have less brilliant coloration, with the ventral parts ash-white, without iridescent plates on the forehead and throat, and without salient fire-red breast feathers. As the male matures, the top of the head and the back of the neck become blue-green, the forehead and throat display iridescent green, and on the breast appear lengthened feathers of fire-red. Afterward the bluish part of the head turns velvet black with blue reflections, and the white band diminishes until it is barely visible. In these species the similarity and distribution of the plates of iridescent plumage on forehead and throat and of the lateral tufts on neck and throat are quite characteristic and cover the same areas. The lateral, slightly recurved white band is also very characteristic of all these species, and is situated in the same pectoral region. Also the postocular white line is present in all these species. The similarities displayed by the young in their varying molting phases are characteristics common to all the species. In the females of all species, the tail has a pronounced metallic brilliance, and a narrow whitish band on the terminal parts of the tail feathers is characteristic. The semi-andromorphism of the females is another factor common to all these species.

GEOGRAPHIC DISTRIBUTION

All of the species considered in the present paper, to be included in the genus *Augastes*, are found in the Brazilian subregion of the A. Russel Wallace Neotropic region. All are sedentary and nonmigratory.

Schistes g. geoffroyi is found in the Oriental Andes of the Subtropical Zone. Its habitat comprises 50,000 sq km, from eastern Peru, eastern Equador, eastern Colombia, and northern Venezuela; from Chaupe, Pozuzo, Rio Napo, Rio Pastaza, Hacienda Rio Negro, Rio Oyacachi, Chaco, El Roble, Nova Granada, Bogotá, Sierra de Perijá, Alto Rio Negro, Zulia, Táchira, and Yaracuy to Aragua, and centered on El Roble, in Colombia.

Augastes scutatus is found in the Eastern Meridional (northern half of Eastern Zone) region of the Brazilian Plateau, in an area comprising about 75,000 sq km, from the Serra da Mantiqueira, Chapada Diamantina, and Serra do Espinhaço, to Minas Gerais; from Ouro Preto, Nova Lima, Bello

Horizonte, Caeté, Sabará, Serra do Cipó, Itacolomí, Diamantina, Montes Claros, to Grão Mongól, and centered on Ouro Preto.

A. lumachellus is found in the Eastern Septentrional (southern half of Eastern Zone) region of the Brazilian Plateau within an area comprising about 12,500 sq km, from the Serra da Mantiqueira, Chapada Diamantina, Serra do Espinhaço, and Serra do Sincorá, to Bahia; from Barra da Estiva, Mucugê, Igatú, Andaraí, Lençóis, to Morro do Chapéu, and centered on Cachoeira do Ferro Doido. I suspect that the specimens now in the European museums were taken from Cachoeira do Ferro Doido, which is about 18 km from the city of Morro do Chapéu. This species is quite rare; in fact, Peters (1945) thought that there were probably no museum specimens with definite data in existence. Its apparent rarity can be ascribed to the inaccessibility of its Brazilian habitat, and the lack of information as to the locality in which the skins in European museums were collected. Most of these skins are simply labeled "Brazil," if indeed any locality is given. In September 1960, I was fortunate to have the opportunity of studying the collection of E. Kaempfer in the American Museum of Natural History where I found four male specimens captured in May 1928, in Morro do Chapéu in Bahia. In February 1961, I visited this region, which contains the oldest diamond mines in Brazil. It is probable that the first skins of *Augastes lumachellus* were brought out from that region together with the diamonds mined there.

I find that the area of distribution extends from Barra da Estiva to Morro do Chapéu and comprises an area of about 12,500 sq km. The species is abundant in this region, and I was able without difficulty to collect 30 living specimens. I discuss elsewhere in greater detail (Ruschi, 1955, 1959, 1962*a* and *b*) the reasons for the lack of recently collected skins of trochilids; these relate to the difficulty in reaching the habitat of *A. lumachellus*, which has not been visited by botanists or zoologists for almost a century.

HABITAT

All of the three species under discussion live in very similar biotopes, viz. in typical tropical arid regions having a climate characteristic of a semidesert. In the Eastern and Western Andes the birds are found in rocky fields or savannahs at altitudes of 1,200 to 2,700 m, where the flowering plants include Cactaceae, Caricaceae, Euphorbiaceae, Bromeliaceae, and trees and bushes growing in a rocky detritus. In the Brazilian habitats the birds are also found in rocky fields at the top of a sierra at altitudes ranging from 950 to 1,600 m, where the flowering plants include more than 15 species of Velloziaceae intermixed with Cactaceae, Bromeliaceae, Orchidaceae, Amaryllidaceae, Euphorbiaceae, and Verbenaceae. In the areas in which there is more soil, there are also grasses and various Compositae. Where the areas are less arid at altitudes of 2,500 to 2,700 m in the Andes and 1,100 to 1,300 in the Serra do Espinhaço, they are found in rocky areas in which the vegetation comprises principally "pluvifolius" bushes and trees, with Compositae, Leguminosae, Loranthaceae, and Vochysiaceae.

The birds feed principally at the flowers of Bromeliaceae, Loranthaceae, Compositae, Verbenaceae, and Vochysiaceae. They rest in or under small bushes where they are protected from the direct force of the wind. Their nesting sites are some small distance (50–200 m) from the feeding area, sometimes on rocky slopes, sometimes in hedges providing protection against the wind, sometimes in the open field without any protective cover for the nest against rain.

In summary, the three species are always found in rocky and stony regions with semi-arid vegetation, predominantly subxerophytic and xerophytic, in fields and savannahs at altitudes of over 1,000 m. There is sufficient variability in the ecology of their habitats to permit them to be readily maintained in captivity, provided the general appearance of their native habitat is created.

BIOLOGY

Certain behavioral characteristics, such as bathing, singing, nesting, flight, and the nuptial display which also are similar for the three species, determine their living conditions. They have also influenced their external morphology and strengthen the considerations that lead us to classify them within a single genus.

The birds usually bathe in running water in small pools; in bathing, they glide over the water with the tail in an open fan, as if they were skating. No other species among the Trochilidae appear to bathe in this way.

The song is also similar for all species; it is a phrased chirping interspersed with a stronger and more sonorous trill and occasionally with a metallic snapping outburst. The call is always a repetition, two times or more, of the syllable *itch.* The nest is Type 3 in the Ruschi (1949) classification and is made entirely of very fine fibers from Cactaceae, Bromeliaceae, Compositae, and grasses with very small lichens on the exterior surface. It is always hung from the branches of herbaceous plants at a height of about 1 m, on rocky ledges, protected from the wind, and appears to be without overhead protection against rain.

The postures of the birds in hovering flight are similar. All of the species hold the bill and tail in a horizontal position. The rest of the body is in an oblique straight line, forming an angle of about 140° with bill and tail. This is a quite typical silhouette of all species of the genus in hovering flight.

The nuptial display is always similar in the attack and in the dance, and is followed by identical reactions on the part of the female. The assault and courtship phases are also similar for all the males. The plumage of the male is exhibited exuberantly, by presenting the iridescent feather plates, erecting and raising them as if in high relief. This occurs with the feathers of the neck, pectoral, cephalic, and lateral neck regions. These presentations are combined with alternate advances and retreats toward and from the female and are followed by ascending flights and slow or violent descents until the male dominates and the female acquiesces.

SUMMARY

In this paper the author examines *Schistes g. geoffroyi* (Bourcier), *Augastes scutatus* (Temminck) and *A. lumachellus* (Lesson). Besides the descriptions of these species given by Gould, Hartert, and Simon, the author sets forth his own observations made in native habitat and on specimens in captivity, and of skins in several museums. The comparisons are based not only on morphology, but also on geographical distribution, biology, and habitat. The conclusion is reached that it is only possible to place the three species under one genus: *Augastes.*

The geographical distribution, until now unknown, of *A. lumachellus,* a species once thought to be extinct, is also shown to comprise an area of about 12,500 sq km on the Brazilian Plateau.

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Hybridization in the Wood Warblers *Vermivora pinus* and *V. chrysoptera*

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The Blue-winged Warbler (*Vermivora pinus*) and Golden-winged Warbler (*V. chrysoptera*) are broadly sympatric over a large part of northeastern North America. The distributions of the two forms during the breeding season are indicated in Fig. 1, which is based on information supplied by Edgar M. Reilly, Jr., and supplemented by my own literature review and field experience. As far as is known, hybridization between these warblers occurs in all areas of sympatry. Individuals of both forms are usually found in small, semi-isolated "colonies," this condition being dependent upon the availability of suitable habitat, and perhaps other factors. The birds are most common in parts of the overlap area, and the Blue-winged Warbler is particularly common in parts of New Jersey and on Long Island, New York. However, in the southwestern part of its range, where it is allopatric, the Blue-wing is apparently uncommon. A recent northward range extension of *pinus* has been well documented by Parkes (1949, 1951), Berger (1958), Scheider (1959), and Short (1962). In some areas (e.g. central New York) the Blue-winged Warbler has virtually reached the northern extreme of the Golden-winged Warbler's range.

Although hybridization between these warblers in an ornithologically well-known area has been recognized for nearly a century, since Brewster (1881) suggested the possibility, relatively little work has been done with this problem. There are several reasons for this. The warblers breed over a short period of 6–8 weeks, following which they move out of the nesting area. The songs are weak and buzzy, and the birds are relatively inconspicuous. Considerable difficulty is encountered in locating nests. The studies of Faxon (1911, 1913) and Carter (1944) represent the main contributions to our knowledge of interactions among hybrids and individuals of the parental types. Attempts at genetic analysis based largely on field observations have been made by several workers, notably Nichols (1908) and, more recently, Parkes (1951). The most recent detailed discussion of the problem, particularly emphasizing recent range expansion of *pinus*, is that of Berger (1958). I have been studying these warblers for parts of several field seasons since 1958, and, more intensively, examining museum specimens during the past 2 years. The aims of this paper are to indicate the extent of hybridization in these warblers and its effects on the parental populations, and to present information on several other facets of their interbreeding.

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This report is based upon data from 1,028 adult warbler specimens, including 500 taken in the breeding season, 288 spring birds, 134 fall specimens, and 88 winter birds. In addition to making standard measurements, color patterns were analyzed by means of the hybrid-index (character-index) technique. Employment of this method is dependent upon the existence of several color character differences between the forms. Extremes for each character must be connected by an intergrading array of intermediate stages in supposed hybrids. The Blue-winged Warbler and Golden-winged Warbler differ in six major features of color pattern. Briefly, the Blue-wing has a

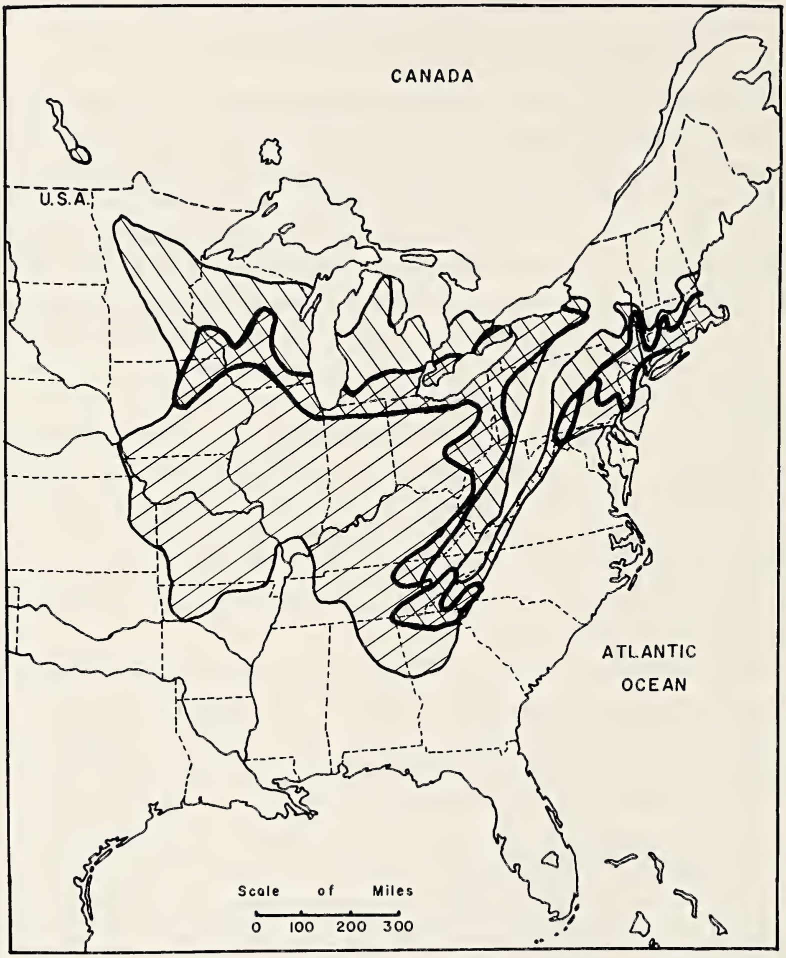

Fig. 1. Map of the breeding ranges of the Blue-winged (indicated by diagonal lines going up to the right) and Golden-winged warblers (diagonal lines going down to the right). The overlap area is shown by cross-hatching, and is surrounded by the heavy, black line.

greenish-yellow hindneck, yellowish rump, greenish-yellow back, no face mask, yellow underparts and two narrow, white wing bars. The Golden-wing exhibits a blue-gray hindneck, rump, and back, a black face mask (throat patch plus broad transocular stripe), white underparts, and a single, broad, yellow wing bar. Both warblers possess bright yellow crown-forehead patches and dark tails with white-tipped outer edges. Sexual dimorphism is not great, females resembling males, but being duller. Females can be distinguished from males in comparable plumage by the duller yellow, more restricted crown-forehead patch. In addition to being duller than the males, female *chrysoptera* have gray rather than black face masks.

METHODS OF STUDY

When one examines the variation shown in the six color characters by which the two warblers differ, one character is found unsuitable for utilization in a character index. The face mask is apparently controlled genetically in a simple Mendelian manner, as previous workers (Nichols, 1908; Parkes, 1951) have noted. Such characters are obviously of little value in studying hybridization, and must be discarded in favor of characters controlled polygenically. An index was constructed based upon the five characters (color of rump, hindneck, back, underparts, and color and extent of wing bars) showing intergradation from one extreme to the other. For each of the five characters the extremes have been assigned values from 0 for the expression of a character as in *pinus* to 4 for its expression as in *chrysoptera* (Table 1). The hybrid index is the sum of the scores for all five characters, and thus ranges from 0 for phenotypically pure Blue-winged Warblers to 20 for phenotypically pure Golden-winged Warblers. All specimens were scored and indexed in this manner. Since face mask was disregarded in this study, a phenotypically pure Golden-wing in this paper can be a bird without a mask.

With respect to wing bars, the 0+ score for narrow white wing bars having yellow edges presents a problem. Many specimens otherwise like *pinus* exhibit this condition. While this may simply be a variant of the normal *pinus* condition (0 score), two facts suggest its relation to hybridization. Specimens indexed at 0+, compared with those indexed at 0, possess longer wings and tails, thus tending toward *chrysoptera*. Also, many specimens with indications of hybridization in other characters also show the 0+ wing-bar condition. Hybridization is probably involved in the incidence of yellow-edged wing bars, but I am unsure as to what extent this is true. At any rate, since some Blue-wings lack yellow traces in the wing bars, it is likely that hybridization was originally responsible for its appearance in that form.

In relation to the similar scoring arrangement for back color, hindneck color, and rump color, it might be argued that these should be treated as a single character complex. However, the three characters show sufficient independence to merit separate treatment, as will be made clear below.

The two warblers are closely similar in measurements. The more northern

TABLE 1.—SYNOPSIS OF COLOR CHARACTERS AND SCORES USED IN HYBRID INDEX

CHARACTER DESCRIPTION	SCORE
COLOR OF UNDERPARTS	
Yellow as in Blue-wing.	0
Yellow, with white traces.	1
Mixture of yellow and white, the yellow usually more evident on the breast and below the eyes, and white more evident on the throat and abdomen.	2
White, but with yellow traces usually on the breast.	3
White, as in *chrysoptera.*	4
COLOR AND EXTENT OF WING BARS	
Two narrow, white wing bars, as in *pinus.*	0
Same as for 0, but with faint, yellow edges of feathers in one or both bars.[a]	0+
Bars slightly broadened, with yellow traces near bases of bars.	1
Bars broadened, yellow and white.	2
Bars converging, yellow with white traces.	3
Single, broad, yellow bar, as in *chrysoptera.*	4
BACK COLOR	
Yellow-green, as in *pinus.*	0
Yellow-green with blue-gray traces.	1
Mixture of yellow-green and blue-gray.	2
Blue-gray with yellow-green traces.	3
Blue-gray, as in *chrysoptera.*	4
COLOR OF HINDNECK	
Color gradations and scores same as for back color.	
RUMP COLOR	
Color gradations and scores same as for back color, except that the rump in *pinus* is much more yellow than the back.	

[a] See discussion of this condition in text.

Golden-winged Warbler tends to have longer wings and a longer tail, a slightly longer bill, and about the same tarsal length as the Blue-winged Warbler. More precisely, *chrysoptera* that are phenotypically pure average longer in wing length by 3–4 mm, in tail length 2½ mm longer, in bill length ½ mm longer, and in tarsal length less than ½ mm longer than phenotypically pure *pinus.* Results of the study of mensural characters will not be presented in detail here. However, specimens ascertained to be hybrids according to color characters were variously intermediate in wing length and tail length.

One reason for our past failure to appreciate the effects of interbreeding on the warbler populations has been the tendency to categorize hybrids into but *two* types, based upon general color of underparts plus the presence or absence of the throat patch and transocular stripe. One of these hybrid types is the "Lawrence's" Warbler, which is simply a hybrid with yellow underparts (*pinus*) and a face mask. The variability of this hybrid is considerable, as suggested by earlier observations (e.g. Brown, 1934; Carter, 1944) and further indicated below. All birds with obviously intermediate (yellow and white) or white underparts and *no* face mask are called "Brewster's" Warblers. The variability of this "type" has been long known (see discussion by Parkes, 1951:10–11). Yet observers commonly note hybrids simply as "Lawrence's" or "Brewster's" Warblers with no attempt at further determination of color variation.

ANALYSIS OF SPECIMENS

By following this simple procedure of categorizing hybrids into the two accepted hybrid types, the 1,028 specimens examined can be separated, as indicated in Table 2. The total number of individuals of these two "types" was 117 (11 percent).

Table 2.—Analysis of Warbler Specimens Based on Two Hybrid Types

Form	No.	Percent
Blue-wings	476	47
"Lawrence's"	31	3
"Brewster's"	86	8
Golden-wings	435	42
Totals	1,028	100

Overall Hybrid Index

Subjecting the same specimens to hybrid-index analysis results in an altogether different picture (Table 3). Specimens indexed at various values from 0 to 20 are pooled in nine groups, for which the inclusive index values are indicated. Individuals phenotypically pure with respect to the five characters are included on the top (*pinus*) and bottom (*chrysoptera*) lines, and together totaled only 113 out of 1,028 specimens, or 10.8 percent. As pre-

Table 3.—Analysis of Warbler Specimens Based on Hybrid Index

Phenotype	Hybrid Index Values	FACE MASK[a]		Total Number Studied
		Present	Absent	
Phenotypically pure *pinus*	0	1 (L)	47	48
	0+	0	111	111
Pinus, slight *chrysoptera* influence	1–2	16 (L)	246	262
Pinus, moderate *chrysoptera* influence	3–4	5 (L)	52	57
Pinus, strong *chrysoptera* influence	5–7	1 (L)	22 (6 B)	23
Intermediate hybrids	8–12	38 (8 L)	45 (41 B)	83
Chrysoptera, strong *pinus* influence	13–15	116	17 (B)	133
Chrysoptera, moderate *pinus* influence	16–17	96	10 (B)	106
Chrysoptera, slight *pinus* influence	18–19	129	11 (B)	140
Phenotypically pure *chrysoptera*	20	64	1 (B)	65
Totals		466	562	1,028

[a] L = "Lawrence's" Warblers and B = "Brewster's" Warblers from Table 2.

viously noted, the 0+ indexed specimens are like Blue-winged Warblers, but have yellow edges on the white wing bars. Specimens indexed at 1–2 or 18–19 show slight indications of hybridization. If one were to disregard evidence for hybridization afforded by specimens indexed 0–2 and 18–20, based on five index characters, there still remain obvious hybrids in these groups. Such obvious hybrids are the "Lawrence's" Warblers, i.e. birds indexed 0–2 having the face mask of *chrysoptera*, and "Brewster's" Warblers indexed 18–20, but lacking the face mask. The height of conservatism in this case would be to regard *all* phenotypically pure specimens and all specimens showing slight effects of hybridization as "pures," except for the "Lawrence's" and "Brewster's" warblers among them. Even if this were done, the definite hybrids, including all specimens indexed between 3 and 17, plus the aforementioned "Lawrence's" and "Brewster's" individuals, would total 431 of 1,028 specimens, or 41.9 percent. Extreme views thus indicate that from 42 to over 89 percent of these specimens show evidence of interbreeding. I feel that, of the 431 specimens I regard as definite hybrids, up to 312 would not be identified as hybrids by most field observers. Counts by observers estimating the frequency of hybrids in an area will thus be biased against the hybrids.

I must stress that this analysis does not purport to demonstrate the exact proportion of hybrids in the warbler populations, as the sample is biased in many ways. However, it strongly suggests that hybrids are apt to be much more common than has previously been realized.

Breeding Populations

The results of index analysis of large samples taken from nine areas during the breeding season are shown in a histogram (Fig. 2). These samples are the largest I could gather, and together represent the bulk of available specimens taken during the breeding season (roughly from 16 May to 10 July), a total of 352 out of 500. This strongly emphasizes the lack of specimens which must be overcome if we are to understand this situation fully. The histogram includes both males and females. Each rectangle represents one specimen, the black ones denoting birds with face masks and the blank rectangles those birds lacking face masks.

The sample from Long Island represents an allopatric Blue-winged Warbler population. The histogram indicates that some introgression from *chrysoptera* is influencing this predominantly *pinus* population. This view is strengthened by occasional reports of "Brewster's" Warblers breeding on the north shore of Long Island (Parks, pers. comm.), and by occasional observations of breeding "Lawrence's" Warblers on Long Island (Nichols, in Carter, 1944:61; and pers. obs.). The occurrence of hybrids may also be indicative of a low level of *chrysoptera* genes present in the population as a result of past interbreeding. Giraud (1844) recorded *pinus* as being

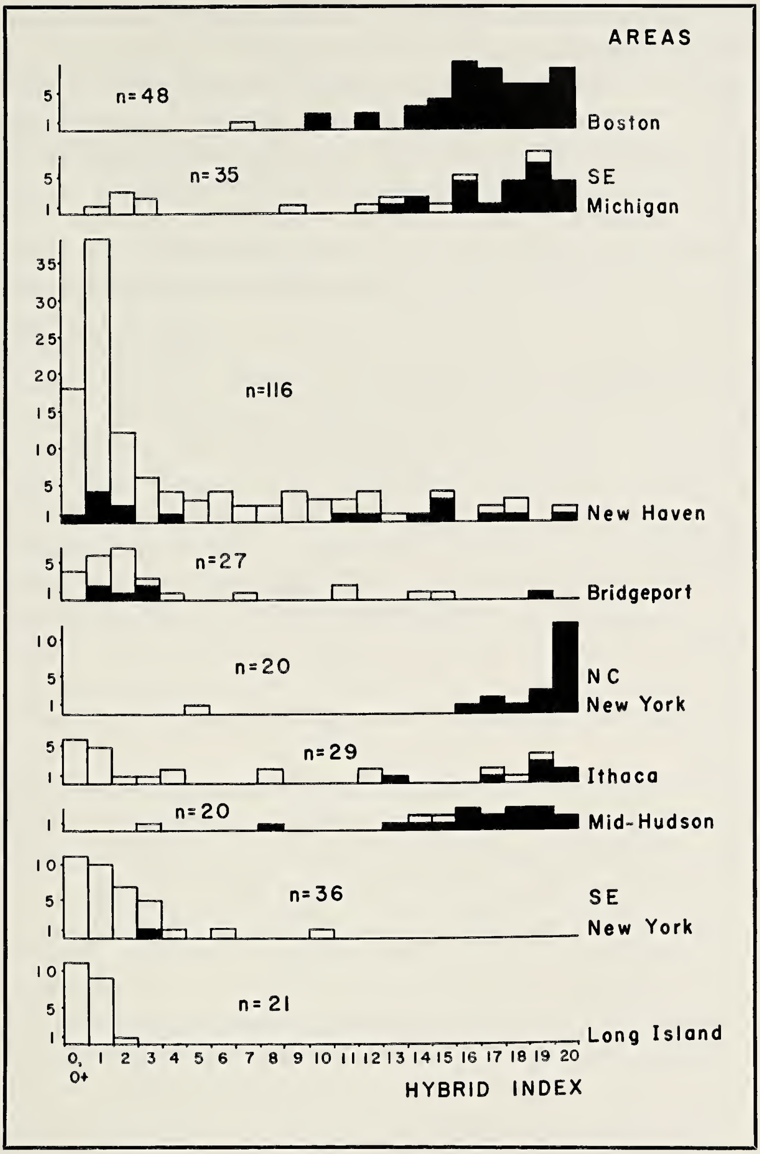

Fig. 2. Hybrid indexes of breeding adult warblers from areas represented by large samples. Black rectangles denote individuals with black face masks, and blank rectangles indicate birds lacking face masks.

nowhere abundant in New York State, and "quite rare" on Long Island, where none were seen in 2 years (p. 67). Although not mentioned as breeding, the Golden-winged Warbler was noted by Giraud (p. 68) as occurring in "small numbers" on Long Island. This suggests that Blue-wings moved into the area in numbers since that time, perhaps submerging a former Golden-wing population through interbreeding.

Birds in the southeastern New York sample come from New York City and southern Westchester County. The population is near *pinus*, but includes some intermediate hybrids. Compared with the adjacent Long Island population, the southeastern New York birds include a significantly greater number of higher-indexed specimens (significant by chi-square test at $P = 0.05$ level). This effect is expected, since New York City is closer to the overlap area.

The mid-Hudson sample comes from Orange and Putnam counties, along the Hudson River in New York. It represents the north end of the overlap area, and indicates that the population is composed mainly of hybrids. These are generally closer to *chrysoptera*, but with some in the intermediate range.

The Ithaca sample from Tompkins County, New York, is a recently secured series. Both parental types are found in this region, although they are outnumbered by hybrids ranging through the spectrum from *pinus* to *chrysoptera*. This situation has undergone recent change, since *pinus* was virtually unknown in the area prior to 1947. An influx of Blue-wings since then has resulted in extensive interbreeding, which continues at the present time. The north-central New York sample represents Cayuga and Onondaga counties, just north of the Ithaca region. The one low-indexed bird was taken recently, while most 20-indexed specimens are much older. The first Blue-wings appeared in this area in the early 1950's (Scheider, 1959). The original *chrysoptera* population is now shifting toward *pinus* as a result of hybridization.

The Bridgeport sample from southwestern Connecticut represents a mainly hybrid population, although it is closer to *pinus*. The specimen indexed 19 is an older specimen, suggesting that *chrysoptera* may have originally been more common in the area, but was gradually replaced by *pinus*.

The largest sample available is that from New Haven, Connecticut, and represents breeding adults taken within 10 miles of that city. The inclusion within the sample of individuals representing nearly every index value clearly emphasizes the need for additional material from other areas. This sample basically represents a Blue-wing population strongly influenced by introgression from *chrysoptera*. A shift toward *pinus* in the past century is clearly evident. The pre-1900 mean hybrid index for that part of the sample is 5.81, while that for birds taken since 1900 is 3.65. Nearly half (22 of 48) of the pre-1900 specimens index above 3, while less than one-third of the post-1900 specimens (20 of 68) do so. The difference between the two groups in the proportion of higher-indexed birds is significant (by chi-square test) at the $P = 0.02$ level. The evidence thus indicates that a more *chrysoptera*-like population previously existed in the area, with a shift toward *pinus* due to hybridization with incoming individuals of the latter form.

The southeastern Michigan sample is taken from an area where *pinus* is also moving into country previously supporting only a *chrysoptera* population (Berger, 1958). Specimens in this sample were mostly taken some time ago, but considerable *pinus* influence is nevertheless evident. Most of the birds indexed close to *pinus* were recently taken. Berger (pers. comm.) now feels that there are more field-identified Blue-wings than Golden-wings in the region.

The Boston sample is drawn from a population formerly more like *chrysoptera*, but changing toward *pinus* with an influx of the latter in recent years. All specimens were secured within 20 miles of Boston.

To permit a more accurate description of the situation, samples are urgently needed from all parts of the overlap area, as well as from areas of allopatry.

Character Combinations

Data concerning the number of color-character combinations at various index values are contained in Table 4. The number of character-score combinations possible with 402 hybrids indexed 3–17 is 394. This, of course, is determined by the number of specimens available per index value (see Table 4). The fact that 139 of these were actually attained indicates the considerable independence of genes controlling the various characters. It also suggests that genetic recombination resulting from hybridization and backcrossing is greatly affecting the populations' gene pools.

Arrangement of the data in Table 4 also permits comparison of the num-

TABLE 4.—COLOR-CHARACTER COMBINATIONS AND TOTAL NUMBER OF SPECIMENS PER INDEX VALUE

Hybrid Index Value	Mask Present (No.)	Mask Absent (No.)	Total No. Studied	Possible Score Combinations	Attained Score Combinations
0	1	47	48	1	1
0+	0	111	111	1	1
1	11	174	185	5	5
2	5	72	77	15	10
3	3	33	36	35	14
4	2	19	21	21	7
5	0	9	9	9	6
6	0	8	8	8	5
7	1	5	6	6	5
8	3	11	14	14	5
9	2	8	10	10	9
10	3	10	13	13	6
11	13	6	19	19	12
12	17	10	27	27	14
13	21	4	25	25	12
14	43	5	48	48	10
15	52	8	60	60	11
16	56	7	63	63	12
17	40	3	43	35	11
18	50	4	54	15	11
19	79	7	86	5	5
20	64	1	65	1	1
Totals	466	562	1,028	436	173

bers of specimens at various index values in relation to the presence or absence of the face mask. Birds lacking the face mask range in hybrid index from 0 to 20, while those having the mask nearly do likewise. This tremendous variation again stresses that the terms "Lawrence's" and "Brewster's" cannot be applied precisely, and should be avoided wherever possible in favor of careful observation and notation of all features of color pattern.

SONG AND HABITAT

The Blue-winged and Golden-winged warblers supposedly differ in song and in habitat preference. Although such differences may have once existed, they are at present poorly defined.

The common song of the Blue-wing is rendered *bee-bzzzzz,* and that of the Golden-wing *bee-bzz-bzz* (additional *bzz* notes may be added in the latter form). Both have an alternate song which is similar, and also a late season song of a quite different nature from those given earlier, but which is again similar in the two warblers. Ficken and Ficken (1962) point out (following Saunders, 1951) that the early "territorial songs" of closely related species are apt to be different, while the "nesting songs" given later in the season tend to be more similar. Any song difference functioning as an isolating mechanism is, then, most apt to occur in the territorial songs. Available evidence suggests that song differences do not function effectively as isolating factors. The fact of widespread hybridization and backcrossing itself indicates this. The alternate territorial songs of the two, as noted above, are similar, the considerable variation of the song in each allowing for overlap. The primary song itself is variable (pers. obs.; F. Gill, pers. comm.) in the two forms. In fact, phenotypically pure individuals of one form may sing only the song of the other (see Table 5). This is true not only in the overlap area, but in allopatric populations, for I have heard a Long Island Blue-wing male on territory singing a passable (although not completely typical) Golden-wing song. Furthermore, Carter (1944), Eisenmann (1946), and I (1962) have noted the interchanging of the primary territorial song of both forms in the *same* individual (see Table 5). Learn-

Table 5.—Songs and Habitats of 38 Warblers in Central New York

Phenotype	Hybrid Index	SONG TYPES[a]			HABITAT[a]		Total Number Collected[b]
		c	p	c–p	c	p	
Chrysoptera	20	1	0	0	0	4	5
"*Chrysoptera*"	17–19	5	0	1	5	3	11
Hybrids	4–18	3	2	1	5	2	7
"*Pinus*"	1–3	2	3	0	4	2	8
Pinus	0–0+	1	2	1	2	3	7

[a] c = *chrysoptera* song type (*bee-bzz-bzz*) and habitat (dry, hillside). p = *pinus* song type (*bee-bzzzzzz*) and habitat (wet, lowland). c–p = both song types sung interchangeably.

[b] Collected in 1958–62 in Tompkins and Onondaga counties. Habitats and song not reported for all specimens.

ing may well play a role in determination of song type in these warblers. Territorial song types of males of various phenotypes taken in the overlap area (central New York) are indicated in Table 5. Each male sang at least 20 times before being collected.

A difference in habitat preference between the two warblers has been noted by various workers. In the eastern overlap areas, Blue-wings supposedly prefer low, swampy, semi-open areas, while Golden-wings occur in drier, upland, woodland-edge situations. However, the exact reverse seems to be the case in western states (Berger, 1958)! Parkes (1951:6) has noted that there is much local variation in habitat preference in the East, with occasional reversal of the usual situation. Olsen (1931) pointed out that Blue-wings were never found (in Michigan) where Golden-wings did not also occur. It is certainly true that Blue-wings moving into central New York have inevitably appeared in previously existing Golden-wing colonies. Habitats of male warblers on territories in central New York are indicated in Table 5. The variability in habitat preference shown by hybrids is interesting, but more important is the information concerning the phenotypically pure individuals. Six of the nine phenotypically pure birds of the two forms for which habitat information was available were in the "wrong" habitat (i.e. that of the other form). These data, although scanty, suggest that a difference in habitat preference between the two forms, if it exists, is ineffective in limiting contact between the warblers. Again, the fact of widespread hybridization further substantiates this.

RECENT HISTORY

Attempts at tracing past histories of extant species with inadequate (or no) fossil evidence are at best hazardous; but, when based upon several kinds of evidence, they are certainly warranted as better than no attempts at all. Some evidence is available suggesting that the present interbreeding between *pinus* and *chrysoptera* is the result of a secondary contact between once isolated western and eastern populations, although the present contact is essentially oriented north–south.

The first line of evidence is derived from the pattern of the winter ranges of the two warblers. The winter distribution of *chrysoptera* is mainly from southern Guatemala and Nicaragua south into Colombia and Venezuela. That of *pinus* is more northerly, from Mexico to Nicaragua (occasional individuals reach South America). Despite the amount of overlap, the general pattern is similar to that found for a number of east–west species pairs (e.g. *Passerina cyanea–P. amoena, Pheucticus ludovicianus–P. melanocephalus, Icterus g. galbula–I. g. bullockii,* and *Piranga olivacea–P. ludoviciana*), in which the eastern forms migrate farther south than their western counterparts.

The breeding distributions of the two birds are also suggestive of an original east–west situation. The range of *chrysoptera* tends to be northern and eastern, and that of *pinus* southern and western (see Fig. 1). The Golden-wing is more common on the eastern slope of the Appalachians, where *pinus* is scarce. The broad area of allopatry for *pinus* is in the Mississippi River region, southwest of *chrysoptera*. The hybrid-index study of northeastern breeding populations (above) indicates that *pinus* has only recently entered the Atlantic coastal states. The general northward movement of this form recently is probably related to man's activities (as suggested by Mayr, 1942), and probably also to natural factors.

Hobbs (1950) has discussed the Pleistocene history of the Mississippi River, especially documenting the Mississippi Embayment concept. At the height of glaciation, the river was a swollen channel of water 100–200 miles in width, extending from near the glacial front in Illinois south to the Gulf of Mexico. A combination of this water barrier and the glacial ice to the north could have separated the ancestral warbler population into eastern and western segments. The geographically isolated populations may then have differentiated into the distinctive western (*pinus*) and eastern (*chrysoptera*) populations, which, however, retained the ability to interbreed. The western *pinus* probably inhabited the prairie-forest edge. To the east, *chrysoptera* must have found suitable habitat along the southeastern coast. With the advent of deglaciation, both forms began to move northward. Continuing amelioration of the climate in the East allowed *chrysoptera* to extend northward to New England, and then westward into the Great Lakes region. The *pinus* population in the Mississippi area was probably prevented from reaching the Great Lakes by increasingly dry climate, culminating in the xerothermic period. At this time, grasslands extended into the north-central and even the northeastern states as the "Prairie Peninsula" (see discussion in Smith, 1957). During this period, *pinus* was restricted by the forested Appalachians and the Prairie Peninsula to the Mississippi region. Perhaps edge habitat along the southern part of the Prairie Peninsula allowed *pinus* to move into the northeastern states for the first time during the xerothermic period. At the same time, *chrysoptera* would have been able to exist north of the Prairie Peninsula from Minnesota to New England, with a subpopulation probably inhabiting the Appalachian Mountains (in burned over areas?). The present contact between the forms in the West appears to have resulted from *pinus* moving northward into the old Prairie Peninsula area, meeting *chrysoptera* along a line from Iowa to Ohio. The eastern contact is more difficult to assess. Man has certainly played an important role in creating new edge habitat and in draining wet areas. At any rate, evidence (discussed above) indicates that *pinus* has entered the eastern overlap areas, if not the East itself, in very recent times.

CONCLUSIONS

Results of this study indicate that interbreeding is strongly affecting populations of these warblers. A crucial point has been reached in the evolution of these populations. If there are any partially isolating mechanisms in the populations, then extensive interbreeding should cause reinforcement of these mechanisms to preserve the integrity of the parental gene pools. On the other hand, if isolating mechanisms are lacking or are ineffective, we may expect a reshuffling of the gene pool based upon selection favoring certain of the genotypes, and perhaps the ultimate resolution of the situation in some form of polymorphism. Needless to say, far more work must be accomplished before we can ascertain what is actually happening and determine what direction selection is dictating. Fortunately, interest in this problem is currently strong, and much progress can be anticipated in the near future.

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SUMMARY

The Blue-winged Warbler and Golden-winged Warbler are broadly sympatric over a large part of northeastern North America. Hybridization between the two occurs throughout the area of sympatry. The hybrids are fertile, and backcrossing is taking place.

Analysis of color patterns of 1,028 adult specimens provides evidence that interbreeding is greatly affecting the parental populations. Samples from breeding populations in the overlap area indicate that hybrids greatly outnumber individuals of the parental types.

Differences in song and habitat preference are not sufficiently strong to provide effective isolating mechanisms. Songs are variable, probably affected by learning, and those of both forms are occasionally given by the same bird. Reversal of supposed habitat preferences of the two are common. In the overlap area both forms are consistently found interbreeding in the same colonies.

It is suggested that the Blue-winged and Golden-winged warblers are in secondary contact following former isolation into western and eastern disjunct populations due to the Mississippi Embayment. Evidence for this is drawn from a study of their winter ranges, analysis of samples from breeding populations in the overlap zone, and recent biogeographic and geologic investigations dealing with the Pleistocene.

Field investigation and specimen analysis have so far failed to provide evidence of any sort for the existence of partially isolating mechanisms. Although hybridization is widespread, phenotypically pure individuals persist, even where interbreeding has been occurring for some time. Continued interbreeding at the present rate may lead to swamping of the differences between the two as they merge, or may result in the establishment of some form of polymorphism.

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Hybridization in Certain Brazilian Fringillidae (*Sporophila* and *Oryzoborus*)[1]

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My special interest in South American finches increased 2 years ago when it became obvious that one of the Brazilian seedeaters, which I had observed and collected on previous occasions, appeared to be identical with the mysterious *Sporophila ardesiaca* described by Dubois in 1894 from a specimen later considered to be *S. nigricollis* that had lost its original color in the alcohol in which it was preserved (Sick, 1962).

When I started on this subject, I was again struck with the extent of variation in the genus *Sporophila*, which is bound to impress anyone who works with these seedeaters. Individual variations in *Sporophila* have been analyzed previously by Chapman (1926), Hellmayr (1938), de Schauensee (1952), and others. Among other peculiarities indicated, there has been noted a recurrent tendency to develop an alar speculum and a moustachial streak. Sometimes, however, new markings show up, like a black throat in some *Sporophila torqueola* from Guatemala.

Very rarely has anyone suggested that abnormalities in *Sporophila* may not be individual variation but the outcome of hybridization. In the literature known to me, I find only three references. Lordello (1957) remarked on a specimen thought to be a cross between *S. collaris* and *S. leucoptera*. The skin was also examined by John Todd Zimmer and by Herbert Friedmann, who both arrived at the same conclusion. The bird in question was a natural hybrid from the State of São Paulo, Brazil. In her check-list of bird hybrids, Gray (1958:278) mentions two further crosses, between *S. albogularis* and *S. intermedia* and between *S. albogularis* and *S. nigricollis*, obtained from captive birds and thus of known parentage.

The scarcity of data on *Sporophila* hybrids contrasts sharply with the wealth of information available on interbreeding of other Fringillidae, e.g. Sibley's outstanding papers on North American towhees (*Pipilo*), buntings (*Passerina*), etc. (Sibley, 1954; Sibley and Short, 1959*a*).

While I was working on *S. ardesiaca*, I came to the conclusion that certain variations described in my paper (1962) were probably the result of hybridization—or of intergradation, if we consider *S. ardesiaca* merely a race of *S. nigricollis* and not an independent species. There were 2 examples of *ardesiaca* with traces of *nigricollis*, 1 *ardesiaca* with traces of *caerulescens*, and 5 or 6 *caerulescens* that suggested the influence of *ardesiaca*. Finally, 1 *Sporophila n. nigricollis* seemed to show traces of *caerulescens*. All were skins

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[1] The paper presented at Ithaca was accompanied by 31 colored slides.

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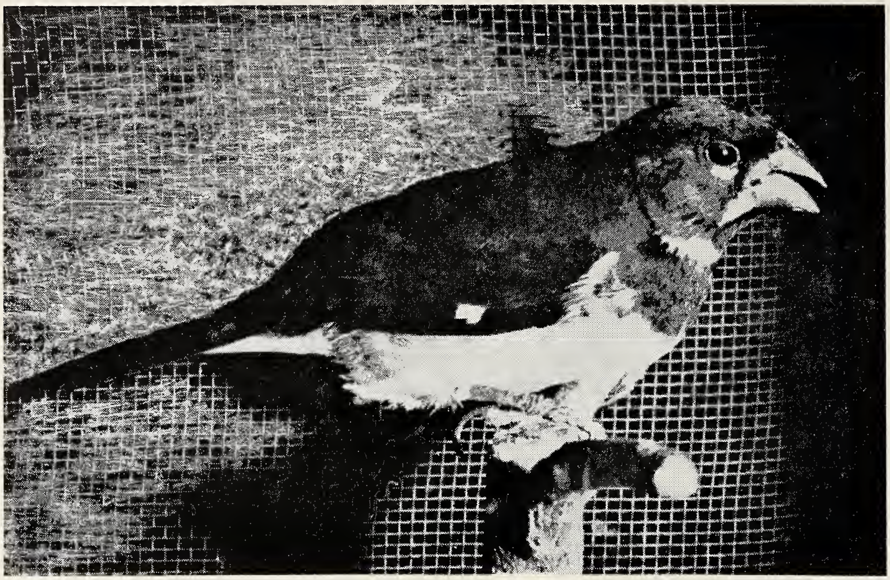

Fig. 1. Suspected hybrid *Oryzoborus angolensis* × *Sporophila caerulescens*, Bird II (Mario 1), Rio, September 1961. Living cage bird.

of wild birds collected in southeastern Brazil (southern Minas Gerais, Espírito Santo, and Rio de Janeiro).

THE PRESENT STUDY—MATERIALS

These surprising findings roused my curiosity and tempted me to go deeper into the matter. Field trips being out of the question at the time, I decided on a simpler method. I visited the bird shops in Rio and got in touch with aviculturists. In Brazil, *Sporophila* and other finches are popular cage birds sold in large numbers (Sick, 1960).

I found a few more *S. ardesiaca* (of uncertain source) and other rare species, such as *S. cinnamomea* (from Campo Grande, Mato Grosso), *S. melanogaster* (from Campanha, Minas Gerais), *S. ruficollis, S. falcirostris,* and a case of gynandromorphism in *S. caerulescens.* I also got data on the problem of "variations" and some hints on hybridization.

One bird fancier showed me a finch (*Bird I*) with the general aspect, size, and tail length of the Chestnut-bellied Rice Grosbeak, or Seed-Finch (*Oryzoborus angolensis*), including the thick black beak, color of back, head, throat, and chest, and large speculum of that species. But it differed in having a faint white moustachial streak, a narrow (3 mm) white band across its throat, a white speck below the eyes, and a pure white (instead of chestnut) belly. Its song, a soft twitter, sounded wholly different from the rich well-pronounced song of *O. angolensis.* It had been bought in Rio de Janeiro.

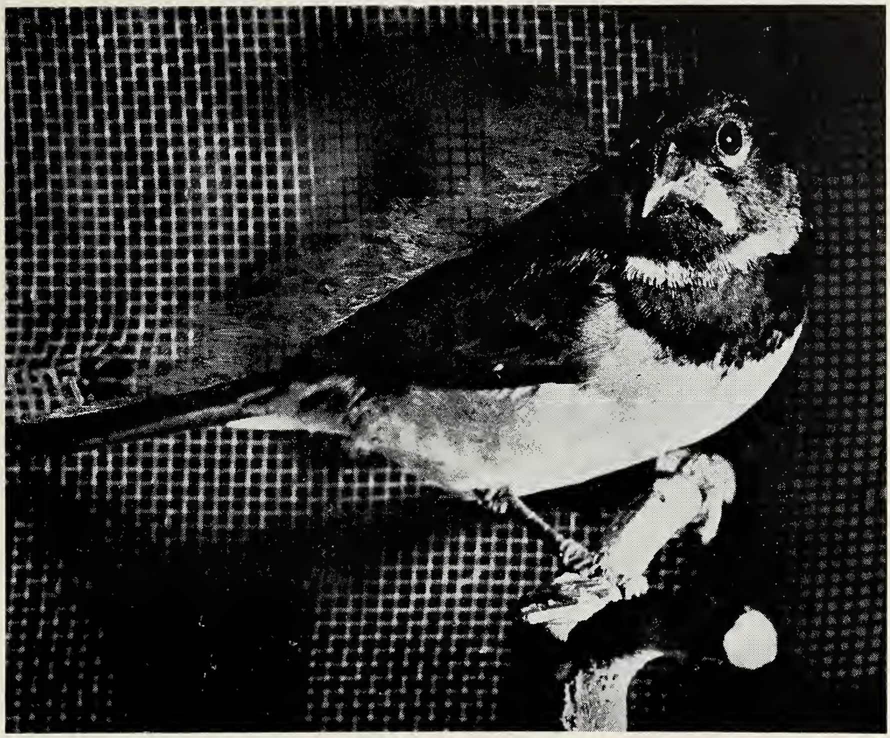

Fig. 2. Suspected hybrid *Oryzoborus angolensis* × *Sporophila caerulescens*, Bird III (Mario 2), Rio, September 1961. Living cage bird.

Another aviculturist surprised me with no less than five fringillids that somewhat resembled the bird I have just described. Their general appearance was also like that of *O. angolensis*. Special traits were as follows:

Bird II—similar to the first one, speck below the eyes, narrow band across throat (broken for 2 mm at center), moustachial streak and belly white (Fig. 1).

Bird III—like the last one, except that the light parts were pale cream-colored not white, especially on the flanks; gap in throat band a little wider (Fig. 2).

Bird IV—whitish speck below the eyes, cheek stripe, throat band, and belly rufous, much brighter than in *Bird III*, but paler than the lower part of the typical *O. angolensis*.

Bird V—moustachial streak enlarged to a fan-shaped cheek spot; this spot and belly rusty yellow, crown and forehead with a suggestion of white along middle; without light throat band; no eye speck (Fig. 3).

Bird VI—back, head, and throat uniform black, no special markings; dark beak like *Birds I–V*; lower parts pure white.

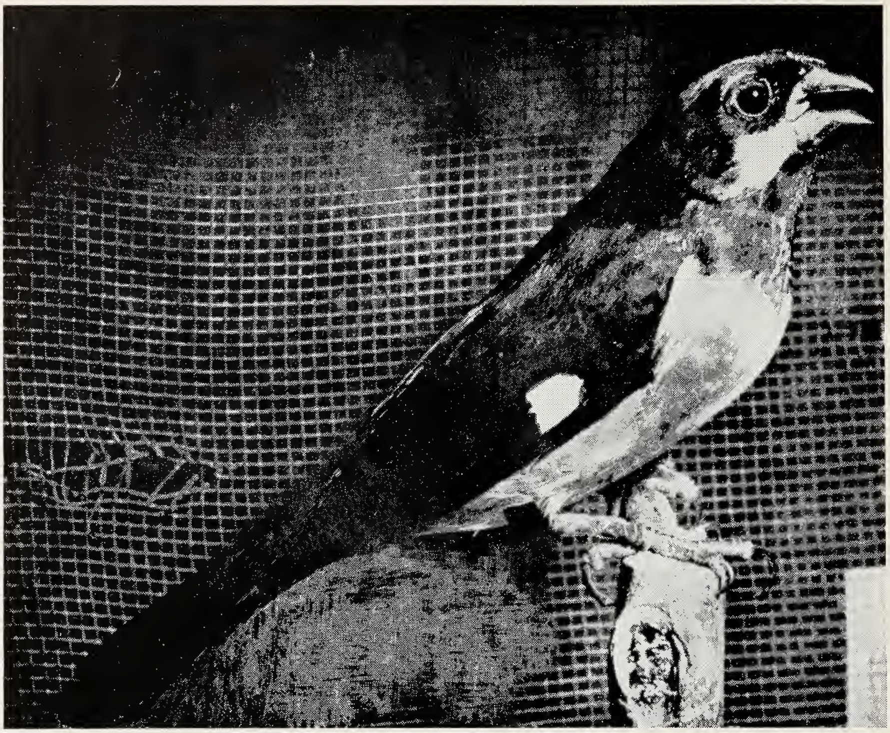

Fig. 3. Suspected hybrid *Oryzoborus angolensis* × *Sporophila lineola*, Bird V (Mario 4), Rio, September 1961. Living cage bird.

All five of these birds called and sang like *O. angolensis*, except for No. VI. Along with the typcial tune of the Chestnut-bellied Rice Grosbeak, this bird sometimes uttered very rapid twittering sounds like the song of a *Sporophila,* such as *caerulescens.* (A tape recording of the vocalization was presented at the XIIIth International Ornithological Congress.) All five birds had been purchased in Rio. Their owner also possessed a number of normal-plumaged seedeaters (*Sporophila*) and no less than 18 normal-colored males of the Chestnut-bellied Rice Grosbeak, whose exuberant singing filled the little suburban home with a deafening noise.

A third Brazilian aviculturist had in his collection four abnormally colored finches. There were two Chestnut-bellied Rice Grosbeaks, one of which (*Bird VII*) looked much like my *Bird V,* the one with the broad light cheek spot, but this spot was vivid rufous, not rusty yellow. Its underparts were of the deep chestnut typical of *O. angolensis.* The bird seemed to be slightly smaller than the ordinary Chestnut-bellied Rice Grosbeak, its beak not so strong. The other (*Bird VIII*) was a little like my *Birds II* and *III,* having a well-marked white moustachial streak and a broad white band on its throat; lower parts yellowish; it was nearly as large as *O. angolensis.* Neither of these birds obliged by singing while I was there.

In addition, this same aviculturist had in his collection the following two interesting seedeaters:

Bird IX—with the characters (I believe) of *S. bouvreuil pileata*, but with a hint of a white crown.

Bird X—with mixed markings of *S. b. bouvreuil* and *S. plumbea.*

The last four finches also came from southeastern Brazil and had been purchased in the market.

DISCUSSION

What are the conclusions that can be drawn from these facts? Eight birds bear unmistakable markings of *Oryzoborus angolensis*, whose influence can be clearly detected in size, proportions, coloring of upper parts, throat, and chest, and, generally, thickness of beak. To account for the abnormalities, one might suppose individual variation within this species of grosbeak. This interpretation has the backing of Hellmayr (1938:245), who comments as follows on *O. angolensis*:

> While throat and chest, as a rule, are uniform black in adult males, there are sometimes a number of half concealed spots of whitish or cinnamon and occasionally even a nearly complete rufous band across the throat, as described by Finsch for his *Oryzoborus specularis.* This is, however, a purely individual variation, since of the specimens so marked two are from Trinidad and one from São Paulo, Brazil.

On the other hand, one cannot but be impressed—at least I am when I look at the live birds before me—by the fact that all these abnormalities resemble plumage traits typical of certain species of *Sporophila.* In at least two cases (*Birds I* and *VI*) the *song* also recalled that of *Sporophila.* In one case it was nearly identical; the other seemed to be a mixture of those of *Sporophila* and *Oryzoborus.*

The possibility of interbreeding between *Oryzoborus* and *Sporophila* was surprising. *Oryzoborus* is a very different kind of finch. Observed at a distance, *O. angolensis* does not seem to have much in common with *Sporophila.* The genus *Oryzoborus* includes such closely related forms as *O. angolensis* and *O. crassirostris*, both found in Brazil. Natural hybrids between these two species have been reported from São Paulo (Lordello, 1957), but I have never heard that rice grosbeaks mix with fringillids of other genera.

If my supposition about interbreeding between *Oryzoborus* and *Sporophila* is correct, it would mean that the two genera are related more closely than has been supposed. Indeed, the idea may not seem so strange if we compare extreme forms of each. The comparatively small Lesser Chestnut-bellied Rice Grosbeak (*Oryzoborus angolensis torridus*), with its short tail and moderately strong beak, does not seem so far apart from the rather large, strong-beaked *Sporophila a. americana.* Both live in the same area in the northern part of South America. The small, all-black *Oryzoborus funereus* of Middle America also has resemblances to the sympatric *Sporophila aurita corvina.*

Whether or not my *Birds I–VIII* are really crosses between *Oryzoborus* and *Sporophila* remains to be confirmed. So far, all I could do was to draw a rough outline of the phenotypes based on the appearance of the live bird. Accurate morphological study will have to wait until the skins are available for inspection. The great advantage of working with live specimens rather than with skins is the possibility of also evaluating behavior patterns and voice. The voice of the Chestnut-bellied Rice Grosbeak differs considerably from that of nearly all *Sporophila* known to me, both in call and song. The song of *Oryzoborus angolensis* is a full descending phrase. Sometimes a series of such phrases is linked by high-pitched twitter. The twitter (stronger when there is competition with another male *Oryzoborus*) resembles somewhat the song of such *Sporophila* as *caerulescens*.

It is my impression that, in the production of the eight birds mentioned here, the following species of *Sporophila* have participated: *S. caerulescens* four times (*Birds I–IV*) and perhaps also in *Bird VIII*; *S. lineola* two times (*Birds V* and *VII*); *S. ardesiaca* once (*Bird VI*). According to Art. 18 of the International Rules of Nomenclature (Richter, 1948), when writing names of hybrids that of the father should precede that of the mother. Alphabetical order is also sometimes used. In naming my surmised hybrids of unknown parentage, e.g. *Oryzoborus angolensis* × *Sporophila caerulescens*, I mean to convey that the traits of *O. angolensis* are more pronounced than those of *S. caerulescens*. As I have said, 2 birds sang like *Sporophila* (one had 2 tunes); 4 sang only like *Oryzoborus*. The voice of the other two I have not been able to investigate so far.

Now let me return to Hellmayr's remarks about individual variation in *Oryzoborus angolensis*. Evidently, Hellmayr referred to the variation of the Chestnut-bellied Rice Grosbeak because he wanted to stress that it cannot be accounted for geographically. The idea of hybridization probably did not enter his mind. Therefore it may be advisable to re-examine the older skins. The two specimens of *O. angolensis* from Trinidad mentioned by Hellmayr perhaps show signs of *Sporophila americana*, and the one from São Paulo may be something like the birds I am working with now. For all we know, this might also apply to Finsch's (1870:583) *Oryzoborus specularis*, also from Brazil, now included in the synonymy of *O. a. angolensis*.

After having found so many abnormalities in the rice grosbeak that probably point to contact with certain seedeaters, it would no longer be a surprise to find abnormalities within the genus *Sporophila* that might have been caused by hybridization. As I pointed out, my *Bird IX* apparently combines markings of *S. bouvreuil pileata* and *S. lineola*, *Bird X* those of *S. b. bouvreuil* and *S. plumbea*.

SUPPLEMENTARY STATEMENT AND CONCLUSIONS

My investigation brings to light two seemingly contradictory facts: (1) Hybridization among a number of Brazilian finches of the genus *Oryzoborus* and *Sporophila* is not uncommon; (2) in the past, almost no variations suggesting interbreeding have been reported, despite the vast number of skins of *Oryzoborus angolensis* and various *Sporophila* that found their way into museums all over the world during the past hundred years.

If my hypothesis of hybridization is correct, the contradiction could be explained either (a) if no crossing took place in the past, or (b), if it did, it was not recognized. In my opinion, hybridization along the lines suspected has gone on to some extent for a long time, but it has increased lately. It is possible that the older skins in museums consist of very few specimens of hybrid origin and that therefore the question of interbreeding did not arise. In the skins I have seen in Brazil, I find the first signs of probable hybrid origin in specimens of *Sporophila ardesiaca* and *S. caerulescens* collected in Brazil by E. Snethlage in 1925–26 in Minas Gerais and Espírito Santo, then in a few specimens of *ardesiaca* and *caerulescens* and in one *nigricollis* collected in the forties in Minas Gerais, Espírito Santo, and Rio de Janeiro: a total of ten specimens, as detailed in my paper (1962) on *Sporophila ardesiaca*. Concerning *Oryzoborus*, I never saw skins that could be considered abnormal, and the only references I know concern the hybrid cited by Lordello and the data quoted from Hellmayr.

The accumulation of findings in recent times, especially regarding *Oryzoborus*, is probably due to a growing interest in the subject, both by the amateurs and myself. Other than the 8 specimens of *Oryzoborus* mentioned, I saw 3 more cage birds that were similar to the ones described in detail above and 1 more abnormal live *Sporophila*, all these probably being hybrids, too.

More frequent interbreeding among these finches in recent times might well be ascribed to the rapid breaking up of their original habitat. The forests are being cut down, which means destruction of natural barriers that previously separated areas of shrub and farmland where these finches occur. Analogous conditions are found in many other cases where hybrid populations have been examined. In South America (including Brazil) the same breakdown of habitat has happened to tanagers of the genus *Ramphocelus*. Where such conditions prevail, sometimes a mixed area of general steadiness developed in the course of time. In other instances, the tendency to crossbreed ceases after a while. Nothing seems to be on record about the occurrence of hybrids having resulted in blurring the borderline between two species (Mayr, 1942). What is happening today with *Sporophila* and *Oryzoborus* in their rapidly vanishing natural habitat in southeastern Brazil remains to be investigated in detail.

While little is known about the ecological demands of most *Sporophila* species, some of these birds have succeeded in adapting to cultivated land. In the new surroundings they meet other seedeaters with which they had little or no contact before.

The case of *Oryzoborus*, however, is probably different. Could lack of mates of the same species play a part? *Oryzoborus angolensis* is one of the fringillids most persistently persecuted by Brazilian aviculturists. Where men arrive, the species soon declines. In no time the grosbeak is rarer than the also much-coveted *Sporophila*. The latter, though, is less endangered because there are so many of them. A situation of this kind may favor interbreeding. Lordello (1957) suggested something like this in view of his hybrid *O. angolensis* × *crassirostris*. He writes that, in his observation area in the State of São Paulo, *Oryzoborus crassirostris* was almost exterminated by continued catching, and that the population of *O. angolensis* decreased steadily. He thinks that, for lack of a male of her own species, a *crassirostris* female may have accepted an *angolensis* male. Actually, more males than females get caught; the males, being singers, fetch a better price in the market. Sibley and Short (1959*b*), studying bulbuls (*Pycnonotus*) in India, come to the conclusion that "hybrids rarely occur except where one species is uncommon."

Many of the problems mentioned in my paper cannot be resolved by study of skins and by field work. The extraordinary likeness of the females of several species of *Sporophila* make definite recognition in the field practically impossible. A given male may have relations with a female of another species without the observer realizing the latter's true identity. Lordello points out that relations of this sort do occur; his conclusion is evidently based on watching captive birds. He mentions occasional courting between *Sporophila caerulescens* and *S. lineola*, and also between *Oryzoborus angolensis* and *O. crassirostris*. It is necessary, therefore, to make observations on a wider scale using captive birds of known parentage housed in proper aviaries. Only then will it be possible to check if hybridization, as suspected by me, actually takes place. In this manner we can hope to obtain complete records on the resulting offspring and their ability to propagate. At present we do not know whether the suspected natural hybrids are first crossings or backcrossings and whether they are fertile. Of special interest is the voice of the hybrids—a rather complex question where inherited traits are hard to tell from those learned by imitation. The identification of female hybrids (they are perhaps rarer than males) will always be a problem.

In Brazil, these finches are nearly always kept in tiny single cages quite unsuitable for breeding. There it is much easier and also cheaper to catch wild birds or buy new ones than to breed them. Nevertheless, the desire to own a hybrid, common to aviculturists all over the world, applies to Brazil as well. The bird fanciers who owned the surmised natural hybrids described here mostly realized their nature correctly and were very proud of them. One of these amateurs offered the astonishing piece of information that for the past 40 years he had repeatedly visited different places in the State of São Paulo (Mogy das Cruzes among others) to release various species of

Sporophila (especially *nigricollis* it seems), "in order to invite interbreeding" he added; but he said nothing definite about results.

In view of the extent of the commerce in Brazilian *Sporophila* (a total of 20 species occur in that country, and over half of them play a considerable role in the market), and the practice of releasing specimens on purpose, it is not out of the question that in time some local fauna may change in composition and puzzle the unsuspecting scientist! In this connection, I would recall a frustrated attempt at explaining the present distribution of the House Sparrow (*Passer domesticus*) in Brazil simply on a theoretical basis. It was not taken into account that the bird had been introduced from abroad time and again at different ports; and that it had been, and still is being, transferred in cages to new places inside the country by people who love to have it around! The result is a widespread and rapidly attained occurrence of the House Sparrow in Brazil, interspersed with unoccupied areas in a manner that cannot be explained by natural range extension.

ACKNOWLEDGMENTS

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SUMMARY

This paper describes the phenotypes of some finches of southeastern Brazil suspected to be hybrids. Eight of the birds dealt with appear to be crosses between *Oryzoborus* and *Sporophila*, as follows: *Oryzoborus a. angolensis* × *Sporophila c. caerulescens* (5 specimens), *Oryzoborus a. angolensis* × *Sporophila lineola* (2 specimens), and *Oryzoborus a. angolensis* × *Sporophila ardesiaca* (1 specimen). Two specimens are thought to be hybrids within the genus *Sporophila*, namely: *S. bouvreuil pileata* × *S. lineola*, and *S. b. bouvreuil* × *S. p. plumbea*. All ten birds had been captured in the wild and were studied alive in captivity. In a few cases, song seemed to confirm mixed parentage.

A moderate amount of crossing of these fringillids may have occurred for some time without having been recognized. It also seems likely that hybridization may have increased recently in consequence of human activity of various kinds in southeastern Brazil: (1) the destruction of forests that formerly functioned as barriers between separated brushy areas where species, which are now in contact, originally occurred separated from each other; and (2) the increasing rarity of certain species, partly due to persistent capturing, which may promote hybridization with other forms.

RESUMO

Descrição de fenótipos de alguns fringilídeos do Brasil austro-oriental, de provavel ascendência híbrida. Oito das aves estudadas parecem provir de cruzamento entre *Oryzoborus* e *Sporophila*, das seguintes espécies: *Oryzoborus a. angolensis* × *Sporophila c. caerulescens* (5 espécimes), *Oryzoborus a. angolensis* × *Sporophila lineola* (2 espécimes), e *Oryzoborus a. angolensis* × *Sporophila ardesiaca* (1 espécime). Dois espécimes denotam cruzamento dentro do gênero *Sporophila*: *S. bouvreuil pileata* × *S. lineola*, e *S. b. bouvreuil* × *S. p. plumbea*. Todas as aves provem de ambiente natural e foram estudadas em captiveiro. Em alguns casos tambem a vôz parece confirmar ascendência mixta.

Admite-se que sempre houve cruzamento entre os fringilídeos mencionados, mas em pequena escala, e sem ter sido reconhecido. Ultimamente, porém, interferência humana nos domínios dessas aves parece ter concorrido para acentuar o fenômeno. Nessa categoria temos, 1.: a derrubada cada vez mais extensa de trechos de mata que formavam barreira entre lugares abertos e meio abertos onde as várias espécies originalmente viviam segregadas umas das outras, mas agora entram em contacto; 2.: diminuição do número de indivíduos de certas espécies, em parte provocada pela perseguição desenfreada que o homem lhes move onde avança pelo sertão. Ambos seriam fatores a fomentar a hibridação.

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Taxonomic Significance of Wing Molt

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A much-neglected field of work is the study of molt. It is well known that the plumage is not renewed at random, but that the process of its replacement follows certain patterns, each of which may be characteristic for certain natural groups. Since the remiges, and especially the primaries, of a bird are of paramount importance to such a highly specialized flying organism, one should expect the way in which they are replaced to be strongly controlled by selection. This consideration has been one of the reasons why my wife and I began some years ago to study the sequence in primary molt. By good fortune we started with the Falconidae, which all show the same most peculiar but regular mode of molting. The results were encouraging, and we decided, therefore, to extend our work to other groups. Yet we could not have reached satisfactory results on a large scale without the privilege of continuing these studies for a couple of months in the superb bird collection of the American Museum of Natural History. Our final aim is to find out the sequence of primary molt in all groups of birds, and we hope to approach it as closely as seems possible with our methods.

This means that we shall have to examine a considerable quantity of skins in addition to the many thousands that have already passed through our hands. In several important cases, even the material of the American Museum proved inadequate for our purpose. Up to the recent past, many collectors seem to have shunned preserving birds in an active stage of wing molt, and in some instances we handled more than 100 skins of the same species without finding a single molting one. Future collectors should therefore be encouraged to value molting birds as objects of scientific importance. We would even suggest that birds with wings in molt should be prepared with one wing fully expanded.

Our attention was directed only to the primaries, and we did not try to extend our work to the secondaries. Those who have ever attempted to investigate wing molt in dry skins will know why we ungrudgingly left work on secondaries to the skill and endurance of someone else.

Of all the sequences in which the primaries are dropped and replaced, the descending mode is the most widespread. This term means that the molt starts with the innermost primary and proceeds gradually to the outermost. In certain orders of birds the sequence is reversed, starting with the outermost primary and ending at the carpal joint. This is called the ascending molt.

The tempo of a strictly consecutive replacement of primaries is subject to considerable variation. One extreme of the scale is represented by some

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groups of tropical species, among them the honeyguides (Indicatoridae) in which we never found more than one primary in some stage of growth. In large birds a considerable slowness of the molt process can be inferred whenever, out of some dozens of skins which have been collected the year round, practically every one has a molting primary. We found this in the large hornbill *Dichoceros bicornis*. On the other hand, there are single species or groups of species with a very fast descending molt. The Common Gull (*Larus canus*), for instance, seems to replace the ten primaries soon after the breeding cycle and within hardly more than 8 weeks. We have seen several specimens in which three consecutive primaries of the distal group were all in early stages of growth, still unfit for sustaining flight, and we wonder how such a bird may manage to feed on the wing at all.

In the most extreme cases, speeding of molt is performed without any regard to the effect on flight—by shedding all remiges simultaneously as do swans, geese, and ducks. This mode has evolved only in species that, while deprived of flying capacity, shelter themselves in the dense vegetation of marshes, or by swimming and diving, or else, in the case of the female hornbill, hide in the safe confinement of the breeding hole.

Many birds that cannot afford temporary flightlessness or much-reduced flying capacity follow another (although less effective) principle for speeding the process—by shedding almost synchronously two or even three primaries separated by not-molting ones. This principle is reflected in two rather different modes of molt, which we shall call *A* and *B*.

A. The molt starts with a primary inserted somewhere between the outermost and the innermost. From this starting point, which may be named the focus, the process spreads in both directions, toward the wing tip after the descending mode, toward the carpal joint after the ascending mode. If, for instance, the focus is represented by the 6th primary, the next to follow jointly will be the 5th and the 7th, then the 4th and 8th, and so on. This is found in *Platycercus* and allied genera of parrots.

B. Two or three foci appear in the wing at the same time or after a short interval. From each of them the molt proceeds in the same direction. To quote an example: The molting wing of the Alcedininae has two foci, represented by the 1st and the 7th primaries, from both of which the molt proceeds distally to end with the 6th and the 10th (Stresemann and Stresemann, 1961*b*).

Usually, however, wings with two or more starting points are molted in a less regular way. Very often only one focus, mostly the proximal one, has its fixed position, it being invariably located in the same primary, while the distal focus may be represented, for instance, by the 7th or the 8th or the 9th primary. This type is connected by intermediate steps with the totally irregular molt, which we found chiefly among larger birds, but also among small ones, such as *Ceryle rudis* and perhaps *Micropsitta*.

Special modes of molt are to be found among the Cuculidae (Stresemann and Stresemann, 1961*a*). *Urodynamis*, for instance, molts the primaries alternately, starting with the even ones (10, 8, 6, 4) followed by the odd ones (9, 7, 5, 3), or vice versa.

In some instances, we discovered that seeming irregularity of sequence was, in fact, masked regularity. In the European Cuckoo (*Cuculus canorus*), the molting wing consists of two independent groups or units, each with its own focus and its own rhythm. They are represented by primaries 1 to 4 and 5 to 9, respectively. The focus of the proximal unit is primary 4 or 1, the focus of the distal unit is primary 9 or 7. The regular sequence in unit *A* is 4, 1, 2, 3; in unit *B* it is 9, 7, 5, 8, 6. Primary 10 may insert itself anywhere in the distal unit. We have illustrated this complicated situation by the following diagram:

$$\begin{array}{l} B \\ A \end{array}\;\frac{9\text{–}7\text{–}5\text{–}8\text{–}6}{4\text{–}1\text{–}2\text{–}3}\;\;10\ \text{independent}$$

In separating unit *A* from unit *B* by a horizontal line, we tend to express their chronological independence from each other. Primary 4 may thus drop before, or together with, or some time after primary 9, which entails a corresponding shift of line *A* in relation to line *B*.

Besides such variable regularity, obvious irregularities are of more or less frequent occurrence in most of the complicated cases. Considerable material is sometimes needed before one can be certain as to what is the rule and what the exception. Frequently the exceptions consist in the fact that the shedding of the focal primary lingers behind that of one of its two neighbors, either the distal or the proximal one. We assume that in such a case the start signal reached the wrong place, or that the true focal primary was not yet prepared for dropping. The more complicated the molting process becomes by insertion of a second or a third focus, the more frequent tend to be the exceptions from the normal sequence. However, in the large family of the Falconidae we never noticed any deviation.

It might be asked which mode has to be considered the more primitive, a regulated or a more or less irregular one. We are strongly inclined to believe that evolution of all other molt patterns started with the descending molt, as it occurs in all Passeres, one single species of the genus *Muscicapa* excepted. To our surprise we found, not only in several genera of the Accipitridae (Stresemann and Stresemann, 1960), but also in several other groups or species that the juvenile wing is molted in a strictly descending sequence, while in the wing of older birds of the same species two or even three primaries may grow at the same time, being isolated by not-growing ones. This difference between young and adult birds can be interpreted as demonstrating two stages in evolution, the young bird recapitulating the original mode. The same difference seems to exist in certain other groups or species, where, however, the age categories are all of the same color and cannot be discerned in the skin. Other facts point to the same direction. *Muscicapa gambagae*, resident in the savanna south of the North African desert, has a descending molt, while this mode has been reversed in its near relative *M. striata,* a Palearctic migrant renewing the wings in and south of the tropics (Diesselhorst, 1961). All members of the order Pici follow the descending molt, except some round-winged Capitonidae which sometimes show a second focus in the distal part of the wing. In the family Caprimulgidae, the long-winged Caprimulginae, which catch flying insects on the wing, have universally a descending molt, while the sluggish Nyctibiinae, Aegothelinae, and Podarginae tend to molt irregularly, with at least two foci. They may have lost the strict regulation in consequence of reduced flying activity.

While the last-named differences seem open to a functional interpretation, there can be no doubt whatsoever that any such explanation breaks down in most other cases.

Many taxonomic groups are characterized as a natural assemblage just as well by their mode of wing molt as by the fact that their members agree in a certain combination of morphological details. This shows that in such cases the mode belongs to the hereditary qualities which go down to a remote past, and that it has not been affected by function.

We are restricted here by space to a few examples. All Falconidae molt the primaries starting with the 4th, whether or not they have pointed or rounded wings (V. Stresemann, 1958). This fact distinguishes them from all Accipitridae. The parrots of the subfamilies Psittacinae and Loriinae start the wing molt with the 6th primary, in contrast to the Cacatuinae and to *Nestor* and *Strigops. Aramus* and *Psophia* have an ascending wing molt, contrary to the Grues. Judged from the pattern of wing molt, *Rostratula* does not belong to the true Limicolae. In the Thinocori the mode differs fundamentally from that of the Limicolae, in which group they have been included in recent classifications. In most genera of the Ralli and of the Jacanae, all remiges are molted synchronously, but in both groups there are genera with consecutive wing molt, and these follow the ascending molt if they belong to the rails, and the descending mode if they belong to the Jacanae (*Microparra* excepted). The pattern of wing molt of the Cuculidae has no resemblance to that of the Musophagidae. All swifts follow the strictly decending mode by ending with the 10th primary, while in all hummingbirds the 8th primary is followed by the 10th, the 9th being the last one to drop.

The importance of molt studies is not at all limited to the fact that they supply a physiological group character supplementing those group characters that are obvious at first sight or that have been discovered by various kinds of morphological comparison. Other aspects can be added. Whenever comparison of molt patterns contradicts certain tentative lumpings of some higher systematic units, the weight of our new argument should not be neglected. Furthermore, the familiarity with the sequence in which a given species renews the primaries may be used as a clue to disclosing its proper place in the system, if its affinities had been misjudged by taxonomists.

Relying on this criterion, we feel sure that *Gampsonyx* does not belong to the Falconidae, but to the Elaninae (V. Stresemann, 1959), that *Pelargopsis* is a halcyonine and not an alcedinine kingfisher, and so forth.

SUMMARY

Almost all Passeriformes strictly adhere to the descending mode of wing molt. This widespread type of molt seems to be primitive. In many other avian orders it has become either considerably disturbed or even obliterated by irregularities, or it has been replaced by another more or less rigid sequence which has the advantage of shortening the process. In the latter case, the mode of wing molt offers a reliable help to phylogenetic induction.

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Morphological Analysis of the Sympatric Populations of Meadowlarks in Ontario

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The study of closely related species living in the same area is perhaps one of the most challenging problems of modern zoology and also one that has received considerable attention during the past 50 years. The problem here is clearly one of coexistence, i.e. the reasons for such species failing or succeeding to maintain a sympatric condition. Since the forms in question are usually closely related to each other and are often very similar as a consequence, studies of this nature invariably involve a careful analysis of the differences that are known to exist between the sympatric species, since such differences may be critical for the coexistence of animals at a given time and place.

The following discussion is presented as part of a broader study of the general ecology, vocalizations, and hybridization of the two sympatric species of meadowlarks in Ontario, and deals with the analysis of their morphology by means of multivariate statistical methods. I shall purposefully refrain from discussing the statistical treatment at length, realizing that such particulars would interest only a few, and instead, I will mainly deal with the results of the analysis and the inferences suggested by these results. A discussion of the statistics employed is included in the appendix at the end of the paper.

MATERIALS AND METHODS

The two species under discussion here are the nominate races of the Eastern Meadowlark (*Sturnella m. magna*) and of the Western Meadowlark (*S. n. neglecta*) which, over the past one hundred years, have extended their breeding ranges and become sympatric over a broad zone running from Canada to Mexico roughly in the middle of the continent (Lanyon, 1956, 1962). Reasons for this range extension are not known exactly but the influence of human activities is suspected as the chief factor. In Ontario, which presumably was inhabited by the eastern form only, the Western Meadowlark first appeared in the early twenties and has since spread over a considerable area (Fig. 1). The population of this species is very thin, however, consisting mostly of small colonies, single pairs, or often single individuals widely separated from each other, with massive populations of Eastern Meadowlarks in between.

Generally speaking, there appear to be three major differences between the two forms:

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1) *Differences in vocalizations.* — Most of the sounds of the Eastern Meadowlark are about 2,000 cycles/sec higher in pitch than the corresponding sounds of the western species.

2) *Differences in habitat selection.*—According to Lanyon (1953, 1962), the Western Meadowlark tends to occupy the drier areas within the zone of overlap, except in Mexico, where a subspecies of the Eastern Meadowlark, *S. m. lilianae*, lives in the more arid parts of the country, while *S. neglecta* is found on irrigated land.

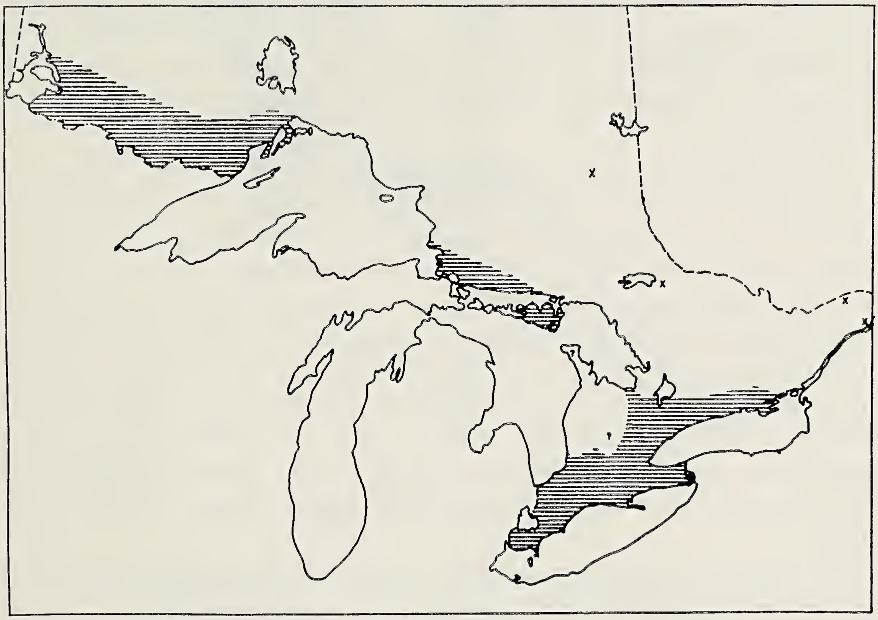

Fig. 1. Approximate distribution of the Western Meadowlark in Ontario. Compiled from surveys in 1958–60 and from data on file at the Royal Ontario Museum. Sporadic references are marked by *X*.

3) *Differences in morphology.* — The nominate races of the two forms show characteristic differences in the intensity of dark coloration, in the shape and size of the dark markings of the upper sides, in the shape of the spotting of the lower sides, and in the extent of the yellow color on the throat. These differences are rather subtle and, at least in Ontario, a convergence of the two morphologies can be demonstrated.

The differences are considered to be stable throughout the range of overlap, and no conclusive evidence of hybridization has been reported in the literature. My own investigations in southern Ontario, however, prove to the contrary. The differences in the pitch of the sound are clearly recognizable, but about one-third of the Western Meadowlarks have Eastern-type vocalizations, songs or calls, or both. The great majority of these birds possess a typical Western morphology and, at least in one case, they are young of typical Western parents. As for the differences in habitat selection, no evidence has been found that members of the Western species would prefer and actually select drier habitats. It appears that these birds occupy identical habitats with Eastern birds, the only difference being in the marginal character of the areas often inhabited by the Western Meadowlarks (such as narrow strips of grassy areas along roads and railway tracks, or close to buildings, construction sites, etc.). An explanation for this apparent lack of habitat differences may well lie in the fact that the area under discussion has no actual prairie-like habitat to speak of and has a rather even moisture gradient increasing from west to east. The present distribution of the Western Meadowlark in Ontario seems to be almost solely governed by two factors: the three routes of entry into the Province and the availability of grassy areas.

Morphological differences appear to be far more consistent, at least in Ontario populations, and it was decided that an analysis of these differences would be the only feasible approach to characterizing the two forms on the basis of existing differences. Other considerations also played a part in selecting morphology. Measurements of morphological characters can be expressed in terms of objective numbers more readily than measurements of other characters. Furthermore, if hybridization and introgression occur between the two species, the morphological phenotype can reasonably be expected to follow such trends. When in 1958 interbreeding was definitely established, it became increasingly important to learn more about the hybrids and, if possible, to find such birds—if any existed—among the wild populations.

Any type of description or analysis aimed at describing and discriminating between two groups of organisms must satisfy certain conditions to serve its purpose. Generally speaking, the two most important conditions are the selection of the characters to be analyzed and the selection of the proper statistical method for the analysis of the sample.

The basic rules for the selection of characters can be stated as follows: (a) They must be reasonably independent in order to convey the maximum information possible, i.e. they should show little interdependence. (b) They should show a reasonable degree of variation in all groups analyzed, with the "pure" types occupying the extremes of an imaginary scale based on total variation. (c) Finally, it will be to the advantage of the investigator if the characters can be measured on field and museum samples equally well—a convenient way to obtain large sample sizes.

With these precautions in mind, four characters were selected and judged to satisfy best the above conditions (Fig. 2):

$X_1 =$ the pattern of the dark markings on the central tail feathers.

$X_2 =$ the pattern of markings on the feathers from the center of the back.

$X_3 =$ the extent of the yellow color on the sides of the cheeks with respect to a line extending from the base of the mandibles down the sides of the neck (apteryal line).

X_4 = the size and shape of the dark spots and streaks on the upper sides of the breast (in the yellow area only).

Each character was divided into six variation groups, arranged to form a continuous graded series, and values from one to six were assigned to each category. An individual bird was "scored" by comparing its morphology to a chart showing the continuous variation series of the four characters (Fig. 3), and the value of each character was simply read from the chart. Each individual thus received a set of four values, referred to as the basic measurements. The values were then summed to form a compound measurement known as the *hybrid index.* The formation of such indices is widely used and accepted in studies of the morphological variation of both plants and animals (Anderson, 1949, 1954; Sibley, 1950, 1954; Huntington, 1952; Dixon, 1955; Sibley and West, 1958; Sibley and Short, 1959; Hatheway, 1962).

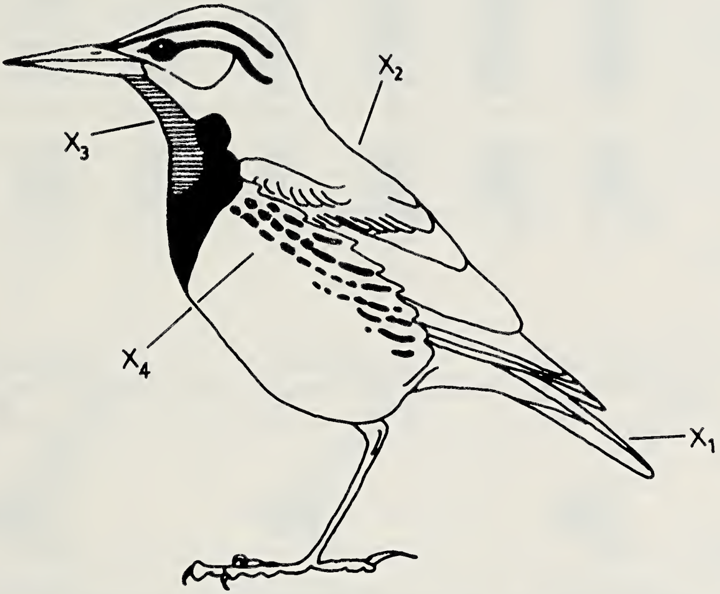

Fig. 2. Morphological characters of meadowlarks analyzed in the study.
X_1 = the markings on the two central tail feathers.
X_2 = the markings on the feathers from the center of the back.
X_3 = the extent of the yellow patch on the throat.
X_4 = the spotting on the sides of the breast (in yellow areas only).

For the statistical treatment of the sample obtained in this way, several methods are available. By far the easiest and simplest method is the construction of a frequency histogram of the hybrid indices to see if separation of the two groups has been achieved, and to test the calculated proportions against the theoretical distribution. While such a method has the advantage of being simple, one must also be reasonably sure that such a test carries the necessary objectivity. The four characters were selected in a somewhat arbitrary fashion, based on the investigator's opinion of their discriminative value. Since the original aim of the study was to show possible signs of introgression in Ontario populations and to detect assumed intermediacy of some portion of this population, the highest degree of separation must be achieved by the analysis. Yet, in the simple arithmetic summation of the

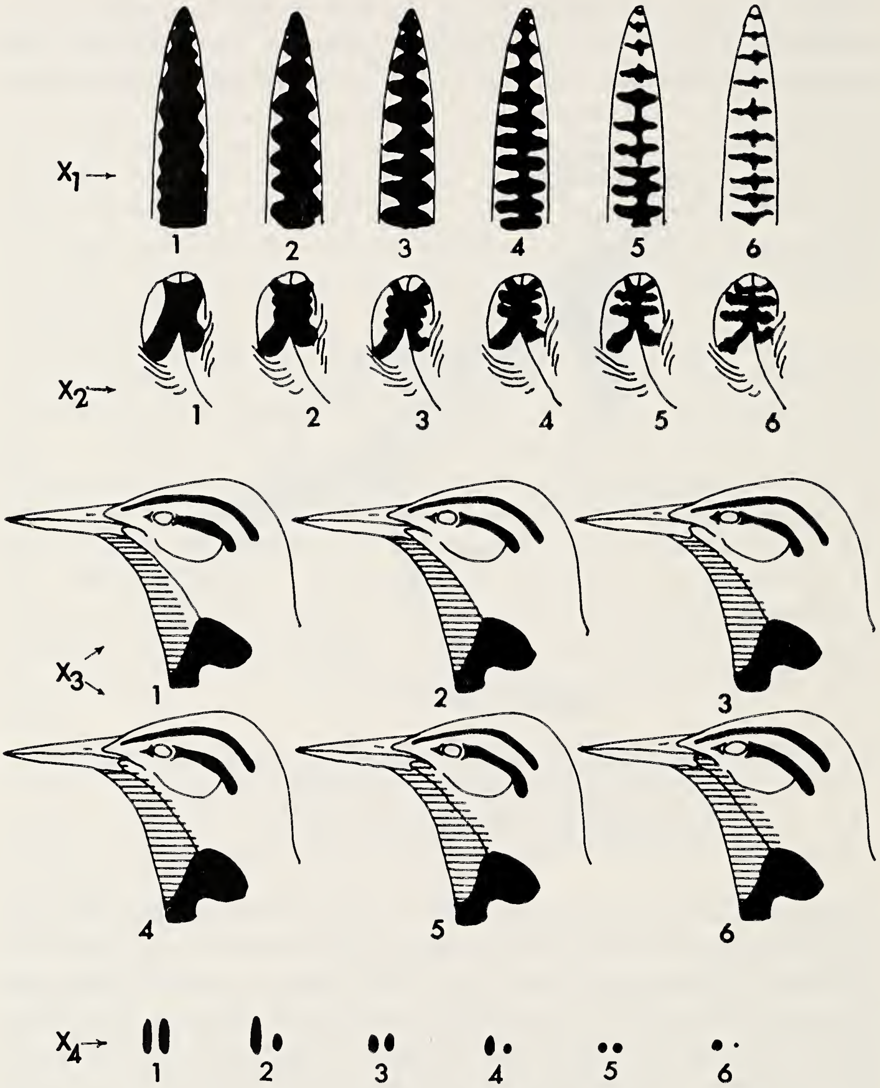

Fig. 3. Scoring system based on the morphological characters.

measurements it is not known how much each character contributes to the discriminative value of the hybrid index since they all carry the same weight. It is far more desirable that "the contribution of a character to an index should be in proportion to its usefulness in demonstrating a known or suspected relationship" (Hatheway, 1962); in other words, characters that contribute more to the value of the composite index should carry more weight, while others showing high correlation and little independent contribution should be assigned proportionately less weight. Assigning proper weights to characters according to their degree of association is then the appropriate method of analysis. Conveniently, such associations can also be measured and expressed as correlation coefficients of the characters measured. Of several multivariate statistical methods that make use of this phenomenon, the one developed by Fisher (1948) was selected because of its relative simplicity. Without going into further details concerning the computation of these so-called discriminant functions, I shall merely illustrate the basic equation used:

$$X = x_1 b_1 + x_2 b_2 + x_3 b_3 + x_4 b_4$$

where X is the discriminant or the weighted sum of the measurements; $x_{1\text{-}4}$ are the measurements proper and $b_{1\text{-}4}$ are the corresponding coefficients of correlation. The new hybrid index obtained in this manner shows several advantages over the index formed by the simple arithmetic sum of the measurements, as can be demonstrated by the results obtained in this study.

RESULTS AND DISCUSSION

The graph of the original sample of 50 birds was easy enough to interpret. The histogram of the unweighted indices or additive scores clearly shows two populations, represented by the two peaks (Fig. 4*A*). It may also be demonstrated that the two populations approach each other very closely but apparently do not overlap. A rather different picture is given by the histogram of the weighted indices (Fig. 4*B*). On this graph the explanation for the extreme closeness of the sample populations is given in the form of a small group located around the combined mean of the samples. Thus, a small intermediate group is chiefly responsible for the convergence of the two populations, rather than a series of intermediate individuals within the groups proper, as suggested by the graph of the unweighted indices. With the new hybrid index, it became apparent that not two morphological types exist as originally suspected, but instead three definite groups could be distinguished.

With known cases of hybridization at hand, it was tempting to assume that the morphological intermediates represented crosses between the parental forms. To prove this theory, efforts were made to raise birds of known-hybrid origin in captivity until they reached adulthood and to compare their morphology with that of the intermediate group. The task, however, proved to be more demanding than originally suspected, because of the reduced viability of the F_1 hybrids. Of 5 young and 4 eggs taken from nests of mixed pairs, only two (a male and a female) were raised successfully, both birds coming from the same nest. Similar efforts with young of conspecific parents gave significantly better results, 5 birds surviving out of 7, taken from nests in the same area. The two hybrids mentioned above reached adulthood and

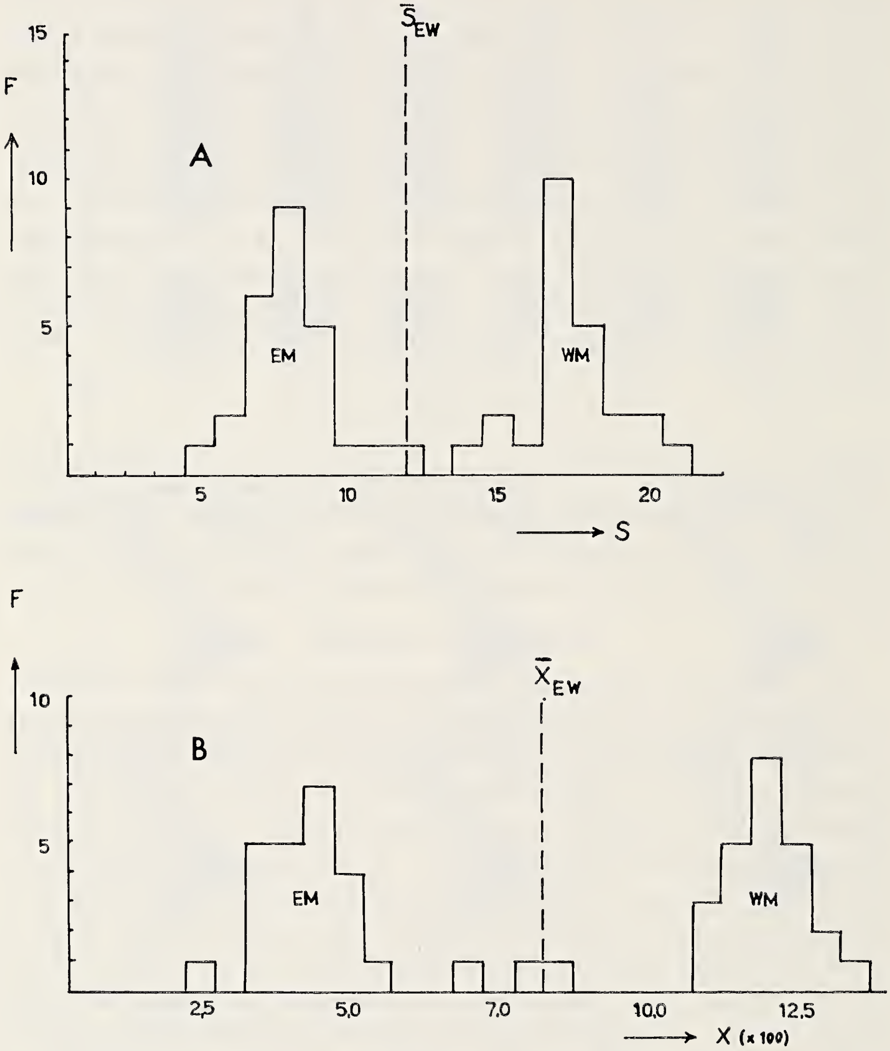

Fig. 4. Frequency distribution of the compound indices in a random sample of 50 meadowlarks taken in Ontario.

A = Unweighted indices (S): Mean = 12.56; $t = 20.17$; $P = 0.01$.
B = Weighted indices (X): Mean = 0.084; $t = 23.66$; $P = 0.01$.
EM = Eastern Meadowlark; *WM* = Western Meadowlark.

were subsequently scored. Their weighted indices were found to match those of the intermediate group discussed earlier. The unweighted indices would have classified them as an Eastern and a Western Meadowlark, respectively.

I realize that a larger sample and more hybrids of known parentage would be needed to establish the exact phenotype of the hybrids beyond doubt. I feel, however, that the use of a weighted statistical method in forming hybrid indices and measuring introgression in wild populations produced preliminary results that may point the way for future investigations of this nature. The reliability of the index described here was tested on a larger sample of 156 Ontario meadowlarks, and the results were in good agreement with earlier findings (Fig. 5).

Perhaps the greatest practical use of a reliable index lies in the fact that it condenses the morphological information into one convenient figure, which then can be correlated with some other ecological or behavioral factor suspected to have some bearing on the morphology, or vice versa. Such an attempt is demonstrated below.

Correlation between Morphology and Vocalizations among Western Meadowlarks.—It was mentioned earlier that a number of Western Meadowlarks were found to have Eastern-type vocalizations, either songs or calls or both. Songs in this group are known to be subject to learning by young birds exposed to sounds other than those of their own species, but calls were thought to be inherited only (Lanyon, 1957, 1960). Experiments with hand-raised young of both species, performed during the course of this study, furnished evidence to the contrary and showed that, although each young bird develops a complete range of the call notes of the species without outside aid, they can be induced to learn the calls of the related species as well (Szijj, 1963). The ability to render the "alien" calls apparently depends on individual skill in these birds. Field studies of the Western population in Ontario indicated a very high incidence of Eastern calls among these birds. Out of 54 Western Meadowlarks recorded during the survey, 16 were found to possess Eastern-type call notes (30 percent)—a ratio which, if calls can only be inherited, would indicate a large number of hybrids or backcrosses among the population. Such an assumption was refuted by the results of 4 years of intensive search in areas where both species were known to occur. Only 9 nests belonging to 5 mixed pairs were found, with an average hatching success of 2 birds/nest, versus 4.8 birds/nest belonging to conspecific pairs. This incidental hybridization with its limited breeding success can hardly account for the production of individuals totaling almost one-third of the Western population, i.e. birds with both types of call notes. Such birds, however, could easily be pure Western Meadowlarks, which simply learned the "alien" notes from Eastern birds plentiful in all areas where Western birds nest. This learning may take place in a fashion similar to that observed during the experiments with hand-raised young. If this is so, Western Meadowlarks with Eastern calls are expected to possess a morphol-

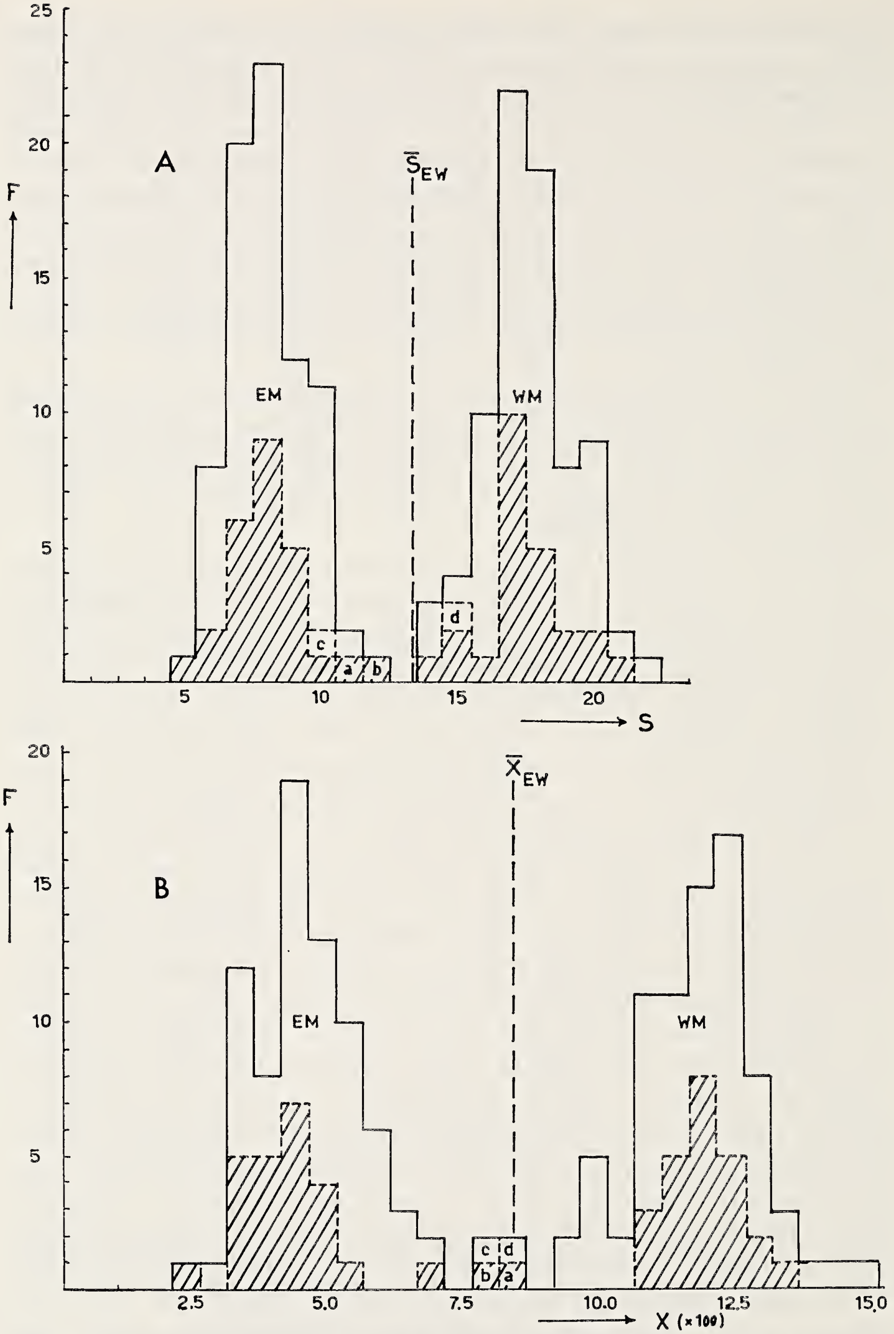

Fig. 5. Frequency distribution of the compound indices in a sample of 156 Ontario meadowlarks. The positions of four individual hybrid birds correspond to *a*, *b*, *c*, and *d* in the histogram. Cross-hatching = sample shown in Fig. 4.

A = Unweighted indices (S): Mean = 12.48; $t = 11.73$; $P < 0.01$.
B = Weighted indices (X): Mean = 0.085; $t = 11.83$; $P < 0.01$.
EM = Eastern Meadowlark; *WM* = Western Meadowlark.

ogy that is characteristic of their species, rather than the one described for the F_1 hybrid generation.

A test of significance of the difference in the mean indices shows that Western Meadowlarks with Eastern-type calls do not deviate significantly in their morphology from the rest of the population. The variance ratio of the samples gave an F value of 3.99 for 51 and 1 degrees of freedom, representing a probability of nearly 10 percent of the population showing deviations of this order by chance alone. On this basis, we may conclude that vocalizations among Western Meadowlarks are not correlated with their morphology (Fig. 6), i.e. on the basis of their appearance, birds with "pure" and "mixed" calls cannot be segregated. Since the morphology does not indicate the hybrid character in birds with Eastern-type calls, the argument presented earlier on the acquisition of "alien" calls by birds of pure parentage is the only logical explanation.

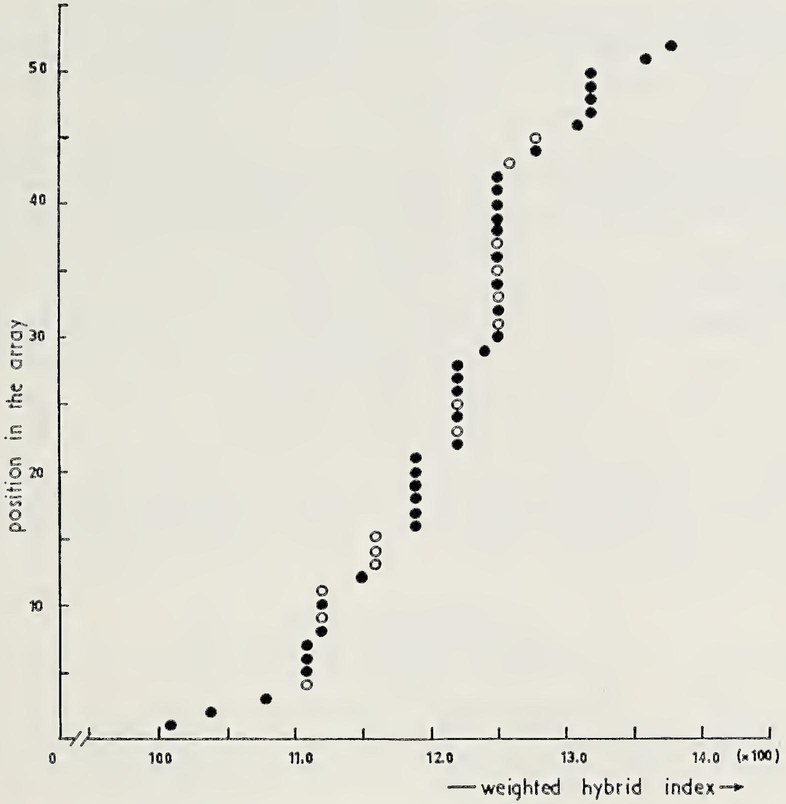

Fig. 6. Frequency array of the compound indices of 52 Western Meadowlarks. The morphology of birds having both Eastern- and Western-type calls (open circles) does not differ significantly from that of birds having Western-type calls only (solid circles). $F = 3.99$; $0.05 > P > 0.10$.

The use of the proper statistical method in analyzing the morphology of the two species of meadowlarks thus helped to confirm other results obtained in the field and in the laboratory, in the course of this study, and became an extremely useful tool in the evaluation of the relationship between two sympatric populations.

SUMMARY

Multivariate statistical methods were used to analyze the morphological characteristics of the two sympatric meadowlarks, *Sturnella m. magna* and *S. n. neglecta*, in Ontario. Four characters were selected for the analysis, each divided into six variation groups (based on the total variation of both groups), and values from 1 to 6 were assigned to these. An unweighted compound index was formed by the arithmetic summation of the values of the four characters for each individual bird. A frequency distribution of these indices shows that a high degree of separation was achieved with this index. To increase the accuracy of the index, each character was weighted according to how much it contributed to the compound by calculating coefficients of their correlation. The new weighted index was accurate enough to characterize not only the two species, but also the F_1 hybrids, showing that the latter group is a morphological intermediate of the parental phenotypes.

Methods of selecting characters for such an analysis and the appropriate statistical treatment are discussed. A practical application of the weighted index is given.

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APPENDIX

Fisher's discriminant functions are designed to calculate that linear compound of the available measurements taken from two populations which will give the smallest possible frequency of misclassification when used as a means of discrimination. With four measurements available, the discriminant (X) is given as:

$$X = b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4$$

where x_{1-4} are the four measurements and b_{1-4} are coefficients chosen so as to maximize the difference between the two populations. Computation of the four values of b involves the solving of four multiple-regression equations:

$$\begin{aligned}
d_1 &= b_1Sv^2 + b_2Svw + b_3Svy + b_4Svz\\
d_2 &= b_1Svw + b_2Sw^2 + b_3Swy + b_4Swz\\
d_3 &= b_1Svy + b_2Swy + b_3Sy^2 + b_4Syz\\
d_4 &= b_1Svz + b_2Swz + b_3Syz + b_4Sz^2
\end{aligned}$$

where: $v =$ deviations from the mean of x_1; $d_1 =$ specific difference of x_1
$w =$ deviations from the mean of x_2; $d_2 =$ specific difference of x_2
$y =$ deviations from the mean of x_3; $d_3 =$ specific difference of x_3
$z =$ deviations from the mean of x_4; $d_4 =$ specific difference of x_4.

After the necessary computations the following equations were obtained:

$$\begin{aligned}
76.00b_1 + 43.60b_2 + 47.20b_3 + 85.00b_4 &= 1.84\\
43.60b_1 + 74.60b_2 + 49.80b_3 + 74.90b_4 &= 1.72\\
47.20b_1 + 49.80b_2 + 98.80b_3 + 101.8b_4 &= 2.32\\
85.00b_1 + 74.90b_2 + 101.8b_3 + 170.5b_4 &= 3.48\,.
\end{aligned}$$

The four equations with four unknowns were solved and values of b_{1-4} were found:

$$b_1 = 0.003105 \qquad b_2 = 0.003319$$
$$b_3 = 0.006205 \qquad b_4 = 0.013700\,.$$

Values of b now enable us to "score" any individual with the four basic measurements known.

To test the significance of the results and measure the degree of separation obtained by the weighted indices, an analysis of the variance of the sample was carried out (Table 1). As indicated by the table, the variance ratio is 21.54, which gives a very high F ratio ($F = 7.19$) as estimated from 48 and 1 degrees of freedom. On this basis, the high degree of separation was achieved.

TABLE 1.—ANALYSIS OF VARIANCE

Item	Sum of Squares	N	Mean Square	Variance Ratio
Between species	$nD^2/2 = 0.06724$	1	0.03362	21.54
Within species	$D = 0.07340$	48	0.00156	
Total	0.14064	49	0.05318	

The reliability of the method can be demonstrated by calculating the probability of a misclassification when one uses weighted measurements. From the table, the ratial difference in X is 0.07340 and the estimated standard deviation of X within species is $\sqrt{0.00156}$, or 0.0395.

A deviation of $D/2 = 0.0734/2$, or 0.0367, will cause misclassification, and such a deviation is $0.0395/0.0367 = 1.076$ times the standard deviation, as estimated from 49 degrees of freedom. Such a value of t_{49} represents just over 20 percent of all cases, but the value of t makes allowance for departures on both sides of the mean. In our case, only departures that lie *toward* the combined means of the sample will result in actual misclassification, and the other half of the deviations that lie *away* from the combined mean will not influence the reliability. The estimated probability of misclassification will then be about 10 percent, or about 5 birds out of 50. The misclassification rate of the two species agrees reasonably well with this expectation. $\overline{X}_A = 0.1208$ and $\overline{X}_B = 0.04746$ and the combined mean $\overline{X}_{AB} = 0.0842$. Therefore, anything greater than $\overline{X}_{AB}$ will be attributed to species A (Western Meadowlark) and anything less than this value to species B (Eastern Meadowlark). Fig. 4*B*, however, shows a third, intermediate group, as well as the two groups referable to Eastern and Western meadowlarks. On closer examination, the two birds located near the combined sample means ($\overline{X}_{AB}$) represent the F_1 hybrid generation, as confirmed by a check of their X values against values found in hybrids of known parentage. The third individual of the group ($X \times 100 = 7$) apparently represents one extreme in the variation among Eastern Meadowlarks, as demonstrated by Fig. 5*B*. From this, the approximate range of the actual hybrid morphology is found to be $X = 0.0817 - 0.0860$. Since only 2 individuals out of a sample of 50 show deviations from the specific mean as great as or greater than 0.0367 (the two hybrids), it is evident that only hybrids are being misclassified by this method. The two individuals represent 1 percent of the sample of 50, which is well within the safe 5 percent level allowed by t_{49}. The large sample of 156 birds shows the same trends and confirms the reliability of the method.

Discussion of the discriminant functions may be found in Fisher (1948) and Mather (1943).

Note.—The scale of the discriminant X in Fig. 4 and 5 is multiplied by 100 to make the illustration more convenient. Rounding off of the values of X in the illustrations was carried out to three decimal places.

Fragen der Anatidensystematik in parasitologischer Sicht

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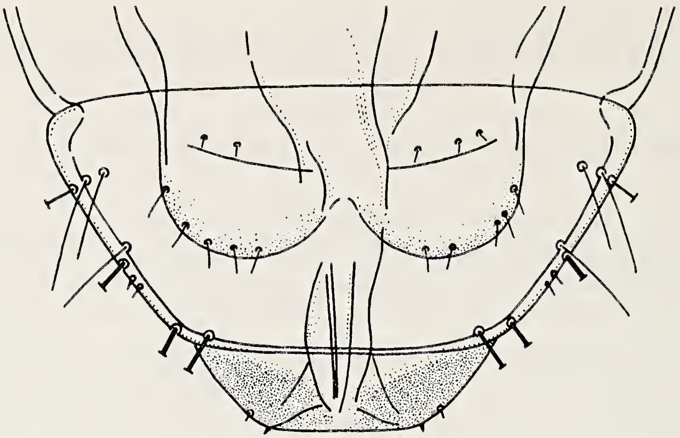
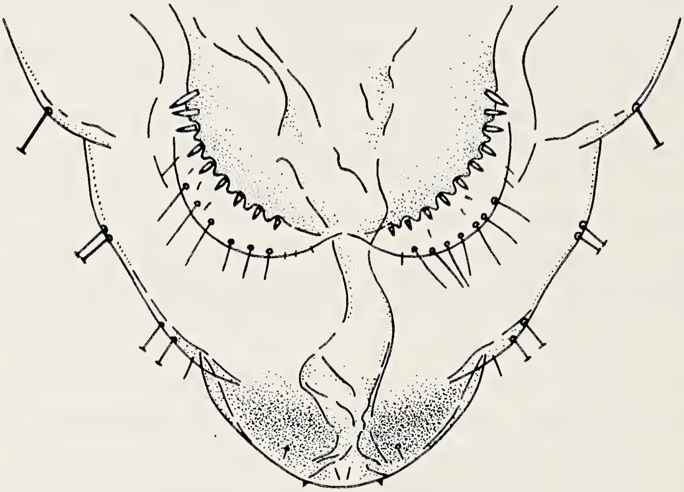
Unter den grossen Vogelabteilungen gehört die Ordnung der Entenvögel heute zu den systematisch am besten durchgearbeiteten. Durch das fruchtbare Zusammenwirken von Morphologie und Verhaltensforschung (ich erwähne nur die Arbeiten von Boetticher, 1952; Delacour, 1954; Delacour und Mayr, 1945; Johnsgard, 1961; und Lorenz, 1941) haben wir im Laufe der letzten 20 Jahre einen zum Teil bis ins einzelne gehenden Überblick über die verwandtschaftlichen Verbindungen der verschiedenen Anatidenabteilungen gewinnen können, der als relativ verlässlich angesehen werden darf. Ich habe daher geglaubt, dass es ein weitergehendes Interesse finden könnte, einmal an Hand von ein paar beliebig gewählten Beispielen zu untersuchen, ob und inwieweit unsere derzeitigen systematischen Vorstellungen in dieser Gruppe mit den Ergebnissen übereinstimmen, die die vergleichende Parasitologie an denselben Objekten erarbeitet hat. Zu diesem Zwecke habe ich dank des freundlichen Entgegenkommens des Britischen Museums Gelegenheit nehmen können, den sogenannten *Ornithobius*-Komplex einer eingehenderen Revision zu unterziehen, einer Vereinigung von drei näher miteinander verwandten Gattungen von Vogelmallophagen, deren Arten ausschliesslich bei Entenvögeln in weiterem Sinn des Begriffes schmarotzen, und zwar in erster Linie bei älteren, stammesgeschichtlich früh ins Dasein getretenen Formen. Erleichtert wurde mir dieses Vornehmen dadurch, dass v. Boetticher und Eichler bereits im Jahre 1952 eine erste Übersicht über die Verbreitung des *Ornithobius*-Komplexes gegeben haben, ohne dabei allerdings in die Erörterung von Einzelheiten einzutreten. Als ein wesentliches, von mir bestätigt gefundenes Resultat dieser Studien darf der Nachweis des Vorkommens der Gattung *Bothriometopus* bei Wehrvögeln (Anhimae), der Gattung *Ornithobius* bei Gänsen und Schwänen und der Gattung *Acidoproctus* bei der Spaltfussgans (*Anseranas*), den Pfeifgänsen (*Dendrocygna*), sowie einzelnen Halbgänsen (*Alopochen*), Glanzenten (*Plectropterus*), und Tauchenten (*Netta, Aythya*) betrachtet werden, die sich damit ornithoparasitologisch als ein zusammengehöriger Verwandtschaftskreis ausweisen. *Acidoproctus hilli* von *Anseranas* ist, der Stellung seines Wirtes entsprechend, eine sehr apart stehende Art, die Harrison sogar zum Genotypus einer besonderen Gattung gemacht hat, was aber meines Erachtens nicht berechtigt ist. Die Möglichkeit einer umfassenden, vergleichend-parasitologischen Interpretation der Befunde des *Ornithobius*-Komplexes und deren Nutzbarmachung für die ornithologische Systematik krankt an zwei Stellen. Von diesen ist die Lückenhaftigkeit der überlieferten stammesgeschichtlichen Zeugnisse nicht zu reparieren, wohl aber unsere zur Zeit immer noch sehr unvollständige Kennt-

Proc. XIII Intern. Ornithol. Congr.: 189–197. 1963



(a) *cygnus*-Gruppe (*bewickii*)



(b) *olor*-Gruppe (*melancoriphus*)

Abb. 1. Weibliche Terminalia je eines Vertreters der bei Schwänen schmarotzenden beiden Verwandtschaftsgruppen der Gattung *Ornithobius*. (Die Speziesnamen beziehen sich jeweils auf die zugehörigen Wirtsvögel.)

nis der letzteren, weshalb ich an alle systematisch interessierten Fachgenossen, insbesondere an alle Jäger und Wasservogelliebhaber unter ihnen, die Bitte richten möchte, die vergleichend-parasitologische Forschung durch das Sammeln von Federlingen unseres Wassergeflügels nach Kräften zu unterstützen.

DIE GATTUNG *ORNITHOBIUS* UND DIE SYSTEMATIK DER SCHWÄNE

Lassen Sie uns jetzt aus der Vielzahl der Probleme ein paar Fragen herausgreifen und zunächst einen kurzen Blick auf die Schwäne und ihre *Or-*

nithobius-Bevölkerungen werfen. Wie Sie wissen, unterscheiden wir bei den Cygnidae insgesamt sieben deutlich ausgeprägte Formen, von denen drei, nämlich unser Höckerschwan, der südamerikanische Schwarzhalsschwan und der Schwarze Schwan Australiens eine lockere Verwandtschaftsgruppe gut abgegrenzter Arten bilden, während die vier restlichen Formen der sogenannten nordischen Schwanengruppe, Singschwan und Zwergschwan der Alten Welt und Trompeterschwan und Pfeifschwan Nordamerikas, andererseits systematisch näher zusammenstehen. Diese taxonomische Zweiteilung der Schwäne in eine *olor*-Gruppe mit *olor*, *melancoriphus*, und *atratus* und eine *cygnus*-Gruppe mit *cygnus*, *bewickii*, *buccinator*, und *columbianus* spiegelt sich in der Morphologie der *Ornithobius*-Arten insofern sehr eindrucksvoll wieder, als die Beborstung der weiblichen Genitalregion in beiden Gruppen eine gänzlich verschiedene ist. Bei den *Ornithobius*-Arten der *cygnus*-Gruppe wird die Vulva jederseits von zwei bogenförmig geführten Borstenreihen umstanden (Abb. 1*a*), während in der *olor*-Gruppe die vordere Reihe dieser Borsten in kräftige Stacheln umgewandelt ist, die die Geschlechtsöffnung halbkreisförmig umgeben (Abb. 1*b*). Was weiter die innere Aufgliederung der *olor*-Gruppe anbetrifft, so zeigt ein Vergleich der männlichen Kopulationsorgane der bei *olor*, *melancoriphus* und *atratus* schmarotzenden *Ornithobius*-Arten (Abb. 2), dass die zuerst genannten beiden Schwäne nach Massgabe des parasitologischen Befundes näher zusammengehören, während *atratus* mehr abseits steht, was ja auch ornithologischerseits seinen Ausdruck in der Begründung der Gattung *Chenopis* für den Schwarzen Schwan gefunden hat.

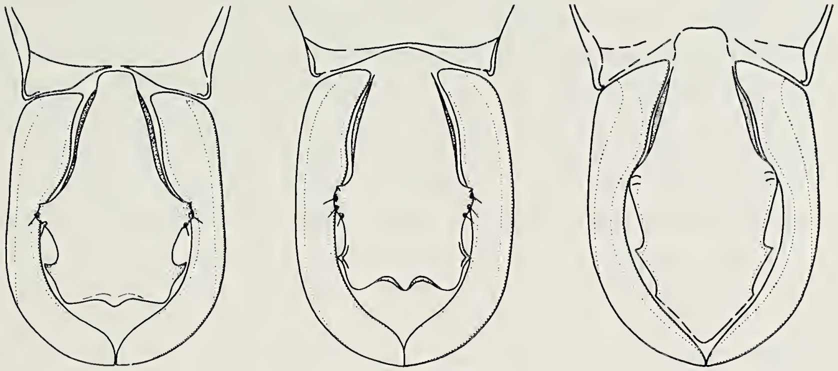
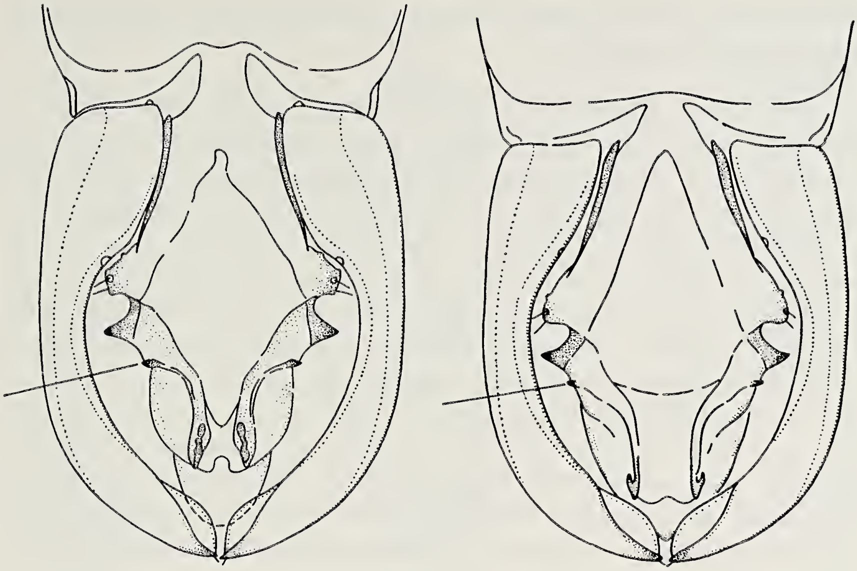

(a) *olor* (b) *melancoriphus* (c) *atratus*

Abb. 2. Männliche Kopulationsapparate der *Ornithobius*-Arten der *olor*-Gruppe. (Die Speziesnamen beziehen sich jeweils auf die zugehörigen Wirtsvögel.)

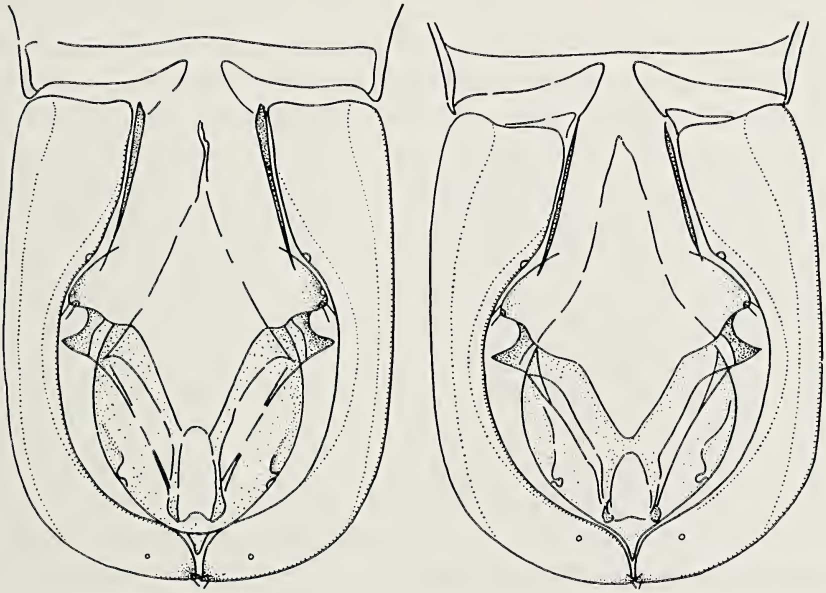
Schwieriger liegen die Verhältnisse hinsichtlich der Klassifikation der vier nordischen Schwäne, die wir in der sogenannten Singschwan (*cygnus*)-Gruppe zusammengefasst hatten. Bekanntlich betrachtete man die vier hierher gehörigen Formen zunächst immer als vier getrennte Arten (und tut dies zum Teil auch heute noch), bis Delacour und Mayr (1945), einer Anregung Harterts aus dem Jahre 1920 folgend, eine Neugruppierung vorschlugen, die nur noch zwei Arten anerkennen möchte, nämlich den nordamerikanischen *Cygnus columbianus* mit dem europäisch-asiatischen *C. bewickii* als Unterart und den altweltlichen *C. cygnus* mit dem amerikanischen *C. buccinator* als Unterart. Dieser Klassifikationsversuch ist inzwischen (1958) von Parkes dahingehend modifiziert worden, nur *columbianus* und *bewickii* weiterhin als konspezifisch zu betrachten, Singschwan und Trompeterschwan aber jeweils als gesonderte Arten zu führen. Die Gründe, die die Entwicklung dieser Vorstellung veranlasst haben, teils zoogeographische und biologische, teils auch anatomische, sind einleuchtender Natur. Dies braucht jedoch noch nicht zu bedeuten, dass die auf sie gestützte Anschauung das Verwandtschaftsverhältnis der vier Schwäne auch tatsächlich zutreffend wiedergibt. Es lassen sich ja, wie Sie wissen, auch morphologische Gesichtspunkte dafür anführen, ich erinnere nur an die Körpergrösse und an die Schnabelfärbung, die darauf hindeuten könnten, dass die stärkeren verwandtschaftlichen Bande zwischen unseren vier Schwänen nicht von Osten nach Westen, sondern von Norden nach Süden verlaufen, dass, mit anderen Worten, die Nordamerikaner *columbianus* und *buccinator* einerseits und die beiden altweltlichen Repräsentanten *cygnus* und *bewickii* andererseits am nächsten miteinander verwandt sind. Jedenfalls ist dies das Bild, das sich bei einer vorläufigen Überprüfung des *Ornithobius*-Befundes ergibt.

Ich habe Ihnen zum Vergleiche die männlichen Kopulationsorgane der *Ornithobius*-Arten der vier in Rede stehenden Schwäne skizziert, um das Gesagte an Hand eines taxonomisch wichtigen Merkmales zu illustrieren (Abb. 3). Die Unterschiede sind im ganzen genommen unbeträchtlich, was darauf hinweist, dass *alle* vier Arten enge verwandtschaftliche Beziehungen zu einander unterhalten. Inwieweit ein einzelnes morphologisches Detail, wie beispielsweise das Vorhandensein einer in unseren Skizzen durch eine Hinweislinie verdeutlichten dritten Protuberanz in der Seitenkontur des Endomeron bei den *Ornithobius*-Arten von *cygnus* und *bewickii* von taxonomischer Bedeutung ist, vermag ich noch nicht abschliessend zu beurteilen. Es mehren sich aber die Anzeichen dafür, dass bei den Vogelmallophagen unscheinbare, mikro- und kryptomorphologische Merkmale, wie einzelne winzige Borsten oder Sensillen, die sozusagen unterhalb des Selektionsniveaus liegen, gerade innerhalb höherer systematischer Kategorien von grossem Wert sein können, während stark in die Augen springenden Gestaltsänderungen vielfach nur ein sehr mässiges Gewicht für die Klarlegung blutsverwandtschaftlicher Zusammenhänge zukommt.

Ausser bei Schwänen kommt *Ornithobius* noch bei Gänsen, nicht jedoch bei Enten vor, womit die engere verwandtschaftliche Zusammengehörigkeit der beiden erstgenannten Gruppen auch parasitologisch unterstrichen wird. Allerdings beschränken sich die bisherigen *Ornithobius*-Funde bei Gänsen auf drei Wirtsarten, nämlich *Branta leucopsis*, *B. canadensis*, und *Cygnopsis*



(a) *cygnus* (b) *bewickii*



(c) *buccinator* (d) *columbianus*

Abb. 3. Männliche Kopulationsapparate der *Ornithobius*-Arten der *cygnus*-Gruppe. (Die Speziesnamen beziehen sich jeweils auf die zugehörigen Wirtsvögel.)

cygnoides, während auf allen übrigen Gänsen bisher noch keine *Ornithobius*-Arten gefunden worden sind. Das gleiche gilt auch für den Koskoroba-Schwan (*Coscoroba*), was umso mehr zu bedauern ist, als die Parasiten möglicherweise Anhalte bieten könnten, die Position dieser eigentümlichen Spezies exakter zu ermitteln.

DIE GATTUNG *ACIDOPROCTUS* UND DIE SYSTEMATIK DER PFEIFGÄNSE

Ein verwickeltes und noch vielfach umstrittenes Problem ist ferner die Systematik der *Dendrocygna*-Arten, der sogenannten Pfeifgänse oder Baumenten. Unter den diese Gattung betreffenden neueren Klassifikationsversuchen will ich zunächst denjenigen v. Boettichers (1952) als Beispiel eines Systems hervorheben, das sich strikte an der äusseren Morphologie orientiert, das heisst die acht *Dendrocygna*-Arten nach dem Grad ihrer habituellen Ähnlichkeit gruppiert. Dass dieses Vorgehen in einer so schwierigen Gattung wie *Dendrocygna* unter Umständen in gefährliche Irrtümer führen kann, war schon 1954 von Delacour hervorgehoben worden. So war es denn auch nicht weiter erstaunlich, dass das 1961 von Johnsgard unter weitgehender Berücksichtigung verhaltenskundlicher Daten entworfene System ein wesentlich anderes Gesicht zeigt, indem es Arten miteinander vereinigt, die auf den ersten Blick gar nicht näher zusammen zu gehören scheinen. Zu den Hauptunterschieden beider Systeme gehört die Beurteilung der Stellung der sogenannten Kubanischen Pfeifgans oder Kubaente, *Dendrocygna arborea,* die ihre nächst verwandte Art nach v. Boetticher in der ganz ähnlich gezeichneten "Tüpfelente" *D. guttata* von Celebes, den Molukken, und Neu-Guinea besitzt, während Johnsgard sie mit der rotschnäbeligen "Herbstente" (*D. autumnalis*) verbindet, *D. guttata* dagegen mit der australischen *D. eytoni* zusammenkoppelt, wobei er davon ausgeht, dass *D. arborea* sowohl wie *D. guttata* Inselformen sind, die ihre gefleckten Alterskleider als Konvergenzbildung sekundär erworben haben dürften. Der mallophagologische Befund, hier repräsentiert durch die Arten der *Ornithobius* benachbart stehenden Gattung *Acidoproctus,* lässt nun kaum Zweifel darüber zu, dass Johnsgard mit seiner Ansicht im Rechten und v. Boetticher im Unrechten ist, wie dies die beistehende Gegenüberstellung (Tafel 1) zeigt. *D. arborea* und *D. autumnalis* werden von gleichen oder sehr ähnlichen Arten parasitiert und dasselbe gilt für *D. guttata* und *D. eytoni.* Besonders die auf *D. arborea* und *D. autumnalis* lebenden *Acidoproctus*-Populationen sind so deutlich charakterisiert, dass ihre unmittelbare Zusammengehörigkeit ausser Frage steht. Entspricht so der *Acidoproctus*-Befund in den Grundzügen völlig der Auffassung, die Johnsgard hinsichtlich der Verwandtschaft der Wirte hegt, so sind doch auch gewisse Abweichungen, ich möchte sagen, solche quantitativer Art, zu registrieren, hinsichtlich derer sich parasitologisches und ornithologisches Bild nicht ganz decken. Diese bestehen vor allen Dingen darin, dass sich die Arten *D. bicolor* und *D. viduata,* die bei Johnsgard verhältnismässig entfernt voneinander stehen, mallophagologisch eng (das heisst durch den Besitz derselben *Acidoproctus-Art*) mit einander verbinden und *D. javanica* und *D. arcuata* näher an *D. guttata* und *D. eytoni* heranrücken sollten als an *D.*

Tafel 1.—Verwandtschaftliche Beziehungen innerhalb der Gattung *Dendrocygna*

Nach von Boetticher, 1952	Nach Johnsgard, 1961	Nach Timmermann (*Acidoproctus*-Befund)
1. *arborea*	1. *eytoni*	1. *eytoni*
	guttata	*guttata*
guttata		
		arcuata
		javanica
2. *bicolor*	2. *bicolor*	2. *bicolor*
javanica	*arcuata*	*viduata*
arcuata	*javanica*	
	viduata	
eytoni		
viduata		
3. *autumnalis*	3. *autumnalis*	3. *autumnalis*
(sehr isoliert)	*arborea*	*arborea*

bicolor und *D. viduata*, in deren unmittelbare Nachbarschaft Johnsgard sie gestellt hat.

Gegen die Ergebnisse der vergleichenden Parasitologie sind in den letzten Jahren eine Reihe heftiger und zum Teil ganz unsachlicher Angriffe gerichtet worden, weil diese nicht in jedem Einzelfall mit den Vorstellungen übereinstimmten, die man zur Zeit ornithologischerseits über die Verwandtschaften der Vögel hegte. Man hat gemeint, dass überall dort, wo morphologischer und parasitologischer Befund einander widersprächen, immer mit der Möglichkeit gerechnet werden müsse, dass Parasitengruppen in der jüngeren oder jüngsten Vergangenheit ihre Wirte gewechselt hätten und so durch ihre Verbreitung verwandtschaftliche Beziehungen vortäuschten, wo in Wirklichkeit keine bestünden. In allen derartigen Zweifelsfällen müsse daher die Morphologie das letzte, entscheidende Wort haben und behalten. Tatsächlich beruht jedoch die sich hierin aussprechende Überzeugung auf einem Missverstehen der biologischen Situation. Ein an seinen Wirt angepasster Schmarotzer ist ein Teil seines Wirtes und kann keinesfalls beliebig gewechselt und ausgetauscht werden. Fälle in rezenter Zeit stattgehabter sekundärer Überwanderungen auf andere Wirte gibt es zweifellos bei Parasiten, aber sie sind als Ausnahme und nicht als Regel zu betrachten, und darüber, ob ein solcher Fall gegeben sein könnte, kann niemals der Ornithologe entscheiden, sondern einzig und allein der Parasitologe nach sorgfältiger Überprüfung des jeweiligen konkreten Einzelfalles im Rahmen der parasitologischen Gesamtsituation.

Ich habe grundsätzliche Bedenken gegen das Verfahren, die letzte, bindende Entscheidung über die verwandtschaftliche Stellung eines Vogels auf der Basis rein morphologischer Befunde vornehmen zu wollen, aber meine

Bedenken gegen die Praxis der morphologisch orientierten Taxonomie, wie sie sich zur Zeit präsentiert, sind nicht geringer. Man braucht die Beispiele nicht weit herzuholen. Wir haben vorhin über die Schwäne gesprochen. 1951 untersuchte Dr. Wetmore den Trompeterschwan und fand, dass die eigentümliche Anatomie von Trachea und Sternum seine Unterbringung in einer besonderen, vom Singschwan getrennten Untergattung erforderlich mache. Drei Jahre später stellte ein anderer berühmter Ornithologe die beiden Schwäne zur selben Art, weil sie angeblich in der Anatomie der Sternalregion miteinander übereinstimmten. 1958 untersuchte Parkes den fraglichen Fall noch einmal und bestätigte Wetmores Befund, stellte also fest, dass sie nicht miteinander übereinstimmten und infolgedessen auch nicht als konspezifisch betrachtet werden könnten. Ich meine, solange noch über die Morphologie zweier unserer grössten und wohlbekanntesten Vogelarten, wie Trompeterschwan und Singschwan, eine solche Unsicherheit herrscht, und zwar nicht etwa nur was die taxonomische Beurteilung von Tatsachen anbetrifft, sondern die Tatsachen selber angeht, solange hat kein ornithologischer Systematiker das Recht, sich auf das hohe Pferd zu setzen und die Ergebnisse der vergleichenden Ornithoparasitologie mit einer Handbewegung abzutun, wenn sie im Einzelfall einmal nicht mit den derzeit gültigen Anschauungen zusammenfallen. Das hohe Ziel eines ornithologischen Verwandtschaftssystems wird, soweit es überhaupt erreichbar ist, nur durch ein harmonisches Zusammenwirken aller am Vogel interessierten Forschungsrichtungen erreicht werden können, aber nicht durch unsachliche Kritik und durch das Beharren auf dem irrtümlichen Standpunkt, wir besässen heute bereits einen Schatz absolut gültiger Erkenntnisse und Einsichten, an denen nicht mehr gerüttelt werden dürfe.

SUMMARY

The Question of Anatine Systematics from a Parasitological Point of View

A report is given on the result of a revision of the so-called *Ornithobius* complex (Mallophaga, Philopteridae), parasitic on Anseriformes, the species of which live especially on phylogenetically old hosts. Of the three genera of the *Ornithobius* complex, *Bothriometopus* is parasitic on screamers; *Ornithobius*, on swans and true geese; and *Acidoproctus*, on the magpie goose (*Anseranas*), the whistling ducks (*Dendrocygna*), the Egyptian goose (*Alopochen*), the spur-winged goose (*Plectropterus*), and pochards (*Netta*, *Aythya*), all of which — according to these parasitological findings — prove to be a group of nearly related forms. On the whole, the host distribution of the genera of Mallophaga mentioned above is still rather unsatisfactorily known and in need of further investigation (collecting of material is therefore urgently desired).

Concerning the swans, the *Ornithobius* findings suggest the separation of two parasitologically well-characterized groups—the Mute Swan group, including the species *olor*, *melancoriphus*, and *atratus*, and the Whooper Swan

group, including *cygnus*, *bewickii*, *buccinator*, and *columbianus*. In the first group, the species *olor* and *melancoriphus* stand closer together, *atratus* somewhat more apart. In the second group, the *Ornithobius* findings speak for a taxonomic arrangement that would connect by stronger bands of affinity the two Eurasian species (*cygnus* and *bewickii*) and the two North American species (*buccinator* and *columbianus*), respectively.

In the whistling ducks (*Dendrocygna*), the Mallophaga largely correspond to the taxonomic conception of Johnsgard (1961). There is no parasitological evidence that the two similar species *arborea* and *guttata* are more nearly related to one another; in fact, the first one should be classified with *autumnalis* and the second one with *eytoni*. The *guttata–eytoni* group joins the two species *arcuata* and *javanica* rather closely, whereas *bicolor* and *viduata* form a separate, independent pair of species.

Objections raised on the part of ornithologists against the results of comparative ornithoparasitology are repudiated, because the morphological findings in ornithology alone do not form a reliable basis for the establishment of relationships. That the host distribution of Mallophaga in individual cases could have been altered and falsified by secondary infestations cannot be criticized by the ornithologist, and only the parasitologist can review the whole actual parasitological situation and get the facts.

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Color Variation and Status of *Parus ater britannicus* and *P. a. hibernicus*

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The purpose of the present paper is to show that, although the English and Irish forms of the Coal Tit (*Parus ater*) have long been accepted as good subspecies, they cannot be clearly distinguished.

The English race, now known as *P. a. britannicus*, was first described by Sharpe and Dresser (1871) in these terms: "*P.* similis *P. atro* sed paullo minor et dorso semper olivaceo-fulvo distinguendus." Although many British specimens, perhaps especially from Scotland, have a much bluer dorsal surface than others, they can probably always be distinguished from *Parus a. ater*, the European form.

The Irish form, now known as *P. a. hibernicus*, was described by Ogilvie-Grant (1910) as *P. hibernicus*, thus: "The pale mustard-colour of the patches on the sides of the head and occipital spot as well as of the breast and belly, also the clear cinnamon-coloured sides, flanks and upper tail-coverts, rendered *P. hibernicus* distinguishable at a glance from *P. britannicus*." This description was based on specimens in the British Museum and in the National Museum of Ireland, and some specimens from County Down were said to be indistinguishable from English birds. The yellow color was said to fade rapidly after death.

Later authors have expanded the distinction between *britannicus* and *hibernicus* without making clear the source of their statements. Thus, in their well-known handbook Witherby et al. (1941) say of Irish Coal Tits: "Some examples, especially from Co. Down, are not separable from *Parus a. britannicus*, others are intermediate, as are coal-tits from parts of S. Wales (Radnor, Brecon, Pemb.) some of which show, varying markedly in degree, some characteristics of the Irish form." And Snow (1955) says: "Irish birds too are similar [to the British form], but in them the whole plumage is suffused with pale yellow, especially noticeable on the underparts and cheeks. Birds from northeastern Ireland are transitional between this and the English form, and some birds from western parts of Gt. Britain show traces of the yellow wash of the Irish birds." Vaurie (1959) has summed the matter briefly by giving the range of *hibernicus* as "Ireland; the birds of the northeast tending towards *britannicus*." Kennedy et al. (1954) recorded birds indistinguishable from the British form in many Irish counties but did not draw the obvious conclusion.

My attention was first directed to the problem by the observation of a bright yellow Coal Tit breeding in Cumberland (England) in 1949; since

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then I have seen 8 yellow Coal Tits in 3 other English counties (Yapp, 1962:253). An examination of museum skins has shown that the situation is much more complicated than has previously been thought. No Irish specimens that I have seen approach the brightest of my wild yellow birds (which seem to be indistinguishable from *P. a. ledousi* from North Africa) in the strength of the color; and the distribution of the pale yellow wash, which is all that they show, is very variable. Of 36 skins that I have examined in detail, only 7 show it on breast, cheeks, and nape. The majority (24) show it on one or two of these surfaces only, as follows:

breast only	1	(Dublin)
cheeks only	13	(Antrim, Down, Dublin, Fermanagh, Sligo, Tipperary, West Meath, Wexford, Wicklow)
nape only	1	(Dublin)
breast and cheeks	2	(Cavan)
cheeks and nape	7	(Antrim, Cavan, Down, Dublin).

On five specimens, from Down, Dublin, and Tyrone, I could find no trace of yellow at all.

The British Museum specimens, which I have looked at only superficially, are not included in this list, nor have I been able to visit the National Museum of Ireland. The former contains, however, the specimens from County Down on which Ogilvie-Grant's statement about nonyellow birds is based. The American Museum of Natural History has two specimens of his from County Down, both of which are determined as *britannicus*. While one (No. 681474) shows no yellow, the other (No. 681475), although very dirty, shows distinct traces of yellow on the cheeks when it is placed against another dirty specimen, such as No. 681509 from Hertfordshire. Three other specimens from County Down, not collected by Ogilvie-Grant, are as yellow as most Irish birds. The same variability is found in birds from other counties; thus, of two birds shot on the same day in Dublin and now at Harvard (although acquired from the National Museum of Ireland), one (No. 80930) has no trace of yellow, the other (No. 80931) is yellowish on breast, cheeks, and nape.

English birds show almost as much variability. In the British Museum, 7 birds are distinctly yellow; these include the specimens from Brecon, Pembroke, and Radnor on which the statement by Witherby is presumably based, but include also birds from Berkshire, Hampshire, Surrey, and Carnarvon. I have examined a total of 279 skins from England and Wales, of which 33 show some yellow. They come from the following counties: Berkshire, Cambridge, Cornwall, Hampshire, Hertford, Lancashire, Middlesex, Nottingham, Suffolk, Surrey, Sussex, and Yorkshire, as well as Brecon, Carnarvon, Pembroke, and Radnor. They were mostly taken during the winter half of the year, from September to March, as indeed are most of the specimens in all the museums. Of 209 skins from Scotland, 16, from the counties of Argyll, Inverness, Lanark, Perth, Renfrew, and Sutherland, show some yellow. As with the Irish birds, the yellow of those from England, Wales, and Scotland is sometimes visible on all three surfaces that are otherwise white, sometimes on two, sometimes on one. It can often be seen only in a good light, and is most visible when the feathers are looked at end-on, that is, from the direction of the tail.

With this interdigitation of yellow and nonyellow forms, the subspecies *hibernicus* cannot be sustained. The yellow forms are certainly commoner in Ireland, but there is not enough evidence to decide whether there is a cline across the British Isles. All the collections that I have examined have skins from a few counties only. Of the specimens taken in England, more than half (137) come from the 7 counties of the southeast, in which Londoners commonly live, while the 9 southwestern counties, of a larger total area, have only 16 specimens. There are only 13 skins from the whole of Wales, and 10 English and 5 Welsh counties are unrepresented. The coverage of Ireland is equally incomplete. With this bias, any statement about the distribution of the yellow forms is unjustified.

There are two possible explanations for the maintenance of the variation. It might be an example of balanced polymorphism, such as has been described for the butterfly *Maniola jurtina* by Dowdeswell et al. (1960). In this animal, isolated populations a few thousand in number are distinct from each other in the distribution of spots on the wing, and a change in the distribution has been shown to be correlated with drought. The spotting is probably not itself important, but is associated with an ability in the early stages to withstand dry conditions. There seems to be no reason why a similar explanation should not apply to birds, and the recognition of this possibility would eliminate many of the assumed entities of geographical subspecies.

On the other hand, the yellowing could be phenotypic. The yellowness of canaries and fowls can be increased if they are fed on chlorophyll-containing food, and it may be that the yellowness of some Coal Tits is due to their diet. This would explain the great variability in the position and degree of the color, and perhaps its fading. By contrast, the yellow of the Great Tit (*Parus major*) lasts well in museum skins, as does that of the bright yellow *Parus ater ledousi.* Some specimens of *P. a. aemodius, amurensis, ater, cabrei, gaddi, insularis, phaenotus,* and *rufipectus* show faint yellow on the cheeks. Some specimens of *charassinicus* are rather more yellow, and one specimen of *gaddi* (No. 328152) in the Smithsonian Institution is as yellow as English juveniles, from which it is in color indistinguishable although apparently full-grown. This wide occurrence of some yellowness in birds from many parts of the world slightly favors the phenotypic explanation.

ACKNOWLEDGMENTS

I thank those in charge of the birds at the following museums, who have given me access to their collections or sent me specimens: American Museum of Natural History, New York; Bolton Museum and Art Gallery; British Museum (Natural History), London; Manchester Museum; Museum of Comparative Zoology, Cambridge (Mass.); Royal Scottish Museum, Edinburgh; Smithsonian Institution, Washington; University Museum of Zoology, Cambridge; Zoologische Staatssammlung, Munich; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; Zoologisches Museum der Humboldt-Universitet, Berlin.

All the observations about yellowness that I have recorded above, except those for the Harvard and Smithsonian specimens, were checked by friends or other workers who were available when I was examining the skins, and I am grateful for their confirmation.

SUMMARY

Examination of 36 skins from Ireland, 279 from England and Wales, and 209 from Scotland reveals that *P. a. hibernicus* cannot be separated from *P. a. britannicus.* Although yellow forms are commoner in Ireland, not enough material is available to establish a cline. They could be an example either of balanced polymorphism or of phenotypic variation.

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Field Tests on the Essential Components of the European Nightjar's Song

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This paper is a brief report on tests to study the responses to auditory stimuli of two members of the Caprimulgidae: the Nightjar (*Caprimulgus europaeus*), which is distributed over most of Europe; and the Red-necked Nightjar (*C. ruficollis*), which is confined to Spain and northwestern Africa. The tests consisted of playing back song records and artificial song to wild nightjars during the summers of 1960 and 1961 near Bonn (Germany) and in May 1961 near Salamanca (Spain). The aim of the study is to understand the essential components of auditory stimuli, to which nightjars respond in a typical manner.

The male Nightjar utters a simple "song," consisting of rattling or buzzing sounds. Usually this is confined to within an hour after sunset. One burst of uninterrupted singing may last for more than 5 minutes. This song has the function of marking a territory.

The song consists of two phrases, each of which consists of components that are short pulses. The "long phrase" shows a mean frequency of 1.7 kc/sec and a pulse rate of 24/sec. Long phrases are followed by "short phrases," which last about half a second and show a lower frequency (1.2 kc/sec) but a higher pulse rate of 40/sec (Fig. 1).

The male Nightjar responds immediately to a playback of its song. He flies over the recorder, claps his wings, calls *quick*, and then buzzes. These responses to auditory stimuli are restricted to an hour after sunset. With this as background, I tried to determine the essential components that release this reaction.

I tested the Nightjar with original and modified song. The latter consisted of an original song transposed with frequencies one-half octave higher and then played back with half the normal speed (Fig. 1). The long phrase of the modified song shows a mean frequency of 1.4 kc/sec and a pulse rate of 17/sec. The corresponding frequency of the short phrase is 1.1 kc/sec and the pulse rate is 30/sec.

Another set of tests consisted of artificial song electronically produced by a square-wave pulse-generator and a special combination of filters. Experiments with artificial song show the advantage of free choice and free combination of melody, pitch, and rhythm. The apparatus used here was developed to simulate human speech vowels. I used this simulator, in spite of

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[1] In connection with the Institut für Phonetik und Kommunikations-forschung der Universität Bonn.

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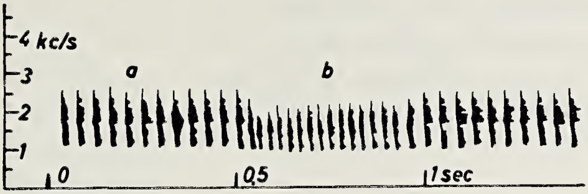
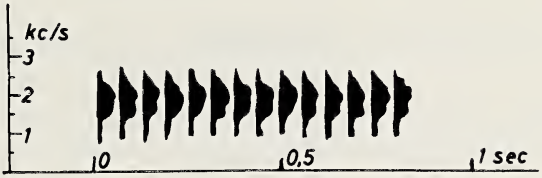
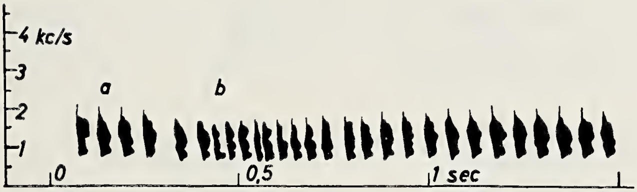


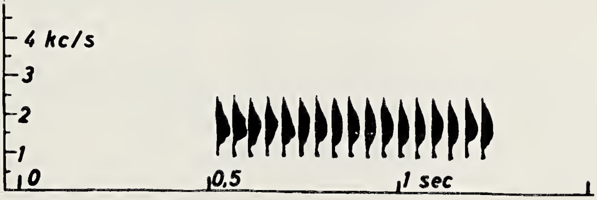
European Nightjar: Original Song.
a: long phrase: 1,7 kc/s mean frequency; 24 pulses/s.
b: short phrase: 1,3 kc/s mean frequency; 40 pulses/s.



Artificial Song:
1,7 kc/s mean frequency; 17 pulses/s.



European Nightjar: Modified Song.
a: long phrase: 1,4 kc/s mean frequency; 17 pulses/s.
b: short phrase: 1,1 kc/s mean frequency; 30 pulses/s.



Artificial Song:
1,7 kc/s mean frequency; 23 pulses/s.

Fig. 1. Sound spectrograms of European Nightjar songs.

the known difference in sound production of humans and birds, because I suggest a principal similarity. I have assumed that the bird's syrinx, like the human larynx, produces a series of pulses. This organ is represented by the square-wave pulse-generator and the integrator (Fig. 2, no. *1* and *2*).

The integrator acts as a smoothing part. The other sound-forming organs (trachea, larynx, bill) are simulated by filters (Fig. 2, no. *3* and *4*).

Two types of artificial song were produced with constant frequency (1.7 kc/sec), equal to the original mean frequency of the long phrase. One had the original pulse rate of 23/sec and the other had a lower pulse rate of 17/sec.

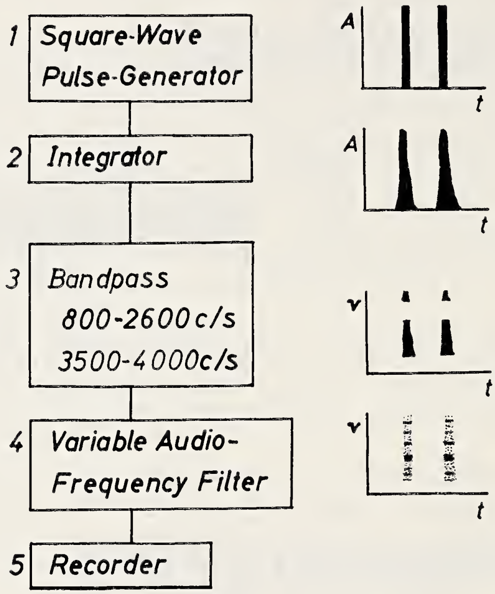


Fig. 2. Circuit diagram for artificial song.

1. Philips GM 4580/02.
2. R-C-Part.
3. Wandel and Goltermann BP.8304.
4. ALBIS 502/74: Frequency and attenuation:

5,210 c/s—10 db	2,510 c/s— 6 db	1,210 c/s—24 db
4,340 c/s— 2 db	2,090 c/s— 0 db	1,010 c/s— 5 db
3,620 c/s—10 db	1,740 c/s— 0 db	841 c/s—25 db
3,010 c/s—26 db	1,450 c/s—13 db	701 c/s—37 db

   and 100–700 c/s—max. att.

5. Burger: Butoba MT4.

Table 1 shows the results of the tests. Experiments were made with 4 individuals, 2 in Germany near Bonn and 2 in Spain near Salamanca. Tests were made from May to July in 1960 and 1961. One sample was played back to an individual 3 or 4 times in one evening. A reaction was called "positive" if the Nightjar gave the above-mentioned behavior; "questionable," if the bird flew silently over the recorder; "negative," if no bird appeared.

The statistics indicate that the best results were obtained with the original and modified song, and a somewhat weaker response with the artificial song

TABLE 1.—RESULTS OF THE TESTS

TYPE OF TEST MATERIAL	NO. OF BIRDS TESTED	NO. OF TESTS MADE	REACTIONS		
			Positive	Questionable	Negative
Original song	2	4	3	0	1
Modified song	2	10	7	0	3
Artificial song					
23 pulses/sec	2	16	5	4	7
17 pulses/sec	2	13	0	4	9
together	4	43	15	8	20

having a pulse rate of 23/sec. There were no positive reactions when tests were made with the artificial song of 17 pulses/sec (Table 1).

The Nightjar's simple song may be described by the pitch, rhythm, and melody. In this case, melody is comprised only of the alternating of long and short phrases.

The tests with modified song demonstrate that changes of pitch and rhythm in a narrow scale have no influence on the results. If one compares the responses to the two types of artificial song, a combination of pitch and rhythm, one notes that a change in rhythm has a remarkable influence. But the question of which combination is sufficient for good results is still unanswered.

Fig. 3. Sound spectrogram of Red-necked Nightjar song.

Another way to prove the significance of the essential components is to compare the song of the European Nightjar with that of the Red-necked Nightjar. Both occur together in Spain as sibling species. The song of the Red-necked species differs strongly in pitch and especially in rhythm (Fig. 3). These investigations will be continued in an attempt to learn something about the "language" of bird sound.

SUMMARY

Analyses of the European Nightjar's and the Red-necked Nightjar's song are given. A series of play-back tests with song records, distorted song, and artificial song was made and the responses of wild nightjars to these auditory stimuli discussed. Pitch and rhythm are essential components of the nightjar's song.

Probleme des Feinderkennens bei Vögeln[1]

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INHALT

A. EINLEITUNG

Jeder Feind jagt auf seine Weise. Daher muss der Vogel dem Angriff ihm gefährlicher Feinde auf jeweils verschiedene Weise zu entgehen suchen. Dies kann er nur, wenn er sie "erkennt." Ein Vogel "erkennt" einen Raubfeind, wenn er auf ihn eindeutig anders antwortet als auf andere Mitbewohner seines Lebensraumes. Das Erkennen ist nur Teil einer Reihe nervöser Vorgänge, die zum passenden Schutzverhalten führen. Beobachtbar ist die oft äusserst komplexe Reizsituation sowie das durch sie ausgelöste Verhalten. Was sich dazwischen abspielt, lässt sich nur erschliessen. Haupteigenschaft der dem Erkennen zugrundeliegenden Apparate, von Lorenz (1950 und später) "Auslösemechanismen"[2] genannt, ist es, aus den schier unbegrenzt vielen Sinnesreizen diejenigen herauszufiltern, die eine biologisch wichtige Situation kennzeichnen und das zu ihr passende Verhalten in Gang setzen; wie spezifisch die vom Auslösemechanismus umgeformte und weitergegebene Nachricht sein kann und sein muss, soll u.a. im folgenden gezeigt werden. Wie er die von einem Feind ausgehenden Reize verarbeitet, ist Gegenstand einer Forschung, deren Ergebnisse uns allgemein lehren, Wahrnehmung zu verstehen.

Noch aus einem zweiten Grunde sind Einsichten in das Erkennen von Feinden hoch bedeutsam. Es ist nämlich etwas historisch Gewordenes und unterscheidet sich sicherlich nicht grundsätzlich vom Ansprechen anderer lebenswichtiger Umweltdinge. Ein besonderer Umstand aber macht die Erforschung der Stammesgeschichte von Auslösemechanismen für das Feinder-

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[1] Mit Unterstützung der Deutschen Forschungsgemeinschaft.

[2] Hiermit identisch ist das "auslösende Schema" (Tirala, 1923; Lorenz, 1935). Dieser Begriff wurde verlassen, weil er nahelegte, das Tier antworte auf eine "schematische," weil einfache Reizkonstellation. "Mechanismus" aber lässt ohne weiteren Zusatz an ein Geschehen *im* Tier denken, auf das eine bestimmte Reizsituation passt.

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kennen so lohnend: ein Feind lebt im Wohngebiet einer Art, oder er fehlt; der Artgenosse oder die Nahrung oder andere lebenswichtige Dinge aber sind notwendig allgegenwärtig. Aus Gründen der Wahrscheinlichkeit muss sich ein Selektionsdruck auf einen Auslösemechanismus dort am drastischsten auswirken, wo er neu auftritt oder in Gänze verschwindet. Und das ist gerade bei dem durch einen Feind ausgeübten Druck der Fall. Artgenosse oder Nahrung ändern sich i.a. nur teilweise und stellen deshalb den auf sie passenden Auslösemechanismus vor die Aufgabe nur teilweiser Umkonstruktion. Tritt aber ein Feind neu auf, so stellt er seine Beutetiere vor die neue Aufgabe, ihn wirksam zu erkennen; sonst frässe er sie. Stammesgeschichtliche Veränderungen im Erkennen von Feinden sollten sich daher leichter nachweisen lassen als solche im Ansprechen anderer Reizsituationen.

B. TERMINOLOGIE UND METHODISCHES

Feind sei hier jeder die Brut oder das eigene Leben bedrohende Räuber sowie auch jeder Brutparasit genannt.

Hasst ein Vogel auf einen Feind, indem er dessen Ort mit bestimmten Rufen und Bewegungen markiert, so versammelt sich i.a. rasch eine lärmende Schar von Artgenossen und anderer Arten, die dem Räuber die Jagd erschweren. Hierzu bedarf es keines Angriffes; es genügt, dass er wahrgenommen wird (Rand, 1941; Hartley, 1950). Im Hassen oder Alarmrufen scheinen sich Angriffs-, Flucht- und Erkundungstendenzen zu spiegeln, und Andrew (1961) wies nach, dass im Rufen der hassenden Amsel viel Flugmotivation steckt. Bei manchen Arten wie z.B. beim Eichelhäher (*Garrulus glandarius*) geht es fliessend in reinen Beschädigungsangriff über. Mitunter erliegt ihm der Räuber (Meinertzhagen, 1959:24).

Schlüsselreiz ist ein Merkmal des Feindes, dessen Veränderung das in Rede stehende Verhalten quantitativ und/oder qualitativ beeinflusst. Nach Lorenz (1935) sprechen angeborene Auslösemechanismen (AAMs) auf eine aus einer überschaubaren Zahl von Einzelmerkmalen bestehende "Schlüsselkombination von Reizen," von Russell (1943) "Schlüsselreize" genannt, an. Die Feststellung, eine im Experiment veränderte Eigenschaft sei Schlüsselreiz für eine Reaktion, sagt noch nichts über die möglichen Grenzen aus, innerhalb deren die die Eigenschaft ausmachenden Parameter variieren dürfen; das ist erst in wenigen Fällen untersucht (z.B. Tinbergen u. Perdeck, 1951).

Auslösemechanismus ist eine reizverarbeitende Funktionsstruktur, die auf biologisch bedeutsame Umweltsituationen anspricht, indem sie das zu ihnen passende Verhalten in Gang setzt (zuletzt Tinbergen, 1951; Lorenz, 1960 u.a.). Die Diskussion darüber, ob man das Sinnesorgan in den Begriff einschliessen soll, hält noch an (z.B. Marler, 1961). Ähnlich lässt sich "stromabwärts" die Grenze zur koordinierenden Motorik sowohl begrifflich wie methodisch bisher nicht befriedigend festlegen.

Ein Auslösemechanismus wird entweder nach der Reaktion, die er auslöst, benannt, oder aber nach dem zu ihm passenden Objekt. Die Benennung nach der Art der Antwort sagt nichts über die auslösenden Reize aus, und die nach dem adäquaten Objekt wird nicht der Tatsache gerecht, dass sehr verschiedene Umweltdinge—hier Feinde—dasselbe Verhalten hervorrufen. So lösen u.a. Eule und Hermelin das Hassen des Buchfinken (*Fringilla coelebs*) aus (Hinde, 1954:I), Würger, Eule, Katze, Mensch u.a. das des Trauerschnäppers (*Ficedula hypoleuca*) (Curio 1959*a*:42). Ähnliches gilt vom "Luftfeindruf" der Amsel (*Turdus merula*) (Messmer u. Messmer, 1956). Die Mehrzahl der Feindantworten gilt demnach vielen verschiedenen Feinden. Hieraus ergeben sich zwei Fragen: 1. Inwiefern ist dann ein gegebenes Schutzverhalten noch reizspezifisch? und 2. Kann ein spezielles, offensichtlich dem Schutz vor Feinden dienendes Verhalten durch mehr als einen Auslösemechanismus enthemmt werden? Auf die hieraus folgenden theoretischen Weiterungen komme ich in Kapitel F zurück.

Der *Attrappenversuch* hilft Feinderkennen zu erforschen. Die Wirkung der Darbietung einer Attrappe auf die folgende Darbietung einer anderen beim selben Vogel kann die zweite Antwort schwächen oder verstärken. Was geschieht, hängt ab von der Dauer der Darbietung, der Pause zwischen den Darbietungen und dem Stärkeverhältnis der benützten Attrappen (Hinde, 1960). Deshalb, und damit individuelle Eigenarten kein Übergewicht bekommen, ist es ratsam, jeden Vogel mit nur einer Attrappe zu prüfen, oder aber wenige Individuen mit einer derart ausgeklügelten Reihenfolge der einzelnen Modelle, dass die angedeuteten, unerwünschten Nebeneffekte unterbleiben. Bei Versuchen mit freilebenden Vögeln ist ferner zu beachten, wie häufig der fragliche Räuber auftritt, weil Gewöhnungsvorgänge (Adaptation) eine grosse Rolle spielen können (Hinde, 1954:II; Schleidt 1961*a*, 1961*b*, u.a.).

Weiter stellt man zu vergleichende Versuche in vergleichbaren physiologischen Phasen an (vgl. Kap. D).

Wie man Feindverhalten am zweckmässigsten *quantifiziert*, hängt vom Einzelfall ab. Fliessen z.B. in eine Alarmhandlung zwei verschiedene Rufe ein, so spiegeln sie i.a. verschiedene Erregungsgrade desselben Verhaltens wider, oder sie sind Mischungen verschiedener Verhaltensweisen. Deshalb darf man sie nicht einfach addieren, um die Stärke der Antwort zu bestimmen. Entweder verwertet man nur den einen—häufigeren—Ruftypus, oder berücksichtigt bei der Auswertung beider Rufe ihr verschiedenes Gewicht; hierzu muss man aber ihre Motivation vorher kennen.

Die *Aufzucht* erfahrungsloser Jungvögel ist die direkteste Methode zum Nachweis eines angeborenen Auslösemechanismus (AAM). Ohne im einzelnen auf die Grenzen des Kaspar-Hauser-Versuches einzugehen (s. Lorenz, 1961), sei hier nur bemerkt, dass der negative Ausfall einer Prüfung des Jungvogels nicht zu dem Schluss berechtigt, die Kenntnis des betreffenden Feindes müsse erlernt werden. Stets ist an aufzucht- oder haltungsbedingte Triebausfälle zu denken (z.B. Nicolai, 1956; Blase, 1960; Thielcke, 1961).

Lernen wäre aber bewiesen, wenn es gelänge, den Vogel *nur* von dem Feind zu isolieren, den er später nicht erkennt.

C. SEHEN UND HÖREN DES FEINDES

a. *Optisches Erkennen*

1. Der ruhende Flugfeind

Nistende Fitisse (*Phylloscopus trochilus*) greifen einen Kuckuck (*Cuculus canorus*) am Nest mit anderen Rufen an als denen, mit denen sie einen ebendort aufgehakten Sperber (*Accipiter nisus*) in respektvollem Abstand umfliegen (Edwards et al., 1949–50; Smith u. Hosking, 1955). Ein Kuckucksbalg ruft Alarm, Drohen oder Beschädigungsangriff bei vielen Wirtsvögeln hervor (*Luscinia luscinia, Erithacus rubecula, Saxicola torquata, S. rubetra, Phylloscopus sibilatrix, P. trochilus, P. collybita, Sylvia atricapilla, S. borin, Acrocephalus arundinaceus, A. schoenobaenus, Anthus pratensis, A. trivialis, Lanius collurio*; sogar *Fringilla coelebs*). *Acrocephalus scirpaceus, Prunella modularis,* beide häufige Kuckuckswirte, *Troglodytes troglodytes, Phoenicurus phoenicurus* und *Turdus merula* scheinen überhaupt nicht zu reagieren. Einzig beim Fitis kennt man einige der für die Kuckucksreaktion nötigen auslösenden Reize, die den Rufen nach feindspezifisch zu sein scheint. Zwar genügt allein ein Kuckuckskopf, doch versagen ein unbemaltes und unbefiedertes Holzmodell mit Glasaugen, Metallschwingen und Schwanz vollkommen sowie weiter ein artgerecht bemaltes flaches Pappmodell. Diese Attrappen führen ganz wie der Sperber nur zu Alarmrufen (Smith u. Hosking, l.c.). Ob das Holzmodell wirksam würde, wenn man es artgerecht bemalte, bliebe ebenso zu prüfen wie die Frage, welche speziellen Qualitäten des Kopfes die Unterscheidung vom Sperber gewährleisten und welche übrigen Eigenschaften des Rumpfes möglicherweise die Antwort verstärken.

Trauer- und Halsbandschnäpper (*Ficedula hypoleuca, F. albicollis*) antworten auf zwei gleichgrosse Flugfeinde grundverschieden und biologisch sinnvoll. Wie spezifisch und wie unabhängig ihre Merkmale wirken, begann ich an freilebenden Vögeln zu untersuchen. Ein in Nestnähe gelandeter Buntspecht (*Dendrocopus major*), ein Plünderer der Bruten von Offen- und Höhlenbrütern (Curio, 1959*a*:46), wird von beiden Nestpartnern augenblicklich schnarrend in Sturzflügen angegriffen. Zwischendurch rufen die Vögel Alarm. Auf einen Rotrückenwürger (*Lanius collurio*) aber hassen sie ausschliesslich, wobei sie ihm stets 3–4 m vom Leibe bleiben. Der Specht sucht nach wenigen Schnarrflügen das Weite, während der Würger unbekümmert bleibt. Nestlinge wie ausgeflogene Junge verstummen und erstarren dort, wo sie gerade sitzen, sobald der Alarm anhebt. Sie regen sich erst wieder, wenn der Alarm verebbt, d.h. der Feind verschwunden ist (Curio, l.c.:47).

Bewegung ist bei beiden Feinden entbehrlich und mindestens für den Würger kein Schlüsselreiz. Wenigstens eine Eigenschaft des Spechtes, die

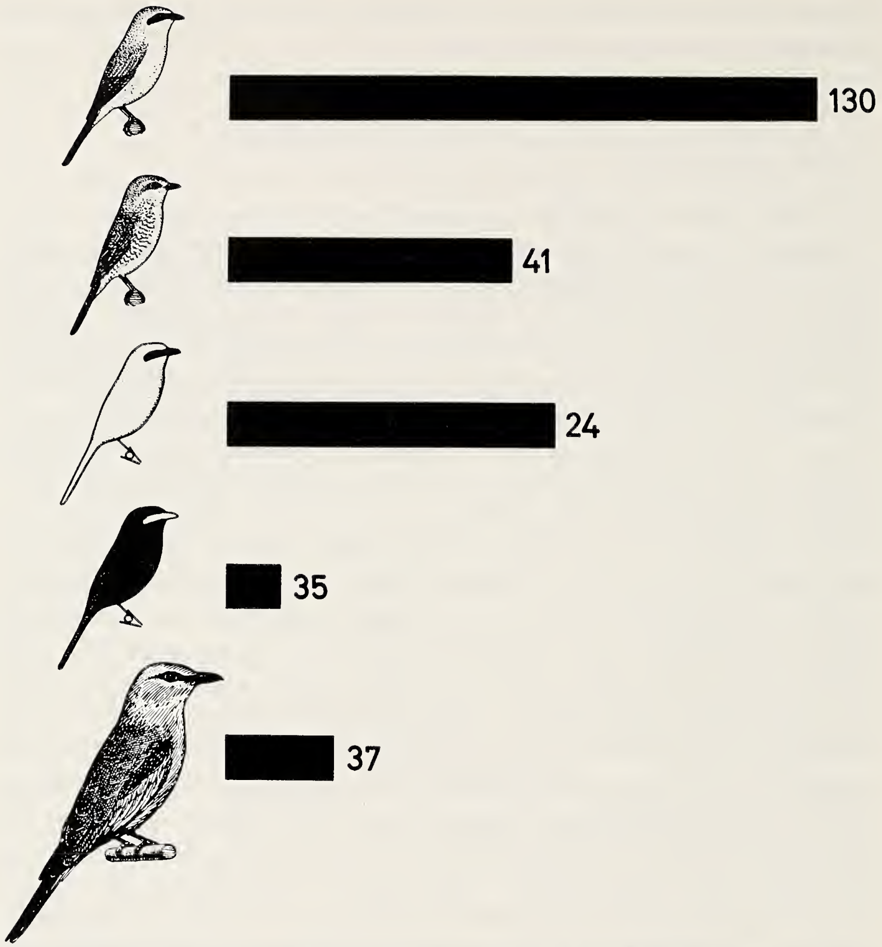


Abb. 1. Hassen revierbesitzender Trauerschnäpper auf Feindattrappen 1,5 m vor der Nisthöhle. Von oben nach unten: Ausgestopftes Rotrückenwürgermännchen, -weibchen, weisses und schwarzes Gipsmodell des Männchens, ausgestopfte Blauracke. Männchenbalg: 65 Rufe/min. Zahlen = Versuche = geprüfte Individuen.

Fig. 1. Mobbing of territorial Pied Flycatchers at enemy dummies placed 1.5 m before the nest hole. From above: mounted Red-backed Shrike male and female, white and black plaster models of the male, mounted Roller. Mounted male: 65 calls/min. Numbers = experiments = tested individuals.

dem Würger fehlt, löst Schnarren aus: er hakt am Stamm, der Würger fusst auf einem Zweig. Versetzt man nämlich den Specht in der aufrechten Kletterhaltung auf einen Zweig, so löst er nur noch Alarm aus und keinen einzigen Schnarrangriff. So kann der Untergrund, auf dem sich ein Feind bewegt, entscheidend mitspielen (Curio, unveröff.). Überdies sichern Merkmale der Würgers seine Unterscheidung von harmlosen Vögeln. Das Weibchen löst nur halb so starkes Hassen aus wie das Männchen, aber etwa ebensoviel wie ein sonst weisser glatter Gipswürger mit schwarzem Augenstreif (Abb. 1). Demnach ersetzt dieser die gesamte Weibchenfärbung. Die farbenfreudige Blauracke (*Coracias garrulus*) wirkt ihrerseits nur halb so stark wie das Würgerweibchen; demnach machen nicht die prächtigen Farben des Männchens seine hohe Wirksamkeit aus. Vielmehr scheint es die spezifische Kopfzeichnung zu sein.

Kommt es aber nur auf einen Hell-Dunkel-Kontrast am Kopf des Würgermännchens an? Dies ist nicht der Fall, denn ein schwarzer Gipswürger mit weissem Streif am Kopf ist seinem Komplementärmodell eindeutig unterlegen (Abb. 1). Demnach muss etwas Dunkles auf hellem Untergrund sitzen; ob nur ein Augenstreif wirksam wäre, das bliebe zu prüfen. Weitere wichtige Schlüsselreize für das Hassen sind absolute Grösse, Haltung und Vogelform, während die Oberflächenbeschaffenheit belanglos ist. Wenigstens Grösse, Vogelform und Farbe müssen zusammenkommen, um überhaupt eine Antwort auszulösen. Die wenigen, bisher schon analysierten Schlüsselreize sind also verwickelte Beziehungen einzelner Parameter. Wie sie quantitativ zusammenwirken, das begann ich zu untersuchen.

Ähnlich antworten Gimpel (*Pyrrhula pyrrhula*) angeborenermassen auf einen weissen würgergrossen Gipsvogel mit schwarzem Augenstreif, doch ist Vogelform für sich auch schwach wirksam, ähnlich wie die Merkmale behaart oder befiedert. Und diese gewinnen ihrerseits durch konvexe Wölbung oder Braunsprenkelung. Diese beiden Schlüsselreize sind aber entbehrlich und verstärken nur eine Antwort auf die anderen, eben genannten Reize (Kramer u. St. Paul, 1951). Nach Versuchen von Dancker (1956) scheinen fütternde Goldammern (*Emberiza citrinella*) eine spezielle Würgerantwort zu haben, doch ergab meine Wiederholung der Vorweisung von Würgerbälgen an einem anderen Paar dafür keinen Anhaltspunkt. Mehrere Meisen, Sylviiden und Rotkehlchen hassen eindeutig auf ausgestopfte Würger in Berlin, Hessen und in der spanischen Sierra Guadarrama. Es hat den Anschein, als sei die Würgerreaktion unter europäischen Singvögeln ähnlich weit verbreitet wie das Hassen auf Eulen (unveröff.).

Ruhende wie fliegende Sperber und Baumfalken (*Falco subbuteo*) ziehen das Hassen von Rauch- und Mehlschwalben (*Hirundo rustica*, *Delichon urbica*) auf sich. Ein sitzender Sperber wirkt stärker als der grössere Habicht (*Accipiter gentilis*) oder ein Wespenbussard (*Pernis apivorus*). Entscheidende Bedeutung haben gelbe Augen, ein Krummschnabel in nicht zu grossem Verhältnis zum Kopf, Räumlichkeit und Befiederung. Alle diese Merkmale sind bis auf die gelben Sperberaugen für die Reaktion unentbehrlich. Natürliche Haltung und Raumlage dagegen sind weitgehend belanglos. (Hängt aber ein Rotrückenwürger kopfab, beachten Trauerschnäpper ihn überhaupt nicht [unveröff.]). Inwiefern Lernen in diese höchst komplexe Reizsituation eingeht, ist völlig offen (Mohr, 1960).

Zahme Dohlen (*Coloeus monedula*) und Nebelkrähen (*Corvus cornix*) fürchten den natürlichen oder aus Gips geformten Kopf von Waldkauz (*Strix aluco*) und Habicht. Die Gesamterscheinung des Räubers wirkt nur wenig stärker. Auch hier dürften die Augen von Bedeutung sein, denn ein Kopf von hinten wirkte schwächer als einer von vorn und ein Habichtskopf wiederum schlechter als einer vom Kauz (Strauss, 1939*a*, *b*). Kontrollierende Versuche, die die spezielle Bedeutung beider Räuber bewiesen, fehlen bisher. Wenig untersucht sind auch die feindlichen Antworten brutpflegender Puten (*Meleagris gallopavo*) auf sitzende Tagraubvögel (Mohr l.c., Löhrl, mdl.) sowie die vieler Singvögel auf Eichelhäher (Edwards et al., 1949–50; Goodwin, 1953). In allen Freilandversuchen ist es besonders dringend, auf vergleichbare Bedingungen zu achten. So griffen brütende Amseln den Häherbalg 30 cm neben dem Nest schneidig an, hassten aber auf ihn, als er 6mal soweit weg war (Goodwin, l.c.; vgl. auch Kramer, 1941).

Erstaunlich ist die Tatsache, dass viele Cardueliden gegen Tagraubvögel und Eulen gleichgültig bleiben, während viele Paridae, Sylviidae, Turdidae, Mimidae, Muscicapidae, Troglodytidae, Sittidae, Spechte, Kolibris u.a. hochspezifische Hass- und Angriffsreaktionen wenigstens auf einen der beiden Räuber ausgebildet haben. Ausnahmen machen vielleicht der Girlitz (*Serinus serinus*) (Strauss, l.c.) und sicher Gimpel und Buchfink unter den Cardueliden. Die sich hieraus ergebende Frage nach der Funktion des Hassens kann hier nicht weiter verfolgt werden.

Als Schlüsselreize für die Eule fanden Hartley (1950) an 33 freilebenden englischen Vogelarten und Hinde (1954:I) an Buchfinken-Wildfängen: (1) Eulenartiger Körperumriss, (2) unaufgelöste Kontur, (3) Räumlichkeit, (4) Befiederung, (5) Braun oder grau, (6) Sprenkelung in diesen Farben auf hellem Untergrund, (7) Augen, (8) Schnabel. Möglicherweise wirken Schleiereulen (*Tyto alba*) deshalb so schwach auf Singvögel, z.B. 4 Nectarinien, weil sie nicht genügend grob gesprenkelt sind (Koenig, mdl.). Nice und ter Pelkwyk (1941) gelang es, durch Randschattierung flacher Eulenmodelle Alarm bei ihren handaufgezogenen Singammern (*Melospiza melodia*) hervorzurufen, desgleichen gestopfte Eulen durch Flügelbewegungen wirksamer zu machen. Ähnlich pickten Benners (1938) Hühner erst dann nach aufgemalten Körnern, als sie durch Schattierung für sie räumlich wurden. “Falsche” Schlagschatten täuschten sie nicht. Hänflinge (*Acanthis cannabina*) und Zeisige (*Spinus*) geraten vor lebenden Sperbern oder Baumfalken im Zimmer erst dann in Panik, wenn diese die Flügel breiten; sonst landen sie auf ausgestopften unbekümmert (Mohr, 1960). Solche Kenntnis machen sich Vogelsteller beim Bau ihrer mit beweglichen Flügeln ausgestatteten Kauzattrappen zunutze.— Viele Vögel lösen Hassen aus, doch Eulen i.a. am stärksten. Dies ist nicht verwunderlich, da alle ähnliche Oberflächeneigenschaften und teilweise ähnliche Gestalt und Grösse haben.

Noch so kunstvoll bemalte Pappeulen lassen handaufgezogene Rotrückenwürger und Rotkopfwürger (*Lanius senator*) gänzlich “kalt” (St. Paul, 1948; s. auch Watson, 1957). Ein entscheidender und unentbehrlicher Schlüsselreiz sind die Eulenaugen für die Würger, und zwei Augen lösen mehr aus als eines (vgl. auch. Portielje, 1926).

Die Körpergrösse der Eule darf schwanken, ist aber auf die durch die eigene Grösse gegebene Bedrohung durch den Räuber abgestimmt. So hassen kleine Singvögel i.a. nicht auf den Hüttenuhu, den Krähen und Tagraubvögel belästigen, und umgekehrt hassen diese schwerlich auf Eulen unter Waldkauzgrösse. Beim Trauerschnäpper liegt das Optimum der Eulengrösse zwischen Sperlings- (*Glaucidium passerinum*) und Waldkauz (unveröff.). Buchfinken hassen auf den Steinkauz (*Athene noctua*) stärker als auf den Waldkauz (Hinde, 1954:I).

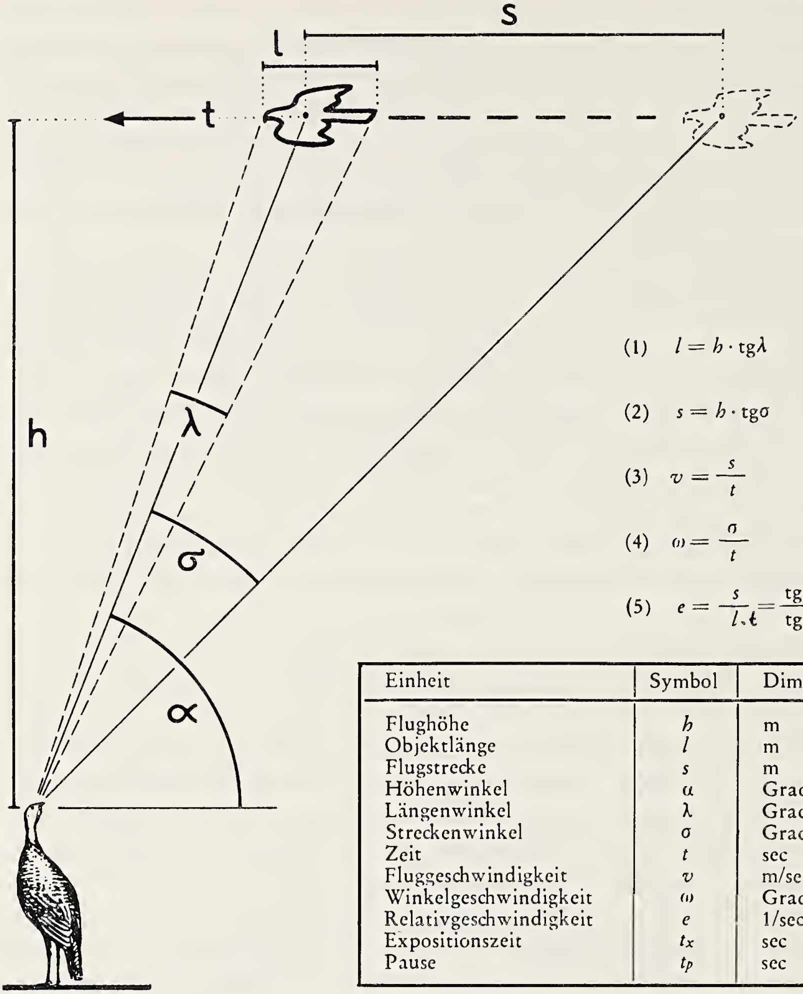
Erreichen Singvögel die Grösse des Würgers, so hassen sie auf ihn nicht, wie z.B. Amseln, oder suchen sogar seine Nähe, wie die Brutgemeinschaften von Sperbergrasmücke (*Sylvia nisoria*) und Neuntöter oder von Wacholderdrossel (*Turdus pilaris*) und Raubwürger (*Lanius excubitor*) zeigen (Heinroths, 1924–33; zuletzt Diesselhorst, 1956; Hohlt, 1957). Der kleine australische *Cuculus pallidus* wirkt auf englische Kuckuckswirte ähnlich oder genauso wie sein grösserer europäischer Vetter (Smith u. Hosking, 1955). Haustauben erschrecken vor dem Sperber nur leicht, vor dem Habicht stieben sie panisch davon (Mohr, 1960). Rabenkrähen (*Corvus corone*) fürchten nur Habicht und Wanderfalk (*Falco peregrinus*), aber nicht Sperber und Bussard (*Buteo buteo*) (Löhrl, 1950*a*).

Sämtlichen hier vorgeführten Fällen ist eines gemeinsam: die überragende Bedeutung des Kopfes als Träger wichtiger Strukturen und Zeichnungsmuster. Im Extrem genügt der Kopf allein (Hosking u. Smith, l.c.; Strauss, l.c.). Eine wohl nicht zufällige Parallele hierzu findet sich in der Ausbildung von Auslösern am Kopf, die im Dienst der innerartlichen Verständigung ausgebildet wurden (Cinat-Tomson, 1926; Immelmann, 1959), oder von individuell besonders variablen Strukturen, die das Erkennen einander bekannter Artgenossen erlauben (Literatur bei Nice, 1943:204 ff.).

Kein einziger im Experiment isolierter Schlüsselreiz wurde auf seine Zerlegbarkeit geprüft, noch auf die vom Auslösemechanismus tolerierten Grenzen seiner Parameter. Weiterhin kennt man nirgends die ungefähre Anzahl der in einen Auslösemechanismus eingehenden Schlüsselreize oder die Art ihrer Verarbeitung. Auch ist nirgends ersichtlich, weshalb z.B. Befiederung im AM einer Art unentbehrlich (St. Paul, s.o.), bei einer anderen entbehrlich, aber wirksam (Mohr, l.c.), und bei einer dritten nicht einmal Schlüsselreiz ist (Curio, s.o.).

2. Der fliegende Flugfeind

Nach Thorpe (1944) schrecken Vögel vor Reizen hoher Intensität, vor allem Fremdem, vor schnell und vor plötzlich Bewegtem. Wirkt ein Lufträuber nur deshalb fluchtauslösend, weil er plötzlich auftaucht, fremd erscheint, oder sich rasch voranbewegt? Einen entscheidenden, methodisch äusserst sorgfältigen Beitrag zu dieser Frage lieferte Schleidt (1961*a*, 1961*b*) mit Versuchen an Bronzeputen (*Meleagris gallopavo* subspec.). Erste Zweifel an der Hypothese, Raubvögel würden an ihrer speziellen Form erkannt



(1) $l = h \cdot \text{tg}\lambda$

(2) $s = h \cdot \text{tg}\sigma$

(3) $v = \frac{s}{t}$

(4) $\omega = \frac{\sigma}{t}$

(5) $e = \frac{s}{l \cdot t} = \frac{\text{tg}\sigma}{\text{tg}\lambda \cdot t}$

Einheit	Symbol	Dimension
Flughöhe	h	m
Objektlänge	l	m
Flugstrecke	s	m
Höhenwinkel	α	Grad
Längenwinkel	λ	Grad
Streckenwinkel	σ	Grad
Zeit	t	sec
Fluggeschwindigkeit	v	m/sec
Winkelgeschwindigkeit	ω	Grad/sec
Relativgeschwindigkeit	e	1/sec
Expositionszeit	t_x	sec
Pause	t_p	sec

Abb. 2. Definition und Ableitung der Begriffe in der Analyse der Flugfeindreaktionen der Pute (aus Schleidt, 1961*b*). Näheres siehe den Text.

Fig. 2. Definition and derivation of terms employed in the analysis of responses to flying predators in the Turkey (from Schleidt, 1961*b*). For further details, see text.

(Heinroths, 1924–33; Lorenz, 1939; Tinbergen, 1939*a*; Krätzig, 1939, 1940; Goethe, 1940), tauchten in Versuchen mit Stockentenkücken (*Anas platyrhynchos*) auf (Melzack et al., 1959; s. auch Hirsch et al., 1955), die aber wegen ihrer unbiologisch hohen Wiederholungsrate nicht die Klärung der Frage erlaubten, inwiefern Gewöhnung an eine bestimmte Form das Erkennen sichert. Mehr Gewicht hatten Befunde an Spaltfussgänsen (*Anseranas semipalmata*), die andeuteten, dass der Jungvogel lernen muss, was er nicht zu fürchten hat (Davies, 1961; historischer Überblick in Schleidt 1961*b*).

Die Pute äussert je nach der Höhe, in der sie einen Raubvogel erblickt, zwei verschiedene Alarmlaute. Obendrein kann sie den Schwanz fächern, in Deckung stürzen, oder sich nur lautlos drücken. Oder aber sie sichert unter Aufmerksamkeitslauten. Die Fluggeschwindigkeit des Räubers darf, gemessen in Eigenlängen, 20–30/sec. nicht übersteigen. Insekten und Kleinvögel bleiben daher unwirksam. Auch darf seine Grösse nicht einen Längenwinkel von 5° überschreiten (Abb. 2). Die eingeführte Symbolik dürfte für die Standardisierung der Befunde verschiedener Forscher nützlich sein. Schleidts zogen Jungputen isoliert von erwachsenen Artgenossen und von Objekten auf, die die Flugfeindreaktion auslösen. Am ersten Tag des Versuchs, im Alter von 11–16 Wochen, sahen die Puten vier flächengleiche Attrappen vor hellem Hintergrund. Alle Attrappen erschienen 2,3 m über dem Boden bei gleicher Geschwindigkeit und einer Darbietungsdauer von 10 sec. (Abb. 3). Keine von ihnen löste stärker aus als die anderen (genauer Versuchsverlauf in Schleidt, 1961*b*, Tab. 6). Am nächsten Tag fiel die Antwort auf alle Attrappen schwächer aus. Nun wurde der Raubvogel R je Tag einmal und die Gans G 10mal geboten, um die Puten an G möglicherweise schneller zu gewöhnen. Zwar sinkt hierbei die auslösende Wirkung beider Objekte, doch bleibt R stets wirksamer als G. Und nach dem 25. Tag lösen Kreis, Rechteck und Bussard mehr Rufe aus als R und G. Demnach antworten erfahrungslose Puten primär nicht unterschiedlich auf die Form fliegender Objekte. Dies liess sich erhärten in weiteren Versuchen an einer führenden Henne. Die durch wiederholte Wahrnehmung eines Objektes einsetzende Empfindlichkeitsminderung ist spezifisch für eine beliebige Form; die jeweilige Reaktionsstärke entspricht der Seltenheit der wahrgenommenen Umrissform (bezogen auf ihre Bewegungsrichtung). (Ob die relative oder absolute Häufigkeit, mit der ein Vogel am Himmel erscheint, den Grad der Adaptation bestimmt, ist noch ungewiss.) Hiermit stehen die Ergebnisse von Lorenz und Tinbergen im Einklang; ihre Puten und Fasane hatten häufig fliegende Gänse und Enten, aber keinen Seeadler (*Haliaetus albicilla*) gesehen; deshalb waren sie gegen jene "voradaptiert" und ängstigten sich vor diesem.

Im Attrappenversuch fiel die Antwortstärke schneller ab als dies nach Flugfeindreaktionen unter natürlichen Bedingungen zu erwarten war (Schleidt, l.c.). Entweder war hieran die Wiederholungsrate der Darbietungen im geschlossenen Raum schuld, oder aber die immer wieder andere Flugbahn, der Flügelschlag, wechselnde Grössen- und Geschwindigkeitsverhältnisse verlangsamen die Gewöhnung an den lebenden Räuber. Dass z.B. der Flügelschlag des Seeadlers—vielleicht erlerntes—Merkmal im Auslösemechanismus der Flucht vor dem Adler sein kann, bewies Markgren (1960) an überwinternden Scharen von Krähen, Möwen und Enten in Südschweden. Zu den Putenergebnissen passt, dass der Adler die im Binnenlande winternden Entenschofe stärker schreckte als die an der Küste, entsprechend seiner Seltenheit an den Binnenseen.

Für Auer- und Birkhühner (*Tetrao urogallus*, *Lyrurus tetrix*) scheinen weniger der Gewöhnungszustand als vielmehr bestimmte Grössen-Geschwindigkeitskorrelationen ausschlaggebend zu sein (Müller, 1961). Auch bei Singvögeln scheinen mehr Dinge als nur Seltenheit des Räubers mitzuspielen. Zwar geben Sumpfmeisen (*Parus palustris*) in Gegenden, wo Turmfalk und Sperber gleich häufig sind, Luftalarm auf beide; dort, wo der Turmfalk aber häufiger ist, wird er weniger gefürchtet (Löhrl, 1950*b*). Doch muss auch die Flugart eine Rolle spielen. Sperber und Baumfalk lösen panische Aufregung bei Rauch- und Mehlschwalben aus, doch nicht die selteneren Mäusebussarde, Turmfalken und Rotmilane (*Milvus milvus*) (Mohr, l.c.). Markgren (l.c.) sah Krähen den Turmfalken erst dann in der Luft necken, als dieser wie ein Merlin (*Falco columbarius*) und nicht im Rüttelflug flog (s. auch Hohlt, 1957: *Turdus pilaris*). Ob Merline ihre Beutevögel durch einen be-

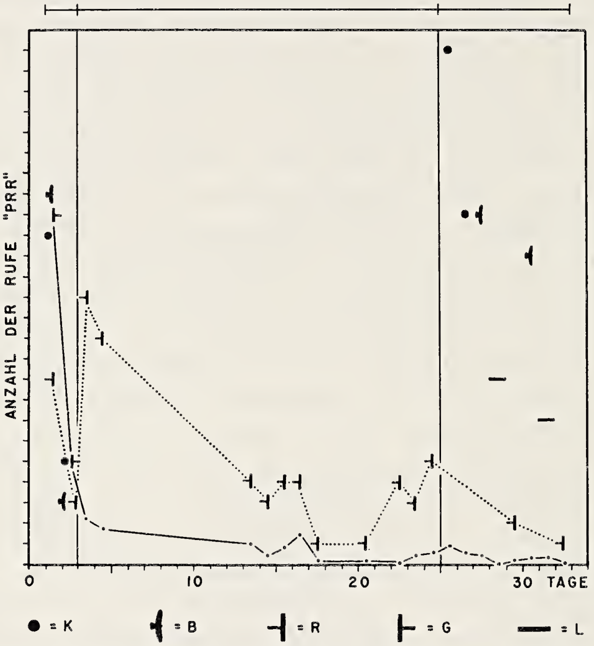


Abb. 3. Anzahl der Reaktionen auf Flugfeindattrappen gleicher Fläche (30 cm^2) an den einzelnen Versuchstagen. Vom 3. Tag ab sind die Mittel aus je 10 Versuchen aufgetragen. Durchmesser von K = 6 cm; die relative Grösse von B in 2,3 m Höhe entspricht der eines Bussards in 27 m Höhe (aus Schleidt, 1961*a*).

Fig. 3. Number of responses to dummies of flying predators of equal size (30 cm^2) at subsequent days of the experiment. After the 3rd day, averages of 10 tests, respectively, were plotted. Diameter of K = 6 cm; relative size of B 2.3 m above ground corresponds to that of a hawk 27 m high (from Schleidt, 1961*a*).

stimmten Flug ("Drossel"- oder "Schwalbenflug") wirklich zu täuschen vermögen (Markgren, l.c.), bedarf wohl noch genauer Nachprüfung.

Oft ist das Schutzverhalten der Jagdweise des Räubers fein angepasst. Krähen übersteigen den Habicht, der ihnen am Boden am gefährlichsten ist, und stürzen vor dem im freien Luftraum jagenden Wanderfalken in Deckung (Tinbergen, 1951). Ob solche Alternanz angeboren ist oder erlernt wird, das wissen wir nicht. Zu lernen, dass der seltenere von zwei am Himmel erscheinenden Vögeln der gefährliche ist, passt gut zu der Häufigkeit des Vorkommens von Räuber und Friedvogel. Habichte und Adler brauchen grössere Reviere und siedeln daher dünner als z.B. Gänse. So ist jener auf Gewöhnung an eine spezielle Form fussende Mechanismus fein den natürlichen Verhältnissen angepasst. Der Vogel nimmt dabei in Kauf, mitunter blinden Alarm zu geben, wenn ein seltener Friedvogel erscheint, wie z.B. ein überhin ziehender Schwarzstorch (*Ciconia nigra*), der unter den Wasservögeln des Essees eine ähnliche Panik wie ein Adler verursachte.

Die Unspezifität der Umrissform im Luftfeind-AAM der Pute, die durch den beschriebenen Gewöhnungsprozess an den Friedvogel wettgemacht wird, steht in auffälligem Gegensatz zu der relativ hohen Zahl meist konfigurationaler Schlüsselreize im AAM des ruhenden Flugfeindes. Möglicherweise ist der Unterschied zwischen diesen beiden Modi des Erkennens nur solange gegeben, wie wir nichts Genaues über die etwaigen Bewegungsreize wissen, die zusätzliche Hilfen beim Erkennen des Lufträubers sein könnten (s.o.).

3. Der Bodenräuber

Meist löst der ruhende oder sich fortbewegende Bodenräuber dasselbe Verhalten aus wie der ruhende Flugfeind. Buchfinken hassen auf Eulen und Hermelin, Singammern auf Eulen und Katzen, Rabenkrähen plärren auf den sitzenden Habicht wie auf Füchse und Katzen (Hinde, 1954: I; Nice u. ter Pelkwyk, 1941; Löhrl, 1950*a*). Trauerschnäpper schnarren auf Spechte, Eichhörnchen (*Sciurus vulgaris*), Hermeline und Mäuse; ein wenig hassen sie dabei auch (Curio, 1959*a*: 46). Die Katze nimmt eine Sonderstellung ein, weil sie ausschliesslich—wie Eule und Würger—angehasst wird. Bepelzt, bewegt und konvex zusammen lösen weder Alarm noch Schnarren aus. Hier fehlen offensichtlich weitere Merkmale (unveröff.), anders als beim Gimpel (s.o.). Die Annahme, der behaarte Säuger "passe" wegen seiner nach vorn gerichteten Augen in den Eulen-AAM, befriedigt wenig: die den Gimpeln vorgezeigten Fellbälle hatten nie Augen (Kramer u. St. Paul, 1951). Weitere Versuche sind nötig, um herauszufinden, ob Eule und Säuger im Erkennen des Gimpels verschiedene Rollen spielen. Auch ist ungewiss, ob australische Kleinvögel nur deshalb auf einen Teddybär hassten, weil er Glasaugen hatte (Sedgwick, 1940). Andererseits genügten allein aufgemalte Augen auf einer weissen Pappscheibe, um gezielte Schnabelhiebe einer bedrängten Rohrdommel (*Botaurus stellaris*) auf sich zu ziehen (Portielje, 1926).

Recht merkmalsarm ist offenbar der AM für Bodenfeinde bei der Pute (verschiedene Hausrassen mit z.T. eingekreuztem Wildblut). Während hörende Putenhennen auf Eiern Kücken ausserhalb der Nestmulde einrollen und hudern, hacken jung ertaubte auf Kücken am Nest sofort wie auf einen Bodenfeind ein, fauchen, spreizen den Schwanz und "knattern" mitunter. Allein der Gehörsreiz entscheidet, ob die Henne Abwehr oder Pflegeverhalten zeigt (Schleidt et al., 1960). Nur mit ihresgleichen aufgewachsene Haushühner hatten erstmals im Alter von drei Wochen Furcht vor einem Kaninchen; von einer Henne geführte Kücken aber ängstigten sich von Geburt an vor ihm (Brückner, 1933).

Ob sich mehrere Insektenfresser (*Phylloscopus* spec. u.a.) an das ihnen gefährliche Mauswiesel (*Mustela nivalis*) so furchtlos wie an tagaktive Wühlmäuse (*Microtus agrestis*) heranwagen (Frank, 1955), bedarf näherer Prüfung. v. Treuenfels (1940) sah einen Zilpzalp (*Phylloscopus collybita*) eine Spitzmaus (*Sorex*) schnabelknackend angreifen.

Gänse und Enten scharen sich stumm, von allen Seiten herbeischwimmend um einen Bodenfeind am Ufer (Kap. E). Viele Limicolen verleiten vor einem Bodenfeind, aber nur in Fortpflanzungsstimmung, indem sie sich krank stellen, einen davonhuschenden Kleinsäuger vortäuschen u.a.m. (Simmons, 1955). Ähnliches tun Grasmücken (*Sylvia*). Manche Bodenbrüter antworten auf weidende Rinder anders als auf vierfüssige Räuber und auf diese wieder anders als auf Menschen. Weil eines der Kennmale des Raubsäugers wahrscheinlich Bewegung ist, sind seine Schlüsselreize bisher experimentell so dürftig untersucht.

Einzig die Spottdrossel *Toxostoma curvirostre* scheint über ein spezifisches Schlangenverhalten zu verfügen[1]. Auf grössere und lebende Schlangen antwortet sie besser als auf kleinere und tote. Wesentlich sind die Windebewegungen des Körpers, blosse Fortbewegung wirkt nur schwach. Bestimmte Oberflächeneigenschaften scheinen erlernt zu werden. Viele andere, von Rand (1941) seinen Spottdrosseln vorgezeigte Tiere (Reptilien, Säuger, Vögel) lösten auch Schlangenverhalten, nur viel schwächer aus; Eulen und Tagraubvögel waren merkwürdig wenig wirksam. Ob Fitisse einen besonderen Schlangenruf haben (Leivo, 1938), muss überprüft werden.

Die in dichtem Dorngezweig nistenden Weber (*Quelea quelea*) geben nur auf Schlangen Alarm, die einzigen ihren Nestern gefährlichen Tiere, aber nicht auf Flugfeinde (Crook, 1960; vgl. auch: Kellogg, 1931; Hicks, 1955; Bowman, 1961; Stickel, 1962).

4. Die Situation "Artgenosse in Gefahr"

Viele Vögel warnen umso heftiger und werden umso angriffsbereiter, je näher ein Feind ihrer Brut kommt. Beim Ansprechen solcher sozialer

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[1] Anm. bei Korrektur: Mindestens 8 Arten der Geospizinae auf Galapagos zeigen ein erstaunlich übereinstimmendes Schutzverhalten vor Schlangen, das auf schlangenlosen Inseln verschieden weit in Verlust geraten ist (unveröff).

Verteidigungsreaktionen braucht sich der Artgenosse nicht in wirklicher Gefahr zu befinden. So fand Kramer (1941), dass Krähen (*Corvus corone, C. cornix*) schon plärren, sobald ein Mensch mit einer zahmen, sich wohl befindenden Jung- oder Altkrähe auf dem Arm in ihr Revier kommt. Ganz ähnlich schnarrten Lorenz' (1931) Dohlen—nachweislich auf Grund schlechter Erfahrung—wenn er nur in die Nähe flügger Jungvögel geriet. Das geschah erst, als seine Kolonie so scheu wie eine beliebige wildlebende geworden war. Angeborenermassen schnarrten seine Dohlen nur auf "Etwas schwarzes Baumelndes, gleichgültig von wem getragen." Selbst ein Artgenosse mit einer schwarzen Feder im Schnabel, einer, der eine Dohlenleiche umwendete und eine schwarze, von Lorenz getragene Badehose lösten Schnarren aus, jedoch nicht eine schwarze, in der Hand gehaltene Haustaube; die wollten die Dohlen augenblicklich umbringen. Und doch ist schwarzes Dohlengefieder einer der schnarrauslösenden Schlüsselreize, denn noch nackte Dohlennestlinge sind wirkungslos, solche mit spriessenden Federn lösen aber voll aus, wenn man sie den Eltern hinhält. (Über die Tradition der Kenntnis des Bodenräubers s. Kap. G b.)

Kolkraben (*Corvus corax*) scheinen dagegen nur Freunde zu verteidigen, unbeschadet ihrer Artzugehörigkeit (Lorenz, 1931). Die Gefährdung des persönlich fernstehenden Artgenossen ruft eher "Umbringenhelfen" als soziale Verteidigung hervor. Eine so weitgehende "Intellektualisierung" der Schutzreaktion, neben der der Schnarrangriff alter Dohlen geradezu reflexhaft anmutet, findet sich bei Krähen nicht. Hier löst die Gefährdung (im Sinne des antwortenden Vogels) des persönlich fremden Artgenossen das Geplärr aus (s.o.), doch wird es augenblicklich verstärkt, sobald der am Nest geschossene Ehepartner aufgehoben wird (Kramer, 1941).

Krähen betrachten interessiert oder sogar plärrend tote Artgenossen oder deren Rupfung. Die fehlende Differenzierung des Verhaltens lässt bisher keinerlei Schlüsse darüber zu, ob hierbei das Umbringen des geschädigten Artgenossen oder soziale Verteidigungsbereitschaft anspricht. Raben wollen ausgesprochen "umbringen helfen," sobald ein Tier, das als Beute in Frage kommt, vom Sozialkumpan gejagt oder gepackt wird (Lorenz, l.c.), und Kramer (l.c.) lockte wilde Nebelkrähen herbei, indem er einen wildfarbenen Zwerghahn im Felde freiliess, einfing, freiliess usw. Eichelhäher liessen eine Häherrupfung in ihrem Flugkäfig unbeachtet, "explodierten" aber förmlich in heftiges Rätschen, als Goodwin (1952) die Federn bündelte.

Merkwürdigerweise steht der Eichelhäher der Dohle in seiner sozialen Hilfereaktion näher als den übrigen Corviden. Er greift einen Raubfeind, der einen Häher trägt, sofort an. Handaufgezogene aber reagieren—anders als Wildfänge—überhaupt nicht, sobald der menschliche Pfleger einen der ihren packt, ganz im Gegensatz zu Lorenz' ebenso zahmen Dohlen. Die Reaktion ist nicht speziell an den gefährdeten Artgenossen oder Freund gebunden wie bei den anderen Corviden: ergriffene Türkentauben (*Streptopelia risoria*) und Amseln lösen ebenfalls Angriff aus, nur schwächer, (Goodwin, l.c.); doch wollen sie hier vielleicht schon umbringen helfen?

Auch Nestflüchter erkennen, wann ein Artgenosse gefährdet ist. Eine Hochbrutente stiess einen Kolkraben aus der Luft nieder, der sich gerade mit einem ihrer Kücken davonmachen wollte (Lorenz, 1935:304; s. auch Johnson, 1961).

Auch werden unpersönliche Gefahrenquellen gemieden. So hörte Lorenz (brfl. in Kramer, 1941) seine Dolen schon schnarren, wenn nur eine der Jungdohlen in einen abgrundartigen Hof geriet (s. auch Lorenz, 1935:306).

5. Das Verhalten des Feindes

Erstaunlich ist die Fähigkeit von Vögeln, dem Verhalten des Feindes, selbst subtilen Feinheiten, anzusehen, ob er jagt oder satt ist. Nordamerikanische Singvögel hassten auf einen satten Bussard (*Buteo jamaicensis*) schwächer als auf einen hungrigen, und, wenn er rudernd flog viel stärker, als wenn er segelte; beim ruhenden spielte auch die Höhe des Sitzplatzes mit (Hamerstrom, 1957). Ähnlich lässt der nahebei fischende Seeadler riesige Entenscharen im Schärenmeer völlig "kalt," während der niedrig übers Eis streichende Ausweichen, Auffliegen oder bei abgesprengten Enten Tauchen auslöst (Markgren, 1960). Rauchschwalben sehen Baumfalken (Tinbergen, 1961: 78), Krähen Habichten und Wanderfalken ihre Jagdstimmung an (Kramer, 1941), und Singvögel "wissen" genau, wann der Sperlingskauz (*Glaucidium passerinum*) auf Mäuse ansitzt oder auf Vogeljagd ist (Schnurre, 1942; s. auch Chenevix-Trench, 1949).

Krähen richten ihr Verhalten nach dem ein, was ihnen andere signalisieren. Rabenkrähen plärren auf den sitzenden oder eine Beute rupfenden Habicht, geben aber Alarm, sobald er fliegt. Beide Laute rufen gänzlich verschiedenes Verhalten hervor: bei Alarm versuchen alle Krähen in Hörweite sofort Höhe zu gewinnen, um den dann stets nahen Habicht zu übersteigen; Geplärr lässt sie nur gemächlich dem Ort zustreben, von dem es herkommt (Löhrl, 1950*a*). (Bei höchster Gefahr rufen sie aber auch Alarm, wenn sie einen Uhu [*Bubo bubo*] nahe ihrem Nest sitzen oder einen Menschen eine zahme Jungkrähe tragen sehen [Kramer, 1941].) Sobald Silbermöwen (*Larus argentatus*) in einer Lachmöwenkolonie (*L. ridibundus*) landen wollen, verstärkt sich der Alarm der ohnehin in Aufruhr geratenen Koloniebewohner (Tinbergen brfl., 1962). Ähnlich lassen segelnde Bussarde nistende Trauerschnäpper "kalt"; schickt sich aber ein Bussard oder ein Waldkauz zu landen an, so löst er schon Hassen aus, genau wie der ruhende. Genauso antwortet der Gartenrotschwanz (unveröff.). Wenn alle Tiere einer Art so handeln, ist solches Verhalten gewiss arttypisch, unabhängig davon, ob es erlernt ist. Es erscheint allerdings schwer vorstellbar, dass derart geringfügig verschiedene Zeitgestalten angeborenermassen erkannt werden.

Viele wehrlose Kleinvögel nisten an oder nahe den grossen Horsten von Reihern, Störchen und Tagraubvögeln. In Südwestafrika brütete z.B. ein Paar *Poliohierax semitorquatus* inmitten einer mächtigen Weberkolonie

(*Quelea*?), ohne Verwirrung zu stiften (Meinertzhagen, 1959: 146; s. auch S. ii ebenda und Cade, 1960: *Falco rusticolus*, *F. peregrinus*). Räuber töten nicht in Horstnähe. Vielleicht verhüten sie eine "tote Zone" um ihren Horst, um selbst bei drohender Gefahr durch andere rechtzeitig gewarnt zu sein. Solch "Burgfriede" freilich gilt nicht uneingeschränkt: nistende Merline schonen die in ihrer Nähe siedelnden Misteldrosseln (*Turdus pilaris*) und vergrämen nestplündernde Corviden. Die "Anwohner" haben daher einen höheren Bruterfolg als andere Drosseln, die sowohl von den Merlinen wie von den Corviden heimgesucht werden. Doch zehnten die Merline, sobald sie Junge haben, auch ihre Drosselnachbarn ganz empfindlich (Hagen, 1947).— Nicht nur Raubvögel halten Burgfrieden. Nahe den Nestern von Carolina-tauben (*Zenaidura macroura*) nistende Stärlinge (*Quiscalus quiscula*) stehlen den Tauben keine Jungen, wohl aber weiter weg nistenden (Dilger, mdl. 1962).

b. *Akustisches Erkennen*

Seit altersher locken Vogelsteller Kleinvögel in ihre Netze, indem sie Eulenrufe nachahmen (Anonymus, 1743, in brfl. Mitt. von Nice, 1960). Auf Trinidad ist die Stimme des dortigen *Glaucidium phalaenoides* wirksam (Hartley, 1950), in Mitteleuropa die gimpelartige Rufstrophe von *G. passerinum* (Schüz u. Schneider, 1921; Schnurre, 1942). Den Indizienbeweis dafür, dass es sich bei jenen Antworten um erlernte Reaktionen handelt, erbrachte Thönen (brfl. 1961). Im Schweizer Jura werden Rufe des Sperlingskauzes nur dort beantwortet, wo er lebt. Weil aber zwischen den Populationen mit und ohne Sperlingskauz keinerlei Kreuzungsschranken bestehen, kann sich kein genetisches Isolat dort bilden, wo er vorkommt, das den Ruf angeborenermassen verstünde. Nur diejenigen Vögel haben Gelegenheit, den Ruf mit dem Kauz in irgendeiner Weise zu verknüpfen, die ihn rufen hören und sehen; als tagaktive Eule stimmt der Sperlingskauz seinen Gesang oftmals weithin sichtbar auf einem Tannenwipfel an. Mit der Theorie, der Eulenruf werde erlernt, harmoniert, dass nordamerikanische Rötelammern (*Pipilo erythrophthalmus*), die wir in Gefangenschaft von ihren wildgefangenen Eltern in Deutschland aufziehen liessen (Curio, 1959*b*), im Herbst nicht auf die Rufe amerikanischer Eulen (*Strix varia, Otus asio* und *Glaucidium passerinum*) reagierten. Auf einen ausgestopften Sperlingskauz hassten sie prompt. In seiner Heimat aber gehört der Rötelammer zu den auf Rufe von *Otus asio* am besten reagierenden Arten, wie viele Emberizinae (Drury, brfl. 1961). Ähnlich blieb ein handaufgezogenes Singammer-Männchen gänzlich unbeeindruckt, als man ihm Rufe von *Bubo virginianus, Strix varia Tyto alba* und *Buteo lineatus* vorpfiff (Nice u. ter Pelkwyk, 1941). Manchmal kommt es genau auf die nachgeahmte Eulenart an: während viele Singvögel in Nordamerika, mögliche Opfer der Schreieule (*Otus asio*) und ähnlich grosser Arten, auf Schreieulenrufe hassten, antworteten Blauhäher (*Cyanocitta cristata*) darauf überhaupt nicht, wohl aber auf die Rufe von

Bubo virginianus (Miller, 1952). Wahrscheinlich sind Schreieulen für den Häher belanglos und daher auch ihre Rufe.

Weil meist mehrere Arten in Rufweite weilen, ist es schwierig auszuschliessen, dass die früh antwortenden die später ins Hasskonzert einstimmenden anstecken. Aus Europa stammende Haussperlinge z.B. wurden in Nordamerika nur durch die schimpfende Schar anderer Arten, aber nicht durch den Ruf selbst angezogen, und Stare (*Sturnus vulgaris*) antworteten auf keines von beiden (Drury, brfl. 1961). Nachdem Hamerstrom (1957) ihren zahmen Bussard, den Wanderdrosseln (*Turdus migratorius*) hart bedrängten, wiederholt herbeigepfiffen hatte, hassten sie schliesslich bei blossem Hören des Pfiffes. In Frankreich fängt man allherbstlich Eichelhäher mit Hilfe nachgeahmter Rufe von Bussard und Eule (Thorpe, 1961: 21), und Fitisse zeigen ihre Kuckucksabwehr mitunter schon bei Anhören des Kuckucksrufes (Smith, 1946). Akustische Signale verraten aber nicht nur einen Feind, sondern dem Feind auch seine Beute. So lockt Hasenquäken z.B. ganze Scharen von Krähen an (Kramer, 1941).— Ob in allen Fällen der wirksame Ruf eines Feindes gelernt wird, und wenn, auf welche Weise, das bleibt zu untersuchen.

D. STIMMUNGSABHÄNGIGKEIT DES ERKENNENS

Wie alles tierische Tun, so ist auch die rechte Antwort auf den Räuber von äusseren *und* inneren Faktoren abhängig. Zur Brutzeit erfährt der Vogel eine tiefgreifende innere Umstellung. Nur dann sind viele Arten bereit, auf bestimmte Feinde überhaupt oder aber anders zu reagieren als während der übrigen Jahreszeit. Wie schon Bolles (1890) feststellte, hassen Singvögel unserer Breiten auf Eulen im Sommer stärker als im Winter. Altmann (1956) beobachtet während der Monate Januar bis September folgenden Verlauf der Bereitschaft (Reaktionsminuten aller Vögel/Versuchsminuten) auf verschiedene Eulenstopfpräparate zu hassen: 0,224–0,089–0,611–0,744–1,900–4,400–0,000–0,000–0,000 (vgl. auch Hinde, 1954:I; Watson, 1957; Mohr, 1960).

Bestimmte Handlungen, deren Sinn es offenbar ist, die Brut zu schützen, sprechen erst an, sobald das betreffende Brutstadium erreicht ist. Kohlmeisen fliehen den Menschen das ganze Jahr über, beschimpfen ihn aber obendrein wie sonst den Kauz, wenn sie ein Brutrevier bezogen haben (Hinde, 1952). Während die Warnrufe also grundsätzlich das ganze Jahr über auslösbar sind, verändert sich die reizverarbeitende Seite der Reaktion zur Brutzeit entscheidend. Ähnlich hasst der Trauerschnäpper nur dann auf den Rotrückenwürger, auf den Waldkauz aber ständig. Hierfür ist nicht allein der Zustand der Fortpflanzungsorgane verantwortlich, sondern eine komplexere Reizsituation, nämlich der Besitz einer Nisthöhle. Brutreife (d.h. körperlich und "seelisch" reife) Männchen, die wegen empfindlichen Weibchenmangels unverpaart umherstreifen, belästigen öfter sesshaft gewordene Schnäpper. Begegnen sie bei ihnen einem Würger, so hassen sie auf den selbst dann nicht, wenn die Revierinhaber dicht neben ihnen ausdauernd Alarm rufen. Diese "Neststimmung" kann schnell verschwinden: ein Weibchen, dessen mehrtägige Junge vom Baummarder geholt wurden, und das mehrere Tage zuvor auf den Würgerbalg hitzigen Alarm gegeben hatte, zuckte nicht einmal mit den Flügeln, als es die Attrappe erneut vor seiner Höhle wahrnahm (unveröff.). Junggesellen des Braunkehlchens (*Saxicola rubetra*) aber verwarnen menschliche Eindringlinge im Revier fütternder Nachbarn leidenschaftlich (Schmidt u. Hantge, 1954).

Bei Fitissen wird die Abwehr des Kuckucks mit jedem Brutstadium vollständiger (Smith u. Hosking, 1955). Eine Nachtigall wurde gegen ihn erst dann gleichgültig, als ihre Jungen das Nest verlassen hatten (vgl. auch Messmers, 1956). Wie die Bereitschaft, den Feind von der Brut zu verleiten, bei Limicolen schwankt, das veranschaulichten Laven (1940), Simmons (1955:134) u.a.

Bei vielen Arten markiert das Schlüpfen der Jungen einen besonders drastischen Verhaltenswandel. Trauerschnäpper hassen dann auf den Würger um 25 Prozent stärker also zuvor (unveröff.), und Stare belästigen Katzen erst jetzt (Schüz, 1943). Dohlen verfolgen Lufträuber nur, wenn sie kleine Junge haben (Lorenz, 1931:75), und Krähen plärren Menschen in Nestnähe stärker an als anderswo oder überhaupt erst, sobald sie Junge haben (Kramer, 1941). Beim Säbelschnäbler (*Recurvirostra avocetta*) tritt zu dem üblichen Gefahrenruf nach dem Picken der Eier ein spezieller Möwenruf, der auftauchende Silbermöwen, die schlimmsten Jungenräuber, vermeldet (Makkink, 1936).

Weshalb werden Vögel nach dem Schlüpfen der Jungen abwehrbereiter? Die Graugans (*Anser anser*) wird schon angriffslustiger, wenn ein Junges beginnt, die Eischale zu durchsägen (Lorenz mdl.). Beim Nesthocker aber könnte die mit dem Füttern der Brut verbundene Anstrengung mitspielen. Um diese Möglichkeit zu prüfen, fügte ich den hochbebrüteten Eiern dreier Paare spanischer Trauerschnäpper (*Ficedula hypoleuca iberiae*) drei frisch geschlüpfte Junge hinzu. Schon nach kurzem Anblick der Jungen hassten die Altvögel auf Feindattrappen in Nestnähe stärker als zuvor. In einem Fall geschah dies nachweislich, ehe der Altvogel das erste Räupchen gebracht hatte (unveröff.). Demnach scheint auch beim Nesthocker allein die Wahrnehmung des Jungen den Fütterer in erhöhte Alarmbereitschaft versetzen zu können.

Eine immer wieder hervorstechende Eigentümlichkeit vieler Feindreaktionen ist ihre hohe individuelle Schwankungsbreite. Sie kommt z.T. zustande durch völlige Gleichgültigkeit einiger Vögel der Population Attrappen gegenüber, die Feinde darstellen, deren Kenntnis nachweislich angeboren ist. Zwar hat ein und derselbe Vogel die Neigung, in einem für ihn typischen Antwortbereich zu beharren, wie wiederholte Reizung mit der gleichen Attrappe zeigt (Hinde, 1954:I), doch kann z.B. ein Trauerschnäpper auf dieselbe Würgerattrappe einmal überhaupt nicht und wenig später im selben

Brutstadium (!) ungewöhnlich stark antworten oder umgekehrt. Es nützt nichts, die Darbietungsdauer im Fall des Versagens um ein Vielfaches zu verlängern; deshalb trägt hohe Reaktionsträgheit hieran wohl keine Schuld. Gründe für derartige Stimmungsschwankungen, die das Experimentieren ausserordentlich erschweren, lassen sich höchstens vermuten.

E. ADAPTABILITÄT DES ERKENNENS

Zeigt man einem gekäfigten Buchfinken wiederholt einen ausgestopften Waldkauz, so hasst er auf ihn von Mal zu Mal schwächer. Bei dreiminütiger Darbietung je Tag ist die Antwortstärke schon am 2. Tag auf 56 Prozent des Ausgangswertes abgesunken und am 6. Tag auf etwa 25 Prozent. Sieht der Fink den Kauz nur kurz jeden Tag, gewöhnt er sich schneller ab zu hassen als bei einer einzigen Begegnung gleicher Gesamtdauer. Je länger eine einzelne Darbietung anhält, desto schwächer ist die Antwort nachher (Hinde, 1954:II).

Bietet man dem Buchfinken nach Auslösung des Hassens durch die Eule ein Wiesel, so hasst er auf dieses deutlich intensiver als auf eine zweite Darbietung der Eule. Demnach muss das Absinken der Reaktionsstärke mindestens teilweise an einer Veränderung der reizverarbeitenden Seite der Antwort liegen. Je mehr Merkmale zwei Feinde miteinander gemeinsam haben, desto höher der Grad der Gewöhnung (“*habituation*”). Weitere Versuche erwiesen jene reizspezifische Schwächung der Antwort als einen langanhaltenden Zustand, während eine mehr in der Motorik zu suchende Abnahme der Reaktionsbereitschaft ausserordentlich kurzfristig ist. Einzelne Zeitcharakteristika der Alarmantwort schwanken verschieden, so dass keine einheitliche, für die Antwort insgesamt verantwortliche nervöse Instanz vorzuliegen scheint.

Ferner kann ein starker Reizkomplex einen ihm folgenden schwächeren verstärken, und umgekehrt kann eine schwächere Reizsituation eine ihre folgende stärkere schwächen. Was hierbei im einzelnen geschieht, hängt in verwickelter Weise von der Dauer der ersten Reizung und von dem auf sie folgenden Ruheintervall ab (Hinde, 1960).

Die rasche Abnahme der Hassbereitschaft nach wiederholter Reaktion auf den Kauz ist nicht recht verständlich. Vielleicht verzögert der lebende die Gewöhnung ohnehin und im Wildleben obendrein der Umstand, dass der Kauz nach einigem Hassen (auch anderer Arten) wegfliegt (Hinde, 1954: II). Möglicherweise spielt die Begegnung an immer wieder anderem Ort mit. In Volierenversuchen allerdings war der Einfluss des wechselnden Ortes von einer Darbietung zur anderen kaum nachweisbar. Im Freien mag das anders sein. So waren Gänse auf dem Essee in Seewiesen vollständig gegen zwei Chows und einen Airdale-Terrier adaptiert. Erschien ich aber mit diesem am gegenüberliegenden Seeufer, an dem die Hunde nie umhertollten, schwammen sämtliche Gänse in Sichtweite zielgerichtet auf den Hund am Ufer zu und versammelten sich um ihn genau in derselben Weise wie um einen ihnen völlig neuen Mungo am anderen Ufer. Auf diese Weise wäre einem Fuchs jegliche Jagd vereitelt worden. Ähnlich gewöhnten sich Gimpel schnell an die Umstände des Attrappenversuchs, so dass selbst wirksame Feindmodelle nicht mehr beantwortet wurden (Kramer u. St. Paul, 1951; s. auch Nice, 1943:264).

Trauerschnäpper im Revier von Rotrückenwürgern, die täglich die Feinde vor Augen hatten, hassten auf ausgestopfte genauso stark wie solche, die in dem betreffenden Sommer wahrscheinlich keine Würger gesehen hatten. Der ständige Anblick des lebenden Feindes hatte die Antwort weder abgeschwächt noch verstärkt. Demnach scheint die Vielfalt der Umstände, unter denen im Wildleben der Feind immer wieder anders erscheint, die Gewöhnung aufzuhalten oder wenigstens zu verlangsamen (Curio, unveröff.).

Um sich an eine Eule zu gewöhnen, braucht der Vogel sie nur lange genug zu sehen. Des Hassens selbst bedarf es nicht, wie die experimentelle Adaptation junger Würger beweist, deren Antwort noch nicht gereift war (St. Paul, 1948).

Die hier abträglich erscheinende Adaptabilität des AAM gewährleistet andererseits das Erkennen des fliegenden Flugfeindes. Durch die Gewöhnung an den harmlosen Friedvogel wird der seltenere Räuber ausgesondert (S. Kap. C a 2).

Ob die erste Antwort im Leben eines Vogels und der damit verbundene Affekt die schon bestehende Bereitschaft zu einer Feindreaktion zu verstärken imstande ist (Nice u. ter Pelkwyk, 1941), bedarf noch der Prüfung.

F. SPEZIFITÄT DES ERKENNENS

Gänzlich verschiedene Feinde lösen bei vielen Arten ein- und dasselbe Schutzverhalten aus. Sprechen in einem solchen Fall verschiedene Auslösemechanismen an, die sämtlich in eine Motorik münden? Oder "passen" so verschiedene Feinde in ein- und denselben Auslösemechanismus? Erkennen zweier Reizsituationen durch mehr als einen Erkennungsapparat läge vor, wenn jede der beiden Situationen durch wenigstens einen, nur ihr eigenen Reiz im Vogel repräsentiert wäre. Dies wäre eine mögliche Definition. Für die Trennbarkeit beider Auslösemechanismen wäre es also belanglos, wieviele Merkmale zweier Reizsituationen sie gemeinsam beanspruchten, falls sie mindestens eines verschieden verarbeiteten. Die hier gestellte Frage lautet allgemeiner: "Wie werden die vom Vogel wahrgenommenen Schlüsselreize verarbeitet?" Aus hier nicht näher zu erörternden Gründen empfiehlt es sich vorerst, für eine spezielle Reizsituation, die ein bestimmtes Verhalten hervorruft, mindestens einen Auslösemechanismus anzunehmen, aber nicht für jeden nachgewiesenen Schlüsselreiz einen eigenen.

Am Trauerschnäpper begann ich die oben gestellte Frage zu lösen. So verschiedene Feinde wie Würger, Eulen und Katzen am Nest lösen sämtlich Alarm aus. Bedeuten Würger und Eule für den Vogel zweierlei oder werden zentral beide in nur einem Auslösemechanismus repräsentiert? Rotrücken-

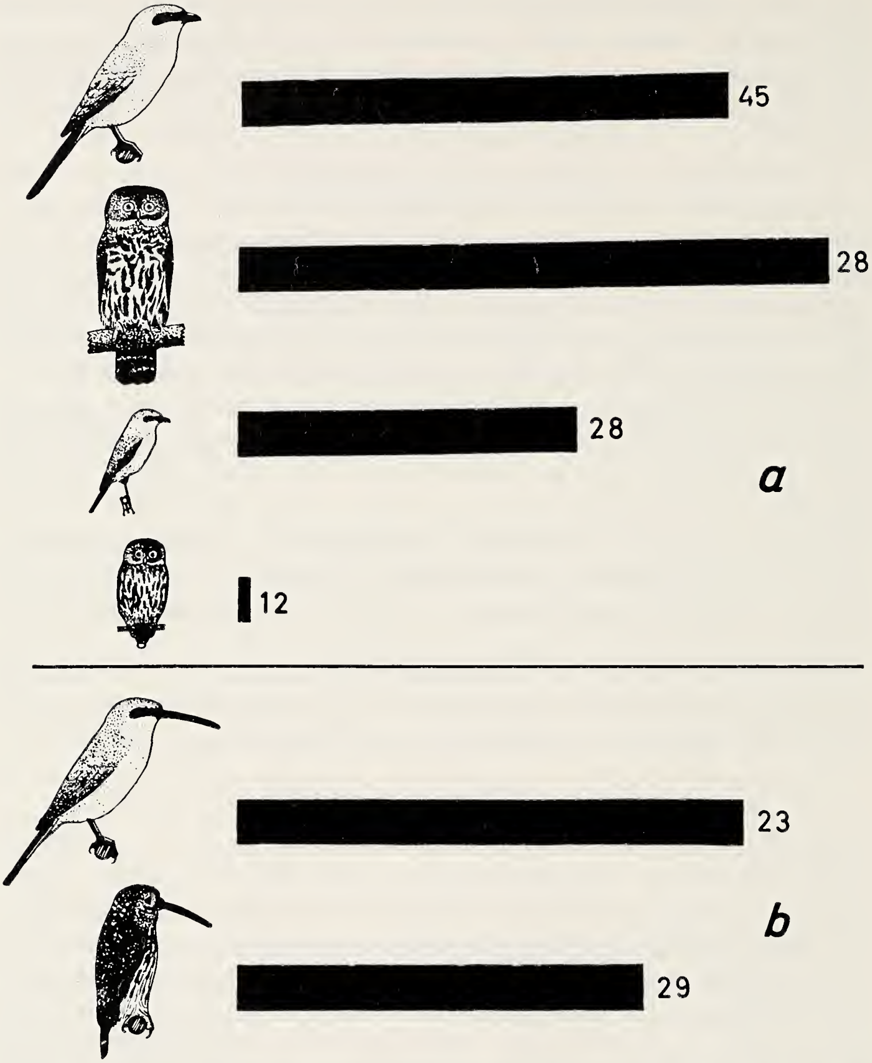

Abb. 4. Hassen fütternder Trauerschnäpper auf Feindattrappen 1,5 m vor der Nisthöhle. Von oben nach unten: Rotrückenwürgermännchenbalg, Sperlingskauzbalg, auf die Hälfte verkleinerte Plastikamodelle beider Feinde; dieselben Bälge wie oben mit mattschwarzem Schnepfenschnabel aus Holz. Zahlen = geprüfte Individuen = Versuche. Stärke der Antwort auf den Würgerbalg: 80 Rufe/min. (aus Curio, 1961*a*).

Fig. 4. Mobbing of feeding Pied Flycatchers at enemy dummies placed 1.5 m before the nest hole. From above: mounted male Red-backed Shrike, mounted Pigmy Owl; models of both enemies at half scale of natural size; the mounted birds with a dull black wooden woodcock's beak. Numbers = tested individuals = experiments. Strength of response released by shrike: 80 calls/min. (from Curio 1961*a*).

würger und Sperlingskauz teilen einige Merkmale: Krummschnabel, Befiederung, Körpergrösse (Sitzhöhe) und etwa aufrechte Haltung. Wäre eines von ihnen Schlüsselreiz für das Hassen, so sollte seine experimentelle Veränderung die Alarmstärke in beiden Fällen nur dann um denselben Betrag und in gleicher Richtung verschieben, wenn nur ein Auslösemechanismus vorliegt. Lägen aber zwei Erkennungsapparate vor, für Würger und Kauz je einer, so sollten die Antworten in beiden Fällen um eindeutig verschiedene Beträge vom Ausgangswert abweichen oder in zwei verschiedenen Richtungen. Der Normal-Würger löst etwas schwächer Alarm aus als der Normal-Sperlingskauz ($P = 5$ Prozent). Verkleinert man jedoch die artgerecht bemalten Attrappen beider auf die Hälfte, so sinkt die auslösende Wirkung des Kauzes fast auf Null ab, während der Zwergwürger noch 70 Prozent der Stärke der ursprünglichen Antwort auslöst (Abb. 4). Demnach wird "Körpergrösse" bei beiden Feinden verschieden bewertet. Dies legt die Annahme mindestens zweier feindspezifischer Auslösemechanismen aber nur nahe. Denn andere mit der Grösse verknüpfte Merkmale wie z.B. "sichtbare Fläche" wurden mitverändert; ihr Anteil am Auslösewert der Gesamtsituation aber ist noch unbekannt. Ergänzende Versuche, in denen der Krummschnabel beider Feinde durch einen Schnepfenschnabel verhüllt wurde, ergaben eine Verstärkung des Würgers und eine Abschwächung des Kauzes; der Unterschied zwischen beiden so veränderten Feinden ist nicht real ($P = 5{,}2$ Prozent). Immerhin weist auch er auf mehr als einen AM hin; doch wiederum braucht die scheinbar identische Abänderung beider Feinde vom Vogel nicht als gleich bewertet zu werden, z.B. der verlängerte Schnabel des Würgers als Vergrösserung des Schlüsselreizes Augenstreif. Weitere, methodisch gänzlich anders ausgerichtete Versuche müssen klären, wie andere Schlüsselreize dieser und anderer Feinde verarbeitet werden (Curio, 1961*a*). (Fünf unabhängige Argumente, deren Vorführung hier zu weit gehen würde, belegen, dass beide Feinde angeborenermassen erkannt werden.)

Zwei weitere Tatsachen sprechen ebenfalls für die Annahme mindestens zweier AAMs für beide Feinde. Zum einen antwortet der Trauerschnäpper auf Eulen das ganze Jahr über und auf den Würger nur, wenn er ein Revier besitzt, und zum anderen antwortet eine Unterart selektiv nur auf Eulen, aber nicht auf Würger (S. Kap. H a).

Versuche mit feindunerfahrenen Rotrücken- und Rotkopfwürgern St. Pauls (1948) deuten ähnlich auf die verschiedene Bewertung von Tagraubvogel und Eule: Augen und Befiederung sind Schlüsselreize im Erkennen der Eule, Krummschnabel und aufrechte Körperhaltung für das des Tagraubvogels. Gemeinsam ist beiden AAMs die Dreidimensionalität der Feinde. Im allgemeinen ist klar, welche Tiere ein Vogel als Feind erkennen muss. Doch sieht man auch Flucht- oder Feindreaktionen (im Sinn der Motorik) auf Objekte, die biologisch belanglos erscheinen. Entweder teilen solche Objekte genügend viele Eigenschaften mit tatsächlich bedeutsamen Feinden, um wirksam zu sein. Oder aber dem Vogel sind gleichsam als zusätzliche Sicherung Erkennungsapparate für unvorhergesehene, von Nicholson (1927) "seltsam" genannte Umweltdinge eigen, d.h. solche, die offensichtlich neu sind. Der Vogel spricht aber nicht auf alles bewegte "Neue" um ihn feindlich an. Das könnte daran liegen, dass ihm vieles als Jungvogel geläufig wurde, ehe seine Feindantwort(en) gereift waren. Beispiele belegen solche rätselhaften Reaktionen: Blaumeisen (*Parus caeruleus*) hassten auf einen ruhenden Wiedehopf (*Upupa epops*) (Tinbergen mdl.), Gartenlaubsänger (*Hippolais icterina*) in Wilhelmshaven auf einen entflogenen Gimpel Kramers (brfl.), mehrere Singvögel auf einen Gummiskorpion am Futtertisch (Meinertzhagen, 1955), Blau- und Schwanzmeisen (*Aegithalos caudatus*) auf eine Schwärmerraupe (Meinertzhagen, 1959:24), Trauerschnäpper, Gartenrotschwänze und Tannenmeisen (*Parus ater*) gelegentlich auf fliegende Fledermäuse (Berndt, 1940). Hertz' (1928:I) Eichelhäher flüchteten zunächst vor jedem neuen Gegenstand in ihrer Voliere, kamen schliesslich argwöhnisch näher und gewöhnten sich allmählich daran. Ähnlich handelten meine Raben. Es bedarf sorgfältiger Versuchsplanung herauszufinden, ob es für den Vogel über die Qualität "neu" hinaus noch eine andere, speziellere "seltsam" gibt (vgl. auch Rand, 1941).

G. ONTOGENESE DES ERKENNENS

a. *Angeborenes Erkennen*

Singammern (Nice u. ter Pelkwyk, 1941), Buchfinken, Goldammern (Hinde, 1954:I), Gimpel (eig. Beob.), Rotrücken- und Rotkopfwürger (St. Paul, 1948), Dohlen (Strauss, 1939), und wahrscheinlich *Corvus brachyrhynchos* (Ramsay, 1950), erkennen Eulen angeborenermassen, d.h. ohne eine schlimme Erfahrung mit ihnen gemacht zu haben. Spottdrosseln (*Toxostoma curvirostre*) reagieren auf Eulen bis Uhugrösse nicht spezifisch, sondern mit einem Verhalten, das sie gegen Schlangen ausgeprägter zeigen (S. Kap. C a 3), und meiden sitzende Bussarde (Rand, 1941). Sitzende Raubvögel wirken ähnlich wie Eulen auf feindunerfahrene Singammern, Dohlen, Krähen, Würger, und Puten (Löhrl mdl.). Vor allem Behaartem fürchten sich junge Gimpel (Kramer u. St. Paul, 1951), vielleicht ebenso Haushühner (Brückner, 1933; s. jedoch Thorndike, 1899; Collias, 1950) und Blauhäher (Rand, 1937), Spottdrosseln aber kaum oder nur kurze Zeit (Rand, 1941). Spottdrosseln und Haussperlinge (Kellogg, 1931) scheinen angeborenermassen auf Schlangen zu antworten; hierbei spielen die spezielle Fortbewegung, Grösse und andere Merkmale eine Rolle, erlerntermassen auch Oberflächeneigenschaften (Rand, l.c.). Singammern, Kanarien, und Blauhäher lässt eine lebende Schlange "kalt" (Nice u. ter Pelkwyk, l.c.; Kellogg, l.c.; Rand, 1937). (Menschenkinder entwickeln im 2. Lebensjahr eine ausgesprochene Schlangenfurcht [Prechtl, 1949; Spindler, 1959]).

Feindspezifische Antworten reifen allmählich. Flügge Buchfinken betrachten neugierig einen Waldkauz, fliehen vor ihm mit zwei bis vier Wochen und hassen dann auf ihn, später noch ausgeprägter. Goldammern tun das etwas früher (Hinde, 1954:I). Bei der Singammer entwickelt sich der Eulenalarm offenbar erst nach mehreren Monaten (Nice u. ter Pelkwyk, l.c.). Bevor

Buchfinken vor dem Kauz fliehen, tun sie es schon vor einer fallenden Schachtel (Hinde, l.c.). Die Motorik scheint dem zugehörigen Erkennen des Feindes immer etwas voraus zu sein (auch eig. Beob.). Diese Feststellung wird aber unmöglich, wenn das artgemässe Verhalten auf Grund körperlicher Unreife notwendig ausbleiben muss. So flüchten Goldfasanküken (*Chrysolophus pictus*) auf den Bodenfeind- wie auf den Luftfeindruf der Mutter in Deckung, baumen aber bei Ertönen des Bodenfeindrufes auf, sobald sie fliegen können (Lorenz, 1935:209).

Spottdrosseln würden sich mit 17 Tagen von einer Schlange erwürgen lassen, lernen in diesem Alter auch noch nichts aus solcher Bedrohung und zeigen erstmals mit 24–30 Tagen das voll ausgeprägte Schlangenverhalten (Rand, 1941). Demnach können feindspezifische Reaktionen unabhängig von Erfahrungen mit dem fraglichen Feind erscheinen, doch ist die Frage offen, welche anderen Reize für die Reifung solchen Verhaltens nötig sind.

Die Frage, ob der feindunerfahrene Vogel schon auf einen Teil der Gesamtsituation antwortet, lässt sich m.W. bisher nur in einem Fall beantworten. Handaufgezogene Rotrückenwürger hassen auf den Waldkauzkopf, ehe sie je einen vollständigen Kauz oder einen anderen Feind gesehen haben (St. Paul, 1948).

b. *Instinkt–Dressur–Verschränkung*

Wie verändern Erfahrung mit dem Feind oder Reize anderer Art das Erkennen eines bestimmten Räubers? Schon die blosse Begegnung mit einem bestimmten Feind kann das Verhalten gegen ihn bestimmen (S. Kap. E). Kommt starker Affekt hinzu, sondert der Vogel mitunter ein bestimmtes Individuum der Feindart aus allen übrigen aus. So lenkte Kramer (1941) das Hassen eines Krähenpaares auf sich, indem er eine Jungkrähe auf dem Arm trug. Später verfolgte es ihn auch dann noch hartnäckig, wenn andere, fremde Personen die Krähe trugen. Die affektive Bindung des Krähenpaares übertönte die viel aktuellere Gefährdung der Jungkrähe durch noch unbekannte Personen, die auch dann unbeachtet blieben, als Kramer sich weiter als sie von dem Jungvogel entfernte. Nachdem bei Dohlen beim Beringen der Jungen heftige Schnarr-Reaktionen ausgelöst worden waren, zog lange Zeit nur der Beringer das Schnarren auf sich (Lorenz, 1958). Ähnliches beobachtete Nicolai (1950:10) bei fütternden Steinschmätzern (*Oenanthe oenanthe*).

Der Vogel lernt auf einen Feind sinnvoll zu reagieren, wenn er von ihm bedroht wird oder andere Vögel, meist Artgenossen, in bestimmter Weise antworten sieht oder hört. Gimpel lernen biologisch bedeutungslose Arten zu fürchten wenn man sie damit jagt (Kramer u. St. Paul, 1951). Junge Dohlen haben keine angeborene Furcht vor Bodenfeinden. Sobald sie aber einem begegnen, den die Altdohlen heftig schnarrend angreifen, nehmen sie sich künftig vor ihm in acht. Angeboren ist der Dohle lediglich, auf das Schnarren hin zu fliehen bzw. mitzuschnarren und die Fähigkeit, einen bestimmten Räuber mit dem Fluchtaffekt zu verknüpfen (Lorenz 1931, 1958). Anders der junge Brachvogel (*Numenius arquata*): er drückt sich, sobald er einen Vogel am Himmel erblickt. Durch den vorher ertönenden Warnruf der Eltern wird er lediglich aufmerksamer als zuvor, drückt sich im allgemeinen aber noch nicht. Hat er einmal beides zusammen, nämlich Räuber und Warnruf, wahrgenommen, genügt künftig der Ruf allein zur Auslösung des Sichdrückens (v. Frisch, 1958). Ob ein Junges den Raubvogel vom Friedvogel unterscheiden lernt, entweder auf Grund eigener Erfahrung oder unter Mithilfe der Eltern, ist eine offene Frage.

Inwiefern Tradition eines bestimmten Erfahrungsinhaltes wichtig sein kann, muss noch gründlich untersucht werden. Einer von Flussseeschwalben (*Sterna hirundo*) aufgezogenen Silbermöwe fehlte die Scheu vor dem Menschen. Ob Flussseeschwalben die von den arteigenen Eltern erlernen müssen, ist ebenso offen wie dieselbe Frage bei Singdrosseln (Brown, 1942) und anderen Vögeln. Junge Steinwälzer (*Arenaria interpres*) antworten normalerweise sinngemäss auf den arteigenen Warnruf, indem sie sich drücken. Rotschenkeln (*Tringa totanus*) zur Aufzucht untergelegte aber sind demgegenüber völlig taub und reagieren nur auf den Rotschenkelwarnruf (Bergman, 1946). Ob sie normalerweise den arteigenen Warnruf erlernen müssen wie z.B. junge Silbermöwen einen von zwei arttypischen Rufen (Goethe in Tinbergen, 1958:251), bedarf weiterer Prüfung.

Wie wirksam Tradition sein kann, das hängt von wenigstens zwei Umständen ab. Zum einen ist es die Autorität des Warners. So stören wenige, gegen Menschen schreckhafte Jungdohlen kaum in einer Kolonie, deren alte Mitglieder den Menschen gut kennen. Die Panik der alten aber steckt zugeflogene junge Dohlen unfehlbar an (Lorenz, 1931). Ähnlich trauen Silbermöwen nur dem Feindalarm zuverlässiger Warner in der Kolonie (Tinbergen, 1958:170). Zum anderen beeinflusst die Menge der antwortenden Schwarmmitglieder das Verhalten nicht vertrauter Neulinge. Das ist allwinterlich der Fall an Futterplätzen für Wassergeflügel, an denen zugeflogene Enten rasch futterzahm werden, sofern die vor ihnen angekommenen ihre Scheu abgelegt haben.

Ein Feind-AAM spricht nicht nur auf die Gesamterscheinung eines bestimmten Räubers an, sondern schon auf einzelne, im Attrappenversuch isolierbare Reize (S. Kap. C a 1). Ob sich das Erkennen des erlernten Feindes hiervon grundsätzlich unterscheidet, scheint zur Zeit noch nicht beantwortbar. Nach Lorenz (1935, 1950) soll eine erlernte Reizsituation als nicht auflösbare Komplexqualität beantwortet werden. Weglassung auch nur einer Einzelheit zerstöre das Erkennen im Gegensatz zur Wirkungsweise des AAM. Indes scheint die Grenze zwischen beiden Weisen des Erkennens nicht so scharf zu sein. (1) Auch der erlernte Feind ist in Grenzen veränderbar; nachdem Gimpel vor einer Eisvogelart Angst hatten, fürchteten sie künftig auch andere Mitglieder der Alcedinidae (Kramer u. St. Paul, 1951; vgl. auch Bingham, 1913; Coburn, 1914; Munn, 1931). (2) Jeder Vogel scheint aus einer für ihn bedeutungsvollen, erlernten Gesamtsituation einige für sein Erkennen wichtige Merkmale herauszugliedern, aber nicht sämtliche Details der Situation zu verwerten, und ein jeder sondert andere aus. So erkannten 4 Dohlen und eine Nebelkrähe ihren menschlichen Pfleger an einer für jeden Vogel typischen, unverwechselbaren Merkmalskombination (Strauss, 1939*a*, *b*; vgl. auch Spindler u. Bluhm, 1935). (3) Einige Schlüsselreize eines Feind-AAM lassen sich von anderen nicht isolieren, bilden mit ihnen zusammen also eine Teilgestalt. Damit sind sie ebensowenig auflösbar wie die hier aus Vergleichsgründen hypostasierte Komplexqualität eines durch Lernen veränderten AAM. Bisher ist nirgends untersucht, wie die Schlüsselreize beider Erkennungsweisen bei derselben Vogelart verarbeitet werden.

Die Fähigkeit bestimmte Feinde kennenzulernen, entwickelt sich erst in einem bestimmten Alter. Bevor der Vogel das erreicht hat, nützen selbst die schmerzlichsten Erfahrungen nichts. Beispielsweise verhielt sich eine Spottdrossel (*Toxostoma curvirostre*) gegen einen Wegläuferkuckuck (*Geococcyx*) gänzlich gleichgültig, nachdem er sie im Alter von 16–18 Tagen am Flügel durch ein Gitter zu zerren versucht hatte. Später, mit über 80 Tagen, flohen alle mit ihr aufgewachsenen Spottdrosseln vor den Wegläufern, gewöhnten sich aber etwas später an sie (Rand, 1941). Dass Jungvögel die Kenntnis von Feinden erlernen können zu einer Zeit, da sie selbst noch nicht mit denselben Triebhandlungen wie die Eltern auf sie antworten, das scheint einzig für die Jungdohle erwiesen zu sein (s.o.).

Kann sich ein Vogel den Ort merken, an dem er einem Feind begegnet ist, so wird er weiteren Zusammentreffen am selben Ort leichter entgehen als einer, der nicht auf der Hut ist. Raben und Singammern meiden den Ort eines schreckhaften Erlebnisses (Lorenz, 1935:205; Nice u. ter Pelkwyk, 1941), und Edwards et al. (1949–50) sahen ein Rotkehlchen (*Erithacus rubecula*) auf einen Platz herabstossen, wo sie vorher einen Kuckucksbalg gezeigt hatten (s. auch Altmann, 1956; Meinertzhagen, 1959:14; Markgren, 1960). Rabenkrähen "bewachen" eine Schonung, in der ein Habicht verschwunden ist, so lange, bis er wieder auftaucht, um ihn weiter zu belästigen; hingegen beruhigen sich Meisen, Amseln und Sperlinge unverzüglich, sobald sich der Räuber ihrem Blick entzogen hat (Löhrl, 1950*a*). Eine Ausnahme scheinen bestimmte Enten zu machen: führende Mütter lernen es nicht, den Ort, an dem sie Junge verloren haben, zu meiden (Lorenz, 1935: 307). Umgekehrt ist aber die schon erwähnte Futterzahmheit streng ortsgebunden (Meinertzhagen, 1950).

Wie Singvögel die Kenntnis bestimmter Eulenrufe erlernen (S. Kap. C b), ist zu erforschen.

H. PHYLOGENESE DES FEINDERKENNENS

a. *Populationsspezifität*

Wie verhält sich ein Vogel gegenüber einem Feind, wo dieser regional fehlt? Diese Frage wirft Licht auf die allgemeinere, wie rasch sich ein AAM ändern kann. Um sie zu beantworten, prüfte ich deutsche Trauerschnäpper (*Ficedula h. hypoleuca*) und spanische (*F. h. iberiae*) auf ihr Würgererkennen. Während *hypoleuca* sowohl auf den Rotrückenwürger wie auf den Waldkauz hasst, tut *iberiae* dies nur auf den Kauz. Das ergab die Prüfung von 130 bzw. 35 Vögeln mit Hilfe derselben Attrappen. Zu diesem rassenspezifischen Benehmen passt die geographische Verbreitung beider Feindtypen: währen *Lanius collurio* mit *hypoleuca* auf weitem Raum sympatrisch vorkommt und in Spanien fehlt, lebt der Waldkauz in fast ganz Europa. (Die beiden in Spanien mit *iberiae* sympatrisch verbreiteten Würger, *Lanius senator* und *L. excubitor meridionalis*, sind ökologisch von ihr getrennt; Curio, 1961*b*). Ob die Rasse *hypoleuca* am nördlichen Rand ihres Verbreitungsgebietes, wo der Rotrückenwürger ebenfalls fehlt, ebenso durch ihn geängstigt wird wie weiter südlich, ist eine noch offene Frage.

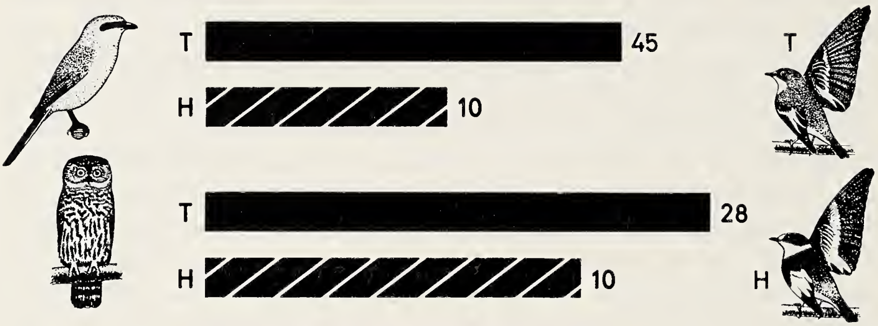

Abb. 5. Hassen fütternder Trauer- und Halsbandschnäpper (T und H) auf den Rotrückenwürgermännchen- und Sperlingskauzbalg. Antwortstärke in *deck*- und *bit*-Rufen/min. (T) bzw. in *deck*- und *siep*-Rufen/min. (H). Übrige Erklärung wie in Abb. 4.

Fig. 5. Mobbing of feeding Pied and Collared Flycatchers (*T* and *H*) at mounted specimens of male Red-backed Shrike and of Pigmy Owl. Response strength measured as *deck* and *bit* calls/min. (T) viz. *deck* and *siep* calls/min. (H). For further explanation, see Fig. 4.

Hasst *iberiae* auf den Würger deshalb nicht, weil schon ihre Vorfahren für ihn kein Auge hatten? Hierzu prüfte ich Halsbandschnäpper (*Ficedula albicollis*), eine dem Trauerschnäpper im Verhalten nächst verwandte und morphologisch sehr nahe stehende Art, und zwar mit denselben Attrappen. Auch hier löst der Sperlingskauz etwas stärker aus als der Würger (Abb. 5), und ein blaugrauer Haustaubenbalg bleibt unwirksam. Da es ausser dem griechisch-vorderasiatischen Halbringschnäpper (*F. semitorquata*) keine Art im System gibt, die dem Trauerschnäpper näher stünde als dem Halsbandschnäpper, dürfte die Würgerantwort beider Arten homolog sein. Auch sind die Bewegungsweisen dieselben und einer von zwei im Alarm geäusserten Ruftypen. Nimmt man hinzu, dass *iberiae* jüngeren Datums ist als diese beiden Schnäpperarten, so erscheint die "Würgerblindheit" der spanischen Rasse als ein sekundärer Verlust. Hierfür sprechen überdies zwei hassende

"Aussenseiter" unter den Spaniern, die Würger-Alarme von gleicher Stärke wie typische *hypoleuca*-Vögel gaben. Demnach kann ein Auslösemechanismus selektiv abgebaut werden, sobald der Selektionsdruck, unter dem er einmal entstand, nämlich die Bejagung der Art durch Würger, wegfällt, und zwar ohne die zugehörige Motorik des Hassen in Mitleidenschaft zu ziehen (Curio, 1961*c*). Eine Gegenselektion lässt sich nicht plausibel machen, denn das Erkennen des Würgers dürfte kaum schaden in einem Raum, wo es ihn nicht gibt.

In welcher Zeitspanne der spanische Trauerschnäpper seinen Würger-AAM verlor, liesse sich nur dann angeben, wenn man wüsste, wann *iberiae* Spanien besiedelte. Weil *Lanius collurio* weder heute noch früher das Verbreitungsgebiet von *iberiae* berührte, wie Verbreitung und Zugwege der europäischen Würger zeigen (Curio, 1961*c*), haben schon die ersten Siedler auf spanischem Boden Ruhe vor dem Rotrückenwürger gehabt.

Ähnliches gilt vom Erkennen des Kuckucks. Während zahlreiche europäische Arten auf *Cuculus canorus* am Nest abwehrend antworten (S. Kap. C a 1), lassen sich nordamerikanische Arten von ihm überhaupt nicht beeindrucken (Stichproben-Versuche E. Mayrs in Smith u. Hosking, 1955). Hierzu passt, dass in Nordamerika kein parasitischer Kuckuck lebt. Auch das Verhalten nesthockender Jungvögel kann dem Vorkommen von Nesträubern fein angepasst sein. So lärmen grönländische Schneeammer-Nestlinge (*Plectrophenax nivalis*) gegen Ende der Hockzeit (Tinbergen 1939*b*), während solche auf dem amerikanischen Festland, vermutlich in Anpassung an die ständige Bedrohung durch Raubsäuger—sich stumm verhalten (Drury, 1961). Allerdings bleibt zu sichern, dass grönländische Jungvögel nicht deshalb lauter sind, weil sie in vielleicht besser sichtgeschützten Nestern heranwachsen.

Weshalb ein Gummimodell eines Skorpions, aber nicht eine Gummieidechse englische Singvögel am Winterfuttertisch schreckte (Meinertzhagen, 1955), bedarf gewiss ebenso der näheren Untersuchung wie regionale Zahmheitsunterschiede (Huxley, 1947).

b. *Genetik*

Die beschriebenen Populationsunterschiede im AAM für bestimmte Feinde fordern geradezu eine Analyse der erblichen Grundlagen des Feinderkennens heraus. Erste Ansätze hierzu liegen beim Puter vor. Junge Mischlinge zwischen Hausputen und Wildputen (*Meleagris gallopavo silvestris*) drücken sich nicht vor Luftfeinden und schenken allem Neuen, was sich ihnen nähert, weniger Aufmerksamkeit als Wildkücken (Leopold, 1944).

I. ZUSAMMENFASSUNG

Der ruhende Flugfeind wird vom Vogel an höchst spezifischen, entbehrlichen und unentbehrlichen Schlüsselreizen erkannt. Häufig bilden diese komplexe Beziehungsmerkmale. Zahl und Verarbeitung der vom Feind ausgehenden Schlüsselreize ist in keinem Fall genau genug untersucht, um die Wirkungsweise des zugrundeliegenden AAM befriedigend zu verstehen.

Der fliegende Flugfeind der Pute ist "etwas Neues am Himmel von bestimmter Relativgeschwindigkeit und bestimmter Grösse"; spezielle Formmerkmale spielen im AAM keine Rolle. Die Pute lernt, welche Art sie nicht zu fürchten hat, indem sie harmlose Vögel häufiger wahrnimmt als den selteneren Räuber. Offen ist, welche Bewegungsmerkmale ausser der geradlinigen Fortbewegung in das Erkennen eingehen.

Das Verhalten des Feindes bestimmt oft entscheidend, wie der Vogel auf ihn antwortet.

Viele Arten lernen es, Eulenstimmen zu erkennen und auf sie wie auf die Eule selbst zu hassen.

Die Bereitschaft, auf bestimmte Feinde artgemäss zu antworten, hängt ab von der Jahreszeit, vom Stadium des Brutzyklus und von ihrem Wesen nach unbekannten Stimmungsschwankungen.

Die Häufigkeit, mit der ein Vogel einem bestimmten Feind begegnet, beeinflusst i.a. entscheidend seine Reaktionsstärke.

Die Frage, ob Vögel für das Erkennen verschiedener Feinde verschiedene AAMs entwickelten, die sämtlich ein- und dasselbe Schutzverhalten auslösen, verdient weitere Untersuchung.

Einige Singvögel erkennen angeborenermassen Eulen, Tagraubvögel, Schlangen, und Säuger, d.h. ohne Schlimmes von ihnen erfahren zu haben. Welche anderen äusseren Umstände zur Reifung solchen Erkennens beitragen, ist eine offene Frage.

Durch Lernen engt der Vogel den Bereich der Schutzverhalten auslösenden Reize ein (Gewöhnung), oder er erweitert ihn. Zwischen der Verarbeitung erlernter und angeborener Reizsituationen scheint kein grundsätzlicher Unterschied zu bestehen.

Zwei geographische Rassen des Trauerschnäppers unterscheiden sich in Anpassung an das Vorkommen eines bestimmten Flugfeindes grundsätzlich im Erkennen des Räubers. Die Rasse, die den fraglichen Feind-AAM aufgab, behielt die zugehörige Motorik des Schutzverhaltens bei. Von den erblichen Grundlagen des Feinderkennens weiss man bisher fast nichts.

SUMMARY

The perched avian predator is recognized by dispensable and indispensable key stimuli, which are often configurational. The number and the mode of evaluation of the key stimuli represented by a given predator is not, in any case, sufficiently known to permit an understanding of the operation of the underlying innate releasing mechanism.

The flying predator is recognized by the Turkey as "some new object in the sky moving at a certain relative speed and of a certain size." The Turkey learns what species not to fear by perceiving harmless species more frequently than the rarer raptor. The movement characters entering into recognition other than linear locomotion are questionable.

The enemy's behavior often determines the response of the endangered bird.

Many species learn to recognize owl calls and will mob in response to them as to the owl itself.

The level of responsiveness of predator reactions depends on the time of year, on the stage in the breeding cycle, and on fluctuations of internal factors, which are not yet understood.

The frequency of encountering a given predator significantly influences the strength of the response to it.

The question of whether or not different enemies releasing identical responses enter into different IRMs demands further investigation.

Some songbirds recognize owls, birds of prey, snakes, and mammals as predators, even though they have not experienced harm from them. Which other stimuli contribute to the maturing of such innate recognition is an open question.

By learning, the bird either reduces the range of stimuli eliciting predator responses (habituation) or widens it. Recognition of learned and innate stimulus situations does not seem to differ basically.

Two subspecies of the Pied Flycatcher differ in their recognition of a perched predator. This correlates well with the predator's distribution. The subspecies which abandoned the IRM in question maintained the motor pattern of the response. Nearly nothing is known about the genetics of enemy recognition.

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Some Aspects of Social Organization in the Carolina Chickadee

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The term "social organization," as developed by Allee (1931:340–346), implies orderliness in the relations between individuals of a social group. "Social" refers only to a group formed as a result of interindividual actions none of which need be amicable if the social tendency (Crook, 1960:126) is sufficiently strong. Social groupings of unconfined vertebrates usually occupy a circumscribed area, and the pattern of utilization of that space may influence the form of social organization exhibited. Spatial restriction tends to minimize the contacts with individuals outside the group, and promotes orderliness within it (see Collias, 1944:84).

Allee (1931) recognized three forms of social organization in vertebrate societies: the social hierarchy, territoriality, and leadership. Our concern will be with the interrelations of the first two, which have been discussed by Collias (1944), Greenberg (1947), Ritchey (1951), and Davis (1959), among others. This study seeks to explore the factors serving as a basis for the forms of organization, and to examine the adaptive value of the organization exhibited. The subject was a free-living population of an arboreal passerine bird, the Carolina Chickadee (*Parus carolinensis*). Since most of the birds studied were color banded, this report will emphasize the histories of individuals.

The Carolina Chickadee is a small bird (ca. 10 g) that forages principally on leaf surfaces in the growing season and upon bark surfaces in winter. Nests are built in cavities, and roost sites may be sought there also. Social organization was studied in autumn, winter, and spring in 5 consecutive years, 1953–54 through 1957–58, on an area 2 miles southwest of College Station, Brazos County, Texas. The study area, some 40 acres in extent, was on rather level terrain and was covered with woodland of open canopy and moderate stature (deciduous oak savannah forest of Braun, 1950:177), with dense clumps of evergreen holly (*Ilex vomitoria*) 6–12 ft in height interspersed. The discontinuous overstory, 15–30 ft in height, was comprised of *Quercus stellata*, *Q. marilandica*, *Ulmus alata*, and *Fraxinus* sp., and the understory was made up of scattered shrubs of the genera *Ulmus*, *Callicarpa*, *Ilex*, *Vaccinium*, *Crataegus*, *Forestiera*, and *Viburnum*. Similar woodland extended to the south and west of the plot. In the course of the study, the vegetation became more dense, largely a result of the closure of small clearings by growth of elm saplings. The area, situated at about 30°40′N lat., was characterized by mild winters. The lowest temperature recorded during the 5 years was 18° F, with snow persisting on the ground for only 1 day. The growing season on an average extended from 8 March to 22 November

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(Norquest, 1941:1129). Census data for other species breeding on the plot were reported by Dixon (1957).

METHODS

Chickadees were trapped at elevated stations baited with pecans or coconut meat. The traps used were of the single-cell, swinging drop-gate, wire-mesh type, described by Bailey (1951). The period of susceptibility to these baits is indicated by extreme trapping dates, 7 October and 23 February. In October and early November the ages of newly trapped chickadees were determined by incision of the scalp and examination of the roof of the skull in the manner devised by Miller (1946). Chickadees were provided with one colored-plastic and one aluminum band on the same leg. Rapidity of movements made observation of color-band combinations difficult, and in many situations the identity of one or more participants remained unknown. In addition, chickadees tended to cover their tarsi with ventral plumage in cold weather. From 1955 onward, patterns painted on the rectrices with Testor's airplane dope facilitated identification of individuals. Sex was determined by breeding behavior, and remained unknown for some individuals. Numbers assigned to individuals (Fig. 2) indicate the year of their first appearance (single digits for 1953–54, 10–19 for 1954–55, etc.). Designations for territories in subsequent figures follow the same scheme.

Baiting of trapping stations did not clearly influence the travels of the birds, for the same flock might visit a given feeding station at different hours on succeeding days. Nonetheless, periods of trapping were followed by intervals of observation without baiting. Chickadees were attracted to each of several trapping stations by a chunk of coconut meat suspended on a wire so that it swung freely 12–18 inches below a branchlet. Access to this pendant bait was limited to a single bird at a time, and the order of precedence at this food was used as one criterion of social ranking in the last 3 years of the study. Nearly all these observations were made at four stations from 500 to 800 ft apart.

Forty Carolina Chickadees were marked in the course of this study, and 27 of these were present on the area during one or more breeding seasons. However, no more than 15 marked birds were under observation at any one time. Other duties prevented my following the birds through the early summer months, and no nestlings were banded.

BEHAVIOR

The social organization in this species was affected by two tendencies exhibited to a greater degree in this population than in most species of *Parus*, as noted by Hinde (1952:61–62). These traits were restriction of activities to a limited area seldom exceeding 20 acres, and permanence of pairing. A female chickadee F1, of undetermined age when trapped initially in January 1954, occupied the area mapped in Fig. 1 continuously in the years indicated, but was not detected in areas to the south and east, where investigation was intensive. Similar constancy in restriction to a limited area was shown by five males (M32, M17, M11, M23, and M34; see Fig. 2), each of which took up its area in its first autumn. This tendency was shown as well as by other males of unknown age. This extreme sedentariness was less evident in females, and some implications are discussed in connection with longevity in a later section. Although site attachment may be weaker (or deferred?) in some females, spatial restriction was shown strongly by F22, F4, F2, and F13, as well as by F1 (see Fig. 1). In most instances the areas occupied by these individuals in winter were somewhat larger than their breeding territories, and could be likened to the "domiciles" of the Great Tit (*Parus major*), as discerned by Kluijver (1951:21). In no instance did a bird known to have nested on the plot shift its subsequent breeding territory outside the area of its winter range other than to move into a contiguous space within the study area. However, permanent displacements of greater magnitude may have escaped detection because of limitations of my areal coverage. A male M3, at least 3 years of age, was not detected on the study plot between April and late October 1956 and probably spent that interval nearby. The arrival each autumn of one or two individuals that certainly were adults,

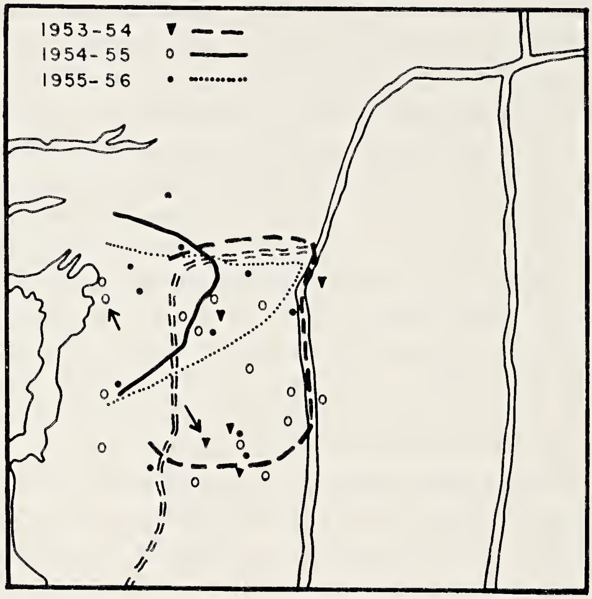

Fig. 1. Individual range of female F1 between January 1954 and May 1956. Sites where she was identified throughout the year, and boundaries of the breeding territories are indicated by the symbols in the key. Nest sites for 1954 and 1955 are shown by arrows pointing to location symbols for those years.

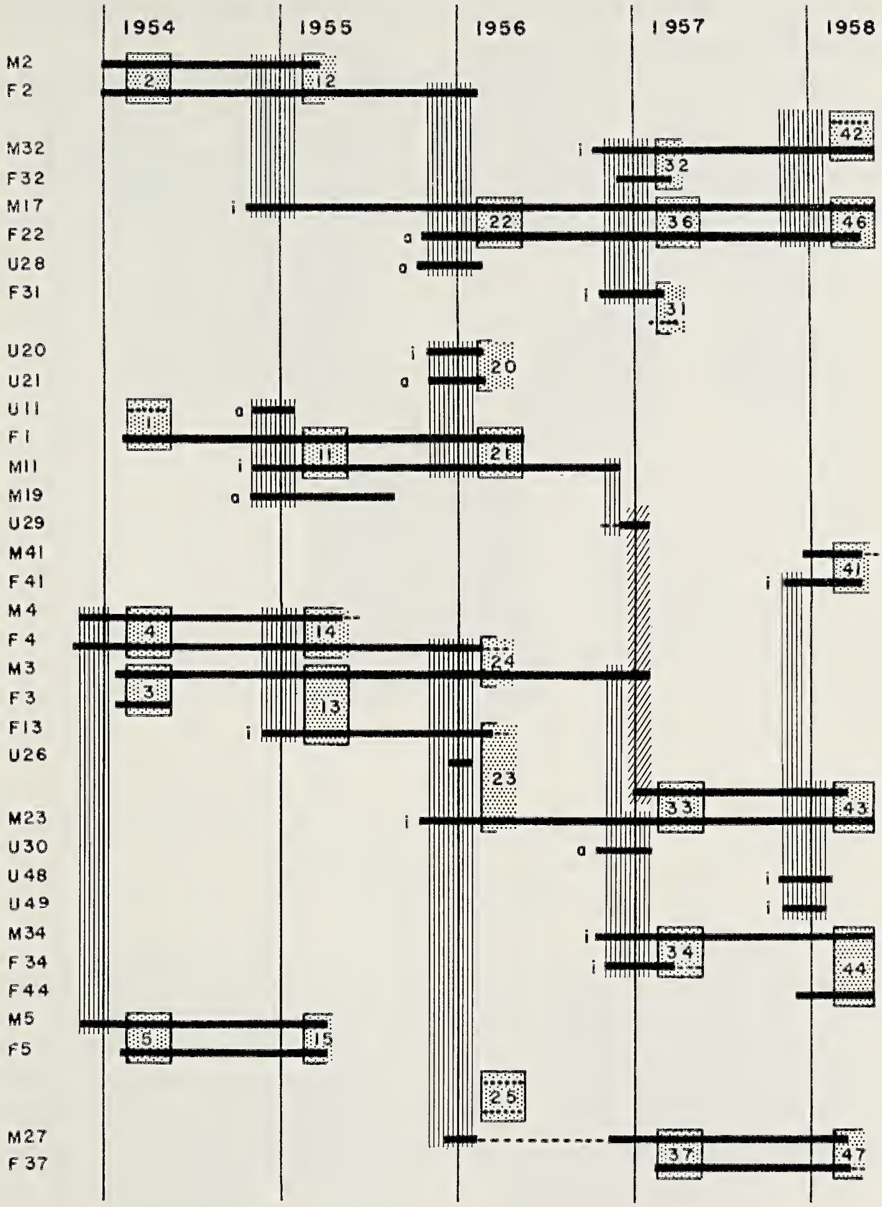

Fig. 2. Temporal and social relations of Carolina Chickadees on the study area. Horizontal bars indicate tenure of marked individuals; rows of dots, that of unmarked birds. Rectangles with background of vertical lines enclose the bars representing members of a given flock during the time interval charted, and rectangles with dotted background denote breeding pairs. Numbers in those rectangles refer to territories mapped in Fig. 3–7. The letters *a* and *i* to the left of certain horizontal bars denote skull-determined ages at the time of initial capture. The diagonally hatched area in 1956–57 indicates a succession of flocks on the same area (see text). Birds of unknown sex are designated by the prefix *U*.

such as F22, M19, and U30, lends support to the assumption that some individuals did shift their domiciles.

Many Carolina Chickadees apparently pair in autumn of their first year (or earlier?), and retain their mates in continuous association for life. In nine instances involving 14 individuals, both members of a pair survived to initiate the following breeding season, and in only one case was there a change of mates. This "divorce," involving M3, F4, and F13, will be discussed below.

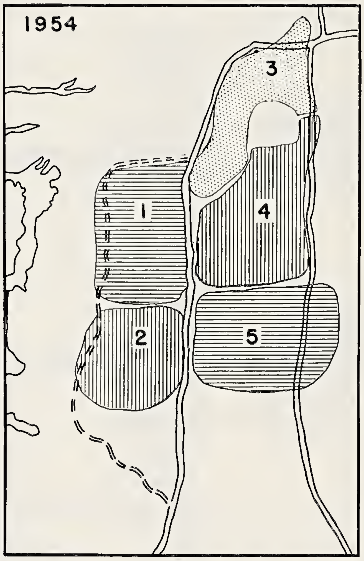

Fig. 3. Breeding territories in 1954.

Annual Cycle. — The following sketch presents background information relating to the populations studied. Additional details may be found in the accounts of Edw. Dingle (*in* Bent, 1946:344–352) and Brewer (1961). Pairs separate from flocks in mid-February, and incubation ordinarily is under way by late March. Broods appear in late April, but more commonly in early May. This species is single brooded as a rule (Simmons, 1925:309). During midsummer the majority of pairs enlarge the area occupied for nesting, and are joined by other individuals (usually juveniles) to form a "winter" flock. Insofar as is known these are not family groups, the dispersal of juveniles presumably having preceded the formation of these flocks. A similar conclusion for the Black-capped Chickadee (*Parus atricapillus*) was reached by Wallace (1941:53). The pairing of flock mates (discussed below) supports this contention. The flocks on this area consisted of from 2 to 6 or 7 individuals and occupied restricted ranges (the domiciles of the nucleus pairs), as shown in Fig. 3 through 7. Thus, the yearly sequence in

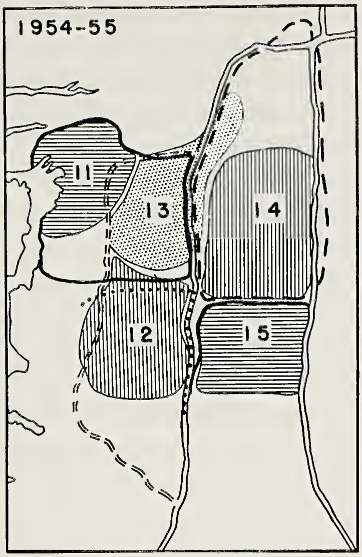

Fig. 4. Configuration of breeding territories (shown by cross-hatching and stippling) and winter flock ranges in 1954–55. Flock membership and pairing relations are diagrammed in Fig. 2.

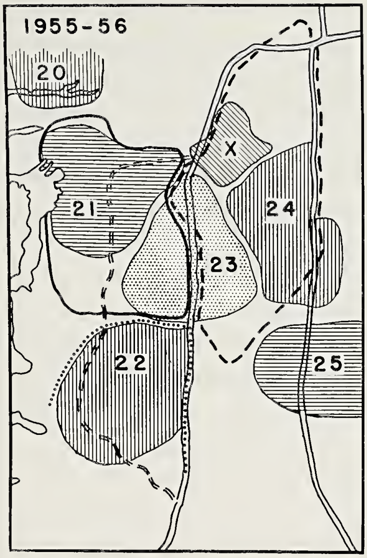

Fig. 5. Winter flock ranges and configuration of breeding territories in 1955–56. Territory *X* was occupied by unmarked birds (see text).

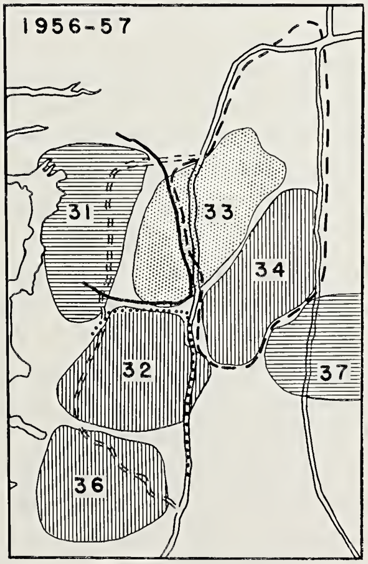

Fig. 6. Winter flock ranges and configuration of breeding territories in 1956–57.

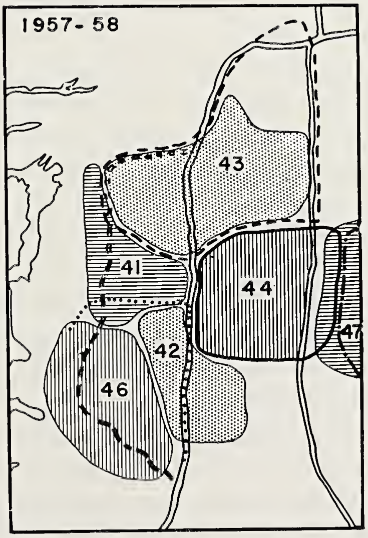

Fig. 7. Winter flock ranges and configuration of breeding territories in 1957–58.

the population studied involves alternation of periods of spacing as territorial pairs (February until early summer), and aggregation in flocks.

Characteristics of the Flocks.—All the flocks studied were constant in membership. No transfer from one flock to another was known, although two couples (pair No. 20 and pair No. 41) separated prematurely from the flocks to which they had belonged earlier in the winter. One individual, U29, was a member of two flocks that occupied the same area successively in the same winter (1956–57).

The ranges of the flocks appeared well defined in any given year and were essentially exclusive. Often the borders of the woodland dictated the limits, but other boundaries were without features conspicuous to me. Infrequently two flocks were noted in proximity, and at those times vocal exchanges and actual skirmishes usually involved the dominant male and sometimes his mate. One such boundary between the flocks of the northwest and southwest sectors (Fig. 3–7) clearly was an outgrowth of contests between pairs No. 1 and 2 in the breeding season of 1954. Thus, the exclusiveness of winter flock ranges reflects the territoriality of the dominants.

The flocks were fairly cohesive (Thompson, 1958:300), although individuals or couples might be found apart from the group, and the presence of some individuals could not always be demonstrated when a flock was visiting a feeding station. However, flock members traveling separately were not observed transgressing those boundaries held in common with other flocks on the study area. (Flocks of the northeast sector made infrequent excursions *as flocks* to the east of the area that they defended. On such occasions, their manner was less leisurely and their unity seemed more pronounced than at other times.)

The structure of seven flocks was determined by observation at feeding stations, and in each flock the resident male was the alpha or dominant individual in what apparently was a peck-right or unilateral hierarchy. In general, the dominant birds fed first at the restricted food source, and returned more frequently. Assigning of rank in a hierarchy on the basis of precedence at food appears valid since Tordoff (1954:356) found no difference in rank determined by fighting and by order of feeding in the Red Crossbill (*Loxia curvirostra*). Further, I observed no reversal in rank in supplanting attacks (Hinde, 1952:22) at natural food sources.

However, data on precedence at food are difficult to quantify, since some individuals avoided the feeding station when the dominants were present, and since the sequence of feeding sometimes was interrupted by the dominance of the chickadees by Tufted Titmice (*Parus bicolor*). Therefore, additional criteria, such as manner of approach to the food, and of supplanting attacks elsewhere, were employed.

The mate of the alpha male appeared to rank second in the flock when her mate was present. However, in the absence of their mates such females did not always hold precedence over subordinate males. F22 generally preceded M32 (a first-year male) to food in the winter of 1956–57, but gave way to him in the following winter on occasions when her mate, M17, was elsewhere. Following F22's deference to M32 on 28 November 1957, M17 appeared and M32 withdrew until his departure. Another established female, F33, was supplanted by a first-year bird, U48, on 28 December 1957 in the absence of M23, again suggesting that the status of the female depended upon the presence of her mate. Sabine (1955:109) reported an observation wherein the rank of a female of *Junco oreganus* increased dramatically after she had paired with the alpha male and prior to the departure of the flock from his territory.

The social structure in flocks of Carolina Chickadees appears intermediate between that of the Red Crossbill, in which all males dominate all females (Tordoff, 1954), and of the Jackdaw (*Corvus monedula*) in which the rank of a given female is determined by that of her mate, whether or not he is present (Lorenz, 1952:151). Since rank in female chickadees is equivocal, males and females will be ranked separately, and the mate of a dominant male will be spoken of as the "alpha female" without reference to her position in the mixed-sex assemblage.

The ages of 16 subordinate individuals that ranked below the dominant pair in 11 flocks were known. Eleven were immature (5 males, 4 females, 2 unsexed) and 5 were adults (3 males, 1 female, 1 unsexed). The three subordinate males that unquestionably were adult were M19, M3 in 1954–55, and M32 in 1957–58. M19 was subordinate to a first-year male, M11, and did not succeed in obtaining a mate or a breeding territory in 1955.

Breeding-season Dispersion.—As the winter flocks disbanded with the onset of the breeding season, the alpha male and his mate retained a portion of the flock range for their breeding territory without exception. The status of 21 subordinate members of 11 flocks was confirmed; there were 19 individuals (9 males, 5 females, 5 unsexed), since 2 held subordinate status in consecutive winters. Twelve of the "21" nested within their flock ranges and three settled nearby. Eight of the 12 were beta males, five of them pairing with flock mates. The five birds of undetermined sex were clearly subordinate flock members, and none was known to have nested within the vicinity. I found no example of appropriation of a part of the flock range by an outsider, although M3 took a semi-isolated part of M4's winter range for nesting in 1954. (It is doubtful that M3 was a member of M4's flock prior to nesting.) Two of the six females that did not pair with birds known to be their flock mates (F31, F41) nested in areas contiguous to the flock range. (Pair No. 41 occupied an area frequented by neither M23's group nor M17's in 1957–58.) Thus, the highest-ranking subordinates usually obtained property rights (at least for nesting), and they might advance to alpha rank with the disappearance of the former dominant. Four males that achieved alpha rank in this manner were M3, M23, M11, and M17.

Boundaries of breeding territories were defended vigorously (prior to nesting) by song exchanges and by highly vocal skirmishes, usually involving only the males, but sometimes both members of the pair. Defense continued into the period of flocking with fledglings. Especially spirited encounters between pairs No. 34 and 37 were noted in May 1957. Although advertising by singing males was less conspicuous than in many passerines, the avoidance of trespassing by the chickadees attested a strong awareness of the boundaries.

A brief chronology is presented as a means of elaborating upon the data presented in the maps and in Fig. 2.

1953–54

Three birds that traveled together in the northeast quadrant of the study area (M4, F4, F5) were the only ones banded prior to January. The flocking relations of individuals marked subsequently could not be ascertained before the flocks disbanded. Five pairs were spaced on territories by about 15 February (Fig. 3). The boundaries of the breeding territories were documented more carefully than in any subsequent year.

1954–55

Eight of 9 marked individuals of the previous breeding season were present in October, and the territorial boundaries of the 1954 season appeared to influence their movements. Those birds found repeatedly in a given area seldom were encountered as flocks, but more often were met as couples and trios. Definite segregation as breeding pairs did not occur until late February.

In the northwest quadrant (Fig. 4), F1 and U11 (possibly her mate of the 1954 season) flocked with M11, M19, and an unmarked bird, ranking in the order listed. Following the disappearance of U11 in January 1955, F1 paired with M11, while M19, a subordinate (but adult) bird wandered widely through territories No. 11, 14, and 15 without acquiring a mate.

The returning pair of the southwest quadrant defended as the northern boundary of their flock range the territorial line held in the previous spring. Their range was occupied by a first-year male, M17, that apparently did not mate. The nesting status of M2 and F2 in 1955 was not ascertained, although defense of the north boundary by this pair was witnessed on 11 March.

In the northeast sector pair No. 4 was joined by M3 and F13 (but not certainly before early December). M3 did not nest again in the isolated grove to the north but expanded his domain into the northwest quadrant (west of the road) as territory No. 13 at the expense of the first-year male M11.

The pair in the southeast corner retained their territory and defended it against pair No. 4 through autumn and winter. They were not accompanied by subordinates, and their winter range was not expanded noticeably.

Nesting in 1955 was disrupted by a late freeze (25 March) that shriveled the fresh foliage of the oaks. The only nesting known to have been successful was that of M11–F1.

1955–56

The population level appeared higher in general, a flock of seven unmarked chickadees being present in October at least. Seven marked individuals survived from the breeding population of 1955 to influence the social and spatial patterns (Fig. 5).

In the southwest quadrant four individuals traveled together, but, since their dominance relations were not clear, data for them are not included in analyses of flock structure. These included carry-overs F2 and M17 and newcomers (both adult) F22 and U28. M17 and F22 paired and occupied the northern part of the flock range. The others were not identified after 20 February.

The returning pair, M11 and F1, held forth in the northwest sector, and was accompanied by two individuals that isolated themselves in an area to the north (territory No. 20) after 4 January.

Following the disappearance of M4 during the breeding season of 1955, the previously subordinate M3 assumed the alpha position in the northeast quadrant (seen with F4 on

2 July and thereafter). Included in the flock was M3's former mate F13. She paired with a first-year male M23 (beta male), and the two pairs shared the flock range. The ranking of this flock in January and early February was M3, F4, M23, M27, F13, and U26. The territorial disputes between M23 and M3 were especially vigorous, and the younger bird gained some ground in a succession of days, 4–8 March. After the disappearance of his mate by early April, M23 wandered widely within the study area and did not defend his territory against pairs with broods. A subordinate male, M27, was seen in the southeast quadrant as late as 9 March, and may have nested farther to the east.

Two unmarked pairs settled on the area, one designated as pair No. 25 in the southeast portion, and the other, territory *X*, in the creek bed north of territory No. 23. It is doubtful that nesting was completed in the latter case, although adults were present as late as mid-May.

1956–57

The nucleus pair of the southwest quadrant was M17–F22; they were accompanied by three unmarked birds as early as 18 August. Three known companions of the nucleus pair in midautumn were M32 (a first-year male) and F32, who paired with him in the flock (or prior to joining it?), and F31. These were ranked in the order listed. The first two pairs subdivided the flock range (Fig. 6), and F31 settled in a contiguous area to the northwest. The flock was constant and cohesive until 28 January, but pairs were dispersed on territories by 4 February.

In the northwest quadrant the returning widowed male M11 was seen repeatedly with two unmarked chickadees in October and November. One of the latter almost certainly was U29, marked on 30 November, the last date on which M11 was seen. U29 subsequently traveled with M3 and F33 *in the area of M11's flock range* as late as 28 January. F33, marked on 30 December, but possibly M11's companion in November, paired with M23 in early February after the disappearance of M3. A breeding territory was established here by an unbanded male and F31, the latter having emigrated from the southwest quadrant.

In the northeast sector the widowed M23, an unsuccessful breeder, was joined by an incoming adult U30 and by three other birds by late September. These formed a cohesive unit (seen together on five days) prior to the return of M3 on 26 October. The relationships of M3 and M23 were not clear, but both were seen to be members of a group of five on 30 November, and were noted together again on 30 December. M3 took precedence over the other members of this flock at a station in the northwest quadrant on 23 November; M23 was not seen there, but was noted nearby with M34 an hour later. M3 was not certainly associated with the flock (M23, U30, M34, F34, ranked in that order) after 30 December. Thereafter he was found in the northwest sector except for visits to a feeding station in the northeast, a site at which he had been the alpha bird in the previous winter. M3 was judged to be paired with F33, this couple (but not U29) visiting the northeast feeding station on 29 January. They departed just prior to the arrival of M23's flock. M3 was not seen after 31 January, and F33 was found to be paired with M23 in the northeast sector on 4 February. M23's presumed mate, U30, had disappeared in the same 4-day interval. The flock range was divided between M23–F33 and M34–F34. The beta male (M34) appeared to avoid contact with M23 at the feeding station, and careful search was necessary to demonstrate his presence at such times. F34 and M34 were noted traveling as a couple in the northern part of the flock range on 20 January (and probably on 27 December).

The southeast quadrant was not regularly occupied by chickadees until the detection of M27–F37 late in January. These birds ranged but little west of the road, pair No. 34 occupying most of the area. Territorial encounters between the two pairs were conspicuous throughout the nesting season.

1957–58

In the southwest sector (Fig. 7), the returning pair M17–F22 again formed the nucleus of a small group that included M32, returning for a second year as the beta male. Two unbanded birds accompanied them, one not seen after banding on 28 October, and the presence of the other not detected after 1 January 1958. The alpha male again held a territory at the southern end of the flock range, and the beta male was situated in the northeastern portion and beyond (contesting M34), apparently unmated. From mid-

April onward, M32 was paired with an unmarked bird and occupied an area along the northern fringe of the flock range after pair No. 41 had vacated that vicinity.

The returning male M23 and his mate F33 formed the nucleus of a flock that ranged on both sides of the road (NW and NE quadrants). This group was detected east of the eastern road to a greater extent than were groups of previous years. Accompanying them in October and November were three birds with immature skulls, U48, U49, and F41. The latter split from the group as early as 30 November (accompanied by one unmarked chickadee), and was associated as a pair with M41, a bird first trapped on 15 December. M41 was not known to have been a member of M23's flock, but the two fed together at the feeding station in the northeast quadrant on 16 December. M41 and F41 did not utilize the northeast quadrant after 16 December, and they neither joined M23's flock nor excluded it from the area west of the road. The post oaks of the northwest corner were defoliated as a pasture-improvement measure, and pair No. 41 shifted its activities to the south into the range of M17's flock. M41 and F41 obtained much of the food for their nestlings from the area of reduced canopy, but apparently moved their fledglings into woodland to the west. U49 was seen last on 14 December, but U48 accompanied pair No. 43 as late as 13 February.

M34 retained his territory in the southeast quadrant rather than returning to the flock range of the preceding winter. He was vigorous in defense of territorial boundaries against M23's flock to the north, and against M27 and associated chickadees to the east. M34 was accompanied by F44, a female first captured on 28 November 1957.

PATTERNS OF SOCIAL ORGANIZATION

The data presented above illustrate reciprocal relationships between alternating patterns of social organization, flocking in groups ordered in hierarchies, and dispersal as pairs on breeding territories. Social rank influenced the pattern of territorial dispersion in that surviving alpha males and their mates nested in the flock range without exception (10 examples, excluding M11 in 1955 since he was not the alpha bird of the flock). High social rank led to the *initial* acquisition of breeding territory within the flock range in the following first-year males: M11 (by succession), M23, M32, and M34. Further, no male judged to be *below* beta rank (among males) nested within the flock range, and the same relationship held for females. Since the wintering area was occupied for breeding year after year, lower-ranking individuals conceivably could have been crowded into habitat that was marginal for breeding.

Territoriality likewise conferred rank in that all known alpha males (1954–55 and after) had nested within the flock range during the previous breeding season (eight examples, excluding M17 in 1955–56 and M27, whose flocking status was never determined). These and similar relations of males of this population are detailed in Table 1.

Isolated Pairs.—In 13 instances territory-holding males survived to initiate the next breeding season, and in only two of these cases did the males continue to occupy the breeding territory. The area occupied was not enlarged, and the pair rather than a larger flock constituted the social unit. In each case the same part of the study area was involved (territories No. 5 and 15, 34 and 44). As a partial explanation for the latter occurrence, I can offer the interpretation that M34, the beta male of M23's flock as a first-year male, was fairly evenly matched with M23. M34 seldom appeared at feeding

Table 1.—Social Rank, Survival, and Related Data for Individual Male Carolina Chickadees

Winter Period and Male	Male's Rank in Flock[a]	Previously Bred in Flock Range	Later Paired with Flock Mate	Later Bred in Flock Range	Male Survived until Next Autumn	Survived through Next Winter	Months on Area after His First 1 March
1954–55							
M2	Alpha	+	++[b]	(+)	—	—	10
M17	Beta?	—	?	(+)[c]	+	+	39[d]
M11	Beta	—	+	+	+	+	21
M19	Gamma	—	—	—	—	—	6
M4	Alpha	+	++	+	—	—	14
M3	Beta	+	+	Part	+	+	35
M5	Alpha[e]	+	++	+	—	—	13
1955–56							
M17	Alpha?	+[c]	+	+	+	+	
M11	Alpha	+	++	+	+	+	
M3	Alpha	+	+	+	+	+	
M23	Beta	—	+	Part	+	+	26[d]
M27	Gamma	—	?	—	+	+	24[d]
1956–57							
M17	Alpha	+	++	+	+	+	
M32	Beta	—	+	+	+	+	15[d]
M11	Alpha	+	—	—	—	—	
M3	Alpha[f]	+	+	—	—	—	
M23	Alpha[g]	+	—	+	+	+	
M34	Beta	—	+	+	+	+	14[d]
M27	?	?	?	(+)	+	+	
1957–58							
M17	Alpha	+	++	+			
M32	Beta	+	?	+			
M41	?	?	?	+[h]			
M23	Alpha	+	++	+			
M34	Alpha[e]	+	—	+			
M27	?	+	++	?			

[a] The flock in which each membership was held can be ascertained from Fig. 2.

[b] ++ indicates breeding with mate of preceding year.

[c] Seen within flock range in breeding season but status undetermined.

[d] Individual alive at termination of study, May 1958.

[e] Remained on breeding territory through the winter (nonflocking).

[f] Relationship to M23 uncertain; formed separate flock after M11 disappeared.

[g] Relationship to M3 uncertain; see text.

[h] Flock relations unknown prior to establishment of territory in midwinter.

stations, but was detected occasionally foraging in nearby trees. Avoidance of contact by closely ranked individuals was found in chickens by Schjelderup-Ebbe (1935). Incipient tendencies toward such year-round territoriality may be inferred from the early isolation from the flock by the pair of territory No. 20 in 1955–56, and in the establishment of territory No. 41 in December 1957.

In contrast to the stronger territorial tendency noted above, M32 rejoined his old master, M17, as a subordinate by late summer in 1957, and M3 joined pair No. 4 (but rather late in the autumn of 1954).

Survival Values of Flocking.—The fact that pairs could overwinter successfully on their breeding territories leads one to question what selective pressures may have favored their more prevalent existence in flocks. Some biological advantages to flocking in birds have been reviewed by Short (1961:344–346). Among those listed, the presence of additional eyes to watch for danger would seem to be a principal advantage to the dominant pair in being accompanied by additional individuals. Carpenter (1935) and Johnston (1942) in Illinois and Morley (1950) in England have shown that the flocking tendency in arboreal birds was stronger in inclement weather. Several species of titmice in Britain were shown by Gibb (1954:516–518) to feed at greater intensity in colder weather. Under such conditions, with increasing concentration on the procurement of food, each individual's awareness of its surroundings would decrease and the value of "warning" calls (as expressions of fear) would increase.

Membership in a stable social group confers obvious advantages on an immature individual. One of these is restriction to a circumscribed range, with the opportunity of learning thoroughly the escape facilities within the area. Eberhard Curio has pointed out that the "traditions" of avoidance by experienced birds of those sites where predators have been seen previously may also be effective here. The establishment of a relatively high social rank may lead to precedence in the presence of food in times of scarcity, and to a mate, a territory within the flock range, and an opportunity to advance to higher rank within the group. Four females known to have lost their mates or to have been first-winter birds paired with flock mates (F1 and F13 in 1955, F4 and F13 in 1956). Others pairing with flock mates were F22, F33 (with M3 prior to his disappearance), F32, and F34. (There is no proof that any of the last four did not join the flock as a pair.) Examples of acquisition of breeding territory by the beta male, and of succession to alpha rank have been given earlier. Thus, the flocking habit appears advantageous to all individuals, whether or not they have "property rights."

Interspecific Comparisons.—A common thread in the social organization of those species of *Parus* the winter flocking of which has been investigated is the subsequent nesting of the dominant birds within the flock range. This tendency has been reported in *Parus atricapillus* by Odum (1942:522), and Hamerstrom (1942:35) noted the corollary, that old residents dominated in winter flocks. The pattern in the Carolina Chickadee resembles that of the Blue Tit (*P. caeruleus*), as reported by Colquhoun (1942:236), in that the dominant individuals traveled beyond the confines of their breeding territories. In contrast, Morley (1953:236) reported that the permanently mated pair of Marsh Tits (*P. palustris*) would accompany the flock only when within the confines of its territory, and boundaries of pair territories were defended only against other territory holders. An even more rigid system exists in the coastal Californian populations of the Plain Titmouse (*P. inornatus*), in which all individuals are excluded from pair-held territories in the nonbreeding period (Dixon, 1956). It would seem that immature individuals would be integrated into the social systems in the Blue Tit and Carolina Chickadee more readily than in the permanently territorial systems of the other two species mentioned.

UNDERLYING BASIS FOR THE SOCIAL SYSTEM

The pattern of utilization of space on a year-round basis appears to be territorial, that is, strongly space-oriented, an interpretation supported by several lines of evidence. The first indication is the relative permanence of the boundaries from 1 year to the next, as evidenced by defense and avoidance of trespass. A second point is the correspondence of the flock-range limits to the boundaries of the breeding territories of the alpha males of those flocks. An instructive example was provided by M3, whose breeding territory in 1955 was enlarged along its western margin at the expense of a first-year male M11 (Fig. 1 and 4). This area clearly had been avoided in the preceding winter by M4 (in whose flock M3 had traveled). In the winter of 1955–56, M3 invaded that portion of M11's flock range corresponding to the breeding territory of M3 in the previous spring. A subordinate member of M3's flock in 1955–56 (M23) appropriated a part of that same area for his breeding territory in 1956 (Fig. 5), and M3 occupied it again in December 1956 and January 1957 after the disappearance of M11. M23 utilized that same segment of the northwest quadrant in the following winter, and in the breeding season of 1958 (Fig. 5–7). The flock ranges clearly reflect the configuration of the breeding territories, and the domiciles of the alpha males are in effect their winter territories.

Defense of Flock Ranges.—One may question whether the enlarged "winter" territories of the dominant males may not be group territories. Although all recognized members of each group confined their activities to these territories, thus meeting the criterion of avoidance of trespass, the ranges were not comparable to the group territories of several species of cuckoos (Crotophaginae) studied by Davis (1942:121), in that the areas were not defended by the group as such. In only 2 of 10 encounters in which the identity of the participants was known did a subordinate member of the flock join in the fray. One of these incidents involved M32 in his second winter as the beta male of the flock, in an exchange with a rival of the previous breeding season. Thus, defense of flock-range boundaries does not appear to be a group response.

Categories of Social Dominance.—A question concerning the social system in the Carolina Chickadee that deserves attention is the suggestion by Marler (1955:115) that the hierarchies in parids may be based upon "peck-dominance" (Masure and Allee, 1934:334), rather than "peck-right," i.e.

the outcome of an encounter between two individuals might differ according to the location with respect to the territorial strongholds of the participants. Such an effect was reported in the Great Tit by Brian (1949:148), and the Blue Tit by Colquhoun (1942:239), with the rank of an individual varying inversely with the distance from its territory. Although I made observations at only one feeding station in a given flock range, I detected no reversal of interindividual relationship and no other evidence that suggested that the same ranking did not obtain throughout the range of the flock. Therefore, I conclude that each flock range had a fixed hierarchy of unilateral or peck-right type, and that restriction to their respective flock ranges would preclude the development of a situation such as that provoked by Brian (1949) in which social rank was found to be inverse to distance from center of subsequent breeding territory.

The Influence of Prior Occupancy.—In each of the units of spatial organization (the enlarged territories of the alpha male), the alpha male was the male of longest residency, and the older subordinate males (M3 in 1954–55, M32 in 1957–58) were of longer tenure than some other members of their flocks. These observations, plus the sequence of replacement, suggest the influence of seniority, as found in domestic chickens by Guhl and Allee (1944:338). These authors found that in flocks in which membership was rotated the hen of longest residence usually was the alpha individual. Sabine (1959:131) found a general correlation between prior occupancy and higher social position following merging of two flocks of Oregon Juncos (*Junco oreganus*). The operation of a "prior-residence" effect in fishes was demonstrated by Braddock (1949). He found that individuals placed in a strange aquarium exhibited a tendency to explore their new surroundings, and this "distraction" could confer an advantage for the resident in an initial encounter. Guhl (1962:97) likewise concluded that the newcomer is at a disadvantage in competitive situations. The prior-residence effect, even among first-year birds, may influence the formation of a hierarchy without reference to territorial hostility (defense of area per se).

Flock Disintegration.—The shift from flocks to dispersed pairs at the onset of the breeding season usually is a gradual one, with intermittent scattering as couples followed by regrouping. In 1955 the flocks persisted as late as 23 February, whereas in 1957 the chickadees were flocked on 31 January and dispersed as bickering pairs on 4 February. Genelly (1955:269) reported similarly rapid dispersal of a flock of California Quail (*Lophortyx californica*) that he attributed to the intrusion of unmated males. I found no evidence of disruption from such a source in the chickadees.

The factors underlying this shift are not well understood. Singing does not increase in frequency prior to flock dispersal. Conceivably, singing by the beta male could be suppressed by the presence of the dominant male, in the manner suggested by Hinde's (1959:118) observation of captive males of the Chaffinch (*Fringilla coelebs*) in adjacent cages. Here, the subordinate male sang only after being screened from the view of the dominant. As subordinate chickadee males and their mates spend increasing amounts of time within the flock range but separate from flock mates, they might become conditioned to a particular part of the area from which the alpha male can be excluded by appropriate displays, especially song. A similar segregation of alpha and beta individuals at opposite "poles" of an aquarium was noted in green sunfish (*Lepomis cyanellus*) by Greenberg (1947:287).

Another factor involved in the subdivision of the flock range is the extent of area that the alpha male can patrol effectively while retaining the "attention" of his mate. Response to the challenges of many now-scattered and displaying males conceivably dictates a decrease in the size of the area over which control is exercised, and the preferences of the female doubtless play a role here as well. Thus, the range of a pair diminishes from 10–12 acres to 4–6, over which the pair travels in a leisurely fashion, presently hole prospecting, with occasional flurries of territorial behavior, often involving females as well, in response to the challenges of neighbors and wandering birds.

The alpha male may be considered as yielding little to his subordinate in the subdivision of the flock range. The beta male temporarily acquires an ability to exclude the dominant from a part of that range, presumably under conditions of hormonal reinforcement. In a rejoining of the free-ranging flock in summer, there probably is little subjugation since beta males, such as M32, avoid contact with the alpha male of the flock. The failure of M4 and M23 to regain the full flock range from M5 and M34, respectively, in 1954–55 and 1957–58 is of interest. In the latter instance, the two males were thought to be evenly matched in the hierarchy, but the former subordinate exhibited pronounced "territorial" responses, quarreling repeatedly with his neighbors, M23 and M27, in December and January. M23 and M34 engaged in boundary disputes in which singing was heard on 29 and 30 November and on 13, 16, and 26 December 1957, whereas no singing was noted in 8 hours afield within the same span of dates in 1955, and none in 6½ hours in 1956.

Social Stability and the Survival of Individuals.—A notable feature of the social system described here is stability of utilization of the space, and of succession of the social units on that space. The survival of established individuals is a prominent factor in promotion of such stability. In 10 of 13 instances (involving seven individuals) the breeding males that had previously held alpha rank remained to be the dominant birds of the subsequent autumn's flock, and 6 of 6 beta males persisted on the area. Thus, in 16 of 19 instances, established males remained to shape the patterns of utilization of the area. Since in an earlier discussion breeding-territory relations were considered to be the most effective in determination of boundaries, it may be noted further that in 13 of 19 instances (excluding M17 in 1955) breeding males survived from 1 March of 1 year to the comparable date of the next. In terms of survival of individuals beyond their first 1 March on the area, 11 breeding males lived an average of 19.6 additional months on the area, and 11 breeding females, 12.9 months. Correspondingly, the "longest-lived" male (M17) was present for 39 months after his first 1 March, whereas the longest tenure of a female was 26 months (F1, F22). Four of the males (including M17) and one of the females were known to be alive at the close of the study. These values are strikingly similar to those cited for the Marsh Tit by Southern and Morley (1950), but their work dates from initial marking rather than a specified calendar date. As was suggested earlier, the shorter tenure of females may not reflect a shorter life span as much as a tendency of some to shift their domiciles. Thus, the established individuals or those subordinates experienced on the area tend to perpetuate prior patterns of utilization.

The formalization associated with either territorial relations between individuals acquainted with one another (see Dixon, 1956:176, for comments on a related species), or those gestures and avoidances serving as substitutes for fighting among flock members, results in a minimization of strife in both forms of social organization interwoven in the annual cycle of the Carolina Chickadee. The prevalent spatial orientation and the resulting stability may confer survival advantage to the dominant birds, as it was judged to do for established adults of the Plain Titmouse.

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SUMMARY

The history of occupancy of a 40-acre tract of deciduous oak woodland in eastern Texas by 40 color-banded individuals of *Parus carolinensis* was studied over a 5-year period. Adults typically restricted their activities to areas 10–15 acres in extent and remained permanently paired. After the nesting season such adults usually permitted other chickadees to join them as subordinates in a winter flock that ranged over an area larger than the breeding territory. Thus, within the annual cycle dispersion as breeding pairs alternated with aggregation as nonbreeding flocks that occupied the domicile of the male of longest tenure.

Each of seven flocks studied was ordered in an essentially linear hierarchy of 3–6 individuals, the senior male being dominant. The mate of the alpha

male took precedence over other females at a restricted food source, but, in the absence of her mate, she sometimes deferred to the beta male.

Surviving males of dominant pairs invariably utilized a portion of the flock range for their breeding territory. The flock range was shared in the breeding season by the highest-ranked males in 6 instances, and 2 males returned to subordinate status under their previous masters for a second year. High social rank led to *initial* acquisition of breeding territory by 4 first-year males, and, in general, distance traveled by first-year birds before they settled for nesting appeared inverse to rank in winter flocks.

The boundaries of the flock ranges were relatively constant from one winter to the next, thus reflecting the breeding-season territoriality of dominant males. Defense of such boundaries seldom involved subordinate individuals. Stability in patterns of utilization of space was enhanced by survival of breeding males, which on an average were present through two breeding seasons.

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Properties of Bird Song Eliciting Responses from Territorial Males

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How does a bird recognize songs of its own species? More precisely, what properties of a song are most important in species recognition? This paper reports an attempt to study this question by experimenting with birds in the field using tape recordings. To limit the problem, observation was confined to the reactions of territorial males to experimentally modified advertising songs of their own species. Ovenbirds (*Seiurus aurocapillus*) and White-throated Sparrows (*Zonotrichia albicollis*) were used. Experiments were carried out in Algonquin Park, Ontario, from 1957 to 1962.

The problem and the means of attacking it were suggested by experience in the use of tape-recorded sounds to study territorial behavior. Weeden and Falls (1959) reported that, when tape-recorded songs of Ovenbirds were played through a speaker located in an Ovenbird's territory, the territory holder reacted in much the same way as in a natural encounter with another male. Movements, a tendency for the bird to approach the speaker, songs, and call notes were noted, and variation in the strength of reactions to different songs was demonstrated by a variety of quantitative and qualitative criteria. Since significant differences were found between reactions to songs of neighboring and strange Ovenbirds, the technique used was reasonably sensitive. Moreover, I have found that Ovenbirds and a variety of fringillids including the White-throated Sparrow, which respond readily to songs of their own species, apparently ignore songs of other species recorded in the same area. Thus, the technique developed in this earlier work provided the basis for the method used in the present study.

EXPERIMENTAL PROCEDURE

At the beginning of each series of experiments, several territorial males were selected that were separated from each other by at least one other territory and were mostly a quarter mile or more apart. Each bird was played a normal song of a nonadjacent individual of the same species. The speaker was placed a few feet above ground in a tree and was 50–75 ft from the observer. If the bird reacted strongly and approached the speaker, all subsequent test songs were played from the same location. If not, a new position or a new bird was tried. Before each experiment, the observer noted the positions and songs of the bird to be tested for 5 minutes. The test song was then played at 15-second intervals (a normal interval for both species), and detailed notes were made of the bird's positions and vocalizations. In 1957, the song was played for two 3-minute periods 3 minutes apart. The playing was stopped at any time after four songs were played if

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the bird approached within 20 ft of the speaker. This was intended to minimize the bird's exposure to the test song but may have given rise to some variation in the results. In all other years, including all the experiments with White-throated Sparrows, the playing period was 5 minutes long. A further 5-minute period of observation followed. After the initial experiment with a normal song, each bird was tested with a series of altered songs. The order in which these songs were presented and the order in which each bird was tested during the day were random. A bird was tested no oftener than every other day, and there was often an interval of several days between experiments. The series always ended with the song of another species and a second normal song to ensure that birds had not become conditioned to react to something other than an appropriate song but would still react to a normal song. In a few cases, birds failed to react to the final normal song. In such cases, only data up to and including the last strong response were used. If this occurred early in the series, data for that bird were discarded. In order to obtain the best possible responses, experiments were confined to the morning and were mostly carried out in June and early July.

The following equipment was used. Songs were recorded with an Electrovoice 635 microphone mounted in a 40-inch parabolic reflector. A Magnecorder PT6AH was used at a tape speed of 15 inches per second. Some sounds were produced by an audio-oscillator. Audio-spectrographs (sonagrams) of sounds were made by means of a Kay Electric Sona-Graph using "high-shape" and "narrow-band" settings. Reproduction in the field was by means of the Magnecorder, an Ampex 600, a Nagra IIIb, or a portable playback machine incorporating an Autovox message repeater. All of these machines operated at 15 i.p.s. Atlas HR-2 metal horns were used unmounted.

CRITERIA OF RESPONSE

Attempts were made to express quantitatively the most obvious features of the bird's response. If a normal song is played, a territorial male usually gives a call note or song and flies toward the speaker. Each time the test song is repeated, the bird calls or sings and may change location until quite close to the speaker. When no visible model is used, as in the present experiments, the bird does not usually approach steadily but moves back and forth, often passing the speaker several times. After the playing period is over, the bird may remain near the speaker and sing frequently for some time. However, the response is variable. Some birds respond more by song, others more by calls. Some sing immediately, others not until after the playing period. Some approach the speaker immediately, others do not. Some birds perform displays but these cannot always be observed. Hence, no single criterion of response is adequate. The following have been used in this paper:

Increase in Song.—In the case of the Ovenbird, the number of songs given in the 5 minutes before the experiment was subtracted from those given in the 5 minutes following the playing period as an indication of the strength of the response. In the case of the White-throated Sparrow, the same system was tried, but since it was found that greater differences were obtained by subtracting songs before the experiment from the average of those given during and after the playing period, the latter procedure was adopted.

Time of First Sound.—This is expressed as the 15-second interval following the first test song in which the bird first gives either a song or a call. If a bird responds immediately after the first test song, a zero is assigned, if after the second song, a one, and so on. In order to combine data for different years for the Ovenbird, only the first 3 minutes of playing were considered and a maximum value of 13 was assigned if there was no response. In the case of the White-throated Sparrow, the maximum value was 20, based on a 5-minute playing period.

Number Vocalizing.—This refers to the number of the total birds tested that gave a song or call during the playing period.

Number Moving.—This refers to the number of the total birds tested that moved at least 10 ft during the playing period.

Number Approaching.—This refers to the number of the total birds tested that approached to within 20 ft of the speaker during the playing period.

The last three criteria are meaningful only when taken together with the total number of birds tested.

ANALYSIS OF DATA

Statistical tests were carried out to determine whether the birds responded to each test song and whether the response could be distinguished from the response to a normal song. Since the standards used in these tests were the results obtained with normal songs and with songs of other species, comparisons were made between years for each of these song types, using t or χ^2 tests. The only significant difference found was between the number of White-throated Sparrows approaching the speaker in response to a normal song in 1960 and in other years. Since these data did not affect either the ranking of the test songs or the significance of the results shown, they were included with the rest. In the case of the White-throated Sparrow, results obtained with artificial songs resembling the normal song were indistinguishable from those obtained with normal songs. Hence, the two were combined to provide the normal standard. In view of the results of these tests, all of the data for all years were combined for each species. Details of the analysis follow.

To determine whether birds responded to a test song, the results obtained using that song were compared with the results using the song of another species. In the case of increase in song and time of the first sound, comparisons were made by pairing the data for each bird and applying a t test to the differences. In those cases where the number of birds responding out of the total tested was considered, the comparison was made between the combined results for all years. These data were arranged in 2×2 tables and tested for significance by χ^2, using Yates' correction for small numbers as required. In all cases, a probability of 0.05 or less that the difference observed between the results obtained with a test song and with the song of another species occurred by chance was taken to indicate a positive response to the test song in question.

To determine whether the response to a test song was as strong as that to a normal song, the two sets of results were compared as outlined above. These comparisons were made using the average of the results obtained with normal songs before and after each test series as the standard. In this way, any change in the strength of responses occurring during the season could be eliminated. Actually, only in 1962 was a significant difference found between the results of these initial and final experiments with normal songs.

TEST SONGS USED

A tape recording of a typical advertising song of an Ovenbird was chosen and altered in various ways. This normal song (Fig. 1*A* and test song 1 in Table 1) is an example of the so-called *teacher* song, and consists of a series of similar phrases, each of three sounds, designated *A*, *B*, and *C* in the figure. The song begins quietly and increases rapidly in volume. These features are typical of most songs examined from the area, although minor differences between songs of different individuals can be detected by ear and seen in sonagrams.

TABLE 1.—REACTIONS OF OVENBIRDS TO TEST SONGS[a]

(1) Type of Test Song	(2) Increase in Song	(3) Time of First Sound	(4) Number Approaching	(5) Number of Birds	(6) Score (* plus †)
1. Normal *ABC*	8.5*†	3.1*†	30*†	35 (21)[b]	6
2. Decreasing loudness	14.0*†	2.7*†	5*†	6	6
3. *BC* only	13.7 †	1.0*†	5*†	6	5
4. Random spacing	4.3*†	3.5*†	8*	15	5
5. *ACB*	7.6*†	5.0	11*†	14	4
6. Backward	3.7	2.5*†	3*†	6	4
7. Even spacing	5.5*†	6.5	8*	15	3
8. Kentucky Warbler	2.9 †	4.9 †	3	7	2
9. Half speed	2.9 †	8.1 †	0	7	2
10. Double speed	0.9	6.5	1	8	0
11. *A* only	0.3	11.0	2	6	0
12. Other species	–0.01	8.2	1	21	0

[a] These reactions are explained in the text under Criteria of Response.

* Reaction differed significantly from reaction to other species (song 12).

† Reaction did not differ significantly from reaction to normal song (song 1).

[b] Twenty-one different birds were used in 35 tests. In the case of other songs, each bird was tested only once.

Test songs 6, 9, and 10 in Table 1 consisted of playing the normal song backward, at half normal speed and at double normal speed, respectively. Playing a song faster or slower than normal alters both its length and pitch. Other test songs were constructed by cutting the tape squarely across at carefully chosen points and splicing the pieces together differently. In song 2 the phrases were normal but were put together in reverse order so that the song became quieter instead of louder. In song 3 (Fig. 1*C*) only the *B* and *C* sounds in each phrase were retained, and in song 11 (Fig. 1*B*) only the *A* sounds were retained. In song 5 (Fig. 1*E*) the sounds in each phrase were in the order *ACB*. In songs 4 and 7 the sounds were in the normal sequence but separated by blanks; in song 7 (Fig. 1*F*) the blanks were all 0.1 second long, while in song 4 (Fig. 1*D*) they varied from zero to 0.2 second in length and were arranged randomly. Song 8 (Fig. 1*G*) was of a Kentucky Warbler (*Oporornis formosus*), a species that does not occur in the area.

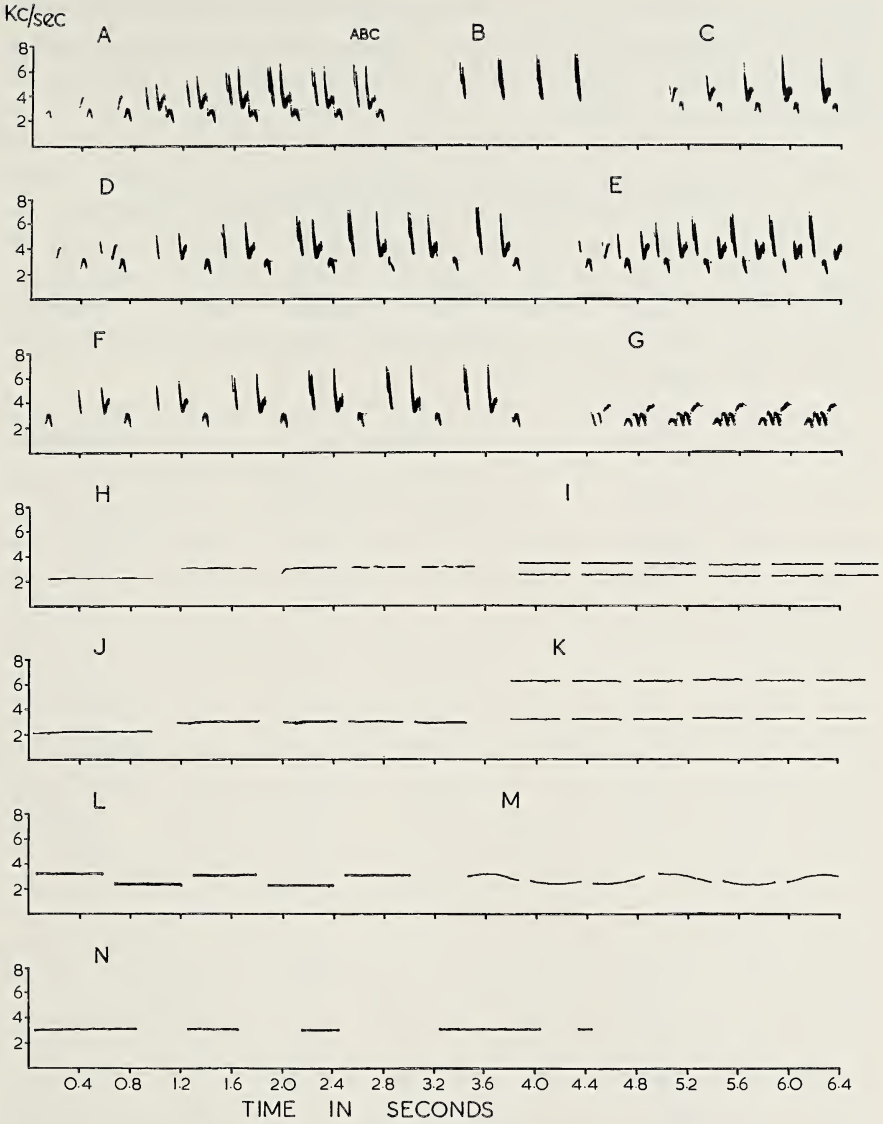

Fig. 1. Sonagrams of representative test songs.

Those played to Ovenbirds (only a part of each is shown):

A—Normal
B—Part *A* only
C—Parts *BC* only
D—Random spacing
E—Parts in order *ACB*
F—Even spacing
G—Kentucky Warbler

Those played to White-throated Sparrows:

H—Normal
I—Unrelated tones
J—Artificial normal
K—Harmonic tones
L—Alternating pitch
M—Varying pitch
N—Random timing

Songs of other species (song 12) were chosen from the following—Savannah Sparrow (*Passerculus sandwichensis*), Vesper Sparrow (*Pooecetes gramineus*), and Hermit Thrush (*Hylocichla guttata*). None of these songs is repetitive like the Ovenbird's.

By comparison with the Ovenbird's song, the song of the White-throated Sparrow (Fig. 1*H*) is comparatively simple, consisting of a series of clear whistled notes. The one chosen represents the commonest pattern in the area, although several others occur. In common with nearly all songs of this species, some of the notes (the second and the last two) are really triplets, and this can be readily detected by ear. There was a difference in loudness of about six decibels between the first and second notes, which were the quietest and loudest, respectively.

An imitation of this song was recorded from an audio-oscillator. This "artificial normal" song (Fig. 1*J*) resembled the normal song in loudness, timing, and pitch but lacked the triplets. All the other test songs were made in the same way but differed in various respects from this imitation of the normal song. Details of all the test songs played to White-throated Sparrows are given in Table 2. Some of these songs are illustrated in Fig. 1, and columns (5) and (7) in Table 2 refer to the figures most closely resembling the pattern of each test song. For purposes of description, these test songs can be divided into four groups (column 1). Songs in the top group have the same pattern with respect to pitch as the normal song, i.e. a low note followed by a series of notes of a higher pitch. Since the required sounds were generated for each song, the higher- and lower-pitched songs were not speeded up or slowed down as in the case of Ovenbirds' songs. The normal pattern of loudness was retained in all but the last song in this group. The latter and all other test songs had notes at a constant level. In the second and third groups, all the notes were pitched at 3,300 cycles per second. In songs of the second group, the notes or intervals varied in length, while in songs of the third group both notes and intervals were constant in any one song but notes varied in length and number between the different songs. Songs in the final group differed in various ways from the normal song in pitch. All songs in this latter group are illustrated in Fig. 1. As far as possible, test songs were of about the same length. Songs of the following other species were used—House Wren (*Troglodytes aedon*), Hermit Thrush, Ovenbird, Mourning Warbler (*Oporornis philadelphia*), and Song Sparrow (*Melospiza melodia*). These species have more complex songs than the White-throated Sparrow.

REACTIONS OF OVENBIRDS

Reactions of Ovenbirds to the various test songs played to them are summarized in Table 1. Test songs are ranked (column 1) with those to which birds reacted most strongly at the top. Each test song was given a score (column 6) based on the responses it received. The number of criteria (columns 2, 3, and 4) in which the responses were positive (indicated by asterisks) were added to the number in which the responses were normal (†). Hence, a perfect score was 6. On the basis of these scores, the test songs were divided into three groups (column 6). The first group includes those songs (1, 2, and 3) to which birds reacted as strongly as to a normal song. The second group (songs 4–7) elicited reactions differing significantly from the reactions to normal songs or to songs of other species, i.e. birds responded to these songs but the responses were weak. In the third group belong the rest of the test songs (8–12) to which responses, if they occurred at all, were so weak or infrequent that the results did not differ significantly from those obtained with songs of other species. Songs 8 and 9 in this group could not be distinguished from normal songs with respect to increase in

TABLE 2.—TEST SONGS PLAYED TO WHITE-THROATED SPARROWS

(1) Type of Test Song	(2) Number of Notes	(3) Length of Notes (sec)	(4) Length of Intervals (sec)	(5) Pattern in Time (Fig. 1)[a]	(6) Pitch of Notes (c.p.s.)	(7) Pattern of Pitch (Fig. 1)[a]	(8) Length of Song (sec)
Normal	5	0.4–0.9	0.1–0.2	H	2,450–3,300	H	3.3
Artificial normal	5	0.4–0.9	0.1–0.2	J	3,300	J	3.3
One octave high	5	0.4–0.9	0.1–0.2	J	4,900–6,600	J	3.3
Two octaves high	5	0.4–0.9	0.1–0.2	J	9,800–13,200	J	3.3
One octave low	5	0.4–0.9	0.1–0.2	J	1,225–1,650	J	3.3
Normal pitch change	5	0.5	0.1	L	2,450–3,300	J	2.9
Normal note length	5	0.4–0.9	0.1	J	3,300	N	3.1
Random timing	5	0.1–0.8	0.3–0.8	N	3,300	N	4.4
Widely spaced	6	0.4	0.4	L	3,300	N	4.4
One long note	1	2.5+	–	–	3,300	N	2.5+
Three notes	3	0.8	0.1	L	3,300	N	2.6
Six notes	6	0.4	0.1	L	3,300	N	2.9
Fifteen short notes	15	0.1	0.1	L	3,300	N	2.9
Alternating pitch	5	0.5	0.1	L	2,450–3,300	M	2.9
Harmonic tones	6	0.4	0.1	K	3,300 & 6,600	K	2.9
Unrelated tones	6	0.4	0.1	I	2,450 & 3,300	I	2.9
Varying pitch	3 or 6	0.4	0.1	M	2,450–3,300	M	1.4 or 2.9

[a] Letter refers to sonagram in Fig. 1 most closely resembling the pattern of each test song.

song and time of the first sound, since in a few cases birds appeared to respond to them. Larger sample sizes might have shifted these songs into the second group.

These results can best be discussed with reference to the properties of a normal song. As pointed out above, an Ovenbird's song consists of several similar phrases delivered at regular intervals (in a rhythmic fashion) with the phrases becoming louder as the song progresses. The strong reactions obtained with song 2 (decreasing loudness) indicate that the crescendo is not essential to elicit these responses. No attempt was made to vary the number of phrases or to introduce a variety of phrases. However, interfering with the rhythm (song 4, Fig. 1*D*) or retaining the rhythmic character of the song but lengthening the intervals between sounds (song 7, Fig. 1*F*) considerably reduced the response. Reactions were stronger to song 4 than to song 7, which may be due to the fact that some of the intervals in song 4 were of the normal length, i.e. this song included bits that were normal. These results suggest that timing is important. This may help to account for the negative results obtained with songs 9 and 10, which were altered in speed as well as in the pitch of the sounds. Unfortunately, pitch cannot be considered separately since it cannot be altered without at the same time changing the length of the sounds. The fact, already referred to, that a few birds reacted to the song of a Kentucky Warbler (song 8, Fig. 1*G*) also suggests the importance of timing, since it is in this respect that the song resembles an Ovenbird's song.

However, timing is not the only essential property of the Ovenbird's song in view of the results obtained with songs 5 and 6, which were normal in this respect. Details of the phrases may also be important. Each phrase normally consists of several different sounds (three in the song used here), each sound having a definite form and the sounds occurring in a definite order. Song 3 (Fig. 1*C*), from which the first or *A* sound in each phrase was deleted, received normal responses, while song 11 (Fig. 1*B*), in which only the *A* sounds were present, produced negative results. This suggests that the *A* sound is unessential. Song 5 (Fig. 1*E*), in which the order of the sounds was altered, and song 6 (backward), in which both the order and form of the sounds were altered, received weak responses. An attempt was made to produce an imitation of an Ovenbird's song using an audio-oscillator. This song was normal in timing and each phrase consisted of three different sounds of about the normal pitch but the quality did not closely resemble that of an Ovenbird's song. Although the procedure was not exactly the same as in the experiments reported here, when this song was played to several Ovenbirds, it did not elicit any responses. Apparently some essential features of the individual sounds were lacking.

To summarize, it would appear that, to elicit the type of reaction studied here, an Ovenbird's song must consist of a rather precisely timed series of phrases, each phrase consisting of at least two sounds having a definite form and occurring in a definite order. Since it would be difficult to go further with a song as complex as the Ovenbird's, more detailed studies were carried out with the simpler song of the White-throated Sparrow.

REACTIONS OF WHITE-THROATED SPARROWS

The reactions of this species to a series of test songs are presented in Table 3, the data being arranged essentially as in Table 1. However, two more criteria of response have been included so that a perfect score for a song in this table is 10. Since more songs and considerably larger samples of birds were used in the case of the White-throated Sparrow, the test songs were divided into five groups according to the way in which birds responded to them (column 8). The first three songs received scores of 6–10, indicating that reactions to them were normal in at least some respects. The next three songs (4, 5, and 6) had a score of 5 since they received positive responses in all respects, but these responses were weaker than normal. The next group (songs 7–10) received positive responses in 2–4 out of the 5 categories, i.e. responses to these songs were incomplete. The next group (songs 11–14)

TABLE 3.—REACTIONS OF WHITE-THROATED SPARROWS TO TEST SONGS[a]

(1) Type of Test Song	(2) Increase in Song	(3) Time of First Sound	(4) Number Vocalizing	(5) Number within 20 ft	(6) Number Moving	(7) Number of Birds	(8) Score (Total * & †)
1. Normal	11.7*†	2.9*†	159*†	135*†	156*†	159 (79)[b]	10
2. Normal pitch change	11.7*	2.9*†	19*	20*†	20*†	21	8
3. Normal note length	9.0*	4.4*†	18*	12*	16*	21	6
4. Three or six notes	6.7*	6.2*	27*	12*	18*	32	5
5. One octave high	4.6*	7.4*	26*	10*	18*	33	5
6. One long note	3.1*	6.5*	23*	8*	18*	29	5
7. Widely spaced	4.3*	8.6	15*	13*	14*	21	4
8. Alternating pitch	1.6	6.8*	27*	12*	18*	34	4
9. Harmonic tones	5.0*	9.2	15	10*	9*	24	3
10. Random timing	1.6	8.4	21*	5	11*	31	2
11. Unrelated tones	2.6	9.1	14	4	6*	23	1
12. Fifteen short notes	2.1	10.4	21	6	13*	33	1
13. Varying pitch	1.3	11.1	21	6	13*	33	1
14. One octave low	0.8	9.3	15	2	7*	32	1
15. Two octaves high	1.5	16.2	9	2	2	32	0
16. Other species	0.02	13.0	31	3	4	69	0

[a] These reactions are explained in the text under Criteria of Response.

* Reaction differed significantly from that to other species (test song 16).

† Reaction did not differ significantly from that to normal song (test song 1).

[b] Seventy-nine different birds were used in 159 tests. In the case of other songs, each bird was tested only once.

received positive responses only in respect to movement. Apparently this indicates a very weak response. Vocalization and close approach occur only in stronger responses. Finally, songs 15 and 16 gave negative results.

Again the results can be considered in the light of the properties of a normal song. Some details of the normal song were obtained from D. J. Borror and W. W. H. Gunn (pers. comm.), who recently analyzed several hundred songs of this species.

The normal song is a sequence of several notes of two or more types. As seen in Fig. 1*H*, the normal song used here included a continuous pure tone, triplets (these two types are invariably present), and a note beginning with an upward slur. Since the artificial "normal" song (Fig. 1*J*), which was made up of continuous tones only, elicited normal responses, it can be concluded that other types of sounds are unessential. Since song 11 (Fig. 1*I*) with complex notes and song 13 (Fig. 1*M*) with notes varying in pitch received scores of only 1, while song 4, made up of unvarying pure tones, had a score of 5, it appears that unvarying pure tones are a necessary feature of the song. Even the addition of a strong first harmonic in song 9 (Fig. 1*K*) considerably reduced the response.

The pitch of notes in a normal song falls between 1,500 and 6,600 c.p.s. Song 5, reaching the upper limit of this range, received slightly subnormal responses, while song 14, which was partly below this range, and song 15, which was considerably above it, are at the bottom of the list. Apparently the normal range of pitch is quite critical, i.e. to be effective a song must lie wholly within this range. In the normal song, notes of two or more pitches are invariably present. The pattern in this respect is variable. Some songs descend in pitch, others ascend (Fig. 1*H*), and in some cases the trend may change direction once or twice. The fact that song 2, with a normal change in pitch, received nearly normal responses, while song 4, with notes all at one pitch but similar in other respects, had a lower score suggests that notes of different pitch are important. Further evidence of the importance of the pattern with respect to change in pitch is that song 8 (Fig. 1*L*), with an abnormal pattern in which the trend changed three times, had a score of 4 although the notes were similar to those of song 2.

Notes in a normal song may vary noticeably in loudness. However, all the notes in song 2, which received strong responses, were of the same loudness. Apparently, this is not an important feature.

The length of notes in normal songs varies from less than 0.1 second to more than a second, and notes in the same song are usually of different lengths (Fig. 1*H*). Intervals between the notes are less variable and are usually 0.1–0.2 second in length. Several of the test songs were designed to study the importance of timing. Since song 3, in which the notes were of the same lengths as in the normal song, had a slightly higher score than song 4, in which notes were of equal length, it may be that the normal variation is of some significance. This might account for the slight difference in score between song 2, with notes of equal length, and the normal song. Songs 6, 4, and 12 represent a series with notes longer than normal, normal, and shorter than normal, in that order. Of these, song 4 received the strongest responses; song 6, slightly weaker responses; and song 12, very little response. Very short notes are apparently ineffective, but beyond a certain length further increase in length makes little difference. This is emphasized by the fact that song 6 was varied from 2.5 to about 15 seconds in length without apparently altering the response. Some natural songs begin with a series of short notes not unlike those used in song 12. However, these songs always include longer notes as well. The notes in song 7 were like those in song 4; but the intervals between them were greatly increased, and this resulted in a decreased response. That long gaps reduce the effectiveness of the song is also indicated by the lower score of song 10 (Fig. 1*N*), in which lengths of both notes and intervals were varied randomly. At the opposite extreme, song 6, with no intervals at all, received slightly weaker responses than song 4 with normal intervals, as already noted. It would appear that, whereas notes must be of a certain minimum length, intervals must not exceed a certain maximum. However, the critical lengths have not been determined. Normal songs vary considerably in length from about 1.5 seconds to perhaps 10 seconds. The longer songs usually end with a long series of triplets, and an individual may vary the number of triplets between songs. Again, the results obtained with songs 4 and 6 suggest that song length, total sound energy, or number of notes are not critical.

In summary, to be effective, a White-throated Sparrow's song must consist of unvarying pure tones within a certain range of pitch. Less important is the presence of notes of different pitch arranged in a certain pattern. The notes should be of a certain minimum length, and the intervals between notes should not exceed a certain maximum.

GENERAL DISCUSSION

In the songs of both species studied, the pitch, form, and arrangement of the component sounds and the length of sounds and intervals between them were shown to be important in eliciting normal responses from territorial males. It appeared that timing was the most important feature of the Ovenbird's song, whereas form and pitch of the notes were more important in the song of the White-throated Sparrow. Thus, several of the most obvious properties of these songs seem to contribute to species recognition. However, a certain amount of variation in pitch, arrangement, and timing was possible without noticeably weakening the response. For some properties the permissible limits of variation corresponded closely with the known range of natural variation, for example, in the case of pitch in the song of the White-throated Sparrow. Some features of the normal song did not seem to be important. Certain sounds could be omitted from test songs, and the characteristic variations in loudness in normal songs could be eliminated without weakening the response. Moreover, some apparently unnecessary features, such as the crescendo of the Ovenbird or the triplets of the White-throated Sparrow, seem invariably to be present in normal songs. What can be the function of these apparently superfluous characteristics?

The present study dealt only with the reactions of territorial males to song, and properties of songs that appear to be unimportant in this context may be significant under other circumstances. For example, they might facilitate species recognition by females. Variation in those properties of song important in species recognition, as well as details not essential for this purpose, may play an important role in permitting individual recognition. Individuals of both species studied here have only one song (occasionally two in the White-throated Sparrow) that remains constant from year to year. Hence, individual recognition must be based on the variations and details of song discussed above. Weeden and Falls (1959) showed that territorial male Ovenbirds can distinguish the songs of neighbors from those of strange intruders. Marler (1960) has pointed out the importance of individual recognition for mates as well as territorial rivals. Finally, it is suggested that some constant characteristics of song, which are unnecessary for species recognition in one area, may serve this function in another part of the range. This does not deny the geographic adaptation of song discussed by Marler, but what I suggested might occur in species whose ranges are not interrupted by ecological barriers, as is the case with both the species studied here in eastern North America. It is tempting to speculate that, where the two species overlap in range, the triplets of the White-throated Sparrow may help to distinguish it from Harris's Sparrow (*Zonotrichia querula*), which has an otherwise rather similar song, or that the crescendo of the Ovenbird is useful in southeastern North America where several other species with repetitive songs occur.

This study was supported by grants from the National Research Council of Canada. I should like to thank Robert Walker and Bruce Thorneycroft, who helped with the field work, and Don F. Robinson, who helped with analysis of data.

SUMMARY

The relative importance of various features of advertising song for species recognition was studied by playing tape recordings of altered songs to territorial male Ovenbirds and White-throated Sparrows in the field. Tapes of an Ovenbird's song were variously modified, while artificial songs recorded from an audio-oscillator were used in experiments with White-throated Sparrows. Responses, measured in terms of vocalizations and movements of birds tested, were compared with responses to normal songs and songs of other species.

In both species, several features of the song were apparently important for species recognition. These included the pitch, form, and arrangement of

the component sounds and timing of the sounds and intervals between them. Permissible limits of variation in these important properties were shown in some cases to correspond with the known range of natural variation. Alternative functions are suggested for some features typically present in normal songs which were apparently unnecessary to elicit the responses studied here.

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A Description of Song Sparrow Song Based on Instrumental Analysis

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Previous descriptions of the song of the Song Sparrow (*Melospiza melodia*) have been based for the most part on audio-analysis in the field, using handwritten notes and a stop watch (Wheeler and Nichols, 1924; Nice, 1943; Saunders, 1951). The prominent features of the song were adequately recorded by this method, and a great deal of information of permanent value has been thus reported. Brand (1935) recorded the song and analyzed it by photographic means; he thus discovered the large number of very short notes and intervals that are present in this and other birds' songs, and that are undetected by the human ear. He also obtained precise frequency determinations (Brand, 1938).

There were several reasons for undertaking the present study. This is a common species whose singing is a very prominent feature of its behavior, and the song differs in an interesting way from that of other rather closely related species. It is very useful, therefore, for the sake of comparative, experimental, and developmental studies of this song to have an objective and quantified description based on analysis with modern instruments. These instruments liberate us from the limitations of the ear, and make precise qualitative and quantitative observation possible. The San Francisco Bay region has four different subspecies of the Song Sparrow available within a short distance; I have studied these races through five seasons during the years 1958–62. The taxonomic status and ecology of these races were described by Marshall (1948) and Johnston (1956), and I wished to know if any difference in song could be detected and correlated with the racial characters they had found. The present paper involves the singing of wild, mature birds.

METHODS

For the tape recordings in the field I used a Magnemite 610-E recorder at a tape speed of 15 inches/sec, with an Altec 633A microphone mounted on a 24-inch parabolic reflector. Playback in the laboratory was done with a Viking 85 recorder, and the analysis was accomplished by two methods. The first was by a Kay Electric Sonagraph machine, and the second was by an oscillograph. Both of these instruments produce a recording of time on the horizontal versus frequency on the vertical axes. In the latter method, a modified version of that described by Fish (1953) was used. It consists of feeding the filtered and amplified signal from the tape recorder into a frequency meter and thence to a voltage-sensitive pen-writing recorder, such as

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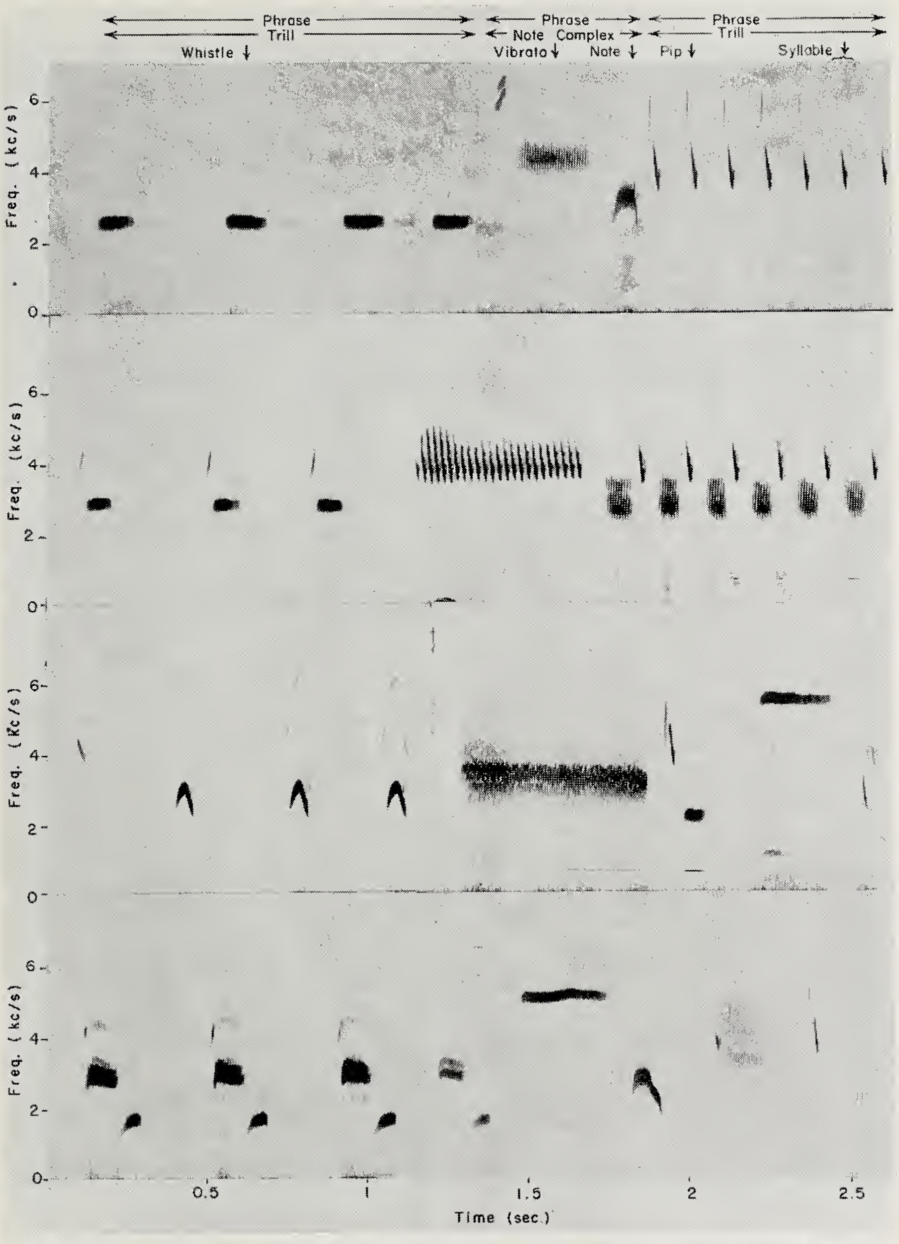

Fig. 1. Sound spectrograms of four Song Sparrow songs of one individual (R/L, St. Albert's College, Oakland) showing the variety of note types characteristic of different songs. The terms defined in the text are illustrated in the upper spectrograph.

an electrocardiograph machine. In this case, a Hewlett-Packard 500B frequency meter was used with a Sanborn Twin-Viso Recorder Model 60-1300. The chart drive of the latter was set at 25 mm/sec, and the tapes were played

(Text continued on page 276)

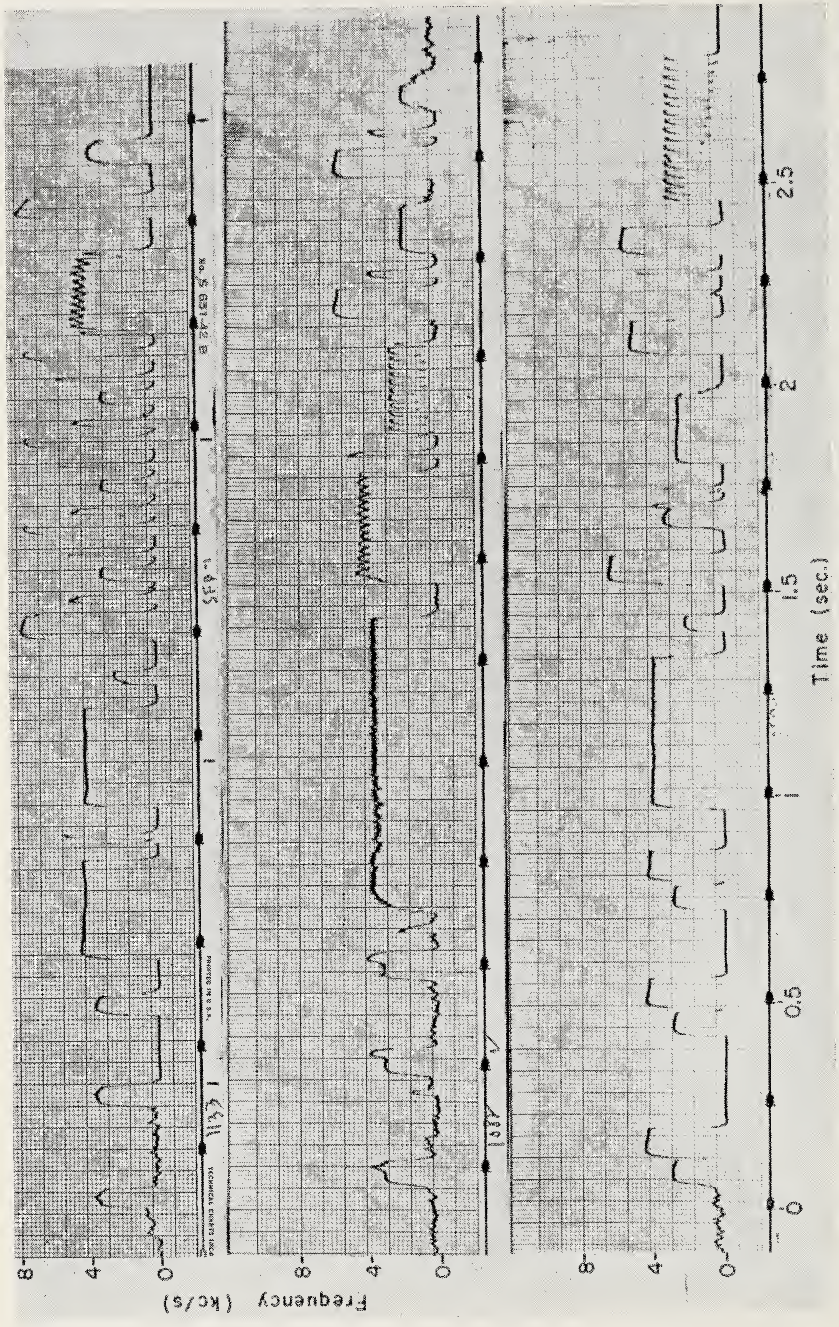

Fig. 2. Oscillograms of four different song types of one individual (SFD-1, San Francisco Bay, near Dumbarton Bridge). The basic patterns of time and structure are displayed by this rapid auxiliary method of analysis.

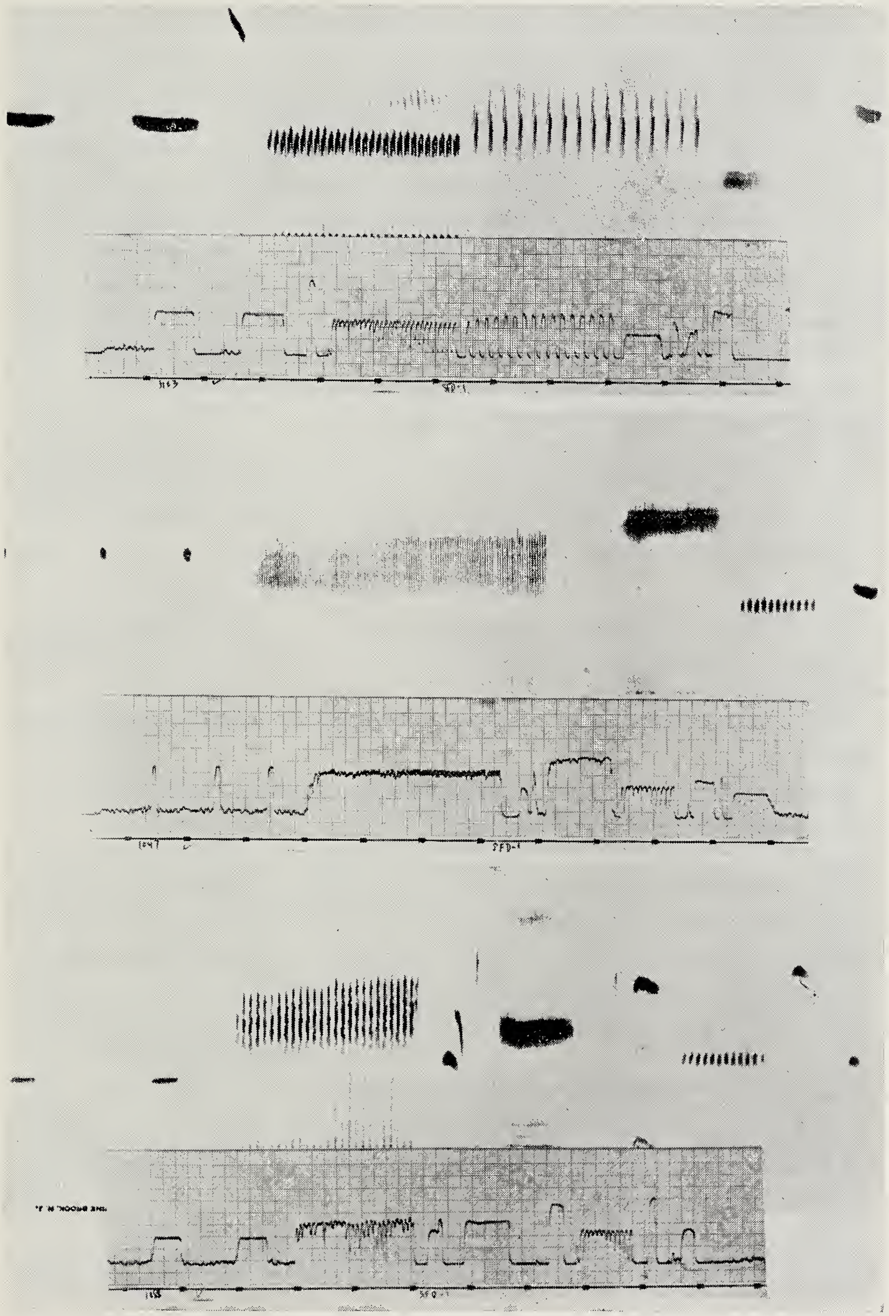

Fig. 3. Comparison of the spectrograms and oscillograms of three songs of one individual (SFD-1).

at quarter speed, 3¾ inches/sec. This method produces a simplified recording in the time required to play the tape. Fig. 1, 2, and 3 are examples of songs and the types of record produced by each method.

Over 1,500 songs were recorded in the field from approximately 75 individuals from three of the above-mentioned races in roughly equal proportions. These were the race *pusillula,* in the marshes of San Francisco Bay; *maxillaris,* in South Suisun Bay; and *gouldii,* the race of the local uplands. A banding program and intensive study of about 20 members of the latter race were carried on during four seasons, 1958 through 1961, in a small area of several acres of especially good habitat. The Song Sparrow is very sedentary in this region, and in a number of cases I observed color-banded individuals continually through two or three seasons on the same territories. No banding of the marsh populations was done. In a few cases, I collected an individual after recording it in order to avoid recording that individual again later. However, I usually relied on the sedentary and highly territorial habits of the birds to prevent this, and was careful to record as different individuals those whose territories were some distance apart. All but a few of the recordings of the marsh populations were made in one season, 1959.

USEFUL DEFINITIONS

Note: a sound producing a continuous trace on the sound spectrograph.

Syllable: a simple or complex element that is serially repeated, i.e. the unit of repetition in a trill.

Trill: a consecutive series of similar syllables; the repetition rate may be rapid or slow.

Note Complex: an unrepeated group of notes, bounded either by trills or by the beginning or end of the song.

Phrase: a natural section of song, either a trill or a note complex.

Song Type: one of the distinctive songs in the repertoire of an individual, recurring in a consistent manner.

Bout: a consecutive series of songs which may vary in minor ways but nevertheless conforms to a particular song type.

Interval: a silent period; this may be between syllables, phrases, songs, or bouts.

Note Types of Frequent Occurrence:

- *Whistle:* a pure tone.
- *Vibrato:* rapid frequency modulation, producing a continuous trace on the spectrograph.
- *Pip:* a note of duration less than 0.05 sec, of whatever shape.

RESULTS AND DISCUSSION

Variation in Structure

It was, of course, anticipated that with spectrographic analysis, this song would reveal a wide range of song, phrase, and syllable types, but at the same time it seemed likely that some structural similarities would appear that had until now been undetected by listening. The latter failure might be due either to limitations of the human ear as an analyzer, or to the inability of one's memory to recall some of the details of songs heard previously. In general, however, the almost endless variety of sounds reported by ear is verified, or rather magnified by the visual display of the spectrographs. Similar syllables in different song types of one individual are infrequent; similar songs in different birds are still more rare. Each song contains an average of five syllable types, and comparison of these with the syllables found in the other song types of the same individual shows that they recur in only one or two other songs. Thus, in a typical individual using 75 syllable types, only about 10 are likely to occur in more than one song type in its repertoire. In a corresponding comparison between individuals, made with color-banded birds, there are about five shared syllable types. Among the banded birds, one or two (and in one case, three) song types were occasionally possessed in common by two birds, which were usually close neighbors. With these exceptions, the repertoire of each bird was unique. It is true, however, as Saunders and Mrs. Nice have observed, that a few song types may recur fairly often in a given population, but this is too insignificant in the total vocabulary, so to speak, to be called a dialect.

No special effort was made to collect the complete repertoires of a large number of birds. The average repertoire size of 13 rather well-studied birds was 15.8, the range being from 10 to 23. These coastal races differ in this respect from the birds in Ohio studied by Mrs. Nice, where the average was less than 10.

Variation within a bout is of considerable interest. Successive repetitions of the same song type are varied continually and in a number of ways. Most common is the addition or omission of syllables in a trill, but the substitution of one syllable or phrase type for another is also frequent, especially in the latter part of the song. Fig. 4 gives examples of such variation, including a rare instance of a drastic change in syllable type in the introductory phrase. Note shape may vary somewhat in successive renderings of a phrase, but this kind of change is largely restricted to slow trills at the start of the song and to unrepeated phrases.

It is clear, then, that structural variation in Song Sparrow song is great, involving repertoire size, a large variety of syllable types peculiar to each individual, and extensive variation on a theme. Whenever the song of other species has been carefully studied, much variation has been encountered; however, there are some exceptions, such as the European tree creepers, *Certhia familiaris* and *C. brachydactyla* (Thielcke, 1961), and the White-crowned Sparrow (Marler and Tamura, 1962). In the latter species, the songs of neighboring individuals are sometimes practically indistinguishable. However, this variation in Song Sparrow song has real limits. The few notable changes of form in any particular song type are used consistently.

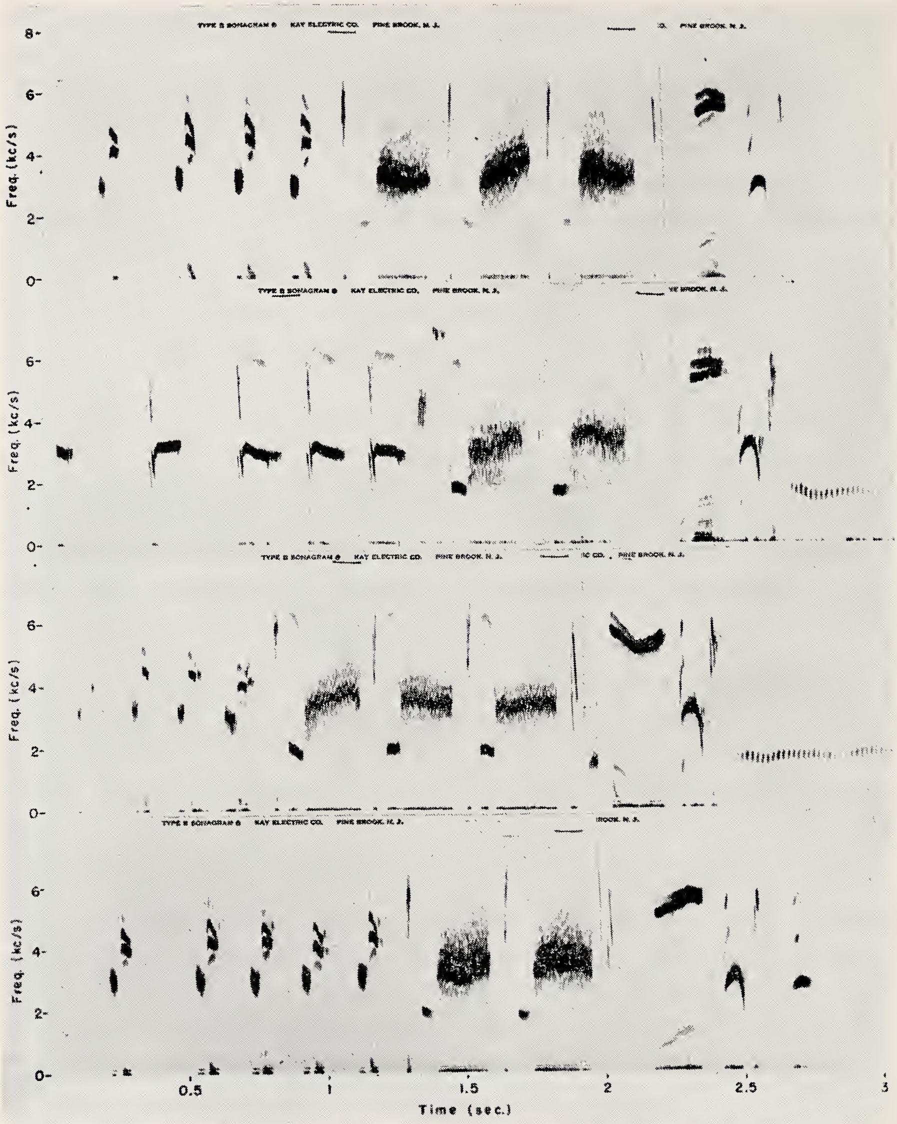

Fig. 4. Four successive renderings of one song type by an individual (SBM-5, Suisun Bay, Martinez marsh) illustrating variations that occur in the number of times that a syllable is repeated, the shape of the notes, and in the substitution of phrases in different parts of the song. In the second song from the top, there is a rare example of substitution of one phrase for another in the introductory part of the song.

Thus, in the course of one season, in subsequent seasons, and apparently throughout the life of the bird, the same variations on a theme are used. The syllable types in these songs remain relatively constant and, in general, the form of the notes composing these syllables varies only slightly.

In the above discussion, the finer detail afforded by the spectrographic record is emphasized. Regarding the relationship between separate Song Sparrow populations, I found that differences between populations exist, but are hardly greater than those to be found within any one of them. To approach the problem from another point of view, a grosser type of analysis and classification was attempted, both as a further search for meaningful variation, and as a means of determining what features are common to the songs of the birds in these populations. It is well known that a Song Sparrow song begins in a distinctive way, often with a series of whistles followed by a rapid trill. Ignoring the finer details of note morphology, I classified all the phrases according to the note types composing them, in the manner defined earlier. Classification of spectrograms and oscillograms of 134 song types from the three populations confirmed that the beginning of the song is distinctively different from the remainder. In the initial phrases, 86 percent contained whistles, 10 percent pips, and 4 percent vibratos. In the second phrase, there were nearly 50 percent vibratos and 25 percent whistles. In the latter parts of the song, there was a greater variety of phrase types, with no consistent trend in the distribution.

Finally, I modified the classes to consist of three categories: trills, vibratos,

TABLE 1.—DISTRIBUTION OF PHRASE TYPES ACCORDING TO SEVEN SUCCESSIVE PHRASES, AS FOUND IN 199 SONGS

NUMBER OF PHRASES IN SONG . . .		2	3	4	5	6	7	Percent of Phrase Total
NUMBER OF SONGS FOUND		2	28	54	71	31	13	
Successive Phrase	Phrase Type	Frequency Found						
I	Trill	2	26	50	69	26	12	92
	Vibrato	0	1	2	1	–	–	2
	Other	0	1	2	1	5	1	5
II	Trill	0	14	17	13	3	2	26
	Vibrato	0	9	23	35	17	7	46
	Other	2	5	14	23	11	4	28
III	Trill		11	17	18	9	4	30
	Vibrato		3	20	31	14	4	37
	Other		14	17	22	8	5	33
IV	Trill			21	25	8	2	33
	Vibrato			9	23	14	7	31
	Other			24	23	9	4	36
V	Trill				21	5	3	25
	Vibrato				24	7	4	30
	Other				26	19	6	45
VI	Trill					12	8	45
	Vibrato					11	3	32
	Other					8	2	23
VII	Trill						3	23
	Vibrato						2	15
	Other						8	62

and all other types, in a manner similar to that used on Mexican Junco songs by Marler and Isaac (1961). A trill here refers to anything repeated, such as a short whistle. Table 1 gives the results of this analysis for 199 songs. The song nearly always begins with a repeated element, which we already know to be a whistle. This is followed by an extended vibrato note in about half of the songs, and the rest of the song is quite variable. No consistent trends were found that would distinguish the different races.

Table 2.—Measures of Song Duration for Song Types, Individual Birds, and Populations

Song Type	Bird[a] or Population	No. of Songs	Mean Duration (in sec)	Standard Error (in sec)	Coefficient of Variation
a	Red/Blue	18	2.8	0.09	14
b	Red/Blue	11	2.75	0.08	10
c	Red/Blue	12	3.0	0.07	8
d	Red/Blue	16	2.46	0.08	13
e	Red/Blue	10	2.5	0.09	11
a	Blue/White	12	2.75	0.12	15
b	Blue/White	11	2.79	0.08	9
a	SBP-1	10	1.99	0.15	25
b	SBP-1	12	2.32	0.09	14
c	SBP-1	17	2.64	0.08	13
d	SBP-1	10	2.62	0.07	8
a	SBM-5	18	2.84	0.15	23
		13	2.64		
a	SBM-22	13	2.64	0.08	8
		INDIVIDUALS			
	Blue/White	86	2.80	0.04	14
	Helio./Yellow	50	2.76	0.06	16
	Red/Blue	94	2.58	0.03	12
	Red/Helio.	48	2.40	0.03	8
	Green/White	68	2.56	0.04	14
	SFD-1	29	2.73	0.08	15
	SFD-2	38	2.84	0.08	18
	SFM-11	64	2.58	0.05	15
	SBP-1	41	2.52	0.07	16
	SBP-5	45	2.60	0.09	22
	SBP-9	79	2.55	0.04	13
	SBP-22	32	2.55	0.05	11
		POPULATIONS			
	gouldii	442	2.65	0.02	17
	pusillula	215	2.62	0.03	19
	maxillaris	214	2.58	0.03	19
All Songs		871	2.62	0.016	18

[a] Individual birds listed in this column are grouped according to race and identified as follows: The color-banded individuals from the upland race (*M. m. gouldii*) are listed by their colored bands; the two marsh races are listed with the beginning letters SF (*M. m. pusillula*) and SB (*M. m. maxillaris*). The letter following SF or SB indicates a particular area, and the number a particular individual. Thus, SBP-1 is individual No. 1, near Pacheco Slough in Suisun Bay, and is a member of the race *maxillaris*.

Temporal Pattern

It has become increasingly evident in recent years that temporal patterns are of great significance in behavior. Once again, modern instruments have made precise measures and careful quantification of this aspect possible. It was especially in this part of the study that I found the oscillographic analysis valuable, since with it I could obtain many records on which time measures could be readily made. I measured the song duration of 871 songs. In about 150 of these, I also measured the duration of the notes, syllables, and phrases, and the intervals between them. Table 2 summarizes the measures of song duration for individual songs, individual birds, and the three races. The songs of about 60 individuals are included in the grand total. Fig. 5 shows the frequency distribution of this total, with a mean of slightly over 2.6 sec. This distribution is approximately normal, as is seen when it is cumulatively plotted on normal-probability paper. An analysis of variance between the races failed to show a significant difference. The sources of variation in song duration are illustrated in Fig. 6. There are significant differences between some songs and between some individuals, but not between populations. The range was 1.2 to 5.2 sec, and the mean corresponds closely with the figure obtained by Saunders (1951) of 2.7 sec for 884 Song Sparrow songs in the eastern United States.

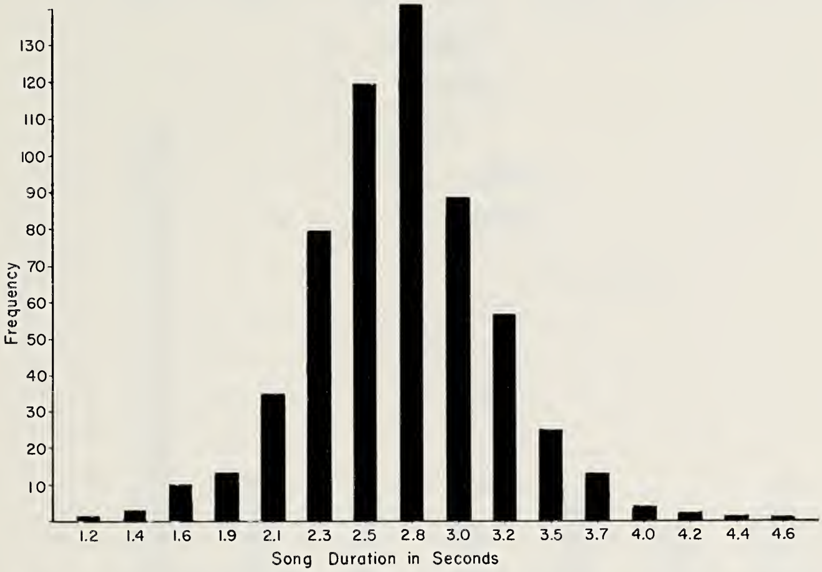

Fig. 5. Frequency distribution of measures of song duration in 871 songs from three populations.

The most significant time measures within the song are the intervals within and between phrases. Fig. 7 shows a comparison of these measures in 125 songs. Once again there is least variability in the beginning of the song; here, the standard deviation of the average interval length within a phrase is only a third of the mean interval length. In later phrases the standard deviation is more nearly equal to the mean. Besides this, the intervals within the first phrase are about five times as long as they are in subsequent phrases. Another peculiarity of this phrase, not shown in Fig. 7, is that the duration of many of the syllables and of the intervals between them shorten markedly as the song progresses. It is as though the bird is picking up speed toward the central part of the song. The upper part of Fig. 7 shows that the interval which terminates the first phrase is much shorter than the intervals within that phrase; this increase of tempo continues through the first half of the song.

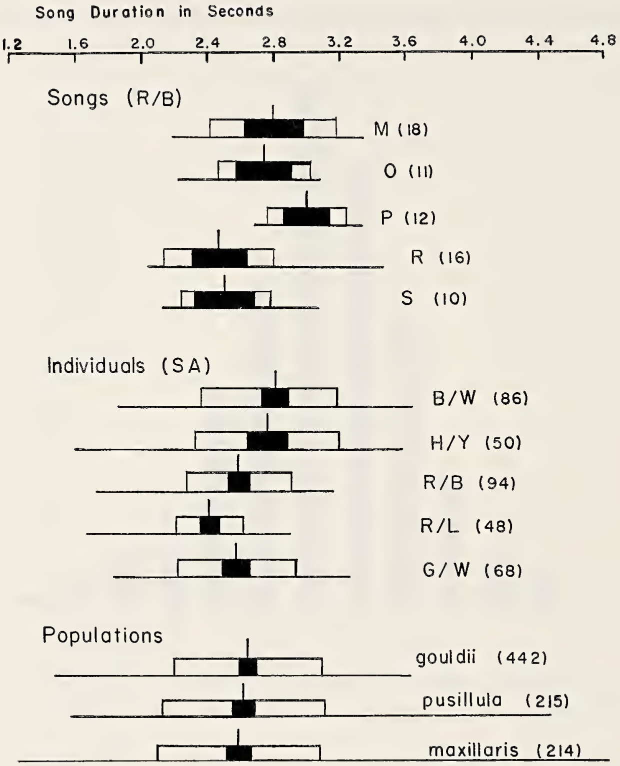

Fig. 6. Groups of song duration measures compared to show the important sources of variability. The horizontal line shows the range, and the vertical line the mean; on each side of the mean the open rectangle shows one standard deviation, and the solid rectangle two standard errors of the mean. The number of measures is given in parentheses to the right.

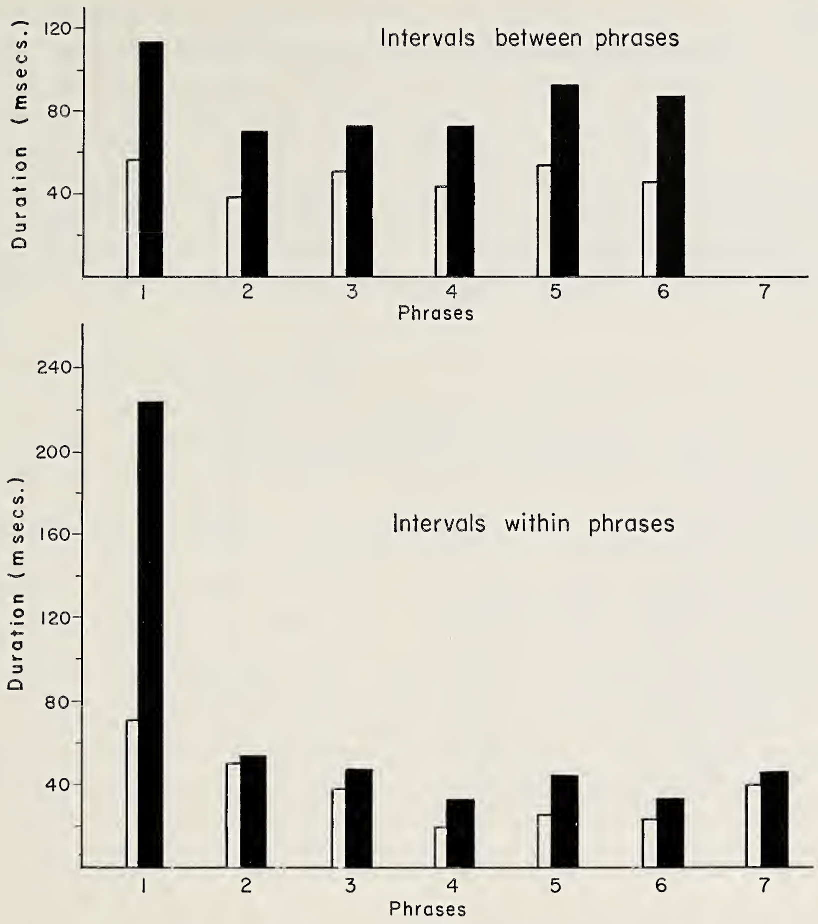

Fig. 7. Comparison of interval lengths within the song. The mean duration of intervals between phrases is shown in the upper graph, and the same for intervals within phrases in the lower graph. The open rectangle represents one standard deviation.

SUMMARY AND CONCLUSIONS

The foregoing results provide a quantified descriptive basis for comparative and developmental studies of Song Sparrow song. Some species-specific characters determined are the duration, 2.62 ± 0.47 sec, the occurrence of repeated whistles in 90 percent of the first phrases, followed by a vibrato note in nearly half of the second phrases. The intervals between the whistle syllables of the first phrase are relatively much longer than in the rest of the song and become shorter from beginning to end of the phrase. In the San Francisco Bay region, males have an average repertoire of 16 song types, consisting of 5 phrases and about 75 kinds of syllables. Within this framework, variation is excessive, ranging from minor changes in numbers of syllables in a trill, or omissions and modified endings, to strikingly different phrase substitutions in successive renderings of the same song type. Each bird has a repertoire of song types that for the most part is unique to the individual. This variation is so great that it masks any differences which may exist between different populations, even though the latter have been given subspecific status on the basis of morphologic characters. In the quantitative measures, at least, there is greater variation between the songs of an individual and the individuals of a population than the variation between populations. It appears that song has not diverged in these color races.

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Color Preference in Fruit- and Seed-eating Birds

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This study concerns selection of differently colored seeds and fruits by birds under natural conditions. There are many experiments with color vision in birds, but relatively little is known about their choice of colored foods in nature. Such selection is especially important when we consider birds as "visual" animals, and it has deep evolutionary consequences on food-bearing organisms (Bruns, 1954).

MATERIALS

The seeds and fruits of indigenous and introduced woody plants were fed to 156 species of European birds. This was done mainly to determine their role in relation to dissemination of diaspores. It has been found (Turček, 1961) that European fruit- and seed-eating birds feed on 274 species (kinds) of diaspores, 88 of which are introduced. Of the total number of diaspores of woody plants in this study, 251 species have been evaluated, namely those in which seeds, fruits, or their consumed (disseminated) parts are of any definite and expressible color. All 251 kinds of ripe diaspores are placed into one of eight color groups. In some cases (e.g. some cones, arilli, pods, etc.), the particular color was difficult to determine, and in these cases some error could be involved. These are mainly those diaspores classified as "brown." An additional possible error originates from the assumption that birds recognize colors in the same manner as does man, i.e. that birds perceive the same spectrum.

Not all seeds and fruits are eaten and, consequently, distributed by birds equally, indicating that birds favor certain kinds. Although the attractiveness and conspicuousness of the diaspores are mainly a function of color, the choice of any fruit or seed does not depend upon color alone. There are many other factors affecting the food that birds select (availability of food, weather, etc.). I shall attempt to demonstrate only the role and importance of color in the selection of fruits and seeds of plants for food by birds. It is possible that the particular colors of at least some diaspores are correlated with other properties but, unfortunately, such correlations could not be examined and demonstrated mainly because of our ignorance of such properties, and especially of their importance to birds.

The diaspores studied here are placed into three groups (categories) according to the number of bird species feeding on them. In the first group are diaspores eaten by 1 or 2 species of birds; in the second those eaten by from 3 to 19 kinds of birds; and in the (most preferred) third group are diaspores eaten by 20 and more (in our materials 20 to 63) bird species. These are groups of qualitative preference, as will be shown below.

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There were some difficulties in determining the colors exactly (i.e. between red and orange, orange and yellow, yellow and green, blue and violet, and black and blue). Therefore, some subjective elements are involved, but these do not influence our results to a decisive degree. The colors of diaspores that were not apparent upon autopsy have been determined from the dendrological literature.

The full list of both bird and woody-plant species studied was given in an earlier work of mine (Turček, 1961). I am indebted to E. W. Jameson, Jr., for reading and correcting the present manuscript.

ANALYSIS OF MATERIALS

Distribution of diaspores according to colors is shown in Table 1. There are some striking differences in frequency of colors, the two extremes being orange with the fewest and brown with the most kinds of diaspores. The most striking and important property of the colors listed in Table 1 is the relatively low frequency of white, orange, yellow, and green diaspores in general, in other words, colors around the center of the humanly visible spectrum (cf. McCabe, 1961; Thompson, 1953; and Wright, 1959). Our crude classification of materials already shows some characteristics, which, in further analyses, will be found and substantiated. It is of paramount interest to what degree these properties can be ascribed to birds. Not all the diaspores eaten by birds are disseminated by them. This is of importance to the natural selection of woody plants and to both the ecological and geographical distribution of the plants. In a statistical test of the values of Table 1, only red and black diaspores are disseminated significantly more than expected, white and blue diaspores are probably more disseminated than expected, while brown diaspores are distributed significantly less frequently. The biological significance of this is discussed below.

Table 1.—Frequency of Diaspores of Different Colors

Number of Kinds of Diaspores						
			Distributed Mainly by Birds		χ^2	Probability
Color	No.	Percent	No. Observed	No. Expected[a]		
White	6	2	6	3	2.7	$P > 0.05$
Red	62	25	55	34	13	$P < 0.01$
Orange	2	1	1	1	—	———
Yellow	7	3	3	4	0.2	$P > 0.05$
Green	19	7	6	10	1.8	$P > 0.05$
Brown	108	43	21	59	25	$P < 0.01$
Blue	11	5	10	6	2.6	$P > 0.05$
Black	36	14	35	20	11	$P < 0.01$
Total	251	100	137	137	56.3	

[a] Number expected = 137 times the percentage shown for each color in column 3.

For three colors some explanations should be given. Although white diaspores are thought to be unattractive and in general rejected by birds, the presence of only one attractive and preferred kind, namely the white mulberry (*Morus alba*), strongly influences the entire "white" group. It is probable that some of the diaspores marked as black are, in fact, blue, and therefore the entire group of blue diaspores would be more numerous and consequently significantly more distributed. The brown diaspores are really distributed less by birds than expected, for this group contains many diaspores with wind-dispersal devices (anemochoria). Thus, excluding the brown group (many of which are dispersed by wind), red and black diaspores, being the most numerous, are the diaspores most disseminated by birds. The last is, in my opinion, not the effect but the cause of the first.

Occurrence of different colors in the three categories (groups) mentioned above is shown in Table 2. The participation of the different colors is given as a percentage of the total number of species of plants (diaspores) in the particular group. Within the three diaspore groups (rejected, mean or according to expectation, and preferred), from the first toward the third group there is an increase of red, blue, and black diaspores, and simultaneously a decrease of green and brown diaspores. The trend of the other colors shows no definite character, probably due to unsatisfactory materials (e.g. low absolute number of kinds of diaspores in such colors). Of these materials, it can be concluded that some diaspores belong to the rejected category because of their color. The same—*mutatis mutandis*—applies to the group of preferred diaspores.

TABLE 2.—COLOR FREQUENCY OF DIASPORES ARRANGED IN THREE GROUPS ACCORDING TO THEIR IMPORTANCE AS FOOD FOR BIRDS

DIASPORES		NO. SPECIES OF BIRDS FEEDING ON SAME	PERCENT DIASPORES,[a] IN COLOR							
Group	No. of Species		White	Red	Orange	Yellow	Green	Brown	Blue	Black
Rejected	42	1–2	2	19	0	2	13	53	2	9
Mean[b]	149	3–19	2	24	1	3	10	42	4	14
Preferred	60	20+	3	30	0	2	0	40	7	18

[a] Based on the number of species shown for each group in column 2.

[b] Or according to expectation.

In this study, the mean number of colors of diaspores selected by each species was 3.5 (Table 3). Only some species, the most polyphagous ones, feed on diaspores of a wide variety of colors. Here again, as in some other trophic relations of birds, the "ecological reciprocity" (*mihi*) will be illustrated: Most birds feed on a few kinds of food and nest in a few kinds of substrate; only a few utilize a wide variety. The birds we examined ate, on the average, diaspores of from 3 to 5 colors, mostly either of 3 or 4 colors. Birds feeding on diaspores of many colors, say 6 and more, belong either

TABLE 3.—NUMBER OF COLORS SELECTED BY VARIOUS SPECIES

No. of Colors of Diaspores	No. of Species of Birds Feeding on Same	No. of Colors of Diaspores	No. of Species of Birds Feeding on Same
1	32	5	13
2	39	6	4
3	22	7	15
4	18	8	13
Total			156

to the well-known polyphages, such as Paridae, or to specialized seed and fruit eaters of the families Turdidae and Fringillidae.

In Table 4 there is calculated the combination of diaspores in different colors in the diets of the 156 species of birds. The number of combinations is $\frac{n(n-1)}{2}$, thus $\frac{8\ \text{colors}\ (8-1)}{2} = 28$. The rows and columns show the frequency with which diaspores of the possible color combinations appear in the diets of different species of birds. The most common combinations contain red, black, and blue diaspores; least common are orange, yellow, and green. If we divide the totals of a particular color column (in Table 4) by the total number of species of birds feeding on diaspores of that color (Table 5), the quotients so obtained give the mean frequency with which that color appears in color combination in the diet per bird species. These quotients are for white (4.8), red (3.2), orange (5.7), yellow (5.8), green (4.6), brown (4.0), blue (4.3), and black (3.1). It is now evident that

TABLE 4.—ASSOCIATION OF THE EIGHT DIFFERENTLY COLORED DIASPORES IN THE DIETS OF 156 SPECIES OF BIRDS[a]

$$\text{Number of combinations} = \frac{n(n-1)}{2}$$

Color	White	Red	Orange	Yellow	Green	Brown	Blue	Black	Totals
White	(1)	52	16	34	36	38	42	50	268
Red	52	(5)	20	38	48	60	62	98	378
Orange	16	20	(0)	16	18	16	20	20	126
Yellow	34	38	16	(0)	30	30	32	34	214
Green	36	48	18	30	(5)	38	38	44	252
Brown	38	60	16	30	38	(4)	42	56	280
Blue	42	62	20	32	38	42	(2)	56	292
Black	50	98	20	34	44	56	56	(15)	358
Subtotals	268	378	126	214	252	280	292	358	2,168
Plus	(1)	(5)	(0)	(0)	(5)	(4)	(2)	(15)	(32)
Totals	269	383	126	214	257	284	294	373	2,200

[a] Numbers in parentheses (n) include diaspores of one color.

diaspores of white, (more pronounced) orange, yellow, or green colors in the center of the spectrum are eaten by birds mainly in combination with 4.5 or more colors and not, or only exceptionally, alone. About the same numbers appear in parentheses in Table 4. Only 32 species of birds (Table 3 and "plus" row of Table 4) feed on diaspores of a single color; this is roughly 20 percent of all birds examined. Evolution has thus favored selection of more than a single color.

TABLE 5.—NUMBER OF BIRDS FEEDING ON DIASPORES OF A GIVEN COLOR

KINDS OF DIASPORES			SPECIES OF BIRDS FEEDING ON SAME		TOTAL COMBINATIONS OF COLORS (from Table 4)
Colored	Absol.	Percent	Absol.	Percent (of $n = 156$)	
White	6	2	55	35	269
Red	62	25	118	76	383
Orange	2	1	22	14	126
Yellow	7	3	37	24	214
Green	19	7	56	35	257
Brown	108	43	70	45	284
Blue	11	5	68	43	294
Black	36	14	120	77	373

Table 5 presents the number, both absolute and relative, of species of birds feeding on diaspores of the particular colors. This is far from proportionate to the number of species of diaspores in that color. Some preferences, as well as rejections, can be observed if we consider that the mean number of species of birds feeding on any color would be $M = 68$, $s = 32$, $s_M = 11$, and $V = 47$ percent. In a chi-square test of equal expectancy, red and black diaspores are strongly preferred ($P < 0.001$), brown not significantly preferred, while diaspores in orange and yellow colors are significantly rejected ($P < 0.001$), white and green probably significantly rejected, and blue utilized according to expectation.

Apart from diaspores of composite colors such as white, brown, and black, the number of bird species feeding on particular colors decreases with the wave length of the particular colors, and is the least about the center of the spectrum (the most brilliant colors).

SIGNIFICANCE OF FINDINGS

The materials analyzed in the present paper—251 species of woody plants and 156 species of birds—are considered to be a fairly representative sample of European plants and birds. As the feeding of birds on particular kinds of diaspores is very different, the birds are highly selective in their choice of diaspores. According to the intensity of use of diaspores as food for birds, it was possible to divide the diaspores (the woody plants) into three categories (as in Table 2). Similarly, according to the number of kinds of diaspores eaten by particular species of birds, it has been possible to divide all birds into three categories: (1) those feeding on 1–6 kinds of diaspores (82 species); (2) those on 7–27 kinds of diaspores (40 species); and (3) birds feeding on 28 and/or more kinds of diaspores (34 species). The first group of birds is considered to comprise occasional fruit eaters, while the third group consists of birds polyphagous not only in relation to diaspores but also to insects (my own materials); in some cases, they are specialized granivorous and frugivorous birds.

In the analysis above, the distribution of eight colors among the diaspores in question is shown. The number of kinds of diaspores of particular colors indicates the following series for Europe, in a decreasing order: brown, red, black, green, blue, yellow, white, and orange. This differs somewhat from the order Ridley (1930) stated for a world-wide distribution of colors. The most striking differences are in yellow and orange, and white and brown seeds and fruits. In Europe there are fewer yellow, orange, and white diaspores, but more brown ones in comparison with the rest of the world. Our data and Ridley's data agree with regard to red and black diaspores: These two colors are—perhaps absolutely—dominant over all. They are, moreover, significantly more widely disseminated by birds than the others and consequently are widely distributed over geographical areas. In this connection, it can be stated that red and black are of positive selective value. Brown diaspores are mainly anemochorous. White ones, although inconspicuous and less palatable, represent a small group composed of extremes; some are rejected, and some mostly preferred, such as *Viscum album* and *Morus alba*, and there are relatively large numbers of birds that consume and disseminate these fruits.

The percentage distribution of the eight colors within the three groups of diaspores (Table 2) enables us to conclude that the number of bird species feeding on diaspores in a particular group is determined, or at least influenced, by the color of diaspores involved. This is confirmed by data in tables 4 and 5. It should be noted that 82 percent of yellow, 66 percent of green, 86 percent of orange, and 71 percent of white diaspores are eaten and disseminated by birds of the third (smallest) category, the so-called polyphages. Thus, while red and black (and probably brown and white) fruits and seeds are disseminated by almost all birds, or at least by a large number of them, yellow, orange, and green diaspores are eaten and disseminated mainly by the relatively small group of polyphagous and specialized birds. If the frequencies of colors of the diaspores and the frequencies of bird species eating as well as distributing them are set on the humanly visible spectrum, the frequencies show a tendency to decrease with the decrease of the wave lengths of colors. It is striking that colors about the center of the spectrum (orange, yellow, and green) are the least utilized. This conclusion suggests that these colors, although conspicuous and very brilliant, are not attractive to birds and therefore are selectively disadvantageous. These colors had proved repellent to birds (mostly) under experimental conditions (McCabe, 1961; Thompson, 1953; and Wright, 1959) and the present analysis of field data tends to confirm the published results of these investigators. These colors, insofar as is known, are probably repellent also when they occur in insects; at least orange and yellow insects are seldom taken by birds. On the other hand, red insects are repellent to birds. Therefore it is probable that besides the color as such there are still more properties determining the selective value of food subjects. This is shown by some of the field experiments of Prop (1960) made on sawfly larvae and tits.

The sole existence of red and black diaspores in predominant numbers, the preferred dissemination of these by birds, and the relatively small number of the orange-yellow-green group, disseminated only a little by birds, classify the selective and survival value of the particular colors and indicate the trend of future selection and evolution, respectively, in the coloring of the diaspores. If this is so, then in insects, which are at least as important in bird food as diaspores, the tendency in color selection should be a reverse one. Here the coloring of orange, yellow, and green (and probably white and red) would be of advantage and protective against birds. In the case of insects, birds are hardly the main factor of natural selection, as they are in woody plants bearing colored diaspores.

Color vision of birds can be assumed to be equal over geographical regions. If, then, there are marked differences in the abundance of certain colors in diaspores, especially in unattractive or repellent colors, between geographical regions (e.g. the relative high number of yellow, orange, and white diaspores in the tropics and partly in the Nearctic Region), not only selection, but an adaptation of whole faunas (birds) to different colors could be supposed. One must not forget the role of the background (e.g. foliage, etc.) and contrasting effects of some colors of diaspores, as stressed by Ridley (1930).

As orange, yellow, and green (and to some degree white and blue) are generally colors of the early stage of ripening, indicating to birds just that stage, two conclusions could be drawn from this: (1) The majority of birds (at least in Europe) consider such colored diaspores to be unripe, and only some of the most adaptive birds (phylogenetically on the top?) recognize the ripe status of such colored (and, in fact, ripe) diaspores; and (2) woody plants bearing yellow, orange, and green (and perhaps blue and white) diaspores in a ripe condition were retarded, respectively, by red, black, and perhaps others surpassed in evolution.

Birds are thus an important factor not only in the dispersal but also in the selection and evolution of plants, on the basis of a mutual adaptation.

SUMMARY

Based on 251 species of diaspores of woody plants, fed upon in the field by 156 species of European birds, the selection of differently colored diaspores for feeding was analyzed. The mean number of colors of diaspores

selected by these birds was 3.5; 42 species of plants were represented in the rejected group of diaspores, and 60 were among the preferred. Apart from diaspores of composite colors (white, brown, black), the number of bird species feeding on particular colors decreased with the wave length of the particular color, and was least about the center of the spectrum.

The number of bird species feeding on diaspores of any particular color was not proportional to the number of diaspore species in that color. Only red and black diaspores were disseminated significantly more than expected, while brown diaspores were disseminated significantly less frequently.

Orange, yellow, and green are, in general, colors of unripe (or early stage of ripening) diaspores (atavistic color in any sense) and are recognized as such by the majority of birds. Plants with these diaspores were, however, surpassed during their evolution by plants bearing diaspores in colors preferred by birds.

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Der Abendflug der Stockente und seine Abhängigkeit von der Lichtintensität

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Seit Jahrzehnten erscheinen zahlreiche Arbeiten, die sich mit dem Erwachen und Zurruhegehen einzelner Vogelarten befassen. Soweit sich die Messungen über einen längeren Zeitraum erstrecken, ist aus ihnen zu ersehen, dass die Zeitpunkte des Erwachens und des Zurruhegehens einer Art sich parallel zu den Sonnenaufgangs- und -untergangszeiten verschieben. Daraus wurde zuweilen geschlossen, dass ganz bestimmte Helligkeitswerte, die für jede Art kennzeichnend sind, den Anfang und das Ende eines Vogeltages bestimmen. Aus der Fülle der Arbeiten sei lediglich eine Auswahl gegeben. Weitere Literaturangaben sind den zitierten Arbeiten zu entnehmen. So haben Černý (1959) und Schoennagel (1959) festgestellt, dass der Star *Sturnus vulgaris* an Tagen mit bedecktem Himmel früher den Schlafplatz aufsucht als an Abenden mit heiterem Himmel. Davis (1955), der ebenfalls den Schlafplatzflug der Stare untersucht hat, findet keinen Zusammenhang zwischen der Beleuchtungsstärke und dem Einfallen in den Schlafraum. Davis gibt zudem eine ausführliche Besprechung jener Literatur, die über unser Thema berichtet. Aschoff (1960) zeigt, dass bei den Schlafplatzflügen der Dohle *Corvus monedula* bestimmte Helligkeiten als Zeitgeber für den Ab- und Anflug massgebend sind. Rappe (1960) hat den Schlafplatzflug der Bachstelze *Motacilla alba* untersucht und kommt zu dem Ergebnis, dass dieser Vogel bei bedecktem Himmel früher auf dem gemeinsamen Schlafplatz einfällt. Frieswijk und Bresser (1961) beobachteten den Abflug der Stare vom Massenschlafplatz. Das Diagramm zeigt, dass die Vögel an heiteren Tagen im Durchschnitt etwas früher abflogen als an Tagen mit bewölktem Himmel.

Ich selbst habe mir als Thema die abendlichen Nahrungsflüge der Stockente *Anas platyrhynchos* und ihre Abhängigkeit von der Lichintensität gewählt. Dieser "Abendstrich" wilder Enten ist allgemein bekannt, jedoch meines Wissens noch nicht einer längeren Beobachtungsreihe unterzogen worden. Tagsüber ruhen die Vögel auf dem Gewässer, das ihnen kaum Nahrung, sondern nur Schutz bietet. In der Abenddämmerung verlassen sie es, um auf Wiesen und Feldern zu äsen. Meines Wissens liegen nur von Brackbill (1952) einige Beobachtungen vor, und zwar von amerikanischen Wasservögeln. Der Forscher kommt zu dem Schluss, dass die Abflüge an Abenden mit bedecktem Himmel früher liegen als an den Abenden mit heiterem Himmel.

Als Beobachtungsgebiet für den Entenstrich habe ich den 20 ha grossen Tönebön-Teich von Hameln gewählt. Er ist eine ehemalige Tongrube und

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liegt in der Südostecke der Stadt. Im Laufe der Jahrzehnte hat sich hier Grundwasser angesammelt. An seinen Ufern grünen Weiden *Salix*, Pappeln *Populus*, Erlen *Alnus*, Eichen *Quercus*, Weissdorn *Crataegus*, usw. Nichts erinnert mehr daran, dass er eine aufgegebene Tongrube ist. Der See besitzt viele Buchten und einige kleine Inseln, so dass er einen natürlichen Eindruck macht. Die Anzahl der rastenden und abends auffliegenden Stockenten kann deswegen nicht gleichzeitig überblickt werden. Das Landschaftsschutzgebiet ist von einem hohen Stacheldrahtzaun umgeben, so dass Unbefugte die Wasservögel nicht stören können. Die Jagd wird nicht ausgeübt. Meine Beobachtungen wurden also in keiner Weise gestört.

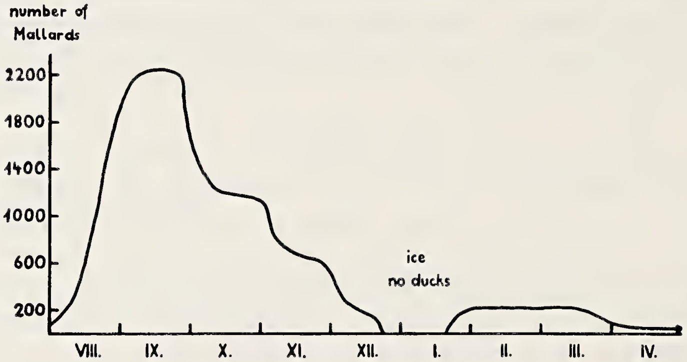

Fig. 1. The number of Mallards studied in the course of a year (1961–62).

Der Herbstzug der Stockente macht sich bereits Anfang August bemerkbar. Die Wasservögel kommen aus ihren weiter nördlich und östlich gelegenen Brutgebieten. Wie Fig. 1 zeigt, wächst ihre Zahl stetig. Anfang September tummeln sich bereits 1 500 Stockenten auf dem See. Mitte September erreichen sie das Maximum mit 2 200 Individuen. Im Oktober sinkt die Zahl auf 1 200. Im Dezember rasten nur noch 200 Vögel auf dem See. Wenn das Gewässer bei starkem Frost von Ende Dezember bis Mitte Januar zufriert, dann weichen die Enten nach dem benachbartem Fluss, der Weser, aus. Sobald aber das Eis taut, kehren sie auf den See zurück. Ende April haben die Wintergäste und Durchzügler den See verlassen. Zurück bleiben etwa 10 Paar Stockenten, die hier brüten und mit ihren Jungen die Wasserfläche beleben. Anfang August setzt dann wieder der Herbstzug ein.

Während des Tages halten sich nicht allzuviel Enten auf dem Wasser auf. Die meisten liegen oder stehen am Ufer, ruhen, putzen sich oder schlafen. Fluchtbereit ist die Brust dem Wasser zugekehrt. Eine Möglichkeit, Nahrung aufzunehmen, besteht nicht. Der See ist am Tage lediglich Zufluchtsstätte. Ein Auszählen der Geschlechter ergibt, dass die Erpel geringfügig überwiegen. Nach Sonnenuntergang aber wird es lebhaft auf dem See. Nun hat der Tönebön-Teich seine hohe Zeit. Jetzt drängen sich z.B. im September über 2 200 Stockenten auf dem See und warten auf den Anbruch der

Dämmerung, um zu den Äsungsplätzen zu fliegen und die leeren Mägen zu füllen. Vor dem Abflug beginnt ein lebhaftes Kontaktgeschnatter. Gleich Mückenschwärmen erheben sich die Stockenten und fliegen mit pfeifendem Schwingengeräusch zielstrebig zu ihren Äsungsplätzen, die bis 10 km entfernt liegen. Diesen Abendstrich halte ich für eine angeborene Handlungsweise. Solch ein September-Abend ist ein eindrucksvolles Erlebnis.

Seit Jahren beobachte ich diese abendlichen Äsungsflüge. Von Anfang August 1961 bis Ende April 1962 habe ich sie aber ausführlich protokolliert. An wolkenlosen Tagen habe ich die Sonnenuntergänge nach Mitteleuropäischer Zeit notiert, für die übrigen Tage durch Interpolation gewonnen. Diese Angaben sind für Hameln keinem Kalender zu entnehmen, da die Sonne hinter einem Höhenzug, dem Klüt, untergeht, der mit seinem Gipfel 194 m über der Weser liegt. Um vergleichbare Werte zu erhalten, schlage ich vor, in ähnlichen Arbeiten den tatsächlichen Sonnenuntergang als Bezugssystem zu wählen, d.h. denjenigen Zeitpunkt, in dem der obere Sonnenrand unter dem Horizont verschwindet. In einigen Arbeiten ist es üblich, den Zeitpunkt der bürgerlichen Dämmerung zu errechnen und als Bezugssystem zu wählen.

Bewölkungsgrad und Wolkendichte habe ich geschätzt. Einen Bewölkungsgrad von 0 bis $^{5}/_{10}$ habe ich mit heiter, den von $^{6}/_{10}$ bis $^{10}/_{10}$ mit bedeckt bezeichnet.

Die Helligkeitswerte habe ich mit dem Lux-Meter "Trilux" der Firma Gossen in Erlangen gemessen. Die Photozelle war gegen den Zenith gerichtet. Im August und September flogen die ersten Stockenten bei einem durchschnittlichen Helligkeitswert von 40 Lux auf. Vom Oktober bis März betrug die Helligkeit nur 5 Lux, d.h. das Lux-Meter sprach kaum noch an. In Fig. 4 sind diese Werte dargestellt. Im April flogen die ersten Enten bei rund 20 Lux auf.

Gleichzeitig habe ich das Verhalten der Enten beobachtet. In Intervallen von je 2 Minuten habe ich die abfliegenden Vögel gezählt. Wegen der zahlreichen Buchten und der Dämmerung habe ich natürlich nicht sämtliche auffliegenden Enten erfassen können. Die Abflüge dauern, wie auch Fig. 3 und 4 zu entnehmen ist, im Durchschnitt 10 Minuten. In Fig. 2 ist der Zeitpunkt eingetragen, in dem 50% der beobachteten Vögel aufgeflogen sind.

Fig. 2 zeigt deutlich, dass die Abstände der Abflugzeiten vom Sonnenuntergang von Tag zu Tag wechseln. Bis zur Wintersonnenwende verfrüht sich das Auffliegen der Enten in demselben Masse, wie die Sonne früher untergeht. Falls der Sonnenuntergang keine Verschiebungen aufweist wie im Dezember, liegen die Zeiten annähernd gleich. Nach der Wintersonnenwende verspätet sich das Auffliegen der Enten in demselben Masse, wie die Sonne später untergeht. Ähnliche Feststellungen sind auch von anderen Vogelarten bekannt. In der Einleitung habe ich bereits auf entsprechende Arbeiten hingewiesen.

Das Protokoll und somit auch das Diagramm lassen aber noch mehr erkennen. Aus ihnen geht eindeutig hervor, dass die Stockenten an Tagen mit bedecktem Himmel und geringer Helligkeit, wie das Lux-Meter zeigt, früher auffliegen als an solchen Abenden mit heiterem Himmel. Man vergleiche die Uhrzeiten vom 28. X. und 2. XI. in Fig. 4! Bei bedecktem Himmel fliegen die Enten im Durchschnitt 38 Minuten nach Sonnenuntergang ab, bei heiterem Himmel aber erst 46 Minuten nach Sonnenuntergang. Man betrachte jetzt neben Fig. 2 auch Fig. 3. Die Abhängigkeit von der Helligkeit ist besonders dann deutlich zu erkennen, wenn auf einen Abend mit geringer Bewölkung ein Tag mit wolkenverhangenem Himmel folgte, bzw. die Wetterlage umgekehrt verlief.

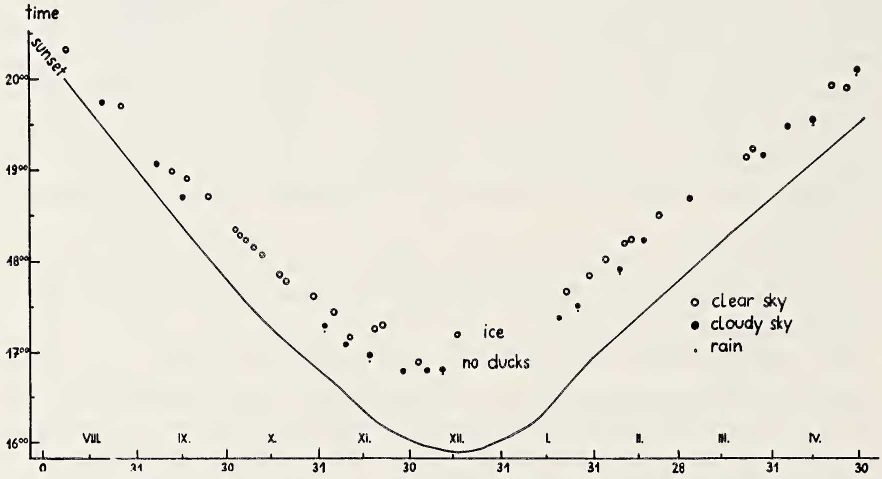

Fig. 2. Departure time when 50 percent of the Mallards left the lake on clear and cloudy evenings.

Übrigens fielen in den Wintermonaten annähernd zur gleichen Zeit an 2 000 Krähenvögel *Corvus corone, C. frugilegus,* und *C. monedula* am Tönebön-See auf ihren Schlafbäumen ein, so dass Fig. 2 auch den Schlafplatzflug der genannten Rabenvögel darstellen könnte.

Fig. 3 zeigt den Verlauf des Abflugs. Ich habe nur die Protokolle vom 20. X.–19. XI. graphisch dargestellt. Auch hier ist wieder zu erkennen, dass die Enten an trüben Abenden früher auffliegen als an heiteren. Die durchschnittliche Dauer des Abflugs beträgt in dieser Beobachtungsreihe 15 Minuten. Somit ist wahrscheinlich, dass sich die Stockente wirklich nach einem bestimmten Helligkeitsgrad richtet. Zumindest spielt er eine grössere Rolle als der Sonnenstand.

Fig. 4 zeigt nochmals den Verlauf des Abflugs, und zwar am wolkenlosen 28. X. und am bewölkten 2. XI. In Intervallen von je 2 Minuten wurden die abfliegenden Vögel gezählt. Die ersten Enten fliegen bei einer Beleuchtungsstärke von 6 bzw. 10 Lux, also fast demselben Helligkeitsgrad, auf. Die meisten starten aber erst, wenn der Helligkeitsmesser nicht mehr ausschlägt.

In diesem Zeitpunkt fallen die Rabenvögel auf ihren Schlafbäumen ein, und die Amsel *Turdus merula* bringt ihren Schlafruf. Es ist jetzt so dämmerig, dass man das Ziffernblatt der Uhr gerade noch erkennen kann.

Im September fliegen gleichzeitig so viele Enten auf, dass man ihre Zahl nur schätzen kann. Vom Oktober bis Dezember gehen kleine Schoofe hoch, wie es Fig. 4 zeigt. Ab Januar fliegen die Enten deutlich zu zweit, also paarweise, ab. Soweit das schwache Licht Farben erkennen lässt, sieht man, dass der Erpel der Ente folgt. Ende April fliegen die wenigen anwesenden Enten ebenfalls paarweise ab. Daneben sieht man auch Männchen allein abstreichen. Nur wenige Enten schliessen sich den abfliegenden Artgenossen nicht an, sondern bleiben auf dem Wasser. Der Abflug erfolgt zielstrebig, Rückkehrer gibt es nicht. Die Vögel fliegen in erster Linie nach den Weser-Wiesen. Entfernungen bis 10 km habe ich festgestellt.

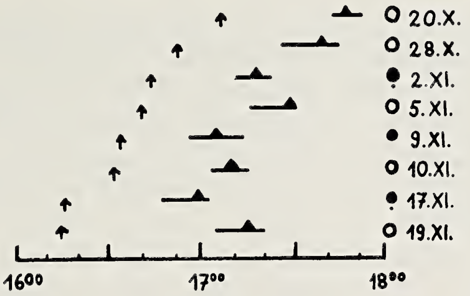

Fig. 3. Duration of the Mallards' departure (abscissa—time; arrows—sunset; horizontal lines — duration of departure; triangles — 50 percent of the Mallards have departed; circles: white — clear sky, dark — cloudy sky, points—rain on date of the observation.

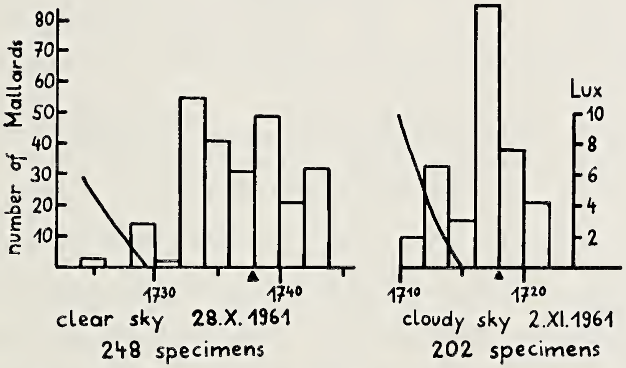

Fig. 4. The number of Mallards departing from Tönebön Lake every 2 minutes in the evening (abscissa—time; triangles—50 percent of the Mallards have departed; curves—intensity of light measured in lux).

In den Morgenstunden kehren die Stockenten weit nach Sonnenaufgang in vielen Schoofen auf den Tönebön-See zurück. Eine geschlossene Heimkehr zu bestimmten Helligkeitsgraden gibt es nicht.

SUMMARY

Dependence of Evening Feeding Flights of Mallards on Light Intensity

In a nature-conservation area near Hamelin, the evening flights of Mallards to their feeding places were observed in relation to the intensity of light. It was established that the time of the Mallards' departure ran parallel to the setting of the sun. It was further observed that the ducks left earlier on overcast days than on clear days. Consequently, it is probable that the Mallard orientates itself to a definite intensity of light. This at least plays a more important part than does the sun's position. Throughout the winter months, the first Mallards leave the lake at a level of brightness of approximately 5 lux. The majority leave shortly afterward when the photometer ceases to register.

In order to compare papers on similar themes, it is suggested that the actual sunset, and not the calculated civil twilight, be chosen as the time element.

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Song Rates and Polygamy in the Long-billed Marsh Wren

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Intensive field studies were carried out by the author during the 1961 and 1962 (through early June) breeding seasons in a Seattle, King County, Washington, population of the Long-billed Marsh Wren (*Telmatodytes palustris*). In addition, alternate weekends during the breeding season were spent observing a population at the Turnbull National Wildlife Refuge at Cheney, Spokane County, Washington, 220 miles due east of Seattle. Seattle is in a temperate marine climate, and its wren population is resident; Cheney's climate is continental, and its wren population migratory. The two wren populations are effectively isolated by the Cascade Mountains; Cheney's has been classified as *T. p. plesius*, Seattle's as *T. p. paludicola.*

The present paper is a preliminary analysis of song rates and mating systems of the marsh wren. The relationships between these two aspects of the species' life history will be discussed, as will the adaptive significance of the mating systems. Comments on conditions favoring evolution of polygamous mating systems will be developed more fully in a later paper to follow completion of the field work.

In 1961, Seattle wrens began building nests in late February, although the first egg was not deposited until 23 March. The last active nest in the study area was destroyed on 5 August. In 1962, nest building commenced on 23 March, and the first egg was laid on 3 April at Seattle, while at Cheney migrants returned in late March and were constructing nests on 1 April. The first egg at Cheney was deposited on 15 April. At the time this paper was prepared, breeding was still in progress in both populations. Seventeen successful, 25 unsuccessful, and 5 incomplete (still in progress) nesting attempts involving 21 males and 23 females have been investigated to date at Seattle. In addition, two Seattle males remained unmated, although on territories, during the full time they were under observation. At Cheney only one nesting cycle had been completed, 7 nesting attempts failed, and 14 were in progress. The Cheney study included 12 males and probably 16 females.

The accumulation of extensive records of time budgeting, principally by males, was accomplished through the use of an elaborate system of shorthand notations whereby all major activities of the birds were recorded in sequence. Observations were conducted from towers erected strategically in the marshes. The standard period of observation was 30 minutes, with time being recorded every minute on signal from an automatic timer. Song-rate data were, perforce, accumulated as a part of the time-budget studies.

I wish to express my appreciation to Gordon H. Orians for his critical

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advice during the preparation of this paper. Thomas H. Frazzetta assisted with the figures.

SONG RATES

It is generally true in monogamous species that song rate drops after pairing, indicating that the presence of a mate inhibits the tendency to sing. Since additional mates may be acquired by polygamous males after their first pairing, it is not surprising that in such forms there have been reports (e.g. Andrew, 1961; Armstrong, 1955) that song rates do not drop after pairing. For the marsh wren, this is well demonstrated by Fig. 1, in which average morning and afternoon song rates are plotted during various portions of the reproductive cycle. Values in this figure are based on 240 hours of observations on 4 functionally monogamous (i.e. monogamous at the time of observation) males at Seattle from 23 March to 6 June 1962. All 4 males show the same trends. Data on functionally polygamous males have not yet been analyzed.

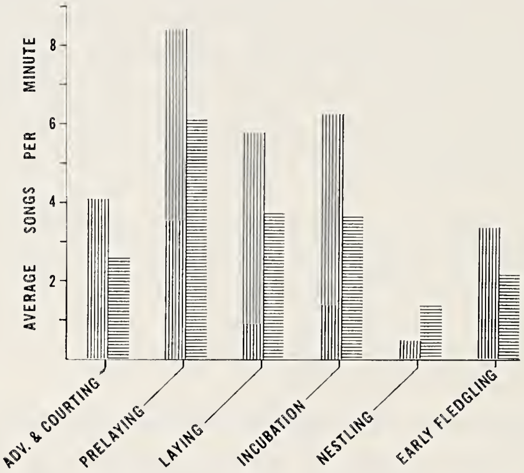

Fig. 1. Variations in songs per minute during different stages of the reproductive cycle. The left column (vertically barred) of each pair is average A.M. rate; the right column (horizontally barred) is average P.M. rate.

The first period, that of advertising and courting, begins with the initiation of construction of courting nests, since this is the first tangible evidence that males are actually seeking mates. The multiple nests built by males of this species have long been called "dummy nests" and have had a variety of functions ascribed to them, including predator decoys and simply excess-energy releasers. They are used as courting sites. A number of these nests are built in a cluster, which I refer to as a courting center.

The second period includes the 3 days prior to laying of the first egg in any nest, be it the first nest of the year or a renesting. The third is the period of laying; the fourth, of incubation; the fifth, of nestlings; and the sixth, that of early fledglings. The morning figure during prelaying and all four figures during the nestling and fledgling periods are based on more limited data than the others.

It is readily apparent that song rate increases after pairing. The very high rates recorded during the 3 days prior to the onset of laying probably serve in at least 2 capacities. It is at this time that the male normally shifts his advertising activities to another portion of his territory, where he proceeds with the construction of a new courting center. This increased song output certainly reflects activity to acquire a second mate. It probably also serves to stimulate his present mate and thus to coordinate the physiological conditions of the pair.

The frequency of singing declines after laying begins and remains fairly constant throughout laying and incubation; but even during these periods there is more song activity than during the period leading to the formation of the first pair bond. This is probably the result of at least two things. First, advertising in the Seattle population begins in mid-March, before feeding conditions are ideal and when average weather conditions tend to be less conducive to song. Moreover, days are shorter and nights longer, so that more food must be accumulated in a shorter time than later in the season to sustain the bird during the night. This means that more time and energy must be spent feeding, leaving less for singing. As the season advances, conditions improve and, theoretically, reach their optimum about the time the young are in the nest. Therefore, during laying and incubation, the time and energy budget can be adjusted in favor of more song. Second, active courtship activities inhibit song to a considerable extent, so part of the lowered early song rate might be the result of courting activities.

A minimum of singing occurs during the nestling period, when the male is actively feeding young. It is not unusual during such periods for a male to be completely songless during the first hour of his active day when, during other periods of the cycle, he normally delivers an average of over 10 songs per minute. Undoubtedly, the demand of foraging for food for the nestlings is the critical factor in this drop. The same applies to the fledgling period. At this stage, however, progressively less time is spent with the young, and the construction of courting nests—the first sign that renewed advertising activities are in progress—may ensue as early as 5 days after the young leave the nest.

The data are, as yet, inadequate to plot song rates during the period leading to the laying of the second clutch; these should provide a test of the notion that the lower rates leading to the first pair bond result primarily from the necessity to spend a greater proportion of time feeding.

Song rates of Cheney males have not been calculated yet, but they appear to be higher than those of Seattle males, and the construction of courting nests proceeds at a more rapid pace at Cheney as well. Furthermore, in contrast to those of the Seattle birds, these activities continue unabated during the nestling and early fledgling periods. These differences are most probably associated with the fact that the males at Cheney do not assist with care of the young, which has definitely had an impact on the evolution of the mating system.

POLYGAMY

The use of the term polygamy is restricted here to cases of simultaneous maintenance of pair bonds with more than one mate. Application of the term to cases of successive pair bonds with different individuals, as has been done by some workers, is not considered correct. Of the Seattle males traced through a major portion of the breeding season 30 percent were polygamous, while at Cheney 50 percent of the males were polygamous. Welter (1935) reported 25–33 percent of the males in New York and Minnesota populations that he studied to be polygamous, with the possibility that one male was trigamous. H. W. Kale II (in litt.) found only 2–3 percent polygamy among male marsh wrens of the *Spartina* marshes of Sapelo Island, Georgia.

In the six bigamous cases investigated to date at Seattle, there was a tendency for the nests of females to be timed in such a way that they did not have young in the nest simultaneously. In Fig. 2, the upper bar of each contiguous pair depicts progressive changes in the reproductive cycle of the first female of a bigamous male. The lower bar depicts that of the second

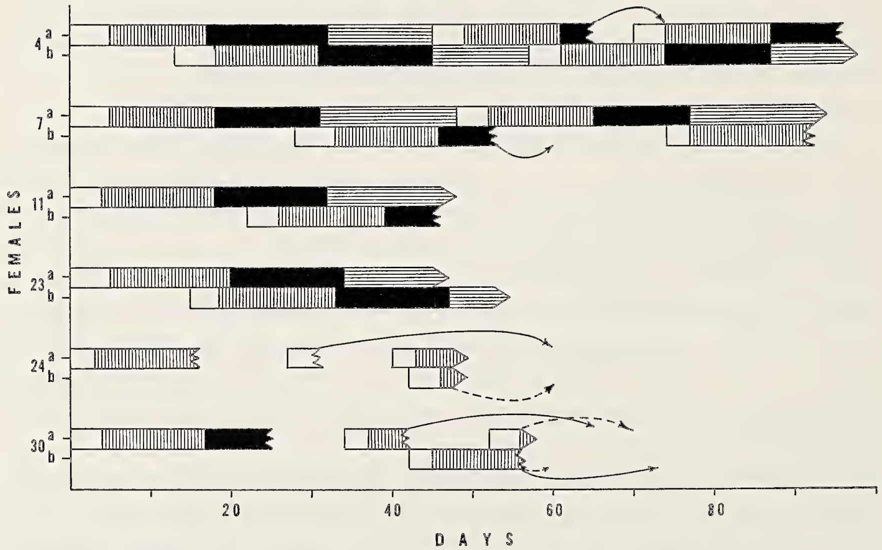

Fig. 2. Coordination of the cycles of females paired to the six polygamous males studied at Seattle. Plain blocks = laying; vertical bars = incubation; black = nestling; horizontal bars = fledgling and prelaying periods. Broken ends indicate nests broken up; points indicate nests still in progress. Dashed arrows denote projected time of hatching; solid arrows denote projected time of fledging.

female, and the cycles of the two females are arranged as they occurred together in time. Females 4*a* and *b* demonstrate an ideal situation in which the later clutches in every case were hatched no more than a day from the time the earlier ones fledged. Even though 4*a*'s second clutch was broken up, an extrapolation of the anticipated date of fledging indicates that 4*b*'s clutch was timed precisely. Moreover, 4*a*'s replacement clutch was timed to hatch on the same day that 4*b*'s fledged. There was no overlap of nestlings in the nests of females 7*a* and *b* or in those of females 11*a* and *b*, although the cycles were not so precisely coordinated as in the first situation. The nest of female 24*b* was timed to hatch about the day the second nest of female 24*a* fledged. However, it is apparent that the last pair of nests of these two females constituted a serious exception to this pattern, since the two birds were laying at the same time and would obviously have had considerable overlap of their nestlings. A possible rationalization of this case is offered below. Finally, the situation with respect to females 30*a* and *b* indicates that their nests may have been timed to incur as many as 6 days of nestling overlap in the first pair of nests and as many as 3 days in the second pair.

Whether or not this timing in general is the result of some unknown mechanism that exerts a control on the onset of laying in the second female cannot be resolved at this point. However, as I shall discuss shortly, there are good selective reasons why this may be true. Furthermore, female 4*a* (Fig. 2) relaid only 5 days after the loss of young 4 days old; so her replacement clutch hatched the day *b*'s fledged. As female *a* wore a distinctive colored-band pattern, there was no doubt of her identification. It is exceptional that she was able to begin laying again so quickly after losing young —a fact borne out by Fig. 3.

As has been found in many other species, the longer a female has been involved with a nest before it is broken up, the longer it is before a replacement is made. Female 4*a*'s performance is indicated by the *X*. Her laying so soon after losing her brood in this case is made more significant by the fact that, after the loss of an earlier brood, she delayed the normal period before relaying. However, in that instance, there was no other female nesting in her territory. It is tempting to suggest that some mechanism triggered an acceleration of oogenesis so that her cycle would be timed appropriately with respect to female 4*b*'s. However, this occurred near the end of the breeding season, which might have affected the time of relaying.

If, in fact, the nesting cycles of the females are coordinated, what possible mechanism could effect this? In a bigamous association, it was a regular occurrence for the second female to visit the nest of the first, during which times lining materials were stolen. A number of changes occurred in the nest of the first female at that time, which might have served to trigger oogenesis in the second female. During laying, the number of eggs increased daily. Toward the end of laying, incubation began, so the eggs were warmer than previously. A timing mechanism could thus rest in either of these factors or a combination of both. Such a system may, in addition, require that oogenesis be inhibited for a period in the second female. The presence of the first female or perhaps the aggressive chases between the two females might serve this function.

It is also reasonable that some behavior pattern of the male could serve to trigger oogenesis in the second female. As observed with changes in song rates of the male, there was a significant increase just prior to laying. That this change could have a releasing function in the case of the second female is a possibility, and its function in this regard could reinforce other selective forces tending to increase song rate at that time, thus resulting in an even greater increase. These mechanisms need not be mutually exclusive but may all be contributing to the control of the cycle in the second female. The following cases, however, tend to favor a mechanism dependent upon the condition of the first female's nest. Female 4*a*'s replacement clutch was begun 5 days after the loss of young 4 days old. At the time 4*a*'s nest was broken up, 4*b*'s nest was in its fifth day of incubation. It seems more reasonable that female *a* was triggered for her replacement by the warm eggs in *b*'s nest rather than by the high song rates of male 4 prior to the laying of female *b*'s clutch, as 10 days had elapsed since the high song rates. Additional evidence in this regard is to be found in a possible explanation of the last pair of nests started by females 24*a* and *b*. In that instance, female *a* began laying her second replacement clutch 2 days before female *b* began laying her first clutch. It was already pointed out that this latter nest would have hatched at approximately the time *a*'s first replacement fledged. Possibly female *b* was stimulated by the eggs in *a*'s first replacement, then, after

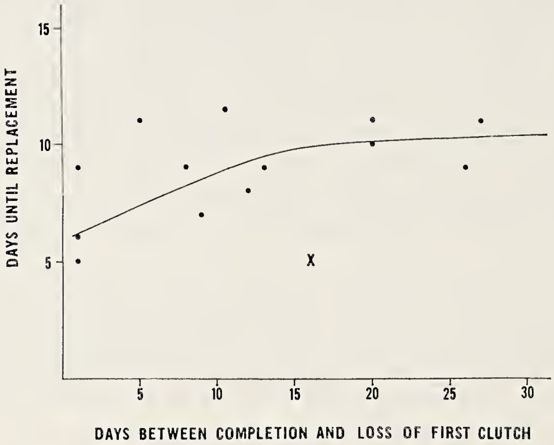

Fig. 3. Number of days required to lay first egg of a replacement clutch as a function of the number of days between the completion and loss of the previous clutch. See text for an explanation of *X*.

the destruction of this nest, oogenesis continued in female *b*, and her eggs were deposited on schedule. Since female *a* began her second replacement before *b* had begun to lay, there may have been no stimulus whereby *a*'s clutch could be timed.

The adaptive significance of such a scheme is clear. In the Seattle population, the males assist with feeding the nestlings and, to a lesser extent, the fledglings. With nestlings in only one nest at a time, the male is free to devote full time to feeding the young in each nest in succession. In this way he probably leaves a higher proportion of offspring than he would were he required to carry food to two nests at once. It is also of advantage to the females for the same reason. There should thus be selection against any tendency to time the cycles with much nestling overlap. The effects of this selection would become more severe the more overlap there is between the nestlings. Overlaps of only 1 or 2 days probably have negligible effect, since the males normally do not begin feeding until 2 or 3 days after the first young hatches. Intuitively, then, any mechanism whereby the cycles of the females could be appropriately timed should be favored by selection.

At Cheney, in the migratory population, where the males do not assist with care of the young, there would be little or no advantage conferred upon females that timed their cycles for nonoverlapping nestling periods. Consequently, one would expect additional females to be acquired in a more random fashion, which is apparently the case. Furthermore, this should increase the total number of females that a male could acquire, since nestling periods could overlap. This notion is supported by the facts that of 6 multiple pairings at Seattle, all were bigamous, while of 5 at Cheney 4 were bigamous and 1 was trigamous. In addition, Welter (1935) reported that males in his New York and Minnesota populations rarely (never?) cared for their offspring, and he found one case that he thought may have been trigamous; Kale (in litt.) found male parental care and only monogamy and bigamy among marsh wrens of Sapelo Island, Georgia.

We can legitimately ask why any female should choose to mate with a male that already has a mate since, even in spite of an arrangement such as that described above, there will be certain disadvantages to the female as a result of inevitable shifts of attention by the male between the interests of the two females. We are probably not faced here with a situation in which there is much, if any, surplus of females. This conclusion can be reached on theoretical grounds alone (Fisher, 1930; Kolman, 1960), but in support of it are records of a number of males that maintained territories, organized courting centers, and sang actively in vain attempts to attract a mate. In some cases, females paired with males that were already mated, even though an unmated male was currently occupying the adjacent territory, and presumably these females could have paired with either male. It follows that there were definite differences, either between the males or their territories, that were somehow responsible for determining which pair bond was formed.

Most likely both these factors were important, and the assumption is reasonable that the more successful males, on the average, were those that defended the more attractive territories. The fact that females selected mated males in favor of unmated ones indicates that, whatever these differences were, the advantages to a female of being able to settle in a more suitable situation outweighed the disadvantages of losing some of the male's attention.

In order for polygamy to evolve in the face of sexual selection, then, the habitat must provide a mosaic in which different habitable areas are qualitatively or quantitatively diverse enough so that a female could rear more young in a polygamous association on a good territory than she could in a monogamous association on a poor territory. Moreover, the population must be large enough so that some males are forced to occupy the poor, or "marginal" sites. Clearly, then, polygamy can evolve in spite of a 1:1 sex ratio, and it is not always correct to think of polygamy as the by-product of an unbalanced sex ratio (Armstrong, 1955; Orians, 1961). In fact, it may be possible to maintain a monogamous mating system in the face of a highly unbalanced sex ratio (see French, 1959).

SUMMARY

Breeding populations of the Long-billed Marsh Wren (*Telmatodytes palustris*) were studied during the 1961 and 1962 seasons at Seattle, Washington, and during 1962 at Cheney, Washington, 220 miles east of Seattle. Seattle's population is resident, Cheney's is migratory.

Song rates of four Seattle males were found to increase after pairing, remain steady throughout laying and incubation, and decrease tremendously during nestling and fledgling periods. These changes are believed to depend upon the polygamous mating system, the role of the male in parental care, and effects of weather and photoperiod on time budgets. Failure of song rates to drop during nestling and fledgling periods in Cheney males was undoubtedly associated with their failure to contribute to the care of their offspring.

Polygamy has been reported in all populations of marsh wrens that have been extensively studied. At Seattle, cycles of females in polygamous associations were timed to incur little or no nestling overlap; this was apparently not true at Cheney, a difference again attributable to the different roles of the males in parental care. Male parental care and cycle timing in Seattle wrens tended to limit those males to bigamy, whereas the Cheney males were not so restricted.

It was suggested that polygamy can evolve in areas providing very diverse, but habitable, sites; that it will evolve in spite of a 1:1 sex ratio; and that monogamy may persist in spite of a highly skewed sex ratio.

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The Breeding Biology of the Orange-breasted Sunbird, *Anthobaphes violacea* (L.)

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The Orange-breasted Sunbird (*Anthobaphes violacea*) is one of the 104 species that belong to the Nectarinidae. This family is distributed over southern Asia, the Philippines, and Africa; to it belong some of the most beautifully colored birds, including the males of the present species (Fig. 1). This species only occurs in the southwestern, southern, and southeastern part of the Cape Province, South Africa, and its distribution coincides with the presence of members of the heath and Proteaceae families. Relatively little is known about its biology. During the period 1951–61, the author carried out a detailed investigation into the breeding biology and behavior of this species. A full account of the results will appear in *The Ostrich* in

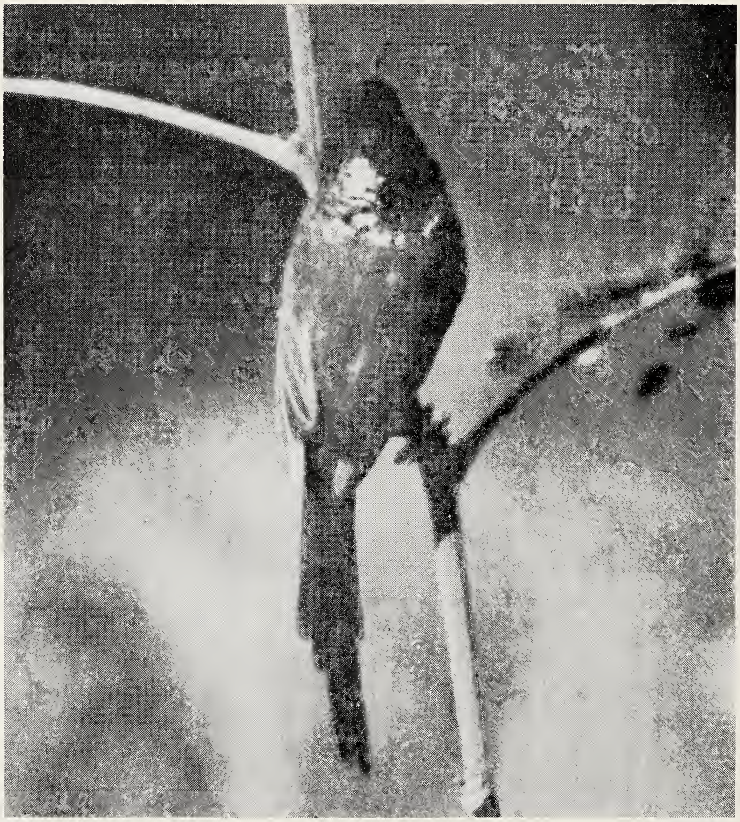

Fig. 1. Orange-breasted Sunbird: male on perch, relaxed.

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1963, but at the XIIIth International Ornithological Congress at Ithaca the author briefly reported on several of the more important aspects of this study, and the present paper must therefore be considered to be an abstract.

During the course of the investigation, most of which was carried out in Kirstenbosch near Cape Town (Fig. 2), it soon became clear that *A. violacea* defends a breeding territory. Evidence obtained from ringed birds showed that during the breeding season, lasting several months, the male and the female spend much of their time in a restricted territory. At the end of the breeding season, territorial behavior wanes, and the male ceases to defend the territory; he and the female may then leave the territory altogether. At the beginning of the year, often from February onward, the males again start defending their territories of the previous year. Gradually the females come back to the territory and later pair again with their former mates. It

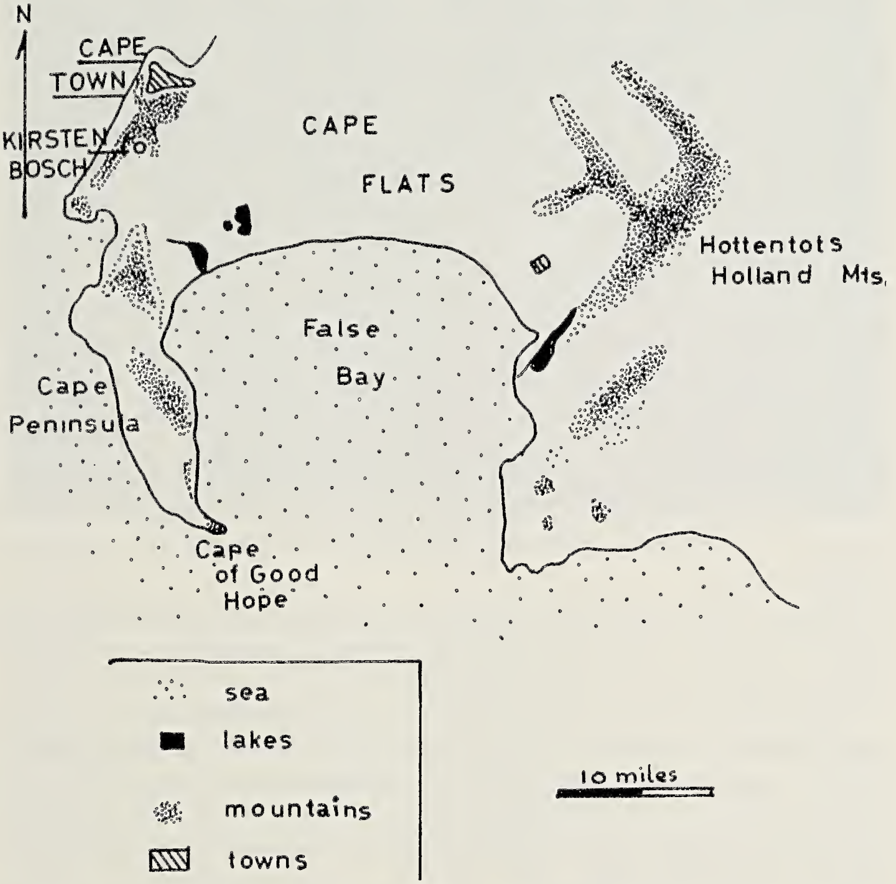

Fig. 2. Map of the area where most of the observations were carried out. The two main observation centers were Kirstenbosch and the northwestern slopes of the Hottentots Holland Mountains.

seems that in the Orange-breasted Sunbird, therefore, one of the consequences of the territory is that the partners of an established pair again come together. In one case the same male defended the same territory for five consecutive breeding seasons. The size of the territory defended by *A. violacea* is rather restricted and seldom exceeds half an acre.

According to published information (Sclater, 1900; Gill, 1936; Roberts, 1940), *A. violacea* is a winter breeder. However, no detailed information based on sufficiently large numbers of breeding records seems to have been published. During the present investigation, use was made of 218 records of nests containing eggs and 130 containing young. In addition to my own observations, use was made of the nest-record cards of the South African Ornithological Society.

It was found that, in general, the breeding season for the vicinity of Cape Town extends from February to the end of November. There is, however, a marked difference between the peak of breeding activity for birds in the Cape Peninsula (June, July, August, and September) and birds occurring on the other side of the Cape Flats, i.e. on the lower slopes of the Hottentots Holland Mountain range (April, May, June, and July). When the results are graphed, the shape of the graph suggests that in this species the female has more than one clutch in a breeding season.

For a total of 194 nests, the type of plant in which the nest was built was recorded. In 48 percent of these cases, the nests were in Proteaceae. In 18 percent they were in heath and Compositae. Proteaceae are, therefore, strongly favored.

Analyses show that 76 percent of 292 nests were not higher than 1 m above the ground. Only 1 percent was between 2 and 3 m, and 6 percent were in the upper branches of trees (Fig. 3).

The position of the nest is the result of selection of nest site. It is usually very difficult to establish which of the two partners makes the decisive selection. It seems, however, that in this species the actual spot where the nest is going to be can be selected by either of the two sexes. They probably both look for suitable spots, and final selection depends on which is the more dominant bird at the time.

Many times the building of the nest was watched, but never was the male seen to build. The female's building technique is very simple. It consists of accumulating nesting material and pressing and molding it into shape by pressing the body against it with quick sideways movements, while legs and feet are pushed backward. By pulling and pushing and rearranging with the bill, the walls and eventually the hood-like roof are formed. The result is a rather neat pouch-shaped nest. In 1,233 observed cases involving five different females, the female was attending to the nest but was actually building in only 123 (10 percent) cases. In the other cases, she was just bringing nest material. In 79 cases, the time during which the female stayed on the nest while "building" was recorded. It was found that in 75 percent of the

Fig. 3. Orange-breasted Sunbird nest in top of silver tree.

cases she did not stay longer than 2 minutes each time, but in exceptional cases she stayed longer, even as long as 11 minutes.

The nest material consisted of small dry twiglets, usually heath, cobweb, and soft vegetable fluff.

For a total of 182 half-hour periods, involving 16 different nests, the rate of building activity was recorded. The figures show a tremendous variation from hour to hour and during any hour of the day. If the means are compared, however, there is a strong indication that building activity was greater during the first part of the day. The mean for the period 07–14 worked out at 9 visits per half hour, while the mean for the rest of the day (14–18) was 6. The difference is significant at the 5 percent level.

Bad weather usually interrupted building activity in this species. The species, therefore, definitely is a *sunbird.* It takes from 10 to 18 days to complete the nest. It was further found that different nests built by the same female could be placed at very different heights, and that a particular female does not have a definite preference as regards the height above ground at which she builds her nest.

For 15 nests the interval was established between the last day that lining material was brought to the nest and the day the first egg was laid. The figures varied between 2 and 8 days, with a mean of 3 days and a standard deviation of 0.68. It therefore seems that in this species there is a rather short interval between cessation of the building urge and the onset of the egg-laying urge.

Birds generally lay in the early morning, and in most cases there is an interval of close to 24 hours between eggs, but there are exceptions (Broekhuysen, 1959:195). The time at which the Orange-breasted Sunbird lays its first egg was determined 8 times, and 15 times for the second egg. It was established that the first egg is laid in the first 2 hours after sunrise and the second the next day, also during the early morning hours.

Of a total of 250 nests of known clutch size, 77 (31 percent) contained only one egg, while the rest had two eggs. Measurements for 120 eggs gave a mean of 12.4 mm (stand. dev. 0.4) × 16.5 mm (stand. dev. 0.7). When 26 first-laid-egg measurements were compared with 16 second-egg ones, no real size differences between first and second eggs could be established. Because several of the females kept under observation were ringed, the number of nests built and clutches produced by the same female during one breeding season could be determined. It was found that as many as 6 nests could be built and 3 successful broods reared.

In all observed cases, incubation started properly only after the clutch had been completed. During the present investigation, the behavior of incubating females at the nest was observed and recorded for a total period of just over 72 hours. In several cases, a nest was kept under constant observation from sunrise until sunset. The time spent by the female covering the eggs during any hour varied from 12 to 100 percent, but if the means are worked out for the different hours of the day, they varied relatively little, i.e. between 51 and 75 percent. The total mean works out at 65 percent, with a standard deviation of 19. The incubation pattern of the Orange-breasted Sunbird female does not show any significant variation during the day.

Observations showed that the incubating female nearly always leaves the nest for only a short period (about 8 minutes). This period, however, was significantly higher during the late afternoon. Seven times when the female left the nest for the first time after the night-incubation session, she left within half an hour before sunrise. On 5 occasions when the female returned to the nest after her last feeding excursion for the day, she settled on the nest for the night during the first quarter hour after sunset. The incubation time in 15 cases appeared to be 14½ days. Hatching was not limited to a particular time of day.

Observations on the parental behavior of birds attending young showed that the female Orange-breasted Sunbird continues covering her young in the nest for a considerable time during all stages of their development. Even in the first days when the young are out of the nest during the daytime, the female still covers them during the night when they return to the nest.

Information on feeding rates, gathered for a total of 111 one-hour periods,

Fig. 4. Female sunbird has just come to the nest to feed the two nestlings.

shows that the birds averaged 5.9 feedings per hour, with a standard deviation of 2.8. The means for different hours of the day indicated that the feeding rate during the whole day was rather constant.

Although the male does not share in the nest building, he does feed the young. Based on eight different nests, the total number of records of parent birds feeding their young was 427 feedings by the female (Fig. 4) and 231 by the male. It therefore appears that 65 percent of the feeding of young was by the female and 34 percent by the male.

In 319 cases, 56 percent of the food brought to the young consisted of insects and 42 percent of spiders. Of the insects, 83 percent were Orthoptera. Very often the parent birds collected food for the nestlings outside the territory. When foraging for themselves, they often fed inside the territory.

The duration of the period between hatching and leaving the nest for the first time varied on 11 occasions from 15 to 22 days and averaged 19 days. The development of the young Orange-breasted Sunbird will be dealt with in the fuller report on this investigation. It appeared that the weight of the recently hatched young is about 11 percent of the weight of the adult. Nice (1943) has shown that in most passerines the weight at hatching is approximately 6–8 percent of the weight of the adult, and the figure for the Orange-breasted Sunbird, therefore, seems to be somewhat higher.

After having left the nest, the young will come back for several days toward evening, and in the beginning they are actually joined by the female. Observations showed that it was the female that led the young back to the nest. At five different nests, the young came back in the evening for periods varying from 6 to 15 days. The female joined them during the first 6 days.

As all young were color-ringed, the duration of the postnestling stage could be determined in a number of cases. It was thus found that Orange-breasted Sunbird young remain at least partly dependent on the parents for just short of 3 weeks after having left the nest for the first time.

Of a total of 93 nests containing eggs, 70 percent produced young, while in 30 percent none of the eggs ever hatched. Of 44 nests containing young, 72 percent reached a stage where young were leaving the nest. The hatching rate of eggs appeared to be 65 percent, and the fledging rate of nestlings 68 percent. Of a total of 142 eggs, 39 percent produced young that reached the fledging stage. These figures were obtained by the conventional method. If they are worked out according to Mayfield's (1961) suggestions, the percentages are somewhat lower but not very much.

The impression was gained that Orange-breasted Sunbirds in the area under observation did not get much older than 2–3 years, although one ringed male was seen in its territory during five consecutive years, after which he very likely came to grief in territorial fights with another male.

SUMMARY

During the breeding season, male Orange-breasted Sunbirds defend a territory seldom exceeding one-half acre. The peak of breeding activity is June–September in the Cape Peninsula, April–July on the other side of the Cape Flats. Nest sites were selected by either sex, most often in Proteaceae, and usually 1 m or less above the ground. Nests were built entirely by the female in 10–18 days. Eggs were laid, on the average, 3 days later, in the early morning. Clutch size averaged 1.7 eggs, no real differences between the first and second eggs being apparent. As many as 6 nests were built, and 3 broods were raised by a single female in one season. Females on an average incubated 65 percent of an hour during the day; incubation time appeared to be 14½ days. Recently hatched young had a weight about 11 percent of that of the adults. Both parents fed the young on an average of 5.9 times per hour; fledging averaged 19 days, and young remained with their parents just short of another 3 weeks. Hatching success was 70 percent, fledging success 72 percent.

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Life History of the River Warbler *(Locustella fluviatilis)* Near Budapest

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The River Warbler is one of the most common bird species in Hungary—in sites suitable for its needs. However, due to its extreme secretiveness, not even cursory observations have as yet been published on its habits.

My intensive and regular researches with regard to the species were carried out in 1960 and 1961. I previously had made occasional observations throughout much of the country, especially at the time of its nesting. Before proceeding, however, I should outline the distribution of the River Warbler in Hungary and refer to its range in general.

The center of its abundance is eastern Europe, from where it spreads in gradually lessening density to the eastern parts of central Europe and western Siberia. It spends the winter in eastern Africa. In Hungary, the bird follows the inundated woods of only the larger rivers, being frequent also in the marshy alder woods sprouting in former swamps. Thus, it is common in the gallery forests mainly of the Danube and the Tisza, and in the alder groves of the peaty marshes of the Hanság and around Ócsa where one may almost always find it living with the Icterine Warbler (*Hippolais icterina*), the Garden Warbler (*Sylvia borin*), the Blackcap (*S. atricapilla*), and the Nightingale (*Luscinia megarhynchos*). It also occurs sporadically on the shores of certain brooks that have been closed over by alder trees, especially in the Sopron and Bakony mountains.

Although my data on its life history are based on observations made at nests found in the alder woods at Ócsa in 1960 and 1961, I shall still submit here every known evidence from earlier experiences in order to present as true and as generally valid a picture as possible of the species in Hungary.

The intensive observations were carried out in April, May, and June in 1960, and chiefly in June and July in 1961. My data gained in the first year related to spring arrival, occupation of the territory, construction of the nest, laying of the eggs, and the incubation period. In the second year, I aimed at studying the fledging period, the activities after the young have left the nest, and the fall departure.

The first River Warbler arrived on 3 May in the alder woods of Ócsa in 1960. Two days later, I could hear its characteristically *churr*ing voice in several places, while on 12 May the whole forest resounded to the calls of many singing males. The belated arrival of 1960 was probably due to the cold spring and the locally high ground water in the woods. According to the nation-wide mean computed from migration data obtained regularly since 1878, the species reaches Hungary on 1 May.

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Any direct observation of the courtship or mating is, due to the extremely secret habits of the female, almost impossible to carry out or is at least an extraordinarily rare occurrence.

The males began to sing almost immediately after their arrival on several locations on the study area. The nuptial song differs in that the bird sings always from exactly the same place, usually low, on the side branch or top of a suitable bush. On the other hand, its notes marking the nesting site are frequently uttered from a very high perch. In the latter case, the male flies in an unvarying direction to its singing tree, from whence it sings and at the same time turns around and around. At such times, its voice has a ventriloquistic quality, and thus it is often very difficult to find and observe the singing bird. Its nuptial song differs from its territory-locating one in its varying strength, causing the same misleading effect as with its turning around. Its well-known disyllabic *churr* is introduced by a melodious but very low strophe, audible only in the immediate vicinity. When, on 17 May in Ócsa, together with Guy Mountfort and Eric Hosking, we recorded and replayed its song on tape, this melodious introductory tune was clearly perceptible.

Owing to the extreme secretiveness of the bird, my observation of the nest construction was successful in a single case only, and even then not encompassing the construction proper but just the rate of construction from time to time. I found this nest on 10 June 1960, when, after a long and extremely careful search, I caught sight of it on the edge of a clearing full of nettles in the alder woods of Ócsa. The outer case or rather the beginnings of the nest was among five nettle stems and consisted of sedge leaves 15–20 cm long and 1 cm wide. The nest was woven on almost the outermost plants of the dense nettle growth of the clearing and was in a favorable light. The bird built the nest for 4 days, and the nest could be observed only because I was able to watch it from the equally dense, dark young alder wood forest without any undergrowth. The bird is so extremely shy and sensitive to any disturbance that it might have been utterly frightened away by my just walking around in the nesting area, if that had been the circumstance. This situation raises the gravest difficulties when one is searching for the uncommonly well-concealed nest in order to study the life of the bird. I may safely assert that, of all Hungarian species, this bird is the most difficult to observe.

The nest was finally finished on 14 June. Its outer, rather heavy (thick) envelope consisted of sedge leaves, interwoven or fastened to the nettle stems carrying it. The internal padding was made from the 1-mm-thick stems of a smooth, rush-like plant. There were also some decaying alder leaves from the previous year inserted in the outer cover. Unfortunately, I was never successful enough to observe the bird during its constructing work. It seems that even the most perfect concealment may be inadequate to allay its apprehension. In all probability, the bird caught sight of me when I approached the hide. In connection with its timidity or cautiousness, I have to remark that, in accordance with the findings of all observers, the River Warbler will—at the very slightest disturbance—always desert the nest that is under construction. Thus, the watching of the nest construction belongs to the rarest of phenomena. The measurement data of the nest mentioned above (Ócsa) are as follows: inner diameter, 6.5 cm; outer diameter, 12.0; cup depth, 5.0; height of nest, 11.5; bottom of nest above ground, 10.5.

Both in the alder woods at Ócsa and in the Hanság, nests of the River Warbler were placed in highly similar situations, but none were at sites that would have allowed direct observation.

The nest described above, by chance in a favorable situation for observation, does not concur, as regards dates, with the regular period of nest construction, since the accumulated ground water in 1960 was unusually high and subsided very slowly. According to my findings in 1960 and those of previous years made in the Hanság, the nests are completed between 20 and 30 May.

The entirely finished nest was yet free of eggs on 15 June, nor did the bird show itself. The first egg must have been laid in the early morning on 16 June, since it was there at 7 A.M. The whole clutch of five eggs was laid in 5 consecutive days, but incubation began only after the laying of the third egg. From then on, the bird sat rather tight, and, even if it left the nest due to some suspicious noise, it soon reappeared. Never did the bird fly directly off the nest; it stepped out and rapidly walked away with a straight, drawnout posture (rather resembling that of the Nightingale), wings tightly closed to its body. Nor did it lurk on its way back, a peculiar and striking behavior as compared to that of the Grasshopper Warbler (*Locustella naevia*) and Savi's Warbler (*L. luscinioides*).

When measuring the eggs, I found the same phenomenon as with the Red-legged Falcon and the Lesser Grey Shrike ("The Life of the Red-legged Falcon *Falco vespertinus* in the Ohat Forest," Acta XI Congr. Intern. Ornithol. 1954, Basel, p. 583–587, 1955; "The Life of the Lesser Grey Shrike *Lanius minor* Gm. in the Great Plains between the Villages Alsónémedi and Ócsa, near Budapest, Hungary," Proc. XII Intern. Ornithol. Congr. Helsinki, 1958, p. 317–326, 1960), namely that the first-laid egg was the smallest and the last one the biggest. The readings are as follows: 20.2 × 14.8; 20.2 × 15.0; 20.4 × 14.9; 20.6 × 15.0; 20.6 × 15.1. Four-egg clutches probably originate from young pairs nesting for the first time. Very rarely does the bird lay six eggs; at least I never found such a clutch. Among 8 full clutches, the mean clutch size was 5 eggs.

In the nest studied at Ócsa, the eggs hatched on the thirteenth day after incubation began (18 June). There were no addled eggs. During my observations, the incubating bird was never relieved by its mate, and thus it is highly probable that only the female incubates. The male sings during incubation, a fact that would substantiate the above assumption.

The River Warbler—and presumably the same pair—nested again on the edge of the small nettle-covered clearing in 1961. This nest was only 4 m away from the site of the previous year. The dry spring suggested the possibility that the birds might nest at the regular time, hence it was not surprising that I found the finished but still-empty nest on 26 May. The 5-egg clutch was again laid in 5 days, and both the measurements of the eggs and the characters of their hue and pattern also indicated their origin from the pair of the previous year. The eggs hatched on 10 June, after an incubation commenced at the time of the laying of the third egg. The adult birds now became shier than ever. The male stopped singing and, together with the female, diligently carried food comprised of insect larvae and small orthopterans. I observed repeatedly that the adult birds flew to the adjacent edge of the woods and then dropped to the ground. Surely they captured grasshoppers on such occasions. Hidden in the edge of the forest, I observed once that one of the adults flew out some 50 m to the nearby meadow hunting grasshoppers. The bird can carry simultaneously more than one insect, so that after a prolonged search it can bring back a considerable load to the nest.

The fledglings left the nest and its vicinity on 27 June after an unusually long period spent in the nest for such a small bird (16 days). They were thereafter always to be found in the dense shrubbery of the nearby forest margin. Very strikingly, the male now began singing again, but on lower perches than before. Its *churr*ing song was always uttered from the low side twig of the same bush, its starting place for hunting insects. I found the family here on 10 July for the last time. Thus, the fledglings may have become independent just 2 weeks after leaving the nest, although I am unable to say whether they became truly free of the nest or were just wandering about with their parents.

Both in the alder woods of Ócsa and the Hanság, the fall departure of the River Warbler took place during the last days of August. In the gallery forests of the Danube, especially in the southern stretches (e.g. in the Béda woods south of Mohács and in the Béllye forest now in Yugoslavia), the birds were still in their nesting area even during the first days of September in previous years. One might come across them during migration also in larger gardens in the vicinity of dwelling houses.

SUMMARY

The average arrival date of River Warblers in Hungary is 1 May. Nesting birds are very shy but common in the inundated woods along the larger rivers, as well as in nearby alder woods. A nest required 4 days for construction. Eggs were laid on consecutive days; incubation, commenced after the laying of the third egg, was apparently carried on by the female only, and required 13 days; young fledged in 16; and the family remained together for at least 14 more days.

Renesting of the Alder Flycatcher

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The Alder or Traill's Flycatcher (*Empidonax traillii*) is a common breeding bird in southern Wisconsin. From 1943 through 1948, this species was the subject of an ecological study on the 1,100-acre University of Wisconsin Arboretum at Madison, Wisconsin. The object of this paper is to discuss one phase of that study, namely the factors associated with the renesting after an initial attempt had failed. To the best of my knowledge, the Alder Flycatcher is single-brooded, and therefore renesting cannot be confused with second nesting. At one point in the second year of the nesting part of the ecological study, two nests disappeared completely from well-marked locations. Although circumstances did not seem to justify the deduction, I concluded that the first of these two nests was taken by vandals. When the second nest vanished in like manner, a thorough search of the ground cover below the nest bush disclosed the *lining* of the missing nest. This evidence was enough to make the nesting pair suspect in the nest destruction. To test this hypothesis, a flycatcher nest was found away from the study area; the eggs were removed, and into the nest were sewn short lengths of colored wool yarn. I reasoned that, if nest material was transferred after breakup, the yarn would also be removed to the new site and the renest could then be identified with certainty. After the test nest had been pulled apart for several days, the site was examined. The nest had been dismantled and, as before, all that remained on the ground was the nest lining plus *all of the colored yarn.*

Another nest was found and again broken up by my removing the eggs. The experiment was repeated, but this time knotted gray cotton wrapping strings similar in color and texture to the nest material were included with the colored yarn. The colored wool additions were rejected as before, but the gray strings were transferred and incorporated in the new nest.

This simple experiment showed that Alder Flycatchers moved the nest material from an original nest to a renesting site and that colored wool yarn was rejected when added to the original nest material. Of these two obvious deductions, only the former seemed important at the time. In all probability, the disappearance of other nests in the ecological study was caused by the shifting of nest material to a renest site.

Nest moving is not rare in ornithological annals. Blathwayt (1903) made these observations on the nests of three Lesser Redpolls (*Linota rufescens*): "The evidence from these three cases also goes to prove that this species, when disturbed in nesting operations, will remove the materials from the spot which has been discovered, and use them in forming a new home." Sim-

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ilarly, Scholey (1922) states of the Reed Warbler (*Acrocephalus s. scirpaceous*): "It is so with the Reed Warbler: if the first nest meets a tragic fate they commence to pull it to pieces and build another with the same material a yard or so away." And, "The use of the [nest] material from number one no doubt facilitates the work on number two and relieves the bird of a considerable amount of hunting for suitable material." What Scholey says may be true, but he does not tell us what reasons, if any, may cause the Reed Warbler to behave as it does.

I suggest two reasons for such behavior by the Alder Flycatcher. First, the source of the chief nesting material, clumps of last year's marsh milkweed (*Asclepeis incanata*), appears to be extra-territorial and used as community property. First-nest building also occurs at a time when "using-area" lines are not as well defined as they are later in the nesting period. Using area (in lieu of territory) is here defined as the area in which the pair is observed during nesting. Generally, these areas are elongate in shape. Thus, what was once regarded as community property at the time of the original nesting may at the time of renesting lie within the using area of another nesting pair. Secondly, if a nest is broken up late in the incubation period, the plant growth around the last year's marsh milkweed stalks may be so tall that the clump is obscured and, from an ecological point of view, may be unavailable.

Some new material is undoubtedly gathered for most renests, and on occasion a renest is built entirely with new material.

Nest moving has also been recorded by Borrer (1923), Lewis (1924), Eastwick-Field (1901), Ingram and Salmon (1923), and Ericksen (*in* Bent, 1950). This list is not complete. In none of these recorded cases were either the birds or the nests marked for absolute identification.

A re-examination of this nest-moving phenomenon some 15 years after its discovery among Alder Flycatchers forms the basis of this report. In the spring of 1960, prompted by the analysis of the earlier nesting data, an expanded series of experiments was undertaken to recheck nest moving by this species, and to re-evaluate the rejection of colored material added to the nests. The tests were continued in 1961.

Nesting of the Alder Flycatcher in the Madison region begins about 5 June. At this time, there is much fighting among the birds, but territories in the conventional sense are difficult to delineate. Nest building takes from 4 days to a week, after which a clutch of four eggs is laid in a nest of plant fibers that is built in a shrub or tree about 4½ ft above the ground. I believe that only the female incubates. The cream-colored eggs with a circle of brown spots on the blunt end hatch in 13 days, and the young remain in the nest for another 13 days before they fledge. The brood moves about the marsh for several weeks after fledging, and by 1 August the nesting area is deserted.

I am grateful for the many services performed by O. J. Rongstad, who

was my field assistant, and also to R. L. Brenckle and E. D. Ables for field assistance. Appreciation is extended to K. H. Gerdes and J. M. Franz, who were consulted regarding clarity of expression in German, and to J. J. Hickey and Marie S. McCabe, who gave advice on improving the manuscript.

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STUDY AREAS

Two study areas were selected, one of 7.6 acres (3.08 hectares) on the University of Wisconsin Arboretum, and one of 12.2 acres (4.94 hectares) in a marsh 3 miles west of Madison at Middleton, Wisconsin. Although the size of the two areas differed, the amount of nesting substrate was about the same. The Arboretum area had a greater diversity of shrubbery suitable for nesting: tartarian honeysuckle (*Lonicera tatarica*), red osier dogwood (*Cornus stolonifera*), elderberry (*Sambucus americana*), swamp birch (*Betula pumila*), and willow (*Salix* sp.) were common. On the Middleton area, elderberry predominated, with some willow and red osier dogwood along the edges. A series of ponds bordered the inside of the long axis of the Arboretum area and a creek ran along the short axis of the Middleton area. Both areas had a wide variety of herbaceous ground cover, and both had a blacktop road running along one of the sides. The distance between the two areas was about 5½ miles. Each could be classed as excellent Alder Flycatcher habitat.

EXPERIMENTAL PROCEDURE

On about 10 June, each of the study areas was searched for active Alder Flycatcher nests. Sites were marked for easy finding and rechecked every 3 or 4 days. When the nests had full clutches, the eggs were removed. Into the nest body was woven five 6-inch lengths of red, orange, yellow, blue, and green darning cotton (as opposed to wool yarn used in the earlier tests), as were five pieces of neutral-gray darning cotton. This latter group of threads simulated the plant fibers from which the nest was built. All threads were given a combination of knots by which the individual nests could be recognized. All singing and nonsinging birds observed were associated with nests, or their movements were checked until such association was established. Notes were kept on the activities of the various pairs, so that searching for the renests was not entirely by trial and error. In several instances, the movement of the nesting material was observed from afar with the aid of field glasses. No close-quarter observations from blinds were made for fear that the original nest would not be moved. After the renest was found, it was checked regularly to determine its fate. When renesting was completed, the distance between the nestings was measured, along with the height of the nest and the height and kind of bush. In 1961, the nest-support angle and the diameter of the principal supporting branch were also measured.

On the Middleton area in 1961, natural predation occurred at three renests early enough in the renest attempt so that a third nest was built. One such case occurred on the Arboretum area. An earlier attempt to get birds to build three nests by destroying the eggs in the renesting effort failed to produce a third nest.

When all young had fledged, the old nests were weighed, measured, and the number of threads transferred determined. Some colored threads were transferred when cotton was used in place of wool, but since not all threads were carried over, the element of color preference, rejection, or confusion was investigated through an appraisal of the number of transferred threads of various colors among the nests.

RESULTS AND DISCUSSION

The data will not be compared between years or between areas. The primary comparisons will be made between the original nesting and the renesting.

If a bird such as the Alder Flycatcher is forced to move its nest because of predation, does it seek out the same physical characteristics from the environment as were used in the original nest, or does it alter the choice in order to give greater security to the second nest? In answer, it may be generalized that no alteration of the original choices was evident between first nests and renests. The individual aspects tested were as follows:

Kind of Bush.—Five species of shrubs and one tree species were used in 25 nesting and renesting attempts. In only two cases between original nest and renest was a shift made in the kind of bush used as the nest substrate: from hazel (*Corylus americana*) to gray dogwood (*Cornus racemosa*), and from tartarian honeysuckle to red osier dogwood. Four of the 25 nestings were triple nestings and in all four the kind of bush was the same (3 in elderberry and 1 in red osier dogwood) in the three nesting attempts.

Height of Bush.—The average height of the shrubs used in the initial nesting attempt was 87.4 inches (2.2 m) and the average height of the bushes used in renesting was 86.0 inches (2.18 m). When these data were paired and tested, no significant difference was found between these mean heights. Thus, the flycatchers observed here chose the same-sized bush for nesting and renesting. One bird nested and renested in tamarack (*Larix laricina*). The measurements from the tamarack nests were not used in the above averages.

Height of Nest.—The average height of 20 original nests was 55.8 inches (1.42 m) and the renests 56.3 inches (1.43 m). Again there was no significant statistical difference between these means. Thus, the Alder Flycatcher may be said to select nest bushes about 7 ft high and to build its nest at 4½ ft. Were it not for the dense cover and the spacing, nests of this flycatcher would be easy to find. Only rarely, however, can a nest be regarded as difficult to locate.

Nest Angle. — The rim of a newly built nest is always parallel to the ground, but the main supporting branch may vary from a perpendicular support directly under the nest (90° angle) to a horizontal support extending laterally under the nest base (180° angle). In 1961, I measured the angles of support on all original nests and renestings. No statistically significant difference was found between the two means. Of 12 pairs measured, 5 increased the angle of support, 4 decreased, and 3 remained the same.

Diameter of the Supporting Stem. — If greater rigidity or strength was sought in renesting, the stem diameter 6 inches below the nest should have been greater. In four cases out of nine the diameter (measured to 1/32 inch) was less than that for the original nest; in two cases it was greater and in three cases it was the same. As in the other comparisons, there was no significant difference between the means of the stem diameters of the original nests and those of the renests.

Nest Relocation and the Using Area.—There was no apparent attempt by the Alder Flycatchers because of nest predation, artificial as it was in this test situation, to alter their behavior toward the environment. Although the nest location changed when the eggs were destroyed, I believe that the renesting is located within the using area of the male. When a nest was moved, it was along the long axis of the using area. The mean distance between the original and the renesting site for 25 relocations was 80.3 ft (24.48 m).

The propensity of the bird to move along the long axis of the using area was shown in the movements made by the four pairs that nested three times. The average distance from the original nest to the renest was 90 ft (27.43 m); from renest to second renest, 101 ft (30.78 m); and from original nest to second renest, 29 ft (8.84 m). Fig. 1 shows the relationship of the using area to the renest locations.

Amount of Nest Materials Moved.—Not all natural nest material is transferred to the renest site when the nest is broken up. Usually when a nest is moved, most of the coarse outer material, largely the bast fibers of marsh milkweed, is transferred. The nest lining of cattail (*Typha latifolia*) and cottonwood (*Populus deltoides*) down, feathers, fine plant fibers, and grass is abandoned. This may result when the lining falls to the ground below the nest as the supporting material is removed. It may also be that fresh lining material is wanted or that such material is readily available and hence expendable.

The original nest could not be weighed because in these experiments it had to be kept intact in the nest bush. The renest was weighed after it had been used or abandoned. Nest material remaining at the original site was also weighed. As a basis for determining the amount of nest material transferred, the weight of that which remained at the original site was computed as a percentage of the total weight of the renest. Of 17 nests, the weight of untransferred material was 25 percent of the renest weight. The paired weights ranged from less than 1 g transferred to the renest to less than 1 g remaining at the original nest site. In at least two instances which came to my attention during the course of this study, no materials were removed from the original nest following breakup.

Transfer of Colored and Gray Threads Added to the Original Nest.—One could determine for certain that a given pair moved the nest by marking the birds. I found that catching even one of a pair was too time-consuming and too difficult for the purposes of this study. To make certain that a renest came from a given original nest, the latter was marked by the addition of knotted colored and gray threads. These threads were transferred along with the other nest material to the new site. Since direct observation showed that a pair moved its nest and because the nest was always found in the using area of the pair, the nest-marking method proved highly satisfactory and required no handling of the birds.

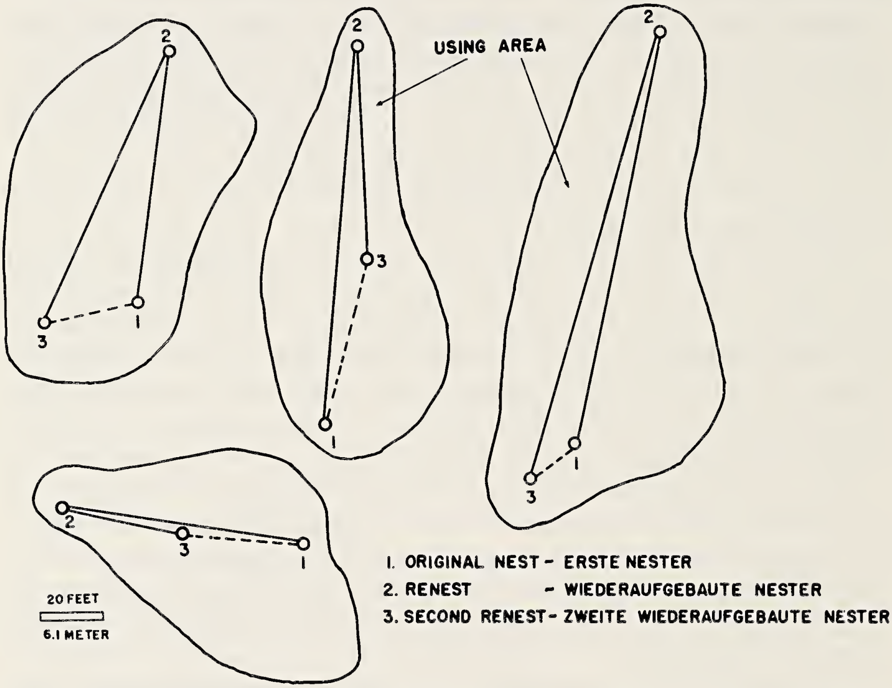

Fig. 1. The locations of three nesting attempts within the using areas of four pairs of Alder Flycatchers. (The arrangement of the four areas is for illustration only.)

Abb. 1. Die Lage dreier Nester (Nestbauversuche) in den Revieren von vier Paaren des Alder Fliegenschnappers. Die Anordnung der vier Reviere dient nur der Veranschaulichung.

Nineteen renests had at least one thread transferred to the new nest. Potentially 190 threads could have been transferred: 95 colored and 95 gray. Actually 19 colored (20 percent) and 66 gray strands (69 percent) were transferred. Statistically, this difference was highly significant.

Some threads were not found at the original nest nor in the renest. Observations indicated that occasionally the bird dropped some material en route to the new nest site, and doubtless this was the way in which the strands were lost. Once dropped, the material was not retrieved. One cannot say that the dropping was purposeful, although twice as many colored threads (33) were missing as were gray threads (15). If a bird wished to get rid of unwanted material, flying it away from the nest and then dropping it would fit the pattern of nest sanitation, as used for eggshells and fecal sacs.

Many of the colored threads were not removed from the original nest, even when virtually all the other material had been transferred. Some gray threads were also abandoned at the original nest, but fewer, 14 (15 percent) as compared to 40 (42 percent) for the colored threads.

In three cases, colored threads (orange, red, and blue) were apparently discarded at the site of the new nest. No gray threads were found unused at the renest site. A general summary of these data is shown in Table 1.

TABLE 1.—THE FATE OF COLORED AND GRAY THREADS TRANSFERRED BETWEEN 19 ORIGINAL NESTS AND CORRESPONDING RENESTS

DER VERBLEIB VON GEFÄRBTEN UND GRAUEN FÄDEN, ÜBERTRAGEN VON 19 URSPRÜNGLICHEN ZU WIEDERAUFGEBAUTEN NESTERN

Threads—Fäden . . .	COLOR—FARBE							GRAY—GRAU	
	O	R	B	G	Y[a]	No.	Percent	No.	Percent
Transferred—übertragen	3	4	6	4	2	19	20	66	69
Missing—verlorn	5	7	5	8	8	33	35	15	16
Left at—Zurückgelassen im									
Original nest—erste Nest	10	7	7	7	9	40	42	14	15
Renest—neuen Nest	1	1	1	0	0	3	3	0	0

[a] Orange, Rot, Blau, Grün, Gelb.

The Role of Color in Thread Transfer.—I had hoped that one or more colors would be clearly accepted or rejected, but the data in Table 1 show no such selectivity. This is not to imply that the flycatchers are not aware of differences among colors. These tests, however, did not indicate color discrimination. The Munsell (1942) notation on these colors is as follows:

Yellow	Gray	Orange	Blue	Green	Red
8Y 8/8	N 7	5YR 6/14	5PB 5/8	7.5G 3/4	5R 2/10

Deane B. Judd (Photometry and Colorimetry Section, National Bureau of Standards, U.S. Dept. of Commerce) with whom I reviewed these tests *ex post facto* suggested that it might have been worthwhile to test a light red, light green, a dark gray, and an olive brown.

The greatest number of colored threads transferred in any one nest was 3 on 3 occasions, while all 5 gray strings were moved on 5 occasions (Fig. 2).

I also looked for a pattern in the use of colored threads in the renest in order to see if the colors were either buried in the nest or displayed toward the outside. The threads were apparently treated the same as wild-gathered nest material.

Miscellaneous Observations.—I was able to account for the movements of all nesting pairs on the study areas. In four cases, however, nest material, including colored and gray threads, was removed from the nest that had been broken up, and I did not find these threads in any other nest. In two instances, no subsequent nest was ever found. These pairs could have moved off the study area or could have moved within the study area in such a way as to have the renest be considered as an original nest. Such is possible but not likely. In the third case, I saw a pair frequent the area in which the "renest" was built, but since no test threads were found in the renest, positive identification could not be made. From this original nest, an orange, red, yellow, and one gray thread were missing and were not accounted for. In the last of the four cases, the original nest with its colored and gray threads remained undisturbed for 14 days, after the eggs were removed, before it was torn apart. The birds associated with this nest remained in the area during this entire period and for almost a month thereafter. This pair was watched periodically for more than 50 man-hours after the nest began to be dismantled. At no time was the pair observed to carry nest material, food for the young, or to act broody as though it were caring for fledglings.

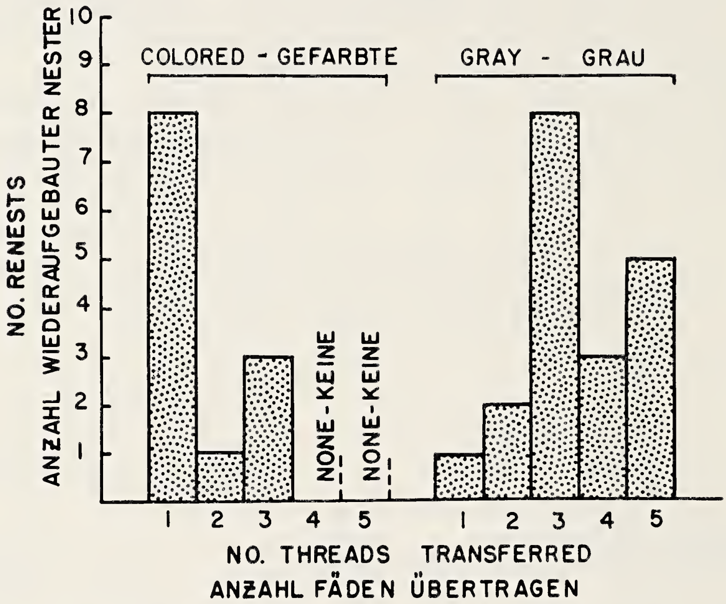

Fig. 2. The transfer of colored and gray threads in 19 renests.

Abb. 2. Die ubertragung von gefarbten und grauen Faden in 19 wiederaufgebauten Nestern.

The bushes on each of the study areas were checked during the winter, when visibility is best, for possible Alder Flycatcher nests that might have been missed. None was found. In the process, I examined several Cedar Waxwing (*Bombycilla cedrorum*) nests and, in one, discovered the missing threads from the Alder Flycatcher nest that had been delayed 14 days before it was dismantled. The Alder Flycatchers apparently had remained in the original using area but did not attempt to renest.

SUMMARY

During the summers of 1960 and 1961, in two separate brush-grown marshes at Madison, Wisconsin, all Alder Flycatcher nests were located. Each nest was broken up by removing the eggs. The nests were then sewn with 6-inch lengths of 5 gray and 5 colored (red, orange, blue, yellow, green) cotton threads that were given a special combination of knots for each nest. The birds then dismantled the eggless original nests and moved the bulk of the material (avg. 75 percent) to be used in the renest. Species of bush, height of bush, height of nest, nest-support angle, diameter of supporting stem, and spatial location were with only slight exception the same for the original nest and for the renest.

The gray threads that identified the renests were transferred between nests significantly more than the colored threads, and no one color was treated differently than any other by the birds.

Four pairs, through natural predation in 1961, nested three times and held the physical requirements constant for each nesting. The move to the first renest, and from the first renest to the second renest was made along the long axis of the using area of the pair.

ZUSAMMENFASSUNG

Während der Sommer 1960 und 1961 wurden in zwei voneinander getrennten, mit Straüchern bewachsenen Sümpfen in Madison, Wisconsin, alle Nester des Alder Fliegenschnappers aufgefunden. Durch Entfernen der Eier blieben die Nester unbenutzt. Sie wurden mit 15 cm langen Stucken aus fünf grauen und fünf gefärbten (rot, orange, blau, gelb und grun) Baumwollfaden bestickt, die eine bestimmte Kombination verschiedener Knoten für jedes Nest aufwiesen. Die Vögel bauten dann die Nester ab und brachten das meiste Material (durchschmittlich 75%) nach einem neuen Neststandort. Die Art und Höhe des Strauches, die Höhe des Nestes uber dem Grund, der Winkel des Tragastes zur Lotrechten, der Durchmesser des Tragastes und die räumliche Lage stimmen mit nur geringen Abweichungen beim ursprünglichen und neugebauten Nest überein.

Mit Hilfe der grauen Faden liessen sich die Neubauten identifizieren. Die grauen Fäden wurden signifikant häufiger als die gefärbten auf die neuen Nester ubertragen. Die gefarbten Faden wurden nicht unterschiedlich von den Vögeln behandelt.

Vier Paare nisteten infolge natürlichen Verlustes des Geleges dreimal. Bei jedem Nestversuch behielten sie die gleichen Nestgewohnheiten bei. In Revieren, die mehr länglich geformt waren, vollzog sich der Umzug zum ersten Neubau und vom ersten Neubau zum zweiten in der Richtung der Längeren Achse des Reviers.

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An Analysis of the Sexual Nexus in the Prairie Warbler

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The sexual nexus, or bond, in a stable population of Prairie Warblers (*Dendroica discolor*) at Bloomington, Indiana, is characterized by unusual variability and flexibility; bonds are established quickly, simply, and opportunistically and are nearly as readily dissolved. Monogamy, although it is the preponderant sexual relationship, is season-long in duration in fewer than half the cases. Polygyny is not uncommon, and such multiple unions sometimes are formed on territories adjacent to others on which unmated males are advertising for females. But so transitory are many bonds that within a week the male that had two females may have none, while his neighbor will perhaps have acquired a mate, or even two.

Underlying this state of diversity and flux are several factors. Over the season, about 80 percent of all nests fail, most of them to predators, and after each case of failure the male and female apparently must be in condition for prompt renesting if their relationship is to continue. Numerous pairs do nest again, the female building and laying eggs in as many as 5, 6, or 7 nests. But when the female, and possibly on occasion the male, is unresponsive to the sex partner and unprepared to breed again immediately, the unit usually dissolves. Because attachment to a particular site, which is highly developed in the male, is comparatively weak in most females, the latter leave the territories of their mates and wander about, ordinarily paying little attention to the courtship almost invariably evoked by the appearance of a female. Formation of a new reproductive bond can be accomplished so quickly that any male, near whose territory a female may be when she is again prepared to breed, can give her the necessary attentions to attach her, almost without regard to the demands already made upon that male by existing marital and paternal responsibilities.

Before turning to the data and the problems they present, it will be useful to outline the history of a breeding season of a population of these parulids. This is a construct based upon 11 years of observation of Prairie Warblers, most of them color banded, on a study area of more or less contiguous old fields, irregular in width and approximately 2 km in length. In late April and early May, shortly after the birds have arrived from their migration from the West Indies, monogamous pairs occupy most territories. An occasional male is unmated and sometimes not yet settled down on a definite territory, and a rare male has won two females even before nesting has begun. Building starts within a few days of pair formation. Nest losses in April and May are about 90 percent, and pair dissolution occurs in small numbers virtually from the outset of the season. Often, before leaving her mate the

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female engages in the preliminaries of renesting, e.g. carrying material or building an abortive nest. Some males abandon the territory after being deserted by their females, but others remain and acquire a replacement. Throughout the season the foregoing processes are repeated, resulting in a gradually accumulating turnover in a substantial number of the females of the original population on the area. There are also a much smaller replacement of males and a considerable shifting in territory lines, as neighbors expand into evacuated territories and as males that have moved away from their original territories take over others. To the numbers of birds thus available for new sexual combinations, monogamous or polygynous, must also be added, in June and July, females that have brought off young and that attempt second broods, sometimes with their original mates and less often with new males. Finally, in a few cases males desert territories on which they have nesting females and move about, singing from time to time on unoccupied land and undoubtedly mating there if opportunity arises. The latest nests are built in mid-July, and I have six records of new pairs formed in that month. Molt is noticeable in July; males usually move little or not at all to molt, but females, unless attending young, leave their home ranges of the breeding season, and marked females are seldom seen in late summer.

PROBLEMS AND METHODS

In attempting to reduce to quantitative terms the data on which the foregoing description is based, I have encountered four problems, which are discussed at this point. Their solutions are less than complete, so that certain numerical conclusions can be only approximations.

1) *Establishing the Unit for Numerical Analysis.*—The complex and kaleidoscopic mating histories of some Prairie Warblers make it almost impossible to use simple units of analysis, such as numbers of monogamous pairs, numbers of bigamous relationships, etc. Even more important, a quantitative description of sexual nexuses formed throughout the season cannot be expressed in terms of numbers or percentages of all males or all females, because a large proportion of birds is present on the study area for only a fraction of the season. On the other hand, all the activities occurring during 1 year on particular tracts of land can be and in many cases are known. Therefore, the analysis in this paper is based upon the segregation of breeding territories into groups, according to the kinds and numbers of reproductive bonds formed on these territories throughout one full season. This also permits expression both of the duration of bonds and of the extent to which they are replaced by new arrangements as summer advances.

2) *Selecting the Sample.*—About 185 territorial histories have been examined, and culling has reduced this number to 84 histories of territories that were inspected daily (with the omission of a day or two in occasional cases), each for a single season. The nesting activities of the Prairie Warbler occupants of these territories are believed to be fully known. Color banding

of the warblers was a factor used in selecting the sample, but banding was not thought to be indispensable to the reliability of all histories. (For example, the occurrence both of polygyny and mate replacement can be ascertained if only 1 of 2 females is marked; and with intensive daily observation the observer can often be confident of the identity even of unbanded birds.) Of the 198 adults breeding on the 84 territories forming the sample, 119 were color banded. A bird was counted once for each season in which it was present.

The selection method just described may involve some risk that the sample will be biased in favor of various multiple sexual relationships and against season-long monogamy. This is attributable to a possible tendency for one to feel that he knows the complete history of a territory on which he has discovered a case of bigamy, but to question the conclusiveness of the negative evidence found on some other territory, i.e. of the fact that no second female or male was found there. In fact, I have excluded from the sample 10 territories on which I know that the same male and female were present at the beginning and at the end of the season, my reason being that the situations in the interim were obscure. However, for the same reason I have excluded three territories not carefully studied but known to have been the scenes of polygyny, and other departures from season-long monogamy were also culled because they occurred on territories visited only intermittently. In sum, I have no reason to suspect the presence of bias.

3) *Determining the Limits of the Breeding Season.*—The constantly changing composition of the breeding population on the area has led me to include a temporal dimension in the present analysis, which is in terms of the individual territorial history for a full season, as I have described. Thus certain territories are classified as having held pairs of birds monogamous for the entire season and others as having involved pairs only temporarily monogamous. By "temporary monogamy" is meant that less than all the reproductive activity of the male and/or the female took place while the birds were mated to each other on that territory. When one member of the pair left its mate and was replaced by another, the "temporary" classification is clearly applicable. The more difficult cases to classify are those in which one or both sexes left the territory, on which no subsequent nexus was formed during the remainder of the season. Even in some of these instances, the birds that disappeared were traced to later relationships on other territories, so that their initial bonds were known to have been temporary. But more often the later activities of the birds that disappeared were unknown, and it is possible only to draw an inference as to how many such warblers mated again, an inference based largely on the dates of the disappearances. To permit classification in these cases, I have selected a date to be used arbitrarily in categorizing a departure as falling before or after the end of breeding activity for the birds involved. This date, 25 June, is thus the dividing line in denominating certain pairs as temporary or otherwise.

The selection of 25 June is based upon several sources of information about the probable subsequent activities of individuals that left the study area. The best of these sources is knowledge of the behavior of the warblers newly appearing on the area before and after 25 June; these newcomers were the opposite numbers of the birds that left. (With one exception, every such female that appeared in midseason and that I examined as she began to build her nest had a fully developed incubation patch, indicating that she had earlier bred somewhere else; the exception was a year-old female that appeared on about 23 May.) The second principal basis for inferring what birds bred again after having departed from the study area is the substantial body of data on the behavior of individuals remaining on the area for the full season; knowledge of the dates of second-brood nests and of replacement nests is particularly instructive.

Nevertheless, different individuals pass permanently out of breeding condition at different times, and the true terminal dates of breeding for the departed birds are unknown. Therefore, all that can be hoped for in fixing an arbitrary date upon which to classify the permanency of a relationship is to find an average, so that the probability of nonremating by an individual leaving before that date will be roughly equal to the probability of remating by one leaving after it. Of the 84 territories in the sample, only 6 involved the dissolution of a pair, with no subsequent replacement, between 15 June and 5 July. Only these six present any real difficulty as regards the classification question under discussion, for birds dissolving the sex nexus before 15 June almost surely mated again and those remaining together until 5 July almost surely did not remate.

4) *Distinguishing between Disappearance Attributable to Dissolution of the Bond and Disappearance as the Result of Death.*—Known or suspected instances of death are, of course, excluded from present consideration, which attempts to assess in quantitative terms an aspect of sex behavior. All other cases of disappearance of females in close conjunction with a nest failure are treated as not caused by death. In addition to the strong reasons already suggested for adopting this position, there may be mentioned the further fact that females that disappear for the season often are seen in later years. All of the relatively small number of male disappearances, in whatever stage of the nest cycle they occurred, are regarded merely as instances of termination of the sex nexus and not of death. As is true with the females, there is plenty of evidence to support this general position, but the possibility that death was involved cannot be excluded in a few cases.

DATA AND DISCUSSION

Table 1 summarizes the data. Its complexity is necessary both in order to reflect the variety of sexual relationships and to permit allocation of each territory to only a single category. The table, however, makes no attempt to break down "polygyny" into possible subgroups.

Table 1.—Territories, according to Forms of Sex Nexus Thereon, during One Full Breeding Season

Form of Nexus on Territory	Number	Percent	Paragraph[a]
Season-long monogamy	35	42–	1
Temporary monogamy—			
Pair formed in midseason	2	2+	2
Pair dissolved in midseason—			
No subsequent sex nexus formed—			
Female disappeared, male remained unmated	9	11–	3
Female disappeared, followed by male	7	8+	4
Male disappeared, followed by female	1	1+	5
Subsequent nexus formed—			
Female lost and replaced	10	12–	6
Male lost and replaced—			
by a male not engaging in polygyny	3	4–	7
by a male engaging in polygyny	1	1+	8
Both sexes disappeared, with replacement—			
by a male not engaging in polygyny, and a female	1	1+	10
by a male engaging in polygyny, and a female	1	1+	9
Polygyny	14	16+	11
Total	84		

[a] Numbers in this column correspond to numbered paragraphs in the text and are given to facilitate reference to the discussion.

The numbers preceding the paragraphs that follow are correlated with the numbers in the right-hand column of Table 1 to facilitate cross-reference. Discussions of the details of particular sex nexuses are based entirely on the behavior of color-banded birds. Copulation was rarely witnessed, so that statements that birds were mates are based on their general behavior toward each other.

1) There were 35 territories on which a single male and female remained for an entire season. Some pairs raised one brood, some two, and some none. Two of the females that brought off young did leave their mates for a day or two and wander several hundred meters to the territories of other males, which courted them. These females then returned to their original mates and raised second broods. Included in this paragraph is a territory on which a pair remained constant throughout a summer, although the male acquired a separate second territory in June and mated temporarily with a female appearing there. The second territory is placed in paragraph 9, below.

2) Two territories were unoccupied until pairs were formed on them well after the breeding season had begun.

3) Nine males were deserted by their mates prior to 25 June and were unsuccessful in acquiring replacements, despite apparent efforts to do so. Four of the females left after bringing young off the nest, five after nest

failure. The lengths of the periods during which the males remained unmated, through 25 June, ranged between 1 and 26 days, and the average was about 14 days. Several males in fact continued to advertise steadily well beyond 25 June.

4) In seven instances the departure of a female was followed by the disappearance of the male, leaving the territory unoccupied except to the extent that there were small boundary adjustments by adjacent males. All disappearances of males preceded 25 June. Five of the seven followed closely after the females' departures, but two males advertised for mates for 22 and 25 days, respectively, before giving up. None of the seven pairs in the present category raised young.

5) One male probably left the territory before his mate did. She then joined an adjacent male as a second female on his territory, which he expanded somewhat.

6) Ten males were deserted by their females but remained on territory and won replacement mates. One of these females later deserted and was herself replaced. Included among the 10 is an intermediate case in which the replacing female brought with her a brood of newly fledged young. The male first courted the female and then followed her about for more than 20 days, apparently paying little or no attention to her young. The female, however, tended them and did not nest again. The effect of the arrival of the female was to cause the male almost to cease to behave as though unmated, hence the placing of the case in the present category. Two of the females that left the 10 territories and were replaced had brought off young; the rest had failed. Ten periods required to attach replacement females ranged from 0 to 25 days and averaged about 8 days in length.

7) Nesting females were deserted in three instances, in addition to that mentioned above in paragraph 5, and in each a new male appeared after from 5 to 7 days, while the female was still on the nest. One nest succeeded, and the female and her new male attempted a second brood. One nest failed before 25 June, and the newly formed pair promptly nested. The third nest failed after 25 June, and the female disappeared; she had never seemed to respond to the courtship of the replacement male.

8) A special category is necessary for one territory on which the original male left his nesting female and was soon replaced. The nest then failed and the new male and the female mated. The replacing male (which was both color banded and marked with paint) meanwhile maintained another (his original) territory, which had a nesting female on it, 1.25 km away. He was found on both territories nearly daily for 37 days, after which he quit visiting his second female; he had never helped in the care of the family he fathered by her. The case of this male may represent a stage intermediate between season-long fidelity to one territory and desertion of the original territory followed by establishment of another. This same male, incidentally, is the one mentioned in paragraph 6, above, as having had

three successive females on his territory, so his total of mates for the year was four.

9) One history somewhat similar to that just described involves the disappearance of the original female and male, the subsequent occupation of the evacuated land by a male from about 100 m away, and the formation of a pair there with a newly appearing female. The male continued to maintain a season-long relationship with the mate on his basic or original territory. See paragraph 1, above.

10) One territory lost its first pair, and after about 2 weeks was taken over by a newly arriving male. This bird acquired a female about a week later.

11) In paragraphs 8 and 9, above, are described two instances of polygyny related to the acquisition of a distinct second territory by a male. The present paragraph adds 14 more cases of polygyny, not involving the complexity of separate territories. These relationships were formed at all dates during the breeding season and without regard to the stage in the nesting cycle attained by the first female at the time the second female appeared on the male's territory. Neither the age of the male nor that of either female appeared to be a factor related to the occurrence of polygyny. In some cases, the original female left the territory early in the summer after a nest failure, while the male's relationship with the second female continued. In other instances, the second nexus was of relatively brief duration. In a single case, the two bonds were formed nearly simultaneously at the beginning of the season and lasted until its end.

Three territorial histories are interesting illustrations of the flexibility of Prairie Warbler relationships: (1) One male with a large territory and two mates yielded about half his ground, and the female nesting on it, to a male that appeared on the area 3 weeks after the season had begun. The arrival treated the female acquired with his land as a mate and, when her nest failed, the two paired for a renesting. But shortly thereafter, the latecomer male disappeared, and the female was taken back by her original mate, which fostered the nestlings fathered by his temporary replacement. (2) A male with two mates acquired at the very outset of the season divided his attentions about equally between them. They built a total of seven nests, all of which failed. The two females left the territory at approximately the same time, within a day or two of the date on which the female on the adjacent territory brought off young. The now-unmated male managed to attach this neighbor, or she won him, and she immediately left her brood to the care of their father and formed a new sexual nexus in July, attempting twice to raise a second brood and succeeding the second time. Possibly the establishment of the new pair was facilitated by the fact that its members had been mates (monogamous for the summer) the preceding year. (3) A male with two mates was deserted by one and replaced her, thus maintaining his *menage a trois*. In fact, it is possible that for a few days this male had all three females simultaneously, which would be my only instance of such an establishment.

SEX RATIOS AND RELATED MATTERS

Engaged in the activities just described were 89 males and 109 females. Full seasonal breeding histories of 68 of the males are known: 43 had a single mate; 9 had two in succession; 14 had two mates simultaneously during part of the summer; 1 polygynous male replaced a mate and therefore had three females; 1 replaced its mate twice on one territory but also had a second territory with a female on it, for a total of four mates. Of the 51 females whose reproductive activities for a summer are known, 44 spent the entire season with one male, but 11 of these shared the male's attentions with a second female during at least part of the time. Seven color-banded females mated with two males in succession; several other associations not leading to nesting are excluded.

TABLE 2.—NUMBERS OF MALES AND FEMALES ON 84 TERRITORIES

Sex	NUMBERS PRESENT				
	15 May	1 June	15 June	25 June	1 July
Male	83	82	77	75	70
Female	86	87	71	67	62

The 89 : 109 ratio in no way represents the ratio of males to females in the breeding population; it reflects instead the transitory character of some bonds, coupled with the lack of site attachment in females. To explore the question of sex ratio, counts must be taken at points of time, not over periods. Table 2 shows such counts of the birds on the 84 territories, from about the earliest date on which pair formation had taken place generally, until 1 July. A small excess of breeding females early in the season yielded after 1 June to an increasing, but nonsignificant, preponderance of males. There is, of course, no statistical support for any conclusion that the sex ratio is other than 1 : 1. However, if either sex is more numerous, it is probably the female. The greater number of males late in the season is likely to reflect the instability of the composition of the population of breeding females, as well as the possibility that the sex drive of the male persists later into the summer.

There is no evidence from the present study that there is any reservoir of nonbreeding birds, as is present in certain other species, waiting to fill vacancies in the nesting population. On the contrary, the habitat has never appeared to be so fully occupied as to leave no room for a male that needed a territory. And it seems fairly clear that all female Prairie Warblers in condition to breed can find immediate opportunity to do so. Polygyny is neither so rare as to be aberrational nor so general as to suggest a surplus of females above the capacity of the males to accommodate. Instead, the indications are of maximum exploitation, at all times, of the available reproductive resources of this population of the Prairie Warbler.

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SUMMARY

In a stable population of *Dendroica discolor* on a study area at Bloomington, Indiana, season-long monogamy, temporary monogamy, and polygyny regularly occur. The sexual nexus is quickly and often opportunistically established and is frequently quite transitory. When pair dissolution occurs, the occasion is usually the loss of a nest to predators (about 80 percent of all nests fail); but dissolution may also follow a successful nesting. It is most often the female which leaves her mate; however, the male sometimes abandons his territory, even when he has a nesting female on it. This breaking up of pairs takes place throughout the season, and, correspondingly, new sex relationships are formed even as late as July, at the very end of nesting.

The reproductive activities of the Prairie Warblers on 84 territories are known for entire single seasons. On 35 territories there was season-long monogamy; on 35 territories there was temporary monogamy, sometimes followed by formation of a new pair, and sometimes not so followed; on 14 territories there was polygyny. Involved in these relationships was a total of 89 males and 109 females; 119 birds were color banded. However, counts of males and females on the 84 territories on various dates throughout the breeding season yield no statistical evidence that the sex ratio of adults is unequal. This study indicates that there is not present in the population any element of nonbreeding individuals that are ready to breed but unable to gain space in which to do so.

Egg-laying Timetable of the Slender-billed Shearwater, *Puffinus tenuirostris*

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The Slender-billed or Short-tailed Shearwater (*Puffinus tenuirostris*), the commercial "muttonbird" of southeastern Australia, affords possibly the best-documented case of a constant and unvarying breeding timetable to be met with among birds. What Fisher (1952:374) wrote of the European Fulmar (*Fulmarus glacialis*) would apply very aptly to this shearwater: "Outside the arctic the fulmar gives the impression of being tied to mid-May [its egg-laying month] with iron bonds; a conservative, unyielding, uncompromising, tradition-steeped, weather-proof automaton. It must be the most predictable of all seabirds of the North Atlantic." This constancy in the Fulmar has been questioned by some authors (cf. Carrick and Dunnet, 1954:364), and the claims for the Australian bird have also not escaped the criticism of doubters.

However, *Puffinus tenuirostris* has been the subject of a commercial industry since the early part of the last century (Serventy, 1958). This industry, now stabilized for a great many years, is dependent on the fact that the timing of the breeding season does not vary from year to year. So a good deal of anecdotal data on the regularity of the nesting cycle has periodically entered the ornithological literature. The earliest record of observed laying dates is that by Davies (1846:13) who, at Green Island in eastern Bass Strait in southeastern Australia, found the first eggs on 21 November and the number of laying birds building up to a peak on 25 November. Later reporters all confirmed egg-laying peaks during the last week in November. Campbell (1901:884) noted the height of the laying season on Chappell Island, near Green Island, as 26 November in 1893. Montgomery (1898) wrote that no eggs were ever known on Chappell Island before 18 November and that he found his first on 20 November. At the northwestern extremity of the range of the species, in South Australia, a lighthousekeeper, Perryman (1937) found the first breeding on 22 November in 1937, with "the big lot" on 25 November, and by 30 November there were eggs everywhere. Some writers embroidered the facts and made the story more sensational by ascribing the egg laying to one particular day only, and the following dates have been variously named in print as *the* egg-laying date: 23 November, 24 November, and 28 November. Others gave a narrow spread, such as 25–29 November or 26–27 November (cf. Elwes, 1859; North, 1914; Littler, 1910).

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OBSERVATIONAL DATA

The published data are suggestive of a constant and well-synchronized nesting season. To gain more particular evidence on its regularity and possible variation between nesting stations, I began a sampling of egg-laying dates at Fisher Island, in the Furneaux Group in eastern Bass Strait, an island situated near the optimum or center of the species' breeding range. As opportunity offered, similar but less frequent samplings were made at other breeding stations by my colleagues (J. H. Calaby, E. R. Guiler, E. R. Hesterman, D. Purchase, and N. E. Stewart) to cover the extremes of the bird's geographic distribution (Table 1).

TABLE 1.—OBSERVATION STATIONS

Station	Latitude	Longitude	No. of Years in Samples
Goat Is., S.A.	32°19′ S	133°31′ E	2
Montague Is., N.S.W.	36°20′ S	150°10′ E	1
Fisher Is., Tasmania	40°10′ S	148°16′ E	7
South Arm, Tasmania	42°58′ S	147°25′ E	2

The observation stations were spread over a band of more than 10½° of latitude and more than 16½° of longitude. Montague and Goat islands are about 1,000 miles apart and Montague Island and South Arm some 500 miles.

The method of study was to select a number of conveniently situated burrows before the egg-laying season began and to examine them each morning

TABLE 2.—EGG-LAYING DATES AT FISHER AND MONTAGUE ISLANDS

ISLAND . . .	FISHER								MONTAGUE
YEAR . . .	1947	1948	1954	1955	1956	1957	1959	Subtotals	1960
19 Nov.	–	–	–	–	–	–	–	–	–
20 Nov.	–	–	–	–	–	1	1	2	–
21 Nov.	4	5	–	–	3	2	2	16	–
22 Nov.	6	11	2	1	0	0	0	20	1
23 Nov.	8	16	1	2	2	2	6	37	0
24 Nov.	22	16	8	11	5	4	3	69	4
25 Nov.	17	12	4	8	2	7	4	54	12
26 Nov.	19	16	12	10	8	6	4	75	18
27 Nov.	9	12	12	2	2	10	3	50	14
28 Nov.	9	6	8	4	1	4	4	36	8
29 Nov.	1	6	8	–	2	2	1	20	3
30 Nov.	6	1	3	–	0	2	0	12	2
1 Dec.	–	3	1	–	0	0	1	5	–
2 Dec.	–	3	1	–	0	–	1	5	–
3 Dec.	–	–	1	–	1	–	–	2	–
Totals	101	107	61	38	26	40	30	403	62

until the season was proved to be over. The number of burrows in the samples varied from 30 to about 100 according to the time that could be devoted to the investigation.

The results obtained are shown in Tables 2 and 3 where the number of new eggs found each morning is recorded for the previous 24 hours.

TABLE 3.—EGG-LAYING DATES AT GOAT ISLAND AND SOUTH ARM

PLACE . . .	GOAT ISLAND			SOUTH ARM		
YEAR . . .	1957	1959	Subtotals	1957	1958	Subtotals
19 Nov.	–	–	–	–	–	–
20 Nov.	–	–	–	2	–	2
21 Nov.	–	–	–	8	1	9
22 Nov.	–	1	1	2	2	4
23 Nov.	4	7	11	6	4	10
24 Nov.	8	11	19	10	12	22
25 Nov.	7	12	19	4	14	18
26 Nov.	6	4	10	6	8	14
27 Nov.	3	5	8	6	6	12
28 Nov.	4	0	4	1	2	3
29 Nov.	1	2	3	2	–	2
30 Nov.	2	2	4	1	–	1
1 Dec.	–	0	0	1	–	1
2 Dec.	–	1	1	–	–	–
3 Dec.	–	–	–	–	–	–
Totals	35	45	80	49	49	98

ANALYSIS OF THE RESULTS

C. A. P. Boundy, of the C.S.I.R.O., Division of Mathematical Statistics, analyzed the numerical data. For each breeding station and each year, the frequency distribution of eggs laid on a given day could be regarded as normal. Excluding Montague Island, the differences in sample variances were not significant, and a pooled estimate of variance (5.2674 days^2) was used. The sampling variance for Montague Island was 2.3027 days^2. With the exception of Fisher Island in 1954, the mean date of laying did not differ significantly from sample to sample for a given breeding ground, so pooled estimates of the means were used.

Table 4 shows the mean date of laying, together with its standard error, for each of the localities.

There appears to be a difference in timing according to latitude on the east coast of Australia. Thus, Montague Island (Lat. 36° S) has a slightly later mean egg-laying date than Fisher Island (except for the 1954 sample), and South Arm (Lat. 43° S) is slightly earlier. That for Goat Island (Lat. 32° S) in South Australia, the most northern breeding station of all, does not differ significantly from Fisher Island. As all the differences vary by only about 1 day from the mean of the main Fisher Island series, it is doubtful under the circumstances that the small differences shown have real bio-

Table 4.—Statistical Summary

Place	Year	No. of Eggs in Sample	Mean Laying Date	Standard Error of the Mean (Days)
Montague Island	1960	62	26.3 Nov.	0.19
Fisher Island	1954	61	26.8 Nov.	0.29
Fisher Island	1947–48 1955–59	342	25.3 Nov.	0.12
Goat Island	1957–59	80	25.4 Nov.	0.26
South Arm	1957–58	98	24.7 Nov.	0.23

logical validity. The statistical results suggest that substantially the same mean laying date holds throughout the breeding range sampled.

Further samples will be taken at the peripheries of the range. It may be pertinent to mention that the Montague Island colony apparently represents a recent northward range extension of the species. The variance in laying date of this sample was lower than that of other areas.

In summary, it appears clear that the egg-laying period is constant throughout the breeding range of the species in southeastern Australia, egg laying beginning on 20–21 November, rising to a peak on 25–26 November, and ending on 1–3 December. The extreme span of laying days is about 13, but 85 percent of the eggs are laid within 3 days on each side of the mean laying date.

From the reports of Davies (1846) and other early writers, it is also evident that the same laying regime obtained over a century ago.

EGG-LAYING DATES OF INDIVIDUAL FEMALES

The foregoing discussion refers to egg laying in the mass in the various colonies studied. We also have some data on the dates of egg laying in individual banded females over two or more succeeding breeding seasons.

There are 69 such cases available, most of them (40) covering only 2 years, but there are 15 for 3 seasons, 9 for 4 seasons, and 5 for 5 seasons (Table 5). It is difficult to present the data in a form suitable for meaningful statistical summary.

The records suggest that certain individuals may have a narrower range of egg-laying dates than the population as a whole. There are some striking cases of same-day layings that involve more than 2-year periods:

No. 12378: This female laid on 24 November in 1954, 1955, 1956, and 1957.
No. 12523: Laid on 24 November in 1952, 1954, and 1955.
No. 12531: Laid on 29 November in 1948 and in 1954.

A not uncommon case is that illustrated by No. 12570, which, starting in 1954, laid on 24, 26, 23, and 23 November. Another is No. 12538, which laid on 26 November (1947), 25 November (1955), 27 November (1957), and 26 November (1959).

TABLE 5.—EGG-LAYING DATES OF INDIVIDUAL FEMALES IN SUCCEEDING BREEDING SEASONS

Number of Years Recorded . . .	2	3	4	5
Layings on same day	2	1	1	0
Range of one day between layings	13	1	0	0
Range of two days between layings	10	7	3	1
Range of three days between layings	7	1	2	1
Range of four days between layings	2	2	2	2
Range of five days between layings	5	2	0	1
Range of six days between layings	1	0	1	0
Range of eight days between layings	0	1	0	0

DISCUSSION

It is inconceivable that *Puffinus tenuirostris* should be a unique example of such a regular and synchronized breeding season. However, this situation is difficult to demonstrate, and its proof is attendant on laborious and time-consuming field studies. In the case of *P. tenuirostris* the existence of the phenomenon was made widely known due to an industry which had developed because of it, and this led to its scientific investigation.

Falla (1934:259) was perhaps the first student of petrel biology to draw attention to the existence of a constant and telescoped egg-laying period in the long-distance migratory petrels as compared with the irregular and protracted period of the relatively sedentary species. *Puffinus griseus* may have a nesting regime similar to that of *P. tenuirostris* (cf. Richdale, 1944:96), and, from the account of the routine egg-harvesting activities of the islanders of Tristan da Cunha, as given by Rowan (1952:106), it would appear that the migratory *P. gravis* behaves similarly.

It is not proposed in this paper to make more than passing reference to the factors that may control this rigid regularity. Marshall and Serventy (1956:499) were of the opinion that the precision of the breeding cycle, unaffected by any local environmental conditions, made it difficult to avoid the conclusion that the cycle was regulated by some astronomical factor. Such a regulatory factor that immediately suggested itself was the seasonal change in hours of daylight. An experimental testing of this hypothesis (Marshall and Serventy, 1959) failed to demonstrate its effect, at least during the first year of experimental exposure to photoperiodic modulation. It was evident from these experiments that, for the first year after the birds' removal from their normal environment, a persistent internal rhythm maintained the gonad cycle on its normal course. Further experiments are in progress in this field.

SUMMARY

The egg-laying dates of the Slender-billed Shearwater have been established over a number of years at one breeding station, Fisher Island, in Bass Strait, southeastern Australia, as well as from occasional samplings at other

stations which, between them, cover the entire breeding range of the species. These have been statistically analyzed to demonstrate a remarkable constancy, throughout, of the egg-laying period, the mean date being around 25–26 November. This period appears to have been unvarying since the first records of the early colonists, some 120 years ago. Observations on banded female birds suggest that these have a narrower range of egg-laying dates than the population as a whole.

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Some Life History Studies of the Stanley Crane

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Lichtenstein (1793) first described the Blue or Stanley Crane (*Tetrapteryx paradisea*) from inner South Africa. Stark and Sclater (1906) gave the range as south of the Zambesi. Roberts, McLachlan, and Liversidge (1958) wrote that the bird was confined to the Karroo and the grassveld areas of South Africa and recorded visually from Mashonaland. Vincent (1952) regarded it as "general in the highveld." As yet, there are no specimens except from South Africa. Blue Cranes are migratory in Natal, South Africa, departing northwestward in March. They return to their breeding grounds in early September.

The Wattled Crane (*Bugeranus carunculatus*) and the Crowned Crane (*Balearica regulorum regulorum*), both much more widespread in distribution, are resident in eastern South Africa. In Natal all three species have been found breeding during the period from November to January. Here, between 7 December 1961 and 9 January 1962, I did my field work on these three species.

Most of my Blue Crane observations were made between Estcourt, Nottingham Road, and Giants Castle, chiefly on the upper reaches of the Mooi, Little Mooi, Hlatikulu, and Bushman rivers. On this area I spent 374 field hours and observed a total of 641 (up to 73 per day) Blue Cranes.

In some of these farming and pasturelands of Natal, breeding Blue Cranes have decreased, while in the highveld regions they have increased (Jack Vincent and William Barnes, pers. comm.).

In Natal, the months of June to August are dry and cold. Often snow lies on the Drakensberg Mountains during this period. However, precipitation in winter is very low. The period from November to February produces a remarkable change. Convectional storms are familiar, forming from cumulus clouds over the high peaks. In summer, these orographic rains, often accompanied by severe hail, produce 82 percent of the annual 34 inches of rainfall (Thorrington-Smith, 1960). These hailstorms produce damage at times to the highveld-nesting Blue Cranes.

Acknowledgments.—I wish to thank Colonel and Mrs. Jack Vincent for all that they did for me to make my studies possible. Colonel Vincent directed me to certain areas for study, helped me secure transportation, aided in plant identifications and testing of water samples, and had some of his men also help me. I wish also to thank John Vincent for checking certain nests after I left, to ascertain their outcome; also William Barnes and the Barnes family for all of their help; the Godfrey Symons family, the Price Moor family, and other landowners who allowed me on their farms.

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NESTING HABITAT

Some Blue Cranes have been found nesting in the dry thornveld (elev. 914–1,219 m) in the region of streams and dams. But the chief breeding grounds are the highland sourveld (6,395 km^2, elev. 1,372–1,829 m) and the lower portion of the bergveld (elev. 2,000 m). These are mostly pastured grass-covered hills, valleys, and plains with a few scattered tree plantings. Besides the Mooi River uplands and a narrow belt along the Drakensberg Mountains, the highland sourveld has an eastward and southward extension into the Orange Free State plateau (Thorrington-Smith, 1960).

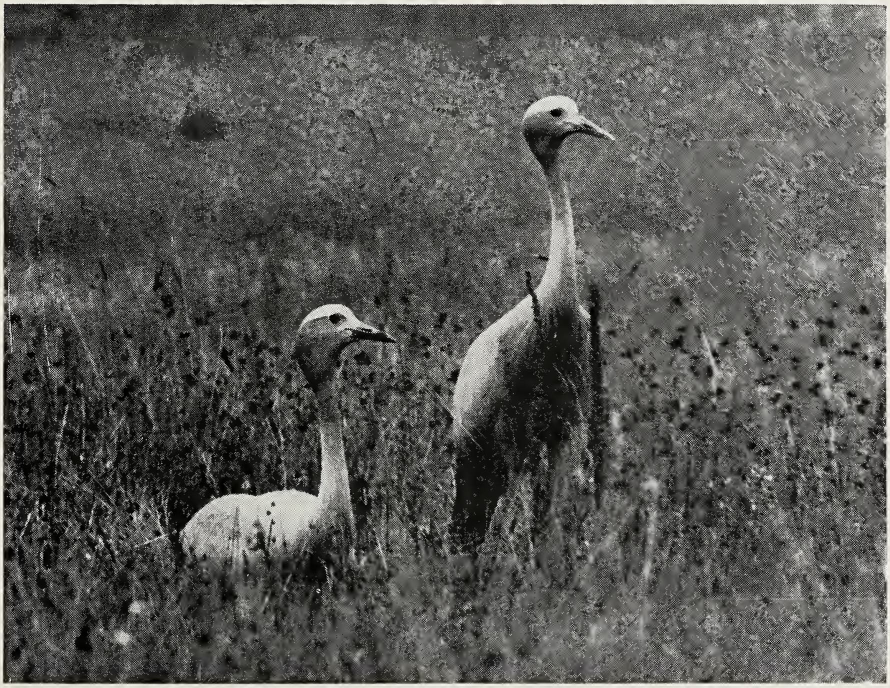

Fig. 1. Stanley Cranes at nest 23 miles west of Mooi River, Natal, 7 January 1962.

I found cranes scattered over the highland sourveld in Natal (Fig. 1). Each pair was separated from the others in favorable places by at least a distance of 400 m. In one situation where nine pairs were breeding, the average distance between nests was 1,711 m. The hilly topography helped isolate each pair from other pairs; but in one long vlei, three pairs nested within sight of each other, and their feeding grounds were contiguous.

The thick grass and sedge growth which helped isolate nests of the Blue Crane were much shorter than the usual cover for nests of other species of cranes. Colonel Jack Vincent helped me identify some of the plants on these pastures and vleis. They consisted of the following.

Graminae: *Pennisetum thunbergii* Kunth., *Andropogon appendiculatus* Nees., *Arundo donax* L. (probably escaped), and *Miscanthidium* (sp.).

Cyperaceae: *Ascolepis capensis* Ridley, *Pycreus unioloides* (R.Br.) Urban =[*P. angulatus* Nees.], *P. oakfortensis* C.B.Cl., *Cyperus fastigiatus* Rottb., *C. denudatus* Linn.f., *Scirpus inclinatus* (Del.) Aschers et Schweinfurth ex Boiss [= *S. corymbosus* (Roth.ex.Roem. et Schultes) Heyne], and *Carex* (sp.).

Orchidaceae: *Disa cooperi* Reichb.fil.

Gentianaceae: *Chironia krebsii* Griseb.

Iridaceae: *Dierama* (sp.), and probably *Cyrtanthus* (sp.).

Some of the larger birds on the nesting marshes were: Black-necked Heron (*Ardea melanocephala*), Cattle Egret (*Bubulcus ibis*), White Stork (*Ciconia ciconia*), Sacred Ibis (*Threskiornis aethiopica*), Hadedah Ibis (*Hagedashia hagedash*), Spurwing Goose (*Plectropterus gambensis*), Secretary Bird (*Sagittarius serpentarius*), South African Crowned Crane, Wattled Crane, and Stanley Bustard (*Neotis denhami stanleyi*).

A crab (*Potamon* sp.) was found in all crane areas and was fed by adults to both Stanley and Crowned crane young. Frogs included *Rana fasciata*, *R. grayi* (in atypical wooded areas), *Cacosternum* (sp.), and a toad, *Bufo regularis*. (These were identified by John Vincent.)

Water in the nesting marshes was neutral to slightly acid (*p*H 7.0–6.0).

THE NEST

Blue Cranes often use the same general nest region for many years. William Barnes reported that a pair had built a nest 4 years in succession on top of a foothill adjacent to Giants Castle. We found a nest there within 1 m of a 1960 nest site. Both nests were built of small pebbles. Other older nests were also found a few meters away. Many others have reported similar findings.

During 1961, nesting lasted from early November until the latter part of January. At first I noted that cranes were often standing or feeding in a definite vicinity for several successive days. Sometimes they were feeding on nearby fields, but before the day was over they were back in a definite spot in their vlei. Here the eggs were later laid.

Nests were of four definite types: (1) in short grass and sedge-grown vleis (marshes) extending through narrow valleys surrounded by short, pastured grass-grown hills; (2) the grass-grown, pastured fields; (3) marshy borders at dam sites; and (4) short-grass foothills of the Drakensberg Mountains.

Nest construction varied according to the type of situation used. In the vleis the first eggs were laid on a mound before any nest material was provided. By the time the second egg was laid, a few pieces of grass were placed on the mound. After the nest had been sat on for some time, the nest, the nest material, and the eggs became stained black from the underlying soil. These nests were nearly always very small. In a pastured field, I found one nest in which there was no nest material at all and the eggs were laid on the short green grass. In the marshes bordering the dams, a small pile of rushes was used for a nest. Here the cranes made their own mound for there were no natural ones.

In the short-grass foothills of the Drakensbergs, the birds built elaborate nests of small pebbles. These ½-inch (1-cm) pebbles were placed side by side over a spot of 30 cm^2 or more, on a flat site surrounded by short green grass. I observed three of these nests, and William Barnes informed me that all of the Blue Crane nests in the Giants Castle situation were of this type.

The average measurements of 13 nests were 44.5 by 51.5 cm in diameter. The one at the dam site was the largest, measuring 61.5 by 84 cm across; the dry-land nests of pebbles averaged 54.2 by 60.9 cm, while the vlei nests were much smaller, averaging 40.7 by 47.7 cm across.

All nests were made of material adjacent to or very near the nest site. All nests, even if not on dry land, were only a few meters from it. Likewise, dry-land nests were not far from water.

Although the nesting season lasted from early November through most of January, the chief nesting season was during December. Of 17 nests, 2 were in use in November and 13 during December, while only 2 others were in active use after 7 January.

THE EGGS

All 17 nests that I observed and all egg sets that I examined in different museums contained 2 eggs, except 1 set of 3 in the Godfrey Symons collection and 2 sets, as reported by Jourdain (1935), each containing 1. In 29 sets, there were 26 of 2, 2 of 1, and 1 of 3, averaging 1.97 eggs per set. Crowned Cranes usually laid 3 eggs, while the Wattled Crane usually laid 1 or 2.

There was considerable color variation in eggs. Even the two eggs of a set often varied. Although many eggs were dirt stained, the ground color varied from smoke-gray, buffy brown to buffy brown-yellow. Over this ground color, usually radiating out along the long axis of the egg, were elongated streaks and spots varying between ½ and 1 cm in length and about ⅓ cm in width (Fig. 2). Sometimes the larger end was covered with great splotches and spots of dusky brown, blackish brown, buffy brown, cinnamon, etc. Eggs were ovate or pointed ovate in shape.

The average measurements of 52 Blue Crane eggs was 90.1 by 59.77 mm. Extremes in length were 80.6 and 99.5 mm, and in width, 55.1 and 65.5 mm. These included eggs in nests, those in the egg collections of William Barnes, Charles H. Jerome, Barry Symons, and Godfrey Symons, and eggs in the British, Durban, Pietermaritzburg, and Pretoria museums.

The actual laying dates were determined in 2 nests and the hatching dates in 4 others, giving evidence that first-laid eggs are smaller usually than second-laid eggs (Table 1).

The average weight of 27 Blue Crane eggs was 171.4 g with extremes of 141.8 and 201.8 g. The average weight of 6 newly laid eggs was 185.3 (168.2–201.8) g; 12 eggs during midincubation, 167.4 (150.4–187.5) g; 9 eggs at hatching time, 156.4 (141.8–183.2) g. The average loss of weight during incubation was about 15.6 percent.

Fig. 2. Eggs of the Stanley Crane. Nest No. 8, 20 miles from Rosetta, Natal, 21 December 1961.

In one nest the eggs were laid 2 days apart; in another nest the second egg was laid 3 days after the first. Eggs were apparently laid during midday. Invariably the eggs in a nest hatched within a few hours of each other. Incubation at nest No. 5 required 30 days for the second egg. I found the nest on 12 December before the birds began setting. On 13 December about noon, John Vincent and I went to the nest, and it contained 1 egg. The second egg was laid on 15 December just prior to noon. William Barnes

Table 1.—Size of Eggs in Same Egg Set as Laid or Hatched

Nest Number	First-egg Measurements in Millimeters	Weight in Grams	Second-egg Measurements in Millimeters	Weight in Grams	Determined by Laying or Hatching
Five	91.8 × 56.2	168.2	96.6 × 56.8	178.1	Laying
Six	93.5 × 61.3	180.0	94.5 × 62.6	187.5	Hatching
Seven	82.4 × 60.2	142.4	86.4 × 58.9	141.8	Hatching
Nine	91.7 × 60.6	201.7	92.1 × 61.2	201.8	Laying
Ten	94.0 × 58.4	154.2	91.4 × 59.2	167.1	Hatching
Thirteen	89.2 × 58.5	168.9	93.3 × 57.3	167.6	Hatching
Average	90.4 × 59.2	169.2	92.4 × 59.3	173.9	

visited it on 13 January and found both eggs pipped. At 1030 on 14 January, John Vincent found both young hatched and a few meters from the nest. Plath (1943:383) gave the hatching date of one egg at the Brookfield Zoo, Royal Oak, Illinois, 6 July 1943 as 33 days after the second egg was laid. John A. Griswold (letter) gave the incubation period at the Philadelphia Zoological Garden, Philadelphia, Pennsylvania, as 30 or 31 days.

BEHAVIOR DURING INCUBATION PERIOD

Incubation commenced immediately after the first egg was laid. It was performed by both parents, and during 2 complete days of observation one pair changed places at least 9 times on the first day and 10 on the other. At one nest the male incubated at night; at the other, the female. During nearly 3 days' observation (1,927 minutes), the male incubated 823 minutes (42.6 percent) of the time while the female incubated 1,047 minutes (54.3 percent) of the time. Eggs were unattended for only 57 minutes (3 percent of the time) and usually then when some man came near to a nest. The first morning change on 2 days was at about 0530 and at 0612. Last changes on three nights were 1815, 1830, and 1812. Sunrise was just prior to 0500 and sunset, 1900.

On 14, 27, and 30 December, 12 periods of incubation by the male averaged 64.25 (29–89) minutes; 11 periods by the female, 93.8 (57–190) minutes. Actual incubation during the average day of 766 minutes consisted of 674 minutes (87.9 percent). During the remainder of the time the incubating bird stood on the nest gazing about, preening, etc.

In the early morning, after the first change, the bird that had been incubating left the nest vicinity for some time and fed some distance away from the nest. After the second change, the second bird did the same. Thereafter, they usually remained closer to the nest. They often fed on grasshoppers and other insects, but more often on the seeds from the heads of nearby grasses and sedges. At times they ate crabs, parts of which they fed their young.

Because of their size and prominent blue color, Stanley Cranes were quite conspicuous. Since the majority of nests were located in situations where the surrounding vegetation was short, they were conspicuous on the nest. Their chief concern was man. When anyone appeared in close proximity to their nest, they walked away. In two cases where the surrounding vegetation was taller, the incubating bird remained on the nest with its head extended in front of it, well hidden from view.

When the incubating bird left the nest, it was almost immediately joined by its mate which was always feeding nearby. Walking a few meters apart, they circled the man near or at the nest—sometimes with wings outspread, sometimes dancing, sometimes calling, sometimes silent. As soon as the man left the nest region, the bird that had been incubating usually returned to the eggs.

Seldom did they pay any attention to other birds, only occasionally chasing one of the larger ones if it came too near their nest. They chased other Blue Cranes immediately if they came into their territory, driving them out by air.

All nests were located where cattle, sheep, sometimes wild mammals, such as eland, grazed. I never saw any of these mammals come very near to a nest. The mammals avoided the nest site. No nests that I found were trampled down by cattle even though there were large herds in some of the fields.

Usually the bird leaving the nest walked to its regular feeding ground, pecking at morsels as it went, stopping to drink at times, occasionally stopping to preen, but always on the alert. Sometimes they walked over a nearby hill out of sight, at times more than a kilometer from the nest. But soon they returned slowly to the nest. Then the second bird repeated the performance. Seldom did they fly.

THE YOUNG

In the 17 nests that I observed, 34 eggs were laid. Four of these were deserted because of some human interference. The outcome of two was unknown. From the remaining 28 eggs, 25 hatched (89 percent). Two eggs from one nest were washed out by heavy rains; 1 egg was infertile. At Giants Castle, several of the park men reported that eggs and young were lost because of heavy hail at times. Others reported that half-grown young were captured at times for food. These seemed to be the chief limiting factors.

Hatching dates at 12 nests were:

9, 10 Dec.
15, 16 Dec.
20 Dec.
20, 21 Dec.
24, 25 Dec.
25 Dec.
27 Dec.
29 Dec.
1, 2 Jan.
ca. 7 Jan.
9 Jan.
14 Jan.

Young could be heard peeping inside the eggs about 24 hours before these were pipped. They hatched 12–24 hours after the eggs were first pipped. After hatching, they remained wet and bedraggled in the nest for several hours. As they dried off, their down acquired a fine sheen, and they became much more stable on their legs (Fig. 3). They remained in the nest about 12 hours. When the birds in a nest hatched on successive days, the older youngster remained longer. The parents then led them to higher land, feeding as they went. On these higher short-grass, pastured fields they were raised.

Among the first things fed the young were the shells of the eggs from which they had just emerged. The adults broke these into small pieces with their bills and passed them to the youngsters.

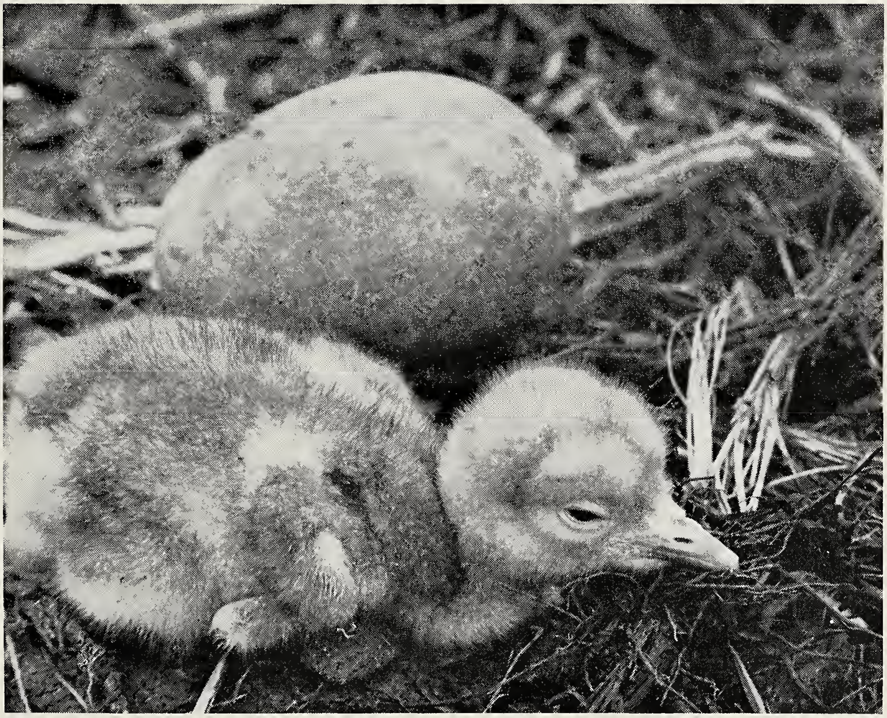

Fig. 3. Downy young of Stanley Crane, 15 December 1961, Natal.

Newly hatched young tried repeatedly to pick up objects. If they were with a nest mate, they often pecked at each other's face and bill, sometimes severely. But on several occasions I observed a pair of adults with two young one-third grown, indicating that they did bring both young through this posthatching period.

Newly hatched young were covered with short buffy-yellow down on the entire head and most of the neck. The shoulders, upper portion of the wings, back, rump, and some on the sides were pearly gray with scattered regions of buffy along the sides. The lower portion of the anterior part of the throat, the breast, and undersides of the wings were nearly white. The eye color, similar to that of the adult, was dark brown. At first, the legs and feet were swollen and bluish gray in color with the undersides of the feet, buffy yellow. When 1 day old, the legs and tops of the toes became much darker gray. The bill was pale bluish gray with the base flesh-colored and the egg-tooth white. There were two small claws on each wing, one at the tip, the second at the bend.

Five young Blue Cranes at hatching averaged in weight 103.1 g, varying between 97.1 and 109.2. Their wing measurements averaged 31.7 (30.3–33) mm; tarsi, 42.5 (40–45) mm; culmen, 19.5 (19.3–20) mm; middle toe, 34.3 (33–37.2) mm.

Four one-day-old chicks averaged 120.1 (111.4–134.2) g in weight. Their wing measurements averaged 33.3 (30–35) mm; tarsi, 43.1 (41.4–49) mm; middle toe, 35.2 (33.5–36.5) mm; culmen, 19.6 (19–21) mm.

The call of the downy young was a shrill *peeep,* sometimes with a burr to it, *peeer.* Young began to fly when about 3 months old.

After the young were full grown, they formed flocks of varying sizes. These gregarious flocks roosted together in shallow water at night, flying shortly after daylight to some nearby field to feed. Sometimes they produced some damage to crops, such as mealies, wheat, etc.

While I was at Pretoria, I visited the Austin Roberts Sanctuary with O. P. M. Prozesky. He showed us two pairs of captive nesting Blue Cranes. One of these had nested for the first time when the birds were 5 years old.

VOICE OF THE ADULT

The alarm call of the adult was a shrill *karrooo,* and a similar call of 3 or more syllables was given by both adults at times when they changed places at the nest. Sometimes one bird gave this call, the other a *tuk-tuk-tuk-tuk-tuk.* When calling the young, they gave a low guttural *purrr.* By imitating this call, I could call the young to me from their hiding places in the surrounding vegetation. Parents also gave this call to each other when everything seemed alright at the nest.

SUMMARY

Blue Cranes were studied during the breeding season in Natal, South Africa, between 7 December 1961 and 9 January 1962. The birds nested in the vleis, in the marshes bordering dams, and on the short-grass pasturelands, and in the foothills. Vlei nests built on mounds contained little nest material; foothill nests were elaborately built of small pebbles; dam-site nests of rushes; some of those built in pastureland contained no nesting material. Nest sites were usually between 1,372 and 1,819 m in elevation. All of the 17 nests that I observed contained 2 eggs which were laid between 11 November and 19 December 1961. At one nest, eggs were laid 2 days apart; at another, 3 days. Incubation required 30 days. Eggs were dark smoky-gray, buffy brown to buffy brown-yellow, spotted heavily with brown, cinnamon, and black. Ovate or pointed ovate in shape, they averaged 89.9 × 59.75

mm across and 171.4 g in weight. Extremes were 80.6–99.5 mm in length, 55.1–64.4 mm in width, and 141.8–201.8 g in weight.

At one nest the male incubated at night; at another, the female. During nearly 3 days' observations, the male incubated 42.6 percent of the time; the female, 54.3 percent; and the eggs were unattended 3 percent. Attentive periods varied between 29 and 190 minutes. Hatching in most cases was between 9 December and 14 January. Downy young, colored buffy yellow on the head and neck, were strongly grayish on the back and buffy below. The average weight of 5 newly hatched young was 103.1 g; at one day, 120.1 g. Wing measurements averaged at birth, 31.7 mm; at one day, 33.3 mm.

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Recent Studies of Bird Migration and Bird Ticks in India

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Of the 2,000 odd species and subspecies of birds that comprise the avifauna of India, some 350 are winter visitors mainly from the Palaearctic Region. Exceedingly little precise knowledge exists about their provenance, their routes, and other details concerning their migratory movements. All that we know is based largely on the scrappy and rather haphazard observations, chiefly of British army and civil-service personnel who happened to be stationed during the last 80 years or so along the strategic northwestern frontier of India and Afghanistan.

Some of these men were excellent field naturalists and have contributed vastly to our basic knowledge of Indian ornithology. Their observational data, although primarily relating to sporting birds such as ducks, geese, and cranes, form the hard core of practically all that is known of Indian bird migration. They outline the broad pattern of the seasonal movements and indicate that the main migratory route between Siberia and central Asia and the Indian peninsula is the Indus Valley in the Northwest. Similar jigsaw bits of information from the northeastern corner of India, even more scrappy, suggest that from northeastern Asia the Brahmaputra River and its affluents constitute the principal flyway. The two migrational streams enter from either end of the Himalayan mountain chain, converge in a pincer movement on the tip of the peninsula, weakening as they advance southward, and trickle over into Ceylon, which virtually forms the terminal.

Increasing evidence is being procured by mountaineers in recent years, however, indicating that many birds also fly directly across even some of the highest sections of the mountain barrier, often at unsuspected heights, thereby shortening their journeys very considerably. Not only have many migrating waders and passerine birds been visually recorded in daytime and heard passing over at night, but mountaineers have also come across the remains of migrating birds such as ducks, cranes, and eagles that had evidently perished in storms and blizzards on high glaciers in the Himalayas and Karakorams. There are now sufficient data of this kind to suggest that perhaps a far greater amount of passage takes place directly over the High Himalayas than had hitherto been suspected.

A large proportion of the migratory land birds that enter India from the northwest sweep down the valley of the Indus River. In order to avoid the inhospitable expanse of the Thar, or Indian, Desert of Rajasthan to the east and find its way into peninsular India, this tide is obliged to fly in a southeasterly direction across the flat salt desert of the Great Rann into Kutch, northern Gujarat, and the Saurashtra peninsula. This is what makes Kutch

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such a particularly rewarding venue for watching visual migration at the appropriate seasons. Not only this, but there is evidence that Kutch lies on the extreme eastern fringe of a broad stream of through migration that flows down from central and northern Asia in a southwesterly direction in autumn and vice versa in spring. This current passes over Afghanistan and the northwestern frontier of Pakistan, Baluchistan, Sind, across the Arabian Sea and the tip of southern Arabia into Somalia, Abyssinia, and farther south. Many of these African-wintering species also pass over Kutch during September and October. They come in great waves as it were, "swarming" during their temporary sojourn, and are completely gone within the course of a fortnight or 3 weeks.

Far less is known about bird migration from across our northeastern border. This is due not only to the steep, rugged, and often awe-inspiring nature of the terrain in the eastern Himalayas—enough to deter any but the most dedicated explorer—but also to the fact of this frontier having had little strategic importance in the past to need permanent military posts there. It is a largely uninhabited, mostly inaccessible, backward tract from which reliable local information concerning bird movements is almost impossible to obtain. Recent geopolitical developments in that part of the world have called for greater vigilance, and it is possible that our knowledge of northeastern bird migration may now improve in proportion.

This, by and large, was the background setting in which the present studies were initiated 3 years ago. Before that, for a number of reasons, organized scientific study of bird migration had received scant attention in India. Chief of these were the lack of competent field ornithologists and the lack of funds for a nongovernmental, unendowed institution like the Bombay Natural History Society to undertake ringing work on any appreciable scale. A modest amount of ringing of migratory ducks was sponsored by the Society in the period between 1927 and 1934 or thereabouts, with the active cooperation of some of the sporting Indian princes and the larger zamindars, or landowners, of Sind. Considering the meagerness and haphazard nature of that experiment, the results proved disproportionately gratifying. Those ring recoveries provide the only positive evidence we have to support the conjecture that most of our ducks come from trans-Himalayan lands—Siberia and central and northeastern Asia—often over distances of 2,000 to 3,000 miles. Apart from our recoveries in U.S.S.R., we also obtained some highly interesting records of European-ringed birds in India, for instance a Green Sandpiper (*Tringa ochropus*) ringed near Moscow recovered over 3,500 miles (5,600 km) away in Kerala (South India), a stork (*Ciconia ciconia*) ringed in Braunschweig, Germany, recovered in Bikaner (3,600 miles—5,760 km), a Rosy Pastor (*Sturnus roseus*) ringed in Hungary recovered in Lahore, and a few others. A scheme drawn up by me in 1945 to study bird migration in Kutch under the financial sponsorship of the late ruler of that State never got under way owing to the untimely death of the sponsor, and the matter had to be shelved, *sine die* as it seemed.

THE TICK-BORNE VIRUS PROBLEM

The present project came as a veritable windfall for Indian ornithology. Its genesis was the discovery in 1955 of an apparently new disease affecting humans and the two monkeys (*Presbytis entellus* and *Macaca radiata*) in the Kyasanur Forest area of Mysore in South India. (This disease has thus come to be known as the Kyasanur Forest Disease, or KFD for short.) It is a form of hemorrhagic fever due to a tick-borne virus closely related to Omsk Hemorrhagic Fever and the Russian Spring–Summer (RSS) encephalitis complex. The epidemiology of this disease is currently one of the major problems under investigation by the Virus Research Centre, Poona, an institution run jointly by the Indian Council of Medical Research and the Rockefeller Foundation. Its principal vector in the epidemic focus has been found to be the tick *Haemaphysalis spinigera.* The disease is active during the dry months from March to May, coincident with greatest tick abundance and activity, and lies dormant during and immediately after the rains when mosquito-borne viruses like Japanese B encephalitis reach their maximum incidence.

Since RSS and allied encephalitides are prevalent in Siberia and eastern Europe—the general area from which many of our migratory birds are known to be derived—the presumption seemed logical that birds could be incriminated in the dissemination of the virus to its "new" secondary focus in India. This could happen in several ways: by infected ticks, normally larvae or nymphs, which had traveled attached to the host—a migrating bird—and dropped off when fully engorged. They could transmit the virus by biting a new host, bird or mammal, or they could perhaps infect it if eaten by the animal as food. The virus could thus circulate for a limited period in the blood of the new host, even though it produced no ill effects upon it. A clean local tick could attach itself to this infected host, become infected itself, and so spread the virus among other hosts and other vectors. In this way, even resident birds could be responsible for maintaining a natural focus. A tick can apparently remain attached to a migrating bird for 5 days or more and thus get carried enormous distances from the primary natural focus to start secondary foci in favorable biotopes. A bird's flying day (or night) ranges from 6 to 11 hours. At a speed of 25–50 miles an hour, depending on size of bird and prevailing weather conditions, some idea can be formed of the distances to which a tick *may* get carried during the period of attachment.

One of the suggestions emanating from an informal meeting organized in Lisbon in September 1958 by A. C. Saenz of the World Health Organization to consider these problems reads: "To organize studies on migrant birds, especially in some areas of the world where large numbers of birds pass through. The birds could be examined for the presence of ectoparasites, bled for antibody studies, and banded to find out their place of origin and of migration. Zoologists and ornithologists should participate in these studies together with virologists already working in this field."

This was followed up in March 1959 by a meeting in Geneva of a "Scientific Group on Research on Birds as Disseminators of Arthropod-borne Viruses" under the auspices of W.H.O. The comprehensive report of this meeting reviewed present information and concepts and outlined areas and methods for future investigations. Among such was a tentative scheme prepared and presented by me on behalf of the Bombay Natural History Society for trapping and banding migratory birds in Kutch and studying their ectoparasites and virology with the cooperation of the appropriate agencies. With the acceptance of the proposals and financial support from W.H.O., it became possible for the first time in Indian ornithological history to start an organized project for the ringing and field study of bird migration in the country.

FIELD OPERATIONS

The field work commenced in Kutch in September 1959, with several members of the Bombay Natural History's staff assisted by a number of amateur ornithologists who joined the camp for varying periods, and a team of technicians from the Virus Research Centre, Poona, to collect ectoparasites from the birds. A. Schifferli, Director of the Swiss Ornithological Station at Sempach, was good enough to accept our invitation to come to India to initiate our workers in the use of Japanese mist nets and the relevant modern techniques of bird-migration study. The advantages of mist nets over fixed traps of the Heligoland and other types, except under very special circumstances, are many and compelling; but they were an innovation for India, and the many initial snags in their use had to be overcome before the full benefit of their effectiveness could be enjoyed. Although perhaps the simplest and most efficient method of catching birds for ringing, and now in almost universal use, mist nets suffer from certain inevitable limitations. In exposed semidesert country like Kutch, for instance, where at most times of the year strong day winds are apt to prevail, it was early realized that mist nets are largely useless—so much so that, even after his long experience with mist netting, the only practical solution Dr. Schifferli could offer was, in his words, to "relax and drink a nice cup of tea." Indeed, under windy conditions little else can be done, and the advice was rigidly followed!

Since that initial session in Kutch, which was more in the nature of a training camp, we have conducted several others in selected areas in Kutch, normally of 2–3 weeks' duration in autumn (September/October) and a like period in spring (March/April). Reports of individual sessions are issued and cyclostyled copies circulated among the participants and other interested persons and institutions. A consolidated report of all the field activities ending with the autumn 1961 session is published in the *Journal of the Bombay Natural History Society* for permanent record.

In the course of the work it was realized that, although Kutch, on account of its favorable location athwart the route of migrating birds, is an exceptionally favorable venue for the visual study of migration, it had certain crippling disadvantages for mist netting. The biggest of these was the absence of any physical features to induce concentration or "funneling" of the migrant birds before or after crossing the Great Rann. The birds consequently are much diffused and spread over so wide a front that netting in bulk is not practicable. This renders the effort uneconomical both as to man-hours and cost. Apart from the fact that during the daytime there is usually a wind blowing to vitiate results, the sun at midday is so fierce that not only is bird movement greatly inhibited but many small birds succumb to the heat if left exposed in the nets even for a few minutes. Consequently, nets have to be folded up at midday, often for 4–5 hours, further reducing the chance of catches. In Kutch, Saurashtra, and even elsewhere, few places can be found, if any, with shade and water which are not at the same time overrun by the spawning village cattle. Our bitter experience is the same as in other parts of the world, namely that cattle and mist nets cannot peacefully co-exist. The losses in nets due to the cattle menace have sometimes proved so heavy that we have been compelled to pack up and depart in haste! Owing to the unpredictable vagaries of the monsoon rains in Kutch—flooding and rendering impassable large tracts of the country in 1 year, and in the next failing completely and creating drought and near-famine conditions—we were obliged to explore the possibilities of extending our field activities to some more dependable parts of the country during the migration season.

Experience has shown that in flat open terrain the most rewarding catches of migratory birds can only be made at their communal roosts. This involves careful staff work and reconnaissance, but once a communal roost is located, very successful bulk netting can be done. In the absence of "guiding" physical features, such as high mountain passes through which migration is funneled—like the famous one of Bretolet in the Alps on the Swiss–Italian frontier—it has become obvious that in the Indian plains communal roosts are our best alternative. Their possibilities are limitless, and it is proposed to concentrate on them in the future. The desirability of locating such roosts has been suitably publicized among bird watchers, and reports are steadily trickling in from all parts of the country. It looks as if we may soon be in a position to conduct the ringing work not only during the few weeks of spring and autumn when migration is actually in progress, but throughout the period of the migrants' sojourn in their winter quarters—practically from September to May. From the angle of expected ring recoveries, tick infestation, and virological study, the advantages of such a possibility are obvious.

Netting at roosts is done by erecting a net, or preferably a row of several nets, in strategic positions after studying the line of flight of the birds to the reedbed or bushes they occupy at night. The birds thus net themselves. Occasionally, as in the case of wagtails in Kerala where the nets were strung out along the edge of a sugarcane field, after the birds have settled in at sunset they are disturbed by a couple of men walking through the roost from the opposite direction. The escaping birds fly out headlong into the nets and provide sizable catches. In the case of the migratory Spanish and Turkestan Sparrows (*Passer hispaniolensis transcaspicus* and *P. domesticus parkini*), a phenomenally populous common roost of a million birds or more was recently discovered in Rajasthan. In addition to setting up nets in the shrubbery across their line of approach, "mobile netting" was tried out with much success. After dark, when the birds were well settled, two men carried a net stretched between bamboo poles from bush to bush in the roosting area. The net was raised and held up against the bush while the roosting birds were disturbed from the opposite side. The birds rushed out into the net in such masses that it was sometimes difficult for the men to cope with the weight. Netting at roosts of overwintering migrants seems to be the answer for large-scale ringing in peninsular India. It has opened up a line of work which holds limitless possibilities and of which we have as yet only seen the beginning.

In the first two or three sessions every bird caught was ringed, whether resident or migratory, but it has now been decided to confine our activities for the present to migrants only. All birds netted, whether resident or migratory, are still carefully examined for ectoparasites, however, the resident ones being released without ringing. Since the project began in 1959, the total number of birds ringed is 19,262, of which more than two-thirds (of over 70 species) are migrants. The largest proportion of migrants comprises wagtails, chiefly the Yellow (*Motacilla flava*), the Yellowheaded (*M. citreola*), the White (*M. alba dukhunensis*), and the Forest Wagtail (*M. indica*). Next come the sparrows (*Passer hispaniolensis transcaspicus* and *P. domesticus parkini*), followed by Rosy Pastor (*Sturnus roseus*), Wryneck (*Jynx torquilla*), Blyth's Reed Warbler (*Acrocephalus dumetorum*), Tree Warbler (*Hippolais caligata*), Orphean Warbler (*Sylvia hortensis jerdoni*), Whitethroat (*Sylvia communis icterops*), Lesser Whitethroat (*Sylvia curruca blythi*), Blackheaded Bunting (*Emberiza melanocephala*), Greyheaded Bunting (*E. buchanani*), and others. The *Motacilla flava* complex covers the races *beema, thunbergi, melanogrisea,* and *simillima*, therefore representing a very wide coverage of breeding ranges in the Palaearctic Region.

TICKS AND THEIR AVIAN HOSTS IN INDIA

Russian workers have found that the most frequent carriers of ticks are such birds that are either terrestrial in habit, like quails, etc. (Phasianidae), or that descend to the ground to pick up food or nesting material. Thus, tree pipits (Motacillidae), buntings (Emberizidae), and thrushes, robins, and chats (Muscicapidae, Turdinae) have been found by them to be the most frequently tick-infested. Our experience here on the whole tends to confirm this, except that the very large sample of wagtails examined (over 2,000 birds) in autumn, winter, and spring, yielded a surprisingly low crop of ticks—under 0.25 percent. Among resident species the ones that we have most frequently found carrying ticks are the babblers (particularly *Turdoides caudatus*), Indian Robins (*Saxicoloides fulicata*), Bush Quails (*Perdicula*), and Bustard Quails (*Turnix*). Among migrants the Rosy Pastor is perhaps our most frequent tick host; other species in the migrant group from which ticks have been collected are *Anthus trivialis, Sylvia communis* and *S. hortensis, Emberiza melanocephala* and *E. buchanani, Erithacus svecicus,* and some others.

Compared with the size of the samples examined, the paucity of infestation on Yellow Wagtails and the two species of migratory sparrows seems to be remarkable.

The ticks collected from birds in all the field sessions so far conducted have been identified at the Virus Research Centre, Poona. The only ixodid (hard) ticks taken have been *Hyalomma m. isaaci* and *Haemaphysalis intermedia.* (I understand that there is some confusion surrounding the name *intermedia* and that it will probably have to be replaced.) The former is a common tick of dry areas in northwestern India, the adults of which commonly occur on cattle in Kutch and Saurashtra. *Haemaphysalis intermedia* is also the species commonly obtained from resident as well as migratory birds in Kutch, Saurashtra, and Rajasthan. *H. spinigera,* the species chiefly incriminated in KFD epidemiology, is apparently a species of a more humid biotope; it is the commonest tick of the Malnad (wet) tract of Mysore, and was not collected from the above areas. Both the ticks are resident in the areas where collected, and could well have been picked up by the birds locally. While the migratory swallows were almost entirely clean, all four examples (i.e. 100 percent) of the resident Cliff Swallow (*Hirundo fluvicola*) taken at a reedbed roost of wagtails in Rajasthan recently (April 1962) carried larvae of argasid (soft) ticks. This species of the genus *Argas* has apparently not been seen before and may represent a new taxon.

RING RECOVERIES

Since so many of our migrants originate in the territories of the Soviet and Chinese republics, their fullest cooperation is essential in order that no recovery of an Indian-ringed bird in their areas goes unreported. The relevant agencies in Moscow, Leningrad, and Peking have been contacted (U.S.S.R. Academy of Sciences, Bird Ringing Bureau, Moscow B-331, Kravchenko Street 12; the Zoological Institute of the Academy of Sciences, Leningrad B-164; and Academia Sinica, Haitien, Peking [53]), and through them our project has been widely publicized and assurance of cooperation secured.

Through the good offices of the Bird Ringing Bureau, Moscow, two most interesting reports have already come to hand: a Yellow Wagtail (*M. flava*) ringed in Bharatpur, Rajasthan, on 14 May 1961 was recovered in Kirghizia (1,900 km distant) on 25 June 1961, and a White Wagtail (*M. alba dukhunensis*) ringed in Kutch on 17 March 1961 was recovered at Kirov (ca. 800 km WNW of Moscow) (4,500 km distant) in June–July 1961. The latter is especially interesting since it represents a somewhat westerly extension of the known range of this race (or it may represent the typical race of Europe not yet recorded in India). A third recovery was the recapture of a Yellow Wagtail in Rajasthan in the same reedbed where it was ringed in late spring, 10 months earlier, indicating that it had been to its homeland (Kirghizia?) and back during the interval. In addition to these recoveries, many other useful data have accrued through recaptures in regard to local movements of migrant species in their winter quarters.

With the proposed development and extension of the ringing work in India, and given adequate cooperation by ornithologists and ringing stations abroad, and by entomologists and virological laboratories within the country, it is confidently expected that data of the highest scientific significance and interest will become available concerning Indian bird migration and the role of our migratory birds in the dissemination of viruses.

SUMMARY

In order to understand the role played by birds in the epidemiology of tick-borne virus diseases, 19,262 birds have been mist-netted and ringed since 1959 on the Indian plains, mostly at communal roosts. Among over 70 species, the most numerous migrants were wagtails (over 2,000) and sparrows.

Resident species most frequently carrying ticks included the babblers, Indian Robins, Bush Quails, and Bustard Quails; among migrants, the Rosy Pastor. The only ixodid ticks taken were *Hyalomma m. isaaci* and *Haemaphysalis intermedia.*

Ringing recoveries from this project include a Yellow Wagtail ringed in Rajasthan and recovered in Kirghizia, a White Wagtail ringed in Kutch and recovered at Kirov, and a Yellow Wagtail recaptured in the same reedbed 10 months later in Rajasthan. Scattered observations over the last 80 years indicate that the main streams of migrants entering India do so from the northwest and the northeast, although many birds evidently attempt a direct flight across the Himalayas and Karakorams.

A Radar Study of the Flight Directions of Nocturnal Migrants

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Radar has enabled ornithologists to probe the physical aspects of bird migration to a degree never before possible by visual means and banding techniques. Bird migrants invisible because of altitude, clouds, or darkness can be tracked by radar, resulting in a new insight into the problems of bird navigation and distribution.

Up to the present time, most radar studies of migration have been made at coastal stations of the North Atlantic Ocean, particularly on the coast of England (Lack, 1959*a* and *b*, 1960*a* and *b*) and the coast of the United States (Drury, 1958, 1959; Drury, Nisbet, and Richardson, 1961). Previously at Kloten, Switzerland, Sutter (1957*a* and *b*, 1958) had studied the passage of birds in the Alps.

In the fall of 1959 we began installation of two aircraft-type radar (AN/APS series) near the cities of Champaign and Havana for the study of nocturnal bird migration in Illinois.

Operation of these units did not commence until the spring of 1960. Aside from numerous temporary breakdowns, both radar units have been in continuing operation during the spring and fall migration periods since the study was initiated. As far as we know, these are the only radar operations established solely for the purpose of tracking migrant birds.

Because Illinois lies well into the interior of North America, terrestrial rather than oceanic features govern the migration pattern of birds. Migration over Illinois would be typical of that occurring over a rather large flat, relatively featureless land mass. Therefore, it was anticipated that the responses shown by migrating birds to their physical surroundings would be different from those reported by Sutter, Lack, Drury, and others in their studies of migration in mountainous and oceanic areas.

The Champaign station was located in an extremely flat agricultural area singularly devoid of significant natural landmarks. The Havana station was adjacent to the Illinois River, a major tributary of the Mississippi River, which bisects the prairie lands of Illinois in a north-northeast–south-southwest direction.

One of the objectives of this study was to evaluate the effects of cloud cover, wind, and altitude upon the flight pattern of nocturnal migrants. The present paper reports on this phase of the study. By defining the navigational attributes of migrants, it is anticipated that the role of topographic and celestial cues can be more precisely determined. Also, assessment of the navigational ability of birds in the absence of landscapes and celestial cues

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might be expected to confirm or refute the necessity for birds to rely solely upon these guideposts.

This is a preliminary report on our findings obtained largely at the Champaign radar station in 1960. It is supplemented by some data obtained at the Havana station in the falls of 1960 and 1961. The findings are based on the tabulation and analysis of over 45,000 separate tracks photographed on the radar scope.

ACKNOWLEDGMENTS

This study was supported by the National Science Foundation and the Illinois Natural History Survey. It was possible to obtain the findings only because many people gave generously of their time and knowledge. Foremost was William W. Cochran, now with the Museum of Natural History of the University of Minnesota who adapted the radar for bird surveillance. Miss Sylvia Sue Hassler and John G. White read much of the radar film from the Champaign station. Gunther Schwartz and Percy Fry of Harvard University's meteor tracking station at Havana assisted Bellrose in many ways. James Likes tabulated much of the data. H. W. Norton of the Department of Animal Science, University of Illinois, provided statistical guidance. Philip Norton coded tape for the Illiac, a digital computer at the University of Illinois. Glenn E. Stout, Head of the Meteorology Section of the State Water Survey, provided encouragement and loaned equipment. Robert E. Potter and Earl E. Rumbaugh of the Coordinated Science Laboratory of the University of Illinois loaned radar equipment.

We have benefited greatly from our talks about migration and navigation with William C. Starrett of the Illinois Natural History Survey Laboratory.

MATERIALS AND METHODS

Graber and Hassler (1962) have described in detail much of the equipment used in this study. They also evaluated the effectiveness of aircraft-type (APS) radar in detecting birds. However, because certain information about the equipment and its operation is deemed essential to understanding of these findings, it is briefly presented here.

An APS-31 radar was installed at the Champaign tracking station in a small building at the University of Illinois Airport. An APS-42-A radar was installed at the Havana station. It was placed at the top of a 100-foot observation tower on the Chautauqua National Wildlife Refuge.

Each radar was equipped with an APS-15 antenna. Its parabolic dish, about 29 inches in diameter, provided a beam width of about 3° to the half-power points. When in operation, the antennas were usually tilted to 30° above the horizon. At this tilt, the altitude of the target was exactly half its range from the radar. For example, a bird showing a range of 1 mile on the scope would be ½ mile high (Fig. 1).

The radar transmitter-receiver had a wavelength of 3 cm, a frequency of 9,375 megacycles, and a peak R-F output of 45–52 kw. The radar was operated on a 5-mile range. Only data from nocturnal surveillance of migration are included in this paper.

The aircraft radar we used was much less powerful than that described by Sutter (1957*a* and *b*) and Harper (1957, 1959) and used by Lack (1959*a* and *b*, 1960*a* and *b*) and Drury (1958, 1959). It could not register echoes from birds much farther away than 4 miles, a much shorter distance than was covered by the radar other investigators used. The chief disadvantage of the low-powered APS radar was its inability to track birds over a long distance; it has an advantage over more powerful sets in that it records fewer and more distinct tracks. Because of the comparatively few targets registered at any one time, it was possible to distinguish among them and enumerate almost every bird echo.

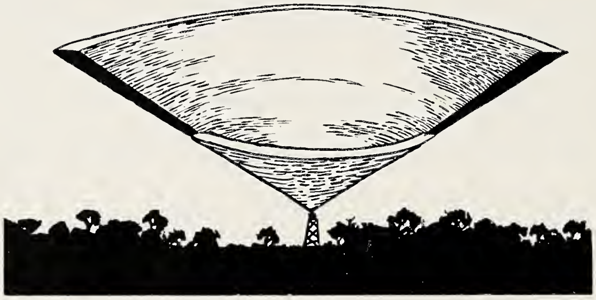

Fig. 1. Landscape profile of the Havana, Illinois, radar station (located in a 100-ft tower) showing the cone-shaped area of coverage of radar energy when the antenna is tilted to 30°. Black edges of the cone represent width of the 3° radar beam. The antenna sweeps one revolution in 6 seconds.

The reflected radio waves were projected on a plan-position indicator scope forming, in essence, a map of the space covered by the radar beam. A 16-mm movie camera was modified so that the shutter remained open continuously except for the brief intervals of frame transfer. Each frame was exposed to the scope for 1 or 2 minutes before a timing mechanism advanced the next frame. Thus, a continuous and permanent record was obtained of the bird targets intercepted by the projected cone of radio energy.

Films of the radar targets were viewed on a large commercial projector which magnified each frame 10 times. Measurements were made of the range, the direction of the tracks, and the speed of the bird echoes. Bird echoes were of two types: (1) those that penetrated the cone directly, and (2) those that penetrated the sides of the cone tangentially.

Bird targets penetrating the cone of radar energy directly formed only a single blip on the scope at the point of entry and again at the point of departure. Bird targets penetrating the cone tangentially left from 2 to 10 dots in a series or "track" resembling a string of beads. Usually single echoes of a "head on" penetration of the radar cone outnumbered track echoes by about four to one.

The dots in a track represented the antenna sweep intercepting a target repeatedly. The antenna rotated once every 6 seconds, the time lapse from the center of one dot to the center of the next dot. By counting the number of dots in a track and determining the length of the track, the rate of movement was determined. Because tracks provided information on speed and direction of flight, they were of greater value than single echoes, which provided information only on relative density and altitude. A track in this paper is construed to mean the flight path of a bird which radar has recorded for distances varying from 200 to 4,000 ft.

Our radar was deficient in one respect, as determined by Graber and Hassler (1962). It recorded but few targets in the lower 1,500 ft of altitude; beyond a range of 6,400 ft, its efficiency in recording bird targets diminished because of the low power output. Targets were blocked out at the lower altitude because of the short recovery time of the pulse and the presence of ground targets. Nevertheless, some birds have been detected at ranges up to 13,000 ft.

Data from radar tracks of migrating birds were tabulated by 10° sectors of the compass and by 500-ft strata of altitude. The mean track and its standard error were computed for each altitudinal stratum for each day. Each category of data was further checked for significance by the chi-square test at 2 degrees of freedom. To show more effectively the distribution of certain observations, standard deviations were calculated for a selected body of data.

Although there is no discussion of the night-to-night variations in volume of migration in this paper, the reader interested in this information can refer to Tables 1 and 2 where we will present the number of tangential targets counted each night. Because the ratio of tangential to penetration targets was about 1 to 4, the total number of targets observed each night was about five times the number of tangential bird targets.

Weather data mentioned in this paper were provided by the U.S. Weather Bureau at Peoria, Illinois, 35 miles north of Havana and 85 miles northwest of Champaign; by the Meteorology Section of Chanute Air Force Base at Rantoul, Illinois; and by the State Water Survey at Champaign–Urbana. The Peoria station was the only source of radiosonde data on winds aloft.

FINDINGS

Seasonal Flight Paths.—The mean daily tracks or flight paths of nocturnal migrating birds during the month of May 1960 at Champaign showed a spread of 71° from 332° to 43° (Fig. 2). They suggested three modes of distribution, one each to the north-northwest, the north-northeast, and the northeast. Most of the tracks occurred between 7° and 17°. Because the bulk of the flight tracks were to the north-northeast, we used a single mean (for all tracks) to expedite comparisons of migration direction under various meteorological conditions.

The spread in the tracks of migrants during May was not unexpected. Most passerines and some shorebirds, probably comprising some 150–200 species, migrated during this period. Birds from innumerable wintering areas flying toward innumerable breeding areas necessarily resulted in many different lines of flight.

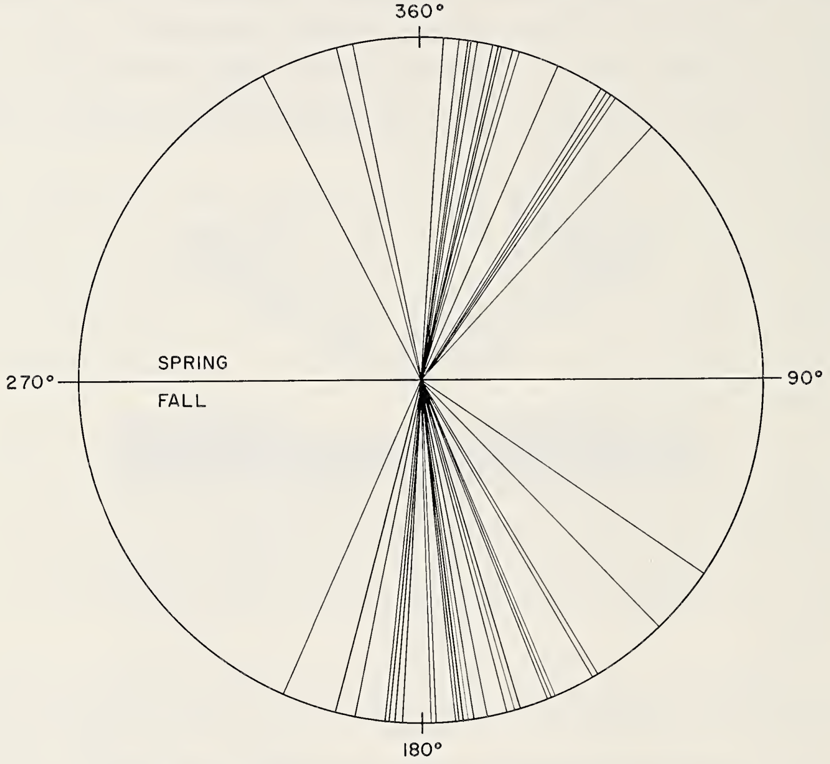

Fig. 2. True courses of nocturnal migrants during spring (upper semicircle) and fall (lower semicircle) in 1960 at Champaign, Illinois. Each line represents the mean course of all migrants tracked on radar during one night. Note that most tracks are east of the north–south plane, both spring and fall.

A similar situation prevailed during the fall migration (Fig. 2), but the daily mean tracks were spread 80° from 124° to 204°. The fall records covered a much longer period of migration, early August to November, and therefore embraced more species of birds than the spring records. In addition to passerines and shorebirds, the fall records included several species of waterfowl.

Most mean fall tracks of nocturnal migrants were directed between 160° and 175°; only a few could possibly have been the back azimuth of the spring lines of flight.

The absence of reciprocal lines of flight for spring and fall months suggested that for many species of birds, the courses of their spring migration were different from the courses of their fall migration.

Effect of Wind Drift.—The track of a migrating bird is the resultant of its heading and the vector of the wind. In evaluating the problem of bird navigation, it is important to determine the influence of the wind vector on the birds' migratory course. The crux of the problem centers on whether the bird recognizes its drift by wind and alters its heading accordingly or whether it maintains the same heading regardless of wind vectors.

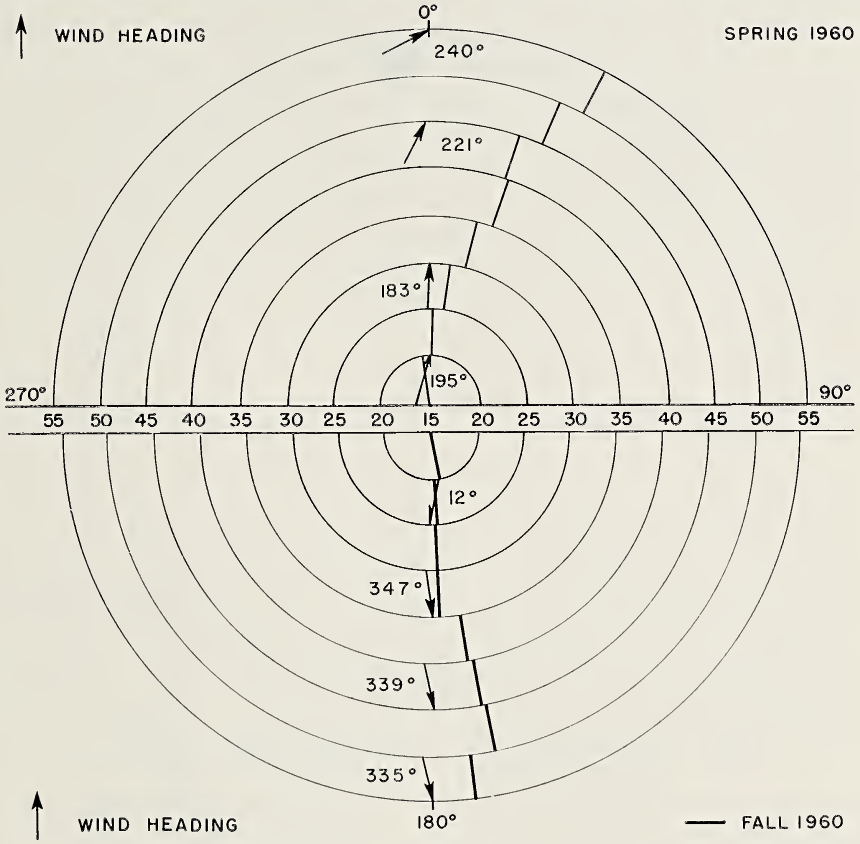

Fig. 3. Wind vectors and average true courses of nocturnal migrants at different altitudes between 1,500 and 5,500 ft in spring (upper hemisphere) and fall (lower hemisphere) 1960 at Champaign, Illinois. Each semicircle represents a different altitude (× 100 ft) above ground. Arrows show wind headings at different altitudes and simple lines show average tracks of migrants at different altitudes. Note that higher-flying migrants have more crosswind in spring than in fall, and that spring migrants at higher altitudes veer definitely eastward.

It would be comparatively simple to evaluate the problem of wind drift if the goals of migrating birds were known. Because the goals of migrating birds were unknown, this problem was approached by investigating the direction of migratory tracks in relation to wind vectors and the headings taken by the birds.

The heading of a bird, that is the direction it is pointed in flight, can be computed from knowledge of its track, its speed of flight, and the direction and velocity of the wind. Radar provides information on the track and speed of flight.

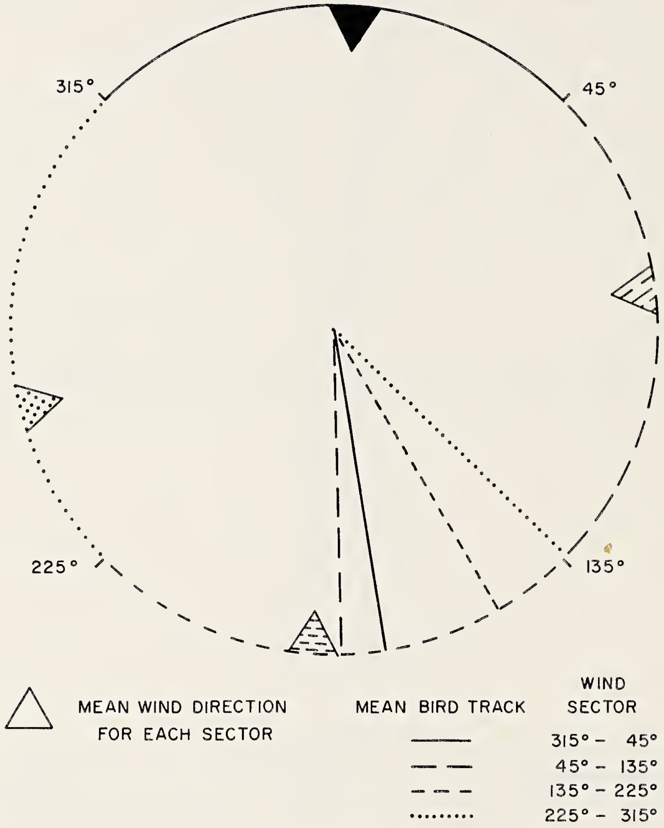

Fig. 4. Fall-flight directions of nocturnal migrants in relation to wind direction. Each radial line represents the seasonal average of migrant tracks coinciding in time with a given wind condition, i.e. westerly, southerly, etc. Note that migrant track was farthest eastward when winds were westerly.

Flight Tracks in Relation to Altitude.—The average track made by nocturnal migrants at different altitudinal strata in May 1960 at Champaign showed an ever-increasing swing from north toward northeast with each increase in strata of altitude (Fig. 3). The wind, too, shifted toward the east as the altitude increased (Fig. 3). Velocity of the wind remained about the same, from 19 to 21 knots, at the several altitudes.

During the autumn of 1960 at Champaign (Fig. 3), average tracks of nocturnal migrants at different altitudinal levels also showed a slight veering of the migration toward the east as altitude increased. Again the wind shifted toward the east with the increase in altitude (Fig. 3) but not to as great an extent as in the spring.

At the higher altitudes in May 1960, the wind blew more or less across the path of the migrants, while at these same altitudes during the fall it tended to be a quartering or following wind. Furthermore, the velocity of the wind was greater during the spring than during the fall months.

Thus, both the direction and the velocity of the wind had a potentially greater influence upon the flight path of birds during the spring than during the fall. The data on the average track taken by birds at the several strata of altitude during these two seasons verified this observation. Furthermore, in both spring and fall, with minor exceptions, the veering of average migration tracks toward the east increased as the wind shifted in that direction.

Further evidence of the influence of wind vectors on nocturnal migrants was apparent from an analysis of mean daily tracks (Fig. 4) in relation to average wind direction. Nightly migration-track data for the spring and fall of 1960 were grouped according to the 90° sector of the compass from which the wind arose. Spring data were not as numerous as fall data, suggesting that the latter findings were more reliable.

It was evident (Fig. 5) that the wind vectors exerted only a minor influence on the flight paths of migrants during the spring, 1960. When winds were from the west sector, the flight paths were farthest west, suggesting some adjustment for wind drift. However, east winds displaced birds farther west than did following or opposed winds, suggesting some wind drifting of the migrants. Flight directions under essentially following or opposed winds in the spring were to the north-northeast. Because wind drift of migrants was negligible or absent with opposed or following winds, it appeared that the birds were intent upon migrating to the north-northeast.

During the fall migration, when the winds were from the west sector of the compass, the mean flight tracks were farthest to the east of south (Fig. 4). Reciprocally, when the winds were from the east sector, the flight tracks of migrants were the nearest to south. With winds from the north and south sectors, the mean flight tracks fell between the two extremes.

Hence, there was evidence both that migrating birds compensated for wind drift and that winds did displace them. Therefore, an analysis was made, relating flight tracks to computed headings of the birds, to evaluate further the problem of wind drift.

Track in Relation to Heading.—A comparison of flight-track directions with heading directions showed that for the several altitudinal strata in any one day there was a greater spread in the heading directions than in the directions of the flight tracks.

During the spring of 1960, there was an average spread of 18° in the flight tracks at several altitudes each night, while the average spread in flight headings was 22°. The nightly average flight tracks during the spring of 1960 were spread over 69°, whereas the average flight headings were spread over 113°.

For the fall of 1960, there was a nightly average spread of 26° in the means of altitudinal track but a spread of 33° in the means of altitudinal headings. Similarly, during the fall months the average nightly flight track spread over 72°, whereas the average nightly heading spread over 98°.

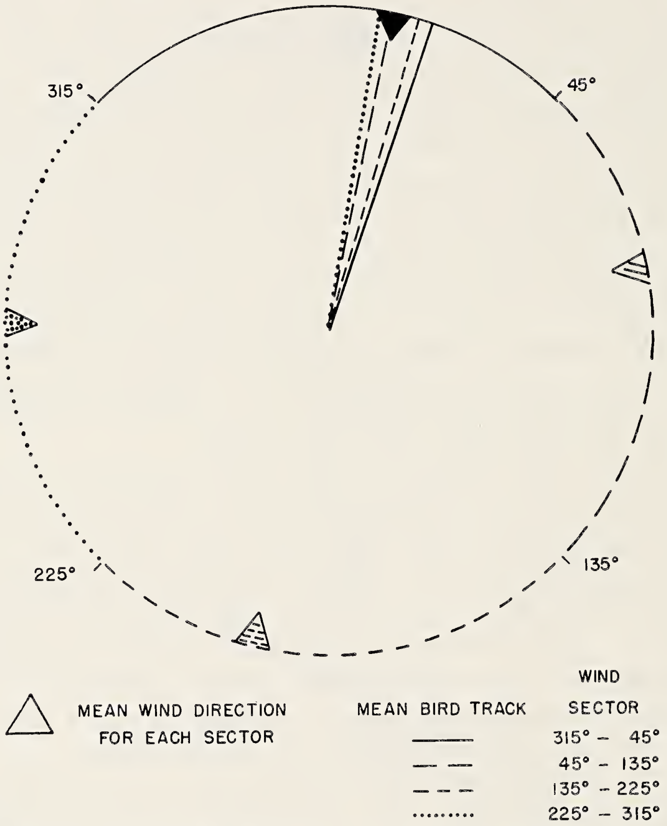

Fig. 5. Spring-flight directions of nocturnal migrants in relation to wind direction. Each radial line represents the seasonal average of migrant tracks coinciding in time with a given wind condition, i.e. westerly, southerly, etc. Note that migrant track was farthest west when winds were westerly.

The average daily flight tracks made by migrating ducks during the fall of 1961 at Havana were spread over 36°. The average daily headings were spread over 63°. Examination of data on several altitudes for certain nights yielded additional evidence of some correction in flight headings to adjust for wind drift. The nights chosen were those having the greatest shift in wind direction with increasing altitude. The track and heading vectors were not drawn to scale, but the length of the wind vector indicated relative wind velocity (Fig. 6).

Wind vectors shifted from 70° at 2,000 ft of altitude to 360° at 4,000 ft and 350° at 5,000 ft on 14 October 1960 (Fig. 6). Bird tracks at comparable altitudes shifted direction approximately 23°. A shift in wind vectors from 20° at 2,000 ft to 290° at 5,000 ft of altitude on 17 October 1960 resulted in a shift of 18° in migration tracks (Fig. 7).

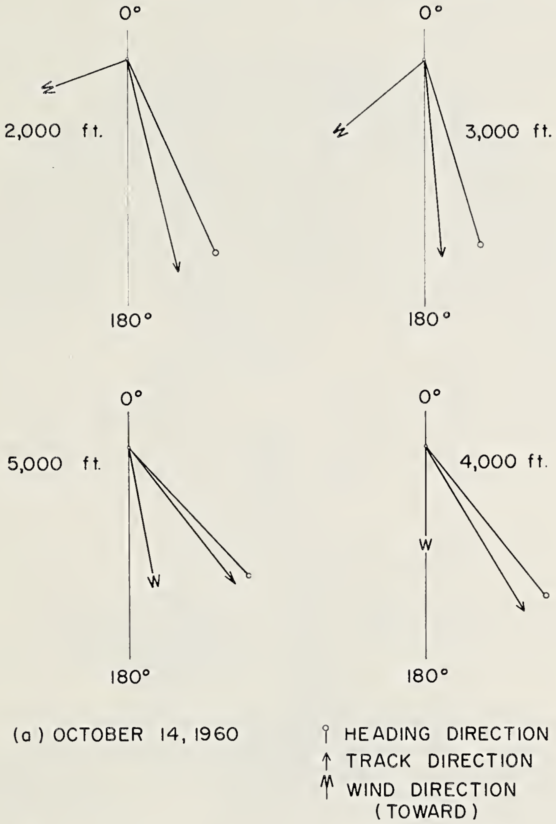

Fig. 6. Variation in true course and true heading of migrants with winds at different altitudes. Headings (direction toward which the bird points) were calculated from radar observations of the track and winds-aloft data for Peoria, Illinois.

It is quite evident that birds correct for wind drift but that the correction is never quite complete. The stronger and more abeam the wind the greater the drift off course. However, further study is needed to appraise the problem of degree of wind drift in relation to degree of correction.

Overcast and Flight Tracks.—On only 2 nights during the spring and 2 nights during the fall of 1960 did we obtain information on nocturnal migration under completely overcast skies. Although other nights were overcast, there were always some periods when the clouds were at least partly broken. On still other instances of overcast nights the birds either failed to migrate in large numbers or the radar was not operational. Observations of migrating birds under a heavy overcast were often blocked or obscured by a heavy return of radar energy from water vapor in the clouds.

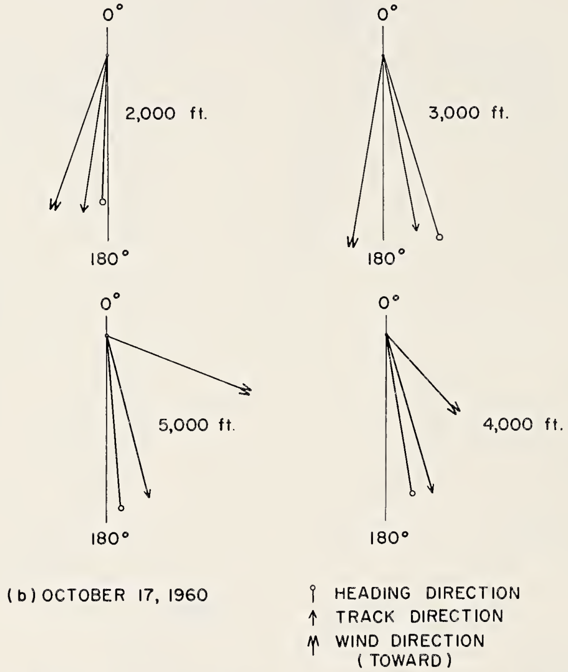

Fig. 7. Variation in true course and true heading of migrants with winds at different altitudes. Headings (direction toward which the bird points in flight) were calculated from radar observations of the track and winds-aloft data for Peoria, Illinois.

One appraisal of the effect of sky cover on the migration of birds was obtained by comparing the direction of movement under complete overcast with that occurring when some sky was visible. How well did the mass of migrants adhere to flight directions under these two opposed conditions?

Data on variability in the direction of tracks of nocturnal migrants at Champaign during the spring and fall of 1960 are presented in Tables 1 and 2. Mean flight tracks, their standard errors, and standard deviations under overcast skies were compared with the nearest night with clear skies, or scattered clouds, or partly broken clouds.

Flight tracks on the overcast night of 24 May were similar in direction to those on 23 May and 26 May, nights when the stars were partly visible through broken clouds (Table 1). The standard deviations of the mean flight tracks for the several altitudinal strata for 18:00 to 24:00 hours on 24 May were almost twice as large as those on the night of 23 May. However, they were not markedly larger than those on 26 May. Moreover, the standard deviations of the mean flight tracks the last half of the overcast night of 24 May were similar to those on 23 May and smaller than those on 26 May.

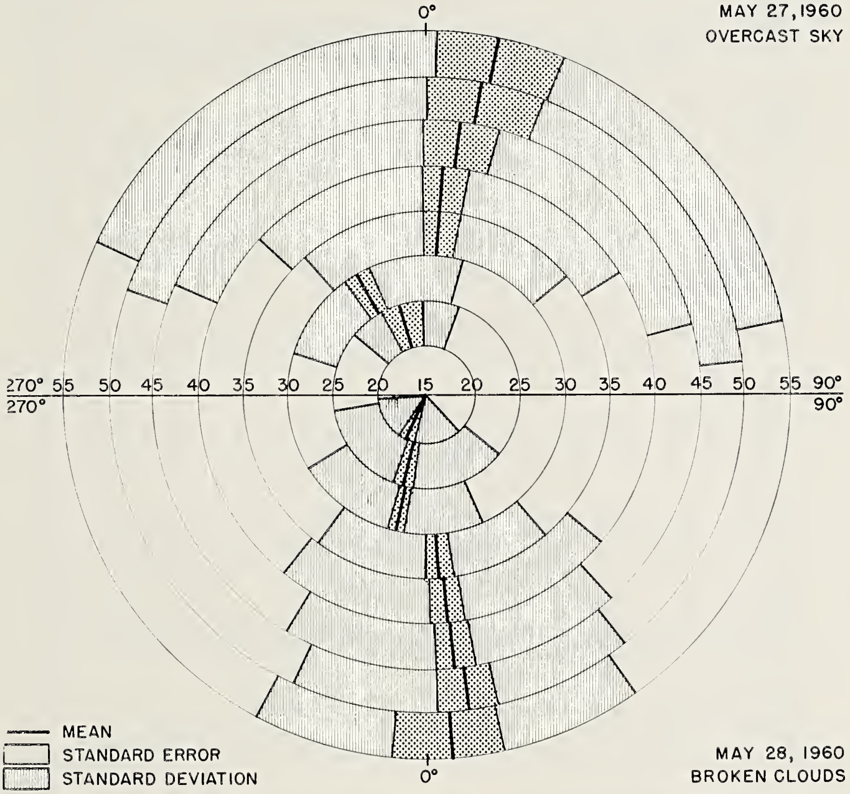

Fig. 8. Variability in flight directions of nocturnal migrants at Champaign, Illinois, on a night with overcast (27 May) versus a night (28 May) with broken clouds. Top of overcast on 27 May was estimated to be 5,000 ft above ground, and broken layer on 28 May was at 5,000 ft.

Standard deviations of the mean flight tracks on the overcast night of 27 May were similar in magnitude to those on 26 May (Table 1), a night when broken clouds prevailed. A comparison of the spread in radar tracks over the compass on 27 May (overcast) with that of 28 May (broken clouds) revealed that there was a markedly better grouping of flight directions about the mean on 28 May (Table 1 and Fig. 8).

During the fall migration the mean flight directions on overcast nights were similar to those on nights when the sky was partly or entirely visible.

(Text continued on page 376)

TABLE 1.—FLIGHT TRACKS (IN DEGREES) OF NOCTURNAL MIGRANTS IN RELATION TO CLOUD COVER, SPRING OF 1960, CHAMPAIGN, ILLINOIS

Date	Amount of Cloud Cover	Data on Flight Tracks	ALTITUDES IN HUNDREDS OF FEET									Number in Sample
			55–60	50–55	45–50	40–45	35–40	30–35	25–30	20–25	15–20	
23 May	Partly	Mean track (°)	—	37.0	34.0	34.4	28.4	24.6	16.4	348.4	335.4	902
	broken	S.E.	—	8.3	4.9	3.6	2.7	2.9	2.3	11.6	14.5	
	clouds	S.D.	—	35.21	38.89	37.24	37.41	42.92	36.51	73.37	48.09	
24 May[a]	Complete	Mean track (°)	—	23.4	23.3	343.1	357.7	359.1	344.3	352.8	5.3	375
	overcast	S.E.	—	8.6	8.1	12.7	11.3	13.1	6.0	12.1	26.8	
		S.D.	—	40.34	37.99	75.13	81.49	107.23	66.54	67.37	92.84	
24 May[b]	Complete	Mean track (°)	—	12.6	10.8	20.3	11.8	10.2	6.9	3.3	318.8	405
	overcast	S.E.	—	18.0	11.7	5.5	5.9	4.4	3.6	10.0	14.2	
		S.D.	—	50.90	43.78	30.62	33.37	37.34	49.75	64.03	56.80	
26 May	Partly	Mean track (°)	18.9	12.9	24.9	5.2	22.5	1.1	355.5	0.1	19.5	418
	broken	S.E.	22.2	10.4	14.1	12.7	11.1	7.2	6.9	9.5	20.5	
	clouds	S.D.	58.74	23.25	50.84	69.56	77.7	69.81	83.37	75.40	54.24	
27 May	Complete	Mean track (°)	18.6	10.8	11.0	7.5	6.1	5.8	329.6	345.4	—	388
	overcast	S.E.	16.3	13.3	11.3	7.6	7.2	6.8	6.6	13.9	—	
		S.D.	76.45	77.55	81.70	67.98	53.40	47.11	44.27	—	34.04	
28 May	Partly	Mean track (°)	11.6	3.2	6.5	5.4	5.2	3.7	347.0	343.5	334.6	754
	broken	S.E.	9.5	8.4	7.1	4.9	5.9	3.9	3.1	5.8	7.2	
	clouds	S.D.	32.91	32.53	32.53	37.96	44.93	41.64	49.70	64.59	59.81	

[a] 6–12 P.M. [b] 12:01–6 A.M.

TABLE 2.—FLIGHT TRACKS (IN DEGREES) OF NOCTURNAL MIGRANTS IN RELATION TO CLOUD COVER, FALL OF 1960, CHAMPAIGN, ILLINOIS

Date	Amount of Cloud Cover	Data on Flight Tracks	ALTITUDES IN HUNDREDS OF FEET									Number in Sample
			55–60	50–55	45–50	40–45	35–40	30–35	25–30	20–25	15–20	
1 August	Clear to scattered	Mean track (°)	—	—	—	—	134.6	172.1	167.1	184.9	183.4	82
		S.E.	—	—	—	—	15.0	30.8	16.6	13.4	20.8	
		S.D.	—	—	—	—	42.42	87.10	62.11	79.28	72.05	
5 August	Complete overcast	Mean track (°)	—	222.5	183.9	202.0	209.4	213.7	201.1	193.0	—	182
		S.E.	—	10.6	11.5	5.2	5.9	5.7	6.0	8.3	—	
		S.D.	—	29.98	44.54	37.50	34.90	25.49	32.31	32.15	—	
6 August	Partly broken clouds	Mean track (°)	—	215.1	151.2	193.4	222.3	197.4	221.8	223.4	—	107
		S.E.	—	7.1	12.2	5.2	7.2	14.2	12.1	6.1	—	
		S.D.	—	28.2	29.83	35.65	31.38	55.0	30.13	14.94	—	
14 October	Overcast to partly broken	Mean track (°)	137.2	143.5	142.6	148.4	157.8	174.7	174.1	166.1	—	654
		S.E.	6.4	5.4	2.9	3.1	2.8	2.4	2.6	6.3	—	
		S.D.	23.95	28.06	23.38	18.07	34.75	32.56	23.83	20.89	—	
15 October	Complete overcast	Mean track (°)	184.0	186.8	188.6	190.4	193.9	187.5	176.0	189.0	196.8	624
		S.E.	5.9	6.0	2.3	2.0	3.7	3.2	4.2	4.1	6.1	
		S.D.	20.44	27.50	26.42	25.30	27.93	28.26	33.06	33.05	29.88	
16 October[a]	Clear	Mean track (°)	180.1	182.5	166.8	168.0	165.8	171.1	175.3	169.6	—	843
		S.E.	11.0	8.1	3.5	2.6	2.3	2.0	2.5	4.1	—	
		S.D.	33.0	35.30	30.11	26.26	29.36	23.58	32.11	31.76	—	
16 October[b]	Clear	Mean track (°)	183.5	180.3	173.1	165.3	161.6	171.4	163.1	178.9	—	628
		S.E.	8.9	4.3	3.5	2.6	2.6	2.2	3.0	7.6	—	
		S.D.	26.70	23.55	26.19	25.87	28.60	30.09	30.15	33.99	—	

[a] 8–12 P.M. [b] 12:01–6 A.M.

Moreover, the standard error and standard deviation indicated that flight tracks were grouped about the mean flight direction as significantly on the overcast nights of 5 August (Fig. 9) and 15 October as on adjacent nights when stars were visible (Table 2).

The similarity in distribution of flight tracks between those on completely overcast skies throughout the night of 15 October and those under partly broken clouds on 14 October is clearly depicted in Fig. 10. On the overcast night of 24 May (Fig. 11), there was a pronounced difference in the grouping of flight directions between those recorded prior to 12 midnight and those recorded after that time.

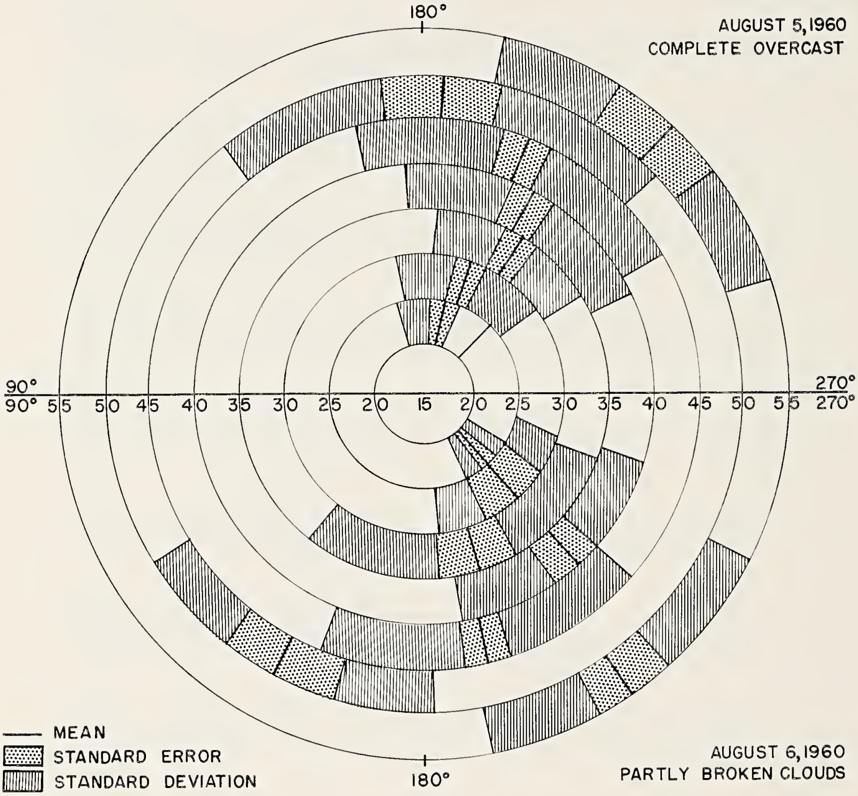

Fig. 9. Variability in flight directions of nocturnal migrants at Champaign, Illinois, on a night with overcast (5 August) versus a night (6 August) with broken clouds. On both nights, the cloud layer was at 10,000 ft.

The closer grouping of the flight tracks on the 2 overcast nights during the autumn, as compared to the grouping on 2 overcast nights during the spring, poses a problem. Perhaps it was the result of different species of birds taking part in migration.

Audio records taken by Graber on the overcast night of 5 August pointed to the Bartramian Sandpiper (*Bartramia longicauda*) as the principal species in migration. Observations for several hours after dawn on 16 October revealed that there had been a sizable migration of ducks into central Illinois the night of 15 October. Passerine birds were also in migration, as shown by smaller-sized echoes.

Audio records indicated that a high proportion of the end-of-the-season migrants from 23 May to 28 May were thrushes of the genus *Hylocichla.*

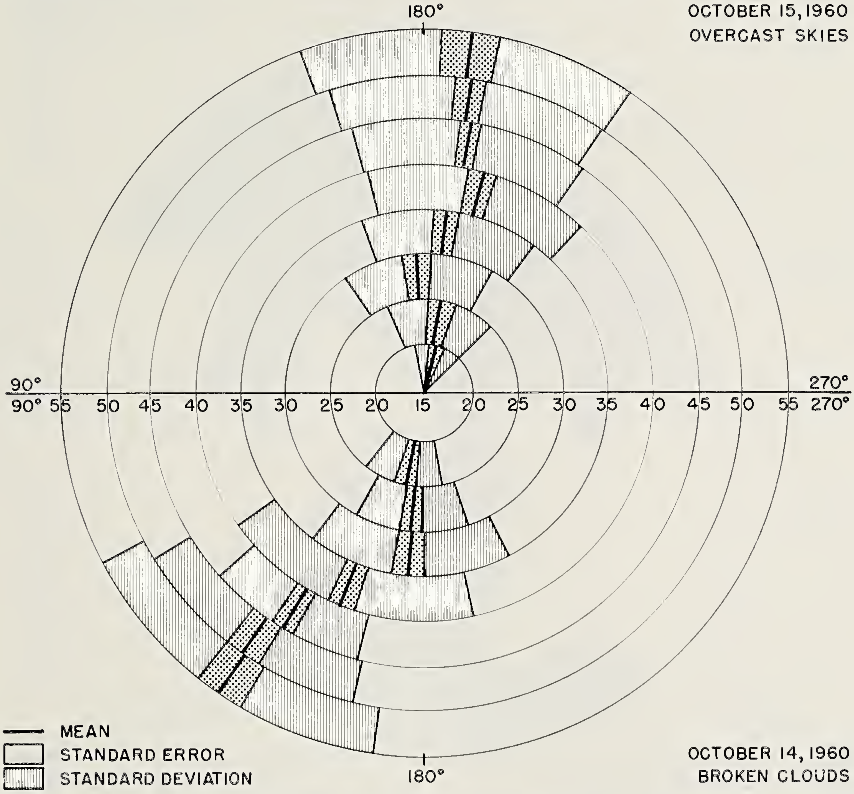

Fig. 10. Variability in flight directions of nocturnal migrants at Champaign, Illinois, on a night with overcast (15 October) versus a night (14 October) with broken clouds. On 15 October overcast base was 3,500 ft above ground.

Altitude of Migrants and Clouds.—The question now arises as to whether or not the migrants tracked by radar on the overcast nights of 24 May, 27 May, 5 August, and 15 October 1960 were above the clouds where the stars were visible, or below the clouds where only the terrain was visible.

The altitudinal distribution of migrants (Fig. 12–15) gave good evidence that some migrants were above the cloud layer, some were below it, and others were in it. Many migrants could not see the ground because of ground fog. A night-by-night analysis of cloud conditions in relation to altitudinal distribution of the migrants elucidates still further the feat of navigation performed by migrating birds.

Cloud Heights.—The solid ceiling on the afternoon of 24 May was measured at a height of 4,700 ft. Tops were estimated at 6,000–7,000 ft. By 21:00 hours the ceiling had risen to 6,000 ft. It continued to rise, reaching 14,000 ft, with tops estimated at 17,000–20,000 ft, at 23:55 hours only to settle down to 8,000 ft during the hours 03:00 to 06:00 on 25 May. Rain, with some thundershowers, occurred from 18:00 to 21:00 hours on 24 May. The solid overcast continued until 08:00 hours on 25 May.

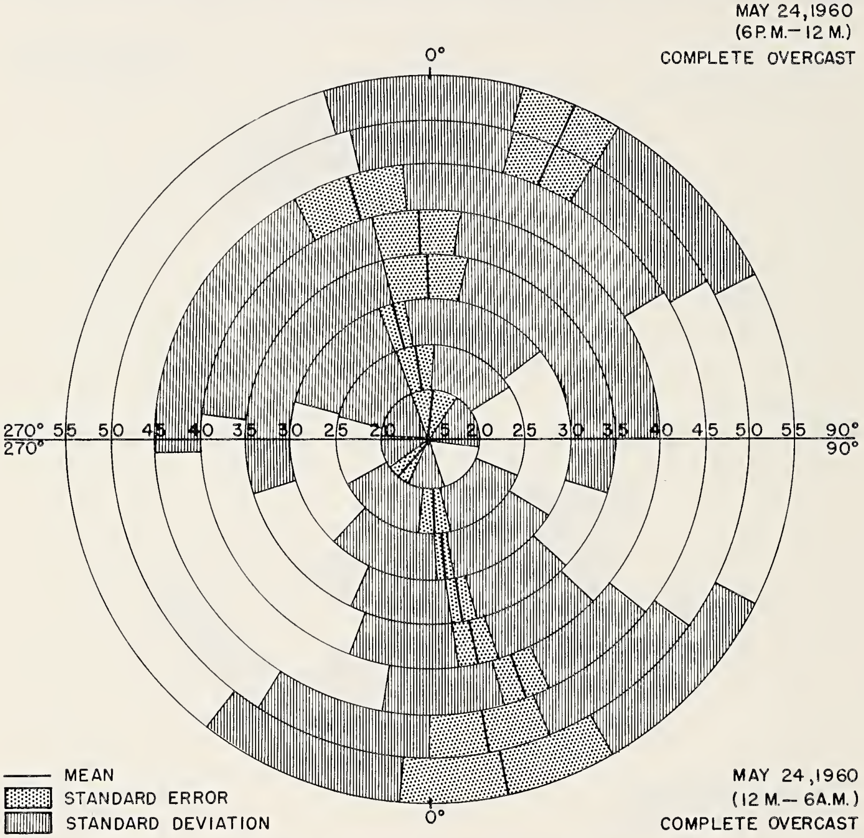

Fig. 11. Variability in flight directions of nocturnal migrants at Champaign, Illinois, on a night with overcast. Birds reaching Champaign before midnight initiated flight under overcast. Birds reaching Champaign after midnight initiated flight under clear skies.

The highest proportion of nocturnal migrants on 24 May was at altitudes extending from 2,500 to 3,000 ft, that is about 2,000 ft under the cloud layer (Fig. 12).

An extremely low ceiling prevailed the night of 27 May. During the afternoon on 27 May, the solid overcast was measured at 1,000 ft above the ground. At 21:00 hours it was 1,200 ft above the ground; at 23:55 hours, it was 900 ft, rising on 28 May to 1,100 ft at 03:00 hours and to 1,400 ft by

06:00 hours. Tops of the clouds were estimated at 4,000–5,000 ft. Fog prevailed throughout the night, reducing visibility from 4 to 1.5 miles. The altitudinal distribution of bird migrants on 27 May indicated that almost all of them were migrating completely shrouded in clouds (Fig. 13).

From 21:00 to 23:55 hours on 5 August 1960, there was a broken layer of altocumulus at 7,000 ft and a solid layer of cirrostratus at 10,000 ft. During the early hours of 6 August, the broken layer varied from 1,000 to 3,000 ft above the ground, while the solid layer remained at a height of 10,000 ft. Because of cloud structure, tops could not be estimated. Rain occurred shortly before daybreak and continued for several hours thereafter. Nocturnal migrants on 5 August were below the solid overcast, with a large proportion in the altitudinal strata at 4,000 to 4,500 ft, below the broken layer of altocumulus clouds (Fig. 14).

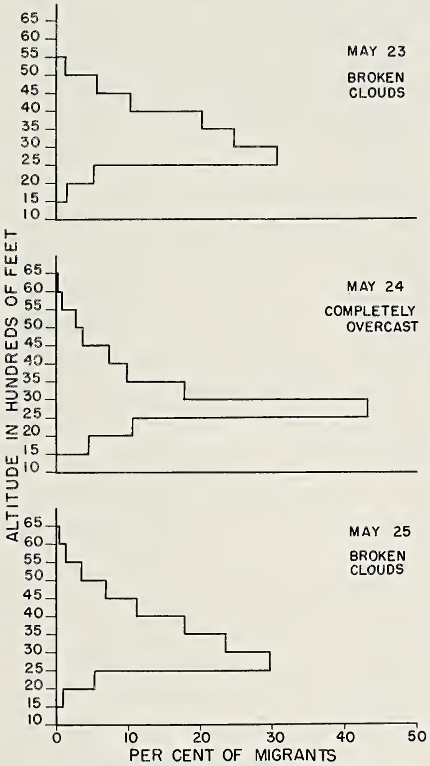

Fig. 12. Altitudinal distribution of nocturnal migrants at Champaign, Illinois, in relation to cloud cover. On 23 May clouds were broken above the migrant swarm. On 24 May base of overcast was at 5,000 ft, and on 25 May broken clouds were at 8,000 ft.

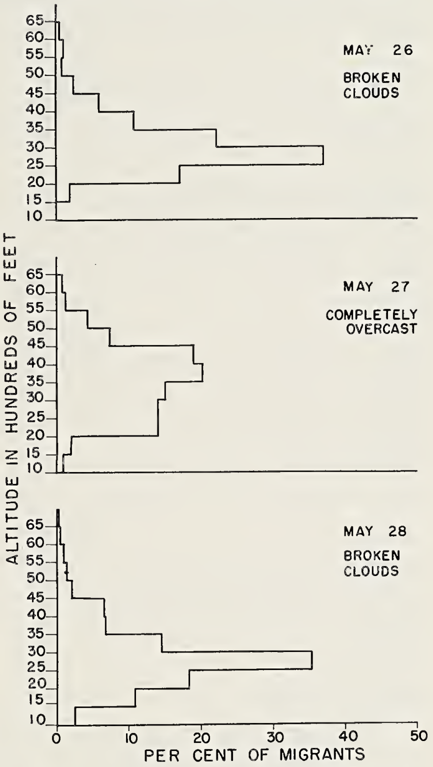

Fig. 13. Altitudinal distribution of nocturnal migrants at Champaign, Illinois, in relation to cloud cover. On 26 May clouds were broken at 10,000 ft. On 27 May overcast base was at 900 ft, the tops possibly as high as 5,500 ft. On 28 May clouds were broken at 5,000 ft.

Overcast measured at from 700 ft to 3,500 ft above the ground prevailed from 07:00 hours on 15 October to 03:00 hours on 16 October. By 05:55 hours the overcast descended to a height measured at 1,600 ft. At 04:00 hours the clouds parted briefly to 9/10 sky cover, then overcast again prevailed from 04:30 to 06:00 hours. Haze and ground fog occurred throughout the night limiting visibility from 2 to 7 miles.

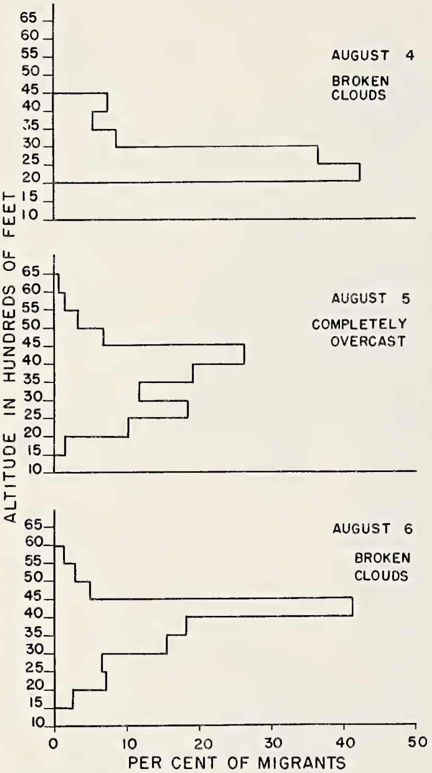

Fig. 14. Altitudinal distribution of nocturnal migrants at Champaign, Illinois, in relation to cloud cover. On 4 August clouds were broken at 3,500 ft. On 5 August overcast base was at 10,000 ft. On 6 August clouds were broken at 10,000 ft.

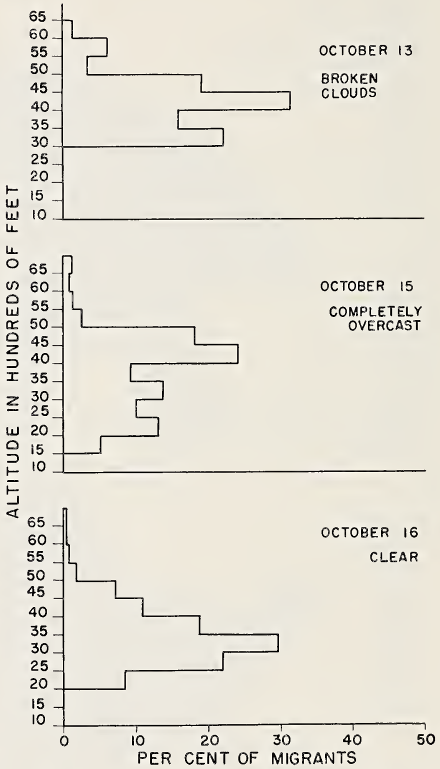

Fig. 15. Altitudinal distribution of nocturnal migrants in relation to cloud cover. On 13 October clouds were broken at 12,000 ft. On 15 October overcast base varied from 3,500 to 1,600 ft. On 16 October the sky was clear.

It was apparent that about half the nocturnal migrants flew above the cloud layer on the night of 15 October, the others flew largely in the clouds (Fig. 15).

Birds in Relation to Clouds.—On 24 May and 5 August 1960, 2 of the 4 overcast nights for which we had migration data, birds migrated almost entirely below the cloud layer. On the overcast night of 15 October, the birds were above, below, and in the clouds. On 27 May, migrating birds were enveloped by clouds.

A comparison of the altitudinal distribution of nocturnal migrants under overcast and clear skies (Fig. 12–15) was most interesting. It showed that birds were prone to migrate at higher altitudes when skies were overcast than when they were clear. Unless the clouds were too high for them to surmount, migrants apparently attempted to fly above an extensive overcast. When this occurred, migrants were usually concentrated in the strata immediately below the cloud layer.

Extent of Overcast.—A review of the extent of the overcast is of paramount importance in evaluating the significance of the radar flight tracks recorded at Champaign.

At midnight on 24 May, the overcast stretched from 175 miles south of Champaign to 100 miles north, and through the northern half of Missouri and all of Iowa.

On 27 May, at midnight, the overcast extended from northern Tennessee through Kentucky, all of Indiana, all of Illinois to as far north and including Minneapolis in Minnesota, Wausau in Wisconsin, and all of Michigan. This overcast embraced an area from 300 miles south of Champaign to over 500 miles north.

At midnight on 5 August 1960, the overcast extended southward from Wausau and Milwaukee, Wisconsin, and covered all of Iowa. To the northwest at Minneapolis, Minnesota, and Fargo, North Dakota, the overcast had begun to break up, for these cities had $\frac{7}{10}$ to $\frac{8}{10}$ cloud cover. The overcast stretched about 100 miles south of Champaign through St. Louis, Missouri, Springfield, Illinois, and Indianapolis, Indiana.

The overcast at midnight on 15 October 1960 extended from about 100 miles north and northwest of Champaign southward to Kentucky. At sunset on 15 October, it had been about 250 miles north and northwest of Champaign.

Initiation of Migration in Relation to Overcast.—We concluded that the overcast was so extensive on 27 May and 5 August, in the direction from which the migrants came, that all the birds tracked by Champaign radar must have initiated their migration below the overcast. The migrants on 27 May were apparently partly enveloped in clouds, while those on 5 August apparently remained below the cloud layer for the entire distance.

If they initiated flight under clear skies, then the migrants on 24 May 1960 had flown under solidly overcast skies for at least 175 miles. Undoubtedly, birds found to be migrating prior to midnight began their migration under overcast skies, while those recorded after midnight initiated migration under clear skies.

Birds migrating on 15 October might have flown as many as 200 miles before being recorded at the Champaign radar station. Those that initiated migration prior to midnight had undoubtedly begun to migrate under overcast skies. Some birds climbed above the overcast, some were flying in it (at least near Champaign), and other birds were flying below the overcast.

On the morning of 16 October, flocks of ducks were observed descending from the low overcast to alight in lakes in the Illinois River valley near

Havana. Some duck flocks arrived late in the morning from the south. It was our considered opinion that these reverse-migrating ducks, which represented the first noticeable migration of Mallards (*Anas platyrhynchos*), had unintentionally passed over the Illinois River valley. The low clouds and ground fog apparently hid the valley from their view, and they "overshot" their goal. Since many other flocks arrived directly at the Illinois River valley, it is problematical whether they discerned it after the ground fog lifted or because they were flying in the base of the clouds and could see the terrain.

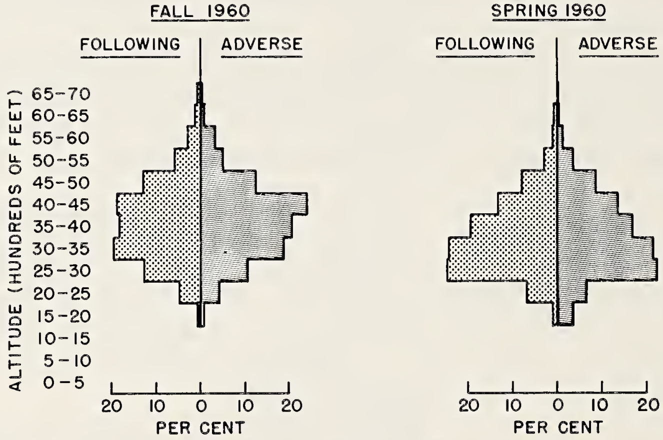

Fig. 16. Altitudinal distribution of nocturnal migrants at Champaign, Illinois, on nights with following (tail) winds and nights with adverse (head) winds in fall and spring, 1960. Note tendency for migrants to occur at higher altitudes in fall than in spring.

Altitudinal Distribution of Migrants.—There was a slight overall seasonal shift in altitude between migrations in the spring and fall (Fig. 16). It was apparent that migrating birds flew at slightly higher altitudes during the fall than during the spring. This was first considered to be a direct response to the wind. Further analysis, however, showed very little difference in the altitudinal distribution of nocturnal migrants between opposed and following winds (Fig. 16) in each of the two seasons. Neither did abeam winds alter the altitudinal distribution of migrating birds.

Fluctuations in the nightly volume of migration during the fall of 1960 suggested that, with opposed winds, many migrants remained on the ground awaiting more favorable conditions (Hassler et al., 1963). It was obvious that the migrants that elected to migrate under opposed winds did not seek the strata that would have offered the minimal resistance to their desired course. There was, therefore, no proximate response to the wind; once aloft they were unaware of changing wind vectors in relation to altitude.

If further study substantiates the finding that fall migrants tend to fly at higher altitudes than spring migrants, then we speculate that there is an ultimate response to the wind. A pattern of altitudinal flying would be advantageous to migrants. In spring, when crosswinds are typical of higher altitudes, a lower flight path would lessen their displacement (Fig. 3). Migration at higher altitudes during the fall, when following winds are more prevalent, would benefit most birds by reducing energy requirements. Thus, an innate pattern of seasonal altitude flying may have evolved as an adaptation to wind direction.

CONCLUSIONS

Migration Tracks.—The easterly declination exhibited in central Illinois in the northbound migration of birds in spring, and, to a lesser extent in their southbound fall migration has some intriguing implications.

Birds may have evolved an elliptical, clockwise migration route between spring and fall as an adaptation to the prevailing westerly and easterly winds. The westerlies occur from about 40° north to about the Arctic Circle. The easterlies occur from about 30° north of the equator to about 30° south of the equator.

The westerlies and the easterlies become more and more dominant in the wind pattern with increasing altitude. Their influence is hardly noticeable below 2,000 ft. The westerlies and easterlies in the northern hemisphere originate from the clockwise flow of air resulting from the rotation of the earth.

Seasonal northeast and southeast flight paths in central Illinois are in accord with the westerly flow of air at that latitude. Even on the Atlantic Coast in Massachusetts, there is evidence that individuals of some species may have an elliptical, seasonal flight path.

Drury et al. (1961:15) reported that radar observations on Cape Cod showed heavy bird migrations in a northeasterly direction during spring. They also reported that from mid-July to mid-October radar showed birds, presumed to be sandpipers and plovers, flying a southeast course out over the Atlantic Ocean. They further stated (p. 14) that in the fall songbirds were often noted migrating south out over the Atlantic. Referring to a reverse migration of birds on three nights in May 1959 (p. 16), they observed by radar a steady southward movement with many birds flying southeastward out to sea. Although the heaviest migration in Massachusetts during the fall appeared to be to the southwest rather than the southeast, a surprising number of migrants apparently head out over the Atlantic to the southeast. While the pattern of an elliptical, clockwise migration for many birds might be modified by the Atlantic Ocean, many species of birds may have different spring and fall migration routes.

Elliptical, clockwise migration routes between wintering and breeding areas would be advantageous to individuals of most species of birds migrating between North and South America. By using such a pattern, northbound migrants, which are vulnerable to westward drift over northern South America, the Caribbean Sea, and the Gulf of Mexico, would utilize the easterly push of the westerlies farther north to return toward their original goal. Again resuming migration in the autumn, those birds breeding north of 40° would be exposed to the eastward force of the westerlies. High-altitude migrants from the easternmost breeding populations would be vulnerable to flight over the Atlantic Ocean. For those species and individuals with sufficient stored energy, this need not be fatal. By remaining aloft 20–30 hours, the easterly winds would return them to Florida and the West Indies. It is increasingly apparent that passerine birds fly much greater distances without stopping than heretofore supposed.

Birds adapted for an elliptical, seasonal pattern of migration may fly in such a manner even when winds do not drift them. In central Illinois, the flight paths with opposed and following winds are to the north-northeast in spring and to the south-southeast in autumn. Therefore, evidence suggests that north of 40°, birds migrate east of north and south even when not drifted by the wind.

The elliptical, clockwise migration of the Golden Plover (*Pluvialus dominica*) has been known for many years. Until recently we have lacked the method (radar) for observing such behavior in other species among the great welter of individuals of a given species migrating from innumerable wintering-ground areas to innumerable breeding areas. Among the multitude of individuals of a given species involved in migration, the geographic distribution of the individuals may provide no tangible clues to an elliptical pattern of flight paths. Because most passerine migration occurs at night, actual flight directions were largely unnoticed before the advent of radar.

Furthermore, the importance of the prevailing westerly winds on bird migration in mid-America was not fully appreciated until radar demonstrated the high altitude at which birds usually migrate (this study and Lack, 1960*a*). Before radar surveillance of bird migration, it was widely believed that most birds migrated at altitudes of 2,000 ft and less. At such low heights, the influence of the high-altitude westerly winds would be nominal.

We wish to make clear that our postulated elliptical and altitudinal pattern of seasonal migration does not pertain to all species, or even to all individuals of the same species, or to all regions of North America.

It is well known that both spring and fall routes of Bobolinks (*Dolichonyx oryzivorus*) breeding west of the Mississippi River extend along a west-northwest, east-southeast axis. On spring migration, North Dakota-bound Bobolinks traveling at high altitudes fly into the westerlies, a decided disadvantage. The north-northwestward migration of the Kirtland's Warbler (*Dendroica kirtlandii*) from the Bahama Islands to Michigan is an example of the northern segment of the spring migration route occurring tangentially to the westerlies.

Our postulation of west to east migration routes between spring and fall is further amended to embrace altitude. The higher birds migrate, the more they are exposed to the influence of the easterly and the westerly winds. We therefore propose that the higher-flying migrants are those that have goals displaced farther laterally from a north–south axis than lower-flying migrants.

Such an ultimate pattern of altitudinal flying would be especially advantageous to long-distance migrants. Lower-flying migrants are more likely to have following winds along a north–south axis, while higher migrating birds north of 40° are more likely to be drifted east. There is more of a following wind in the spring for migrants at lower altitudes, and in the fall for migrants at slightly higher altitudes. If the favoring influence of the wind accounts for our finding birds at higher altitudes during the fall than during the spring, we speculate that this is an ultimate seasonal pattern that is innate. We have previously shown that there is little proximate response of nocturnal migrants to wind vectors.

Innate adaptiveness to wind patterns may have evolved over the eons of time. Those individuals that, by chance, climbed to the most advantageous altitudes and utilized the wind to the greatest extent would be favored in survival, whereas those that did not take advantage of wind patterns would be less likely to survive.

There is the possibility that migrant birds might correct for displacement by westerlies and/or the easterlies in the zone between the two air flows. This zone, in which a southerly air flow predominates, extends from about 30° to about 40° north. Radar studies will be made in this zone to attempt to determine the direction of migration paths in relation to that in the zone of the westerlies.

Only further radar study of nocturnal passerine migration will eventually confirm, refute, or modify the concept of a clockwise, elliptical migration route, spring to fall, among birds in mid-America.

Wind Drift.—The problem embracing the wind displacement of birds in migration is most important, especially along the Atlantic coasts of North America and of Europe. Williamson (1952, 1955, 1959) in a series of papers maintained that many European species of birds reached Great Britain only because they were drifted westward from the continent by easterly winds. He believed that under overcast skies birds would reorient by flying downwind.

Baird and Nisbet (1960:44) concluded from a study of bird migration along the northeast coast of the United States that ". . . most of the birds that reach the outlying islands do so as a result of wind drift from migration routes over the mainland; there is as yet no evidence for the recent suggestions that the islands form part of the normal migration routes of the birds. The largest number of birds arrive after being drifted toward the coast by northwest winds, but southeastward movements also occur in southwest winds."

Lack (1959*b*:392) observed by radar that birds migrating over the North Sea assumed a fixed flight heading which was altered by wind vectors. He stated that ". . . sideways displacement from a heading determined by the sun or stars is evidently the general rule on overseas migration." Lack thus differed with Williamson on the influence of wind on migrants over the North Sea.

Our studies suggested that migrating birds over a large, comparatively featureless land mass attempted to compensate for wind drift by altering their headings. Although they were partly successful in compensating for wind drift, they were not completely successful. The higher the birds flew, the more likely they were to be drifted by the wind. We have already noted that in spring, at least, this drift might reflect the change to more abeam winds with increasing altitude. It may also be related to the distance that migrants are above points of reference on the earth. The higher migrants are above the earth, the more difficult it is for them to ascertain wind drift, because the angle of displacement lessens as the altitude increases.

Birds migrating at night over the sea might be unable to compensate for wind drift whereas those over land might try to counter wind displacement. Over the sea at night fixed points of reference would be almost nonexistent. On land at night, the lights of civilization and salient landscape features would offer points of reference to migrating birds. Thus, Lack's findings that birds are completely displaced (over the sea) by wind, and our findings that wind only partially displaced them, may not be contradictory.

The whole problem of wind drift of migrants over land deserves a great deal more study.

Overcast Skies and Navigation.—Because of the current interest in the problem of celestial navigation, it is important to examine the flight behavior of bird migrants under overcast skies. Where celestial navigation ends and another type of navigation begins in bird migration is conjectural. Some ornithologists believe that celestial cues are the only ones used by birds in migration.

As previously discussed, birds migrating on overcast nights make a pronounced effort to surmount the cloud layer. This intent is further attested by a report (Lack, 1959*b*:393) that, when some captured migrants were released in a thick mist at a Swiss mountain pass, the birds rose vertically until lost to sight.

The desire of birds to fly above the overcast implies that it is advantageous for them to view the sun or the stars, probably as aids in navigation.

Flight paths on the night of 15 October, the only night on which we found an extensive migration above the clouds, were well grouped as to direction, although most of these migrants probably initiated flight under the overcast and perhaps had flown part of the night under it.

The flight tracks of Bartramian Sandpipers and perhaps other migrants were well grouped as to southward direction (Table 1) on 5 August 1960.

Yet these birds had apparently initiated migration under high overcast skies and had flown at least 200 miles under complete cloud cover.

The directional tracks made by thrushes of the genus *Hylocichla* starting migration under overcast skies on 24 May (6–12 P.M.; Table 1) were more diverse in their flight directions than those made by individuals that started farther south under clear skies during the same night (12:01–6 A.M.; Table 1). It is evident that individuals of the same species that obtained views of the sky before migrating under solid cloud cover navigated better than those that did not see the nocturnal sky. Birds that started under clear skies and then flew under solid cloud cover were able to maintain well-grouped directional tracks for at least 175 miles without reference to celestial cues.

It is also apparent that birds were able to maintain directional flight for a short distance without seeing landscape features. Ground fog occurred in the area of the radar station on 3 of the 4 overcast nights on which migration occurred. The altitudinal distribution of the migrants indicated that most birds were above the fog layer. The well-oriented flight paths on 5 August 1960 were made in spite of ground fog and a high overcast.

Evidence for the ability of birds to migrate in an oriented manner under overcast skies is conflicting. Sutter's (1957*b*) radar observations showed birds migrating both above and below extensive overcast in the Alps near Kloten, Switzerland. He believed that the diverse flight directions that occurred on 19 October 1956 might have resulted from heavy cloud cover. On 16 October 1956, Sutter (1957*b*) reported birds flying both above and below a layer of fog. The following day, he found birds migrating above a fog layer and below a light overcast. On 20 October 1956, he reported a large migration occurring, probably between two layers of fog.

Without more detailed information on the extent of the cloud cover and the flight tracks of birds, it is difficult to evaluate the significance of Sutter's (1957*b*) radar findings made under overcast and/or fog conditions. In a later study, Sutter (1958) reported that when flocks of migrating birds met a bank of clouds they either climbed above the overcast or alighted.

In his extensive radar studies of bird movements over the North Sea, Lack (1960*b*:52) reported that on two occasions he observed birds flying in random directions. In one instance, birds emigrating from England encountered fine rain over the sea, and on the other occasion they encountered fog. Lack considered that under these conditions the birds "lost all power of navigation."

Visual records of massive migrations of birds across the Gulf of Mexico (Bullis and Lincoln, 1952; Bullis, 1954) disclosed that birds flew toward the coast in an oriented manner in spite of a low, extensive, solid overcast. We have observed waterfowl migrating under overcast skies on numerous occasions (Bellrose, 1957; Bellrose and Sieh, 1960). On several occasions waterfowl have been observed to depart in migration under overcast skies.

It is difficult to reconcile the conflicting observations, both radar and visual, in regard to migration under overcast skies. From our own visual and radar observations, we are inclined to believe that some birds can initiate migration under overcast skies and can maintain proper directional flight lines without resorting to the use of the sun or the stars for cues. However, most species show better navigation under clear than under overcast skies. Some species of birds show better directional orientation when they view the nocturnal sky before the onset of an overcast than individuals of the same species that have no view of the sky.

We conclude from our observations of bird migration under overcast skies that: (1) Many species of birds and perhaps individuals of other species are reluctant to initiate migration under an overcast. (2) The species and individuals that do initiate migration under an overcast attempt to surmount the cloud deck but, failing in that, they continue in migration below the clouds. (3) Some species that initiate migration under a solid overcast are able to determine direction without celestial cues, and are able to pursue a directional path in migration. Other species have greater difficulty in determining direction under overcast skies. (4) Birds that initiate migration under clear skies and later fly under an overcast are able to maintain proper flight directions.

SUMMARY

Aircraft-type radar was operated during the spring and fall of 1960 at Champaign and Havana, Illinois, for the sole purpose of studying bird migration. Data were obtained from a continuous (1- or 2-minute time-lapse) exposure of 16-mm film to the radar scope.

Flight paths of birds tended to be east of north in the spring and east of south in the fall. The absence of reciprocal flight directions between northbound and southbound migrants in central Illinois suggested the following postulation.

Individual birds of many species migrate along elliptical, clockwise routes between their wintering grounds in Central and South America and their breeding grounds in North America. Birds using such a pattern of migration would take advantage of the easterly drift by the westerly winds north of 40° and the westerly drift by the easterly winds south of 30°.

The higher birds flew, the more they were drifted eastward by the westerlies in both spring and fall. However, the eastward drift appeared intentional on the part of migrants rather than unintentional, because it occurred not only with abeam winds but also with following and opposed winds.

Although birds migrating over central Illinois are drifted by the wind, there is evidence that they correct to some extent for wind drift. Computed flight headings varied more in direction than did flight tracks. The degree of unintentional drift by migrants appeared to be related to altitude and wind velocity.

Migrating birds flew slightly higher during the fall than during the spring. This may relate to the winds during the fall being more favorable for south-

erly migration at higher altitudes, while winds at these altitudes in the spring would be less favorable for northerly migration.

Once in migration, birds appear to be unable to detect the velocity of wind in relation to altitude. The altitudinal distribution of migrants is similar, regardless of whether winds are opposed or following.

Birds migrating under overcast skies attempt to fly above the clouds unless they are too high. When they are not able to surmount the cloud deck, the migrants continue in flight, sometimes in the clouds but usually immediately below.

Some birds initiating migration under a solid overcast are able to pursue a directional flight without reference to celestial cues. Other birds migrating under similar overcast skies do not determine direction as precisely as with celestial cues. Having once determined direction from celestial cues, birds may continue to migrate under overcast skies with good directional flight paths.

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Radar Observations of Bird Migrations in the Southeast of England

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This paper describes a bird-migration film presented to the International Ornithological Congress at Cornell. The film consisted of a series of radar records that were obtained at the Marconi experimental-radar station on Bushy Hill, Essex, England (lat. 51°36′ N, long. 00°37′ E).

The radar operates on a wavelength of 23 cm at a power level of 2 MW. The aerial provides a cosec^2 type of cover diagram in the vertical plane and possesses a horizontal beam width of 0.7°; the performance is such that a range of 65 nautical miles is achieved upon a bird possessing a radar cross section in the order of 10 sq cm, e.g. a single sea gull.

Time-lapse ciné-recording technique was employed whereby one rotational scan of the aerial was recorded on a single frame of the film. The aerial rotated at 4 r.p.m. so that a time-compression ratio of 240 was achieved when the film was projected at the normal rate of 16 frames per second. In this way the various movement patterns of the migrating birds can be rendered clearly apparent, while the direction and speed of flight of the birds can be accurately measured.

SPRING MOVEMENTS

The first part of the film provided a summary of the springtime bird movements that take place in the neighborhood of the southeast corner of England. This location is an extremely interesting one from the bird-migration point of view by reason of the complex movements of birds that are taking place at all seasons of the year between the British Isles and the Continent; movements between Spain and the Scandinavian countries can be similarly monitored for the purpose of learning more about the interesting bird migrations to and from these regions.

The film demonstrated that the major movement of the spring, i.e. February to May, consists of a great eastward surge of birds from the British Isles to northern Europe and the Scandinavian countries. I assume that the species in question were mainly passerines, such as the Blackbird (*Turdus merula*), Chaffinch (*Fringilla coelebs*), and Starling (*Sturnus vulgaris*), which were moving to more northerly breeding grounds. There were also two smaller movements directed to the north-northwest and north-northeast, respectively. The first of these movements involved British passerine residents, e.g. warblers, while the second movement was formed by passerines and waders moving between Spain and Scandinavia.

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AUTUMN/WINTER MOVEMENTS

The second part of the film traced the movements of the autumn and winter, i.e. from September through December to early February, when the main feature was the westerly stream of migrants to the British Isles. It seems safe to assume that these birds were, in the main, the passerines that were returning to the British Isles as winter visitors. A sudden transition between the westerly movements of the winter and the easterly movements of the spring was shown in the film and took place quite abruptly during the early part of February, the precise time depending upon the severity of the winter. As in the case of the spring movement, two other movements also took place in the autumn/winter period; these were directed south-southeast and south-southwest, respectively, and were the reciprocals of those noted above.

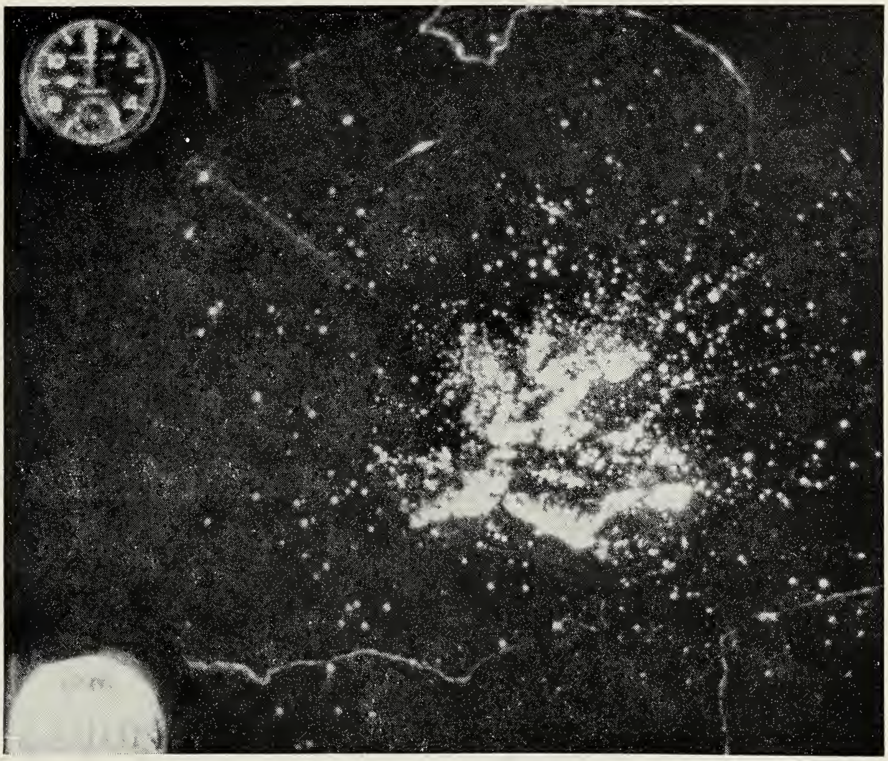

Fig. 1. Appearance of the plan position indicator at sunset.

MOVEMENTS CHARACTERISTIC OF CERTAIN SPECIES

The third part of the film illustrated movements that are characteristic of Lapwings (*Vanellus vanellus*), Swifts (*Apus apus*), and Starlings, respectively, at various times throughout the year.

Hard-weather Movement of Lapwings.—In the British Isles it is a common occurrence for wintry weather during January and early February to provoke a movement of birds to the south, so constituting a form of reversed migration. Illustrations were given of typical movements of Lapwings southward across the channel to France during such periods of hard weather. The birds returned to England immediately after the termination of the wintry spell.

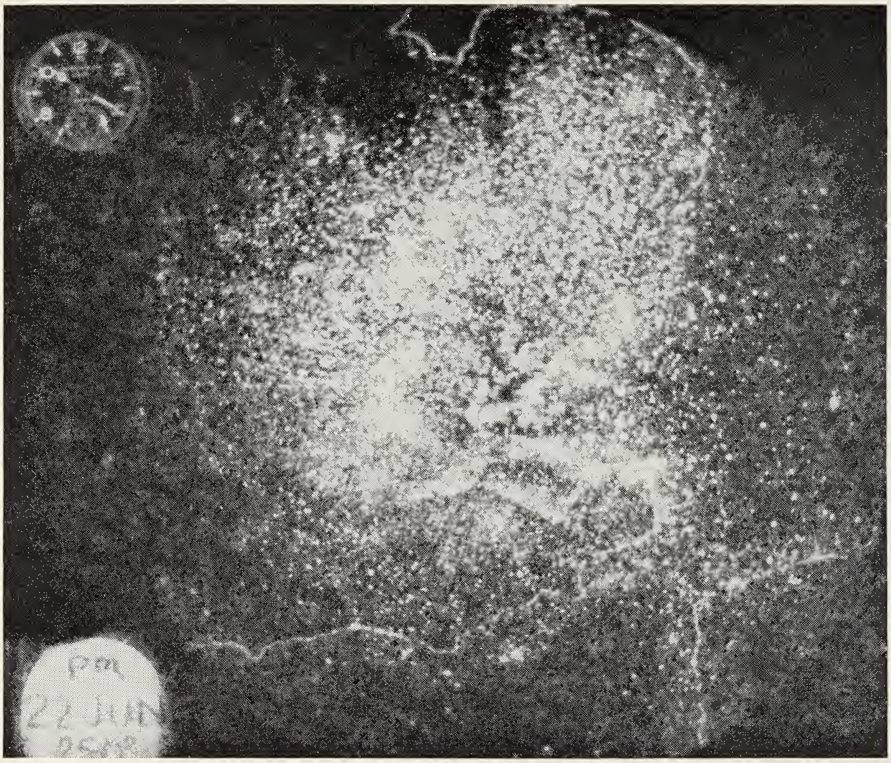

Fig. 2. Swifts in flight after sunset.

Vesper Flights of Swifts.—The "vesper flight" of the male Swift was illustrated by a portion of film that showed how the Swifts take to the air about 1 hour after sunset and continue airborne for most of the night. The radar echoes from the birds were photographed from a cathode ray tube known as a plan position indicator (P.P.I.); the rapid transition from a comparatively clear P.P.I. to a tube showing a heavy density of Swifts was particularly impressive. The film revealed that the birds tend to concentrate more heavily about the towns rather than the open country. This concentration was particularly noticeable at the various coastal towns, such as Hastings and Eastbourne in England, Boulogne and Calais in France.

Once the birds are airborne, they partake of the general air movement characteristic of the season and the region, i.e. they are slowly drifted sea-ward. The film illustrated this effect in a vivid way since the coastline and the coastal towns are apparently drifting into the sea as the night advances; in reality it is the Swifts drifting out to sea and so causing radar echoes to be produced from over the English Channel (Fig. 1 and 2).

Soaring Birds at a Sea-breeze Front.—Another type of bird flight that has been monitored by the radar is the soaring movements that take place at a sea-breeze front. It is a characteristic of the high summer in this part of England for sea breezes to penetrate over the land during the afternoon. The line of demarkation between the cooler, moister air of the sea and the drier air overland is barely observable by the radar in consequence of the small discontinuity of refractive index that takes place at the sea-breeze front, but the presence of the front is clearly revealed by the numbers of soaring birds that congregate there and that are revealed as moving points in the vicinity of the front. The speed of motion of the bird echoes was measured as 30 miles per hour, as compared with the normal speed of progression of such a front of 7 m.p.h. (Fig. 3). It is probable that both Swifts and gulls

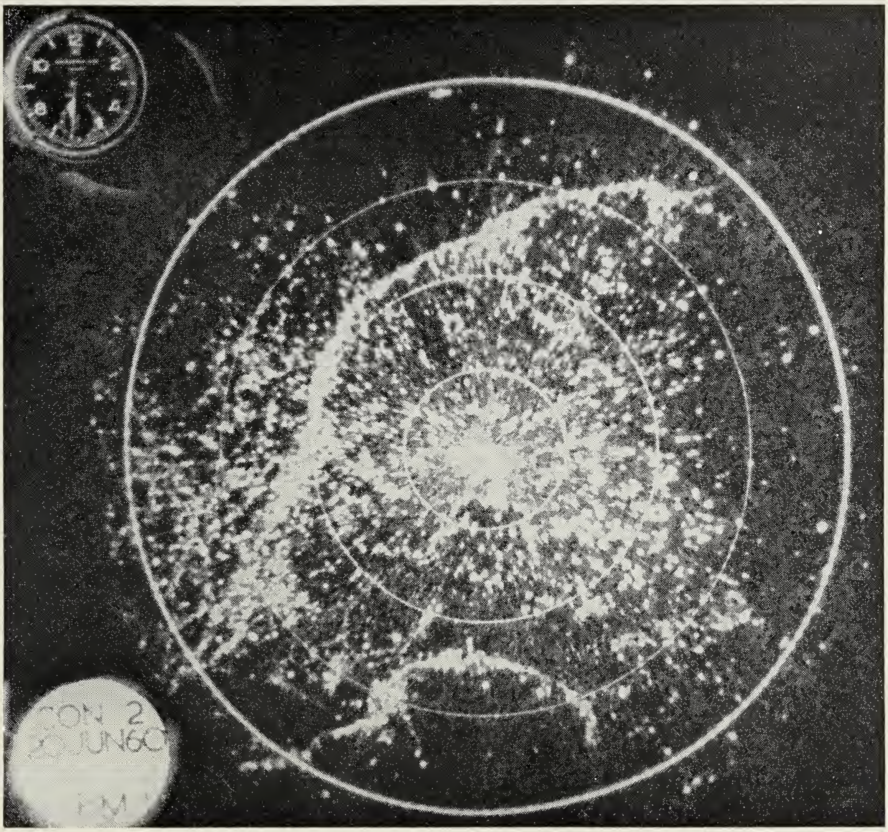

Fig. 3. Soaring Swifts and gulls at a sea-breeze front.

were involved in this soaring movement; the speed measurements do not rule out either of these species.

Ring Angels from Starling Dispersals.—The characteristic roosting habit of the Starling makes this bird peculiarly suitable for detailed radar study. The film illustrated the expanding "ring angels" which are produced by Starlings dispersing from their roost at sunrise (Fig. 4). Illustrations were also given of the nocturnal dispersal of Starlings from their roost; this took place on nights in the early spring when a suitable following wind prompted the birds to join the general migrant stream eastward to the Continent.

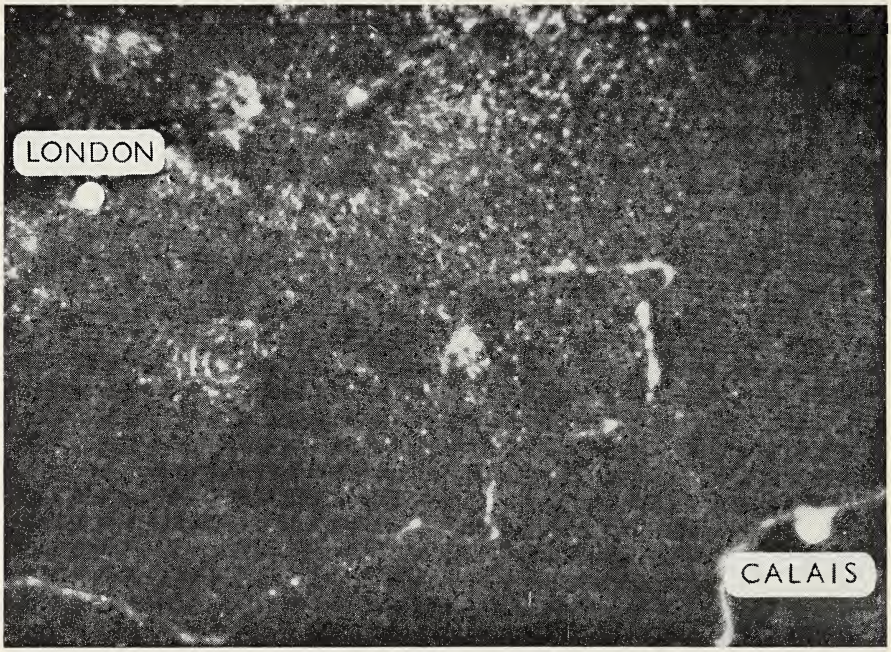

Fig. 4. "Ring-angel" dispersal of Starlings.

Curved Nocturnal Flight Paths.—The final radar record that was shown presented a dense movement of passerines across the English Channel at night. The birds followed a curved path from the French coast and did not take the shortest route across the Channel. The form of this curve toward the northwest was not made in order to correct for any wind effects, nor was it apparently conditioned by any view of the English coast that the birds might have had during the hours of darkness. Execution of this type of movement is obviously related to the navigational ability that these birds possess, but it demands a clear view of the stars at night or the sun by day for its operation.

SUMMARY

Time-lapse ciné recording of a radar in southeast England demonstrated that the major movement of migratory birds in spring consisted of a great

eastward surge to northern Europe and Scandinavia with two smaller movements north-northwest and north-northeast. Reciprocal movements in autumn terminated quite abruptly in early February. Hard-weather movements of *Vanellus vanellus* were recorded in January and early February across the Channel to France. Male *Apus apus* took to the air after sunset and continued airborne for most of the night. Swifts and gulls also concentrated at sea-breeze fronts in the afternoon. Passerines crossed the Channel at night in a curved flight path. The dispersals of Starlings from their roosts at sunrise are shown to be in the form of expanding, discrete rings.

Probleme des Vogelzuges in Peru

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I. EINLEITUNG

Es gibt bisher nur wenige zusammenfassende Veröffentlichungen, die sich mit dem Vogelzug in Südamerika befassen. Schon aus diesem Grunde dürfte es von einigem Interesse sein, eine kurze Übersicht der Vogelwanderungen zu geben, die man in einem tropischen orographisch und klimatisch vielseitig gegliederten Lande wie Peru es ist, beobachten kann. Daten über Vogelwanderungen und Zugvögel in Peru sind spärlich und in der Literatur sehr zerstreut. Einige Angaben bringt schon Taczanowski (1884), und über Wanderungen bei Meeres- und Küstenvögeln berichtet Murphy (1936). Obwohl in den letzten 20 Jahren eine grosse Anzahl von Guanovögeln durch die peruanische Guanogesellschaft beringt worden ist, liegen doch nur wenige zusammenfassende Arbeiten über die Beringungsergebnisse vor, von denen die Arbeiten von Vogt (1942), Schweigger (1959), Jordan (1958, 1960), und Jordan und Cabrera (1960) an erster Stelle genannt seien. Darüber hinaus gibt es noch eine grössere Anzahl in der Spezialliteratur zerstreute Angaben über Vogelzug nach Peru, die in einer späteren ausführlicheren Arbeit behandelt werden sollen.

Die folgenden Ausführungen zeigen, dass noch sehr viel Feldarbeit getan werden muss, bis wir einigermassen über die Wanderungen bei peruanischen Vögeln orientiert sind. Wie in dieser Arbeit gezeigt wird, ist Peru ein Land, das sich zur Erforschung der Anfangsstadien der Entwicklung des Vogelzuges besonders gut eignen dürfte, weil es eine ungewöhnlich grosse Anzahl von natürlichen Lebensgemeinschaften auf relativ engem Raum und dazu noch eine Reihe bedeutsamer Ausbreitungshindernisse besitzt (vergl. M. Koepcke, 1954; H.-W. Koepcke, 1961). Der Artenreichtum der peruanischen Vogelfauna im Zusammenhang mit der Vielseitigkeit des Landes ermöglicht die Aufstellung von biologischen Reihen im Sinne von Böcker (1935–37), in denen die einzelnen Fälle des Wanderverhaltens nach ihrem Ausprägungsgrad angeordnet werden können. Lincoln (1942) hat unzweifelhaft Recht, wenn er schreibt: "The study of movements of birds in South America is of great importance, and this favored region may prove to be the testing ground for some of the theories that have been evolved to explain migration phenomena."

II. STANDVÖGEL

Wie es für ein tropisches Land nicht anders zu erwarten ist, gibt es in Peru sehr viele Standvögel (es sind aus Peru bisher etwa 1 450 Arten mit rund 2 200 Unterarten bekannt). Die meisten Standvögel findet man in

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solchen Lebensgemeinschaften, in denen der Jahreszeitenwechsel verhältnismässig unbedeutend ist, so dass diese Vögel das ganze Jahr über unter fast unveränderten ökologischen Bedingungen leben. Derartige Lebensgemeinschaften, die sich niemals grundlegend verändern, sind z.B. Teile des immergrünen tropischen Regenwaldes, die Mangrovewälder, die Grundwasserwälder an den Flüssen im Gebiet der Küstenwüste, oder auch die *Typha*- und *Scirpus*-Bestände an den Süsswasserteichen der Küste.

Die Standvögel können in drei Hauptgruppen eingeteilt werden: 1. Vögel, die dauernd in ein und derselben Lebensgemeinschaft leben, 2. Vögel, die eine solche Lebensstätte bewohnen, die in kleinen und von einander isolierten (inselartigen) Teilbeständen vorkommt, die über eine grosse Fläche zerstreut sind. 3. Vögel, die zwei oder mehr verschiedenartige Lebensstätten zu ihrer Existenz benötigen.

Die zweite und dritte Gruppe, zu der die Besucher von Blumen, die Aasfresser und auch die peruanischen Guanovögel gehören, leiten zu den Arten mit Tageswanderungen über. Die erstgenannte Gruppe, also die Vögel, die ihr ganzes Leben in nur einer Lebensgemeinschaft verbringen, muss noch in bezug auf das von den Exemplaren in Anspruch genommene Territorium in die folgenden drei Untergruppen unterteilt werden:

a. Vögel mit einem relativ kleinen Territorium, das ungefähr mit der Reichweite ihrer Stimme übereinstimmt. Als Beispiele seien *Cinclodes taczanowskii* am Felsufer des Meeres, *Ochthoeca albidiadema* in den oligothermen ("temperierten") Bergwäldern, sowie eine Reihe weiterer Tyrannen und viele Formicariiden und Pipriden der Regenwälder des Amazonasgebietes angeführt.

b. Vögel mit einem grösseren Territorium, das grösser ist, als die Reichweite ihrer Stimme. Die Sturzbachente *Merganetta leucogenis* ist ein für diese Gruppe zu nennendes Beispiel.

c. Vögel, die sich ausserhalb der Brutzeit mit ihresgleichen oder mit anderen Arten zu Flügen zusammenschliessen, welche in einem verhältnimässig grossen aber abgegrenzten Territorium umherwandern, wie es viele Tangaren der Regenwälder tun, oder wie es bei den aus *Cranioleuca*-, *Leptasthenura*- und *Spizitornis*-Arten und manchen Spechten zusammengesetzten Trupps in den immergrünen Bergwäldern beobachtet werden kann.

Wahrscheinlich haben alle Vögel, also sämtliche Standvögel mit einbegriffen, eine Ausbreitungsphase, die wohl häufig in die Jugendzeit fällt. In dieser Zeit wandern die Vögel solange umher, bis sie einen noch freien Platz finden, der ihre Lebensansprüche befriedigt. Derartige Ausbreitungsbewegungen, die der Arterhaltung förderlich sind, sind als eine normale Erscheinung bei allen Tieren überhaupt aufzufassen und sollen deshalb hier nicht als eine besondere Form der Wanderungen behandelt werden, obwohl sich sicherlich die Wanderungen mancher Arten von dieser Erscheinung ableiten lassen.

III. WANDERUNGEN BEI VÖGELN, DIE IN PERU BRÜTEN

Tageswanderungen

Die Tageswanderungen sind eine Sonderform lokaler Ortsveränderungen, die man, wie schon in Kap. II gesagt wurde, als eine notwendige Begleiterscheinung des Bewohnens mehrerer Lebensstätten oder des Besuchens von "Mikrohabitats" bezeichnen kann, worunter wir kleine inselartig weit voneinander getrennte Kleinlebensstätten verstehen wollen. Als weitere Ursache von Tageswanderungen ist auch der tägliche intensive Wechsel der abiotischen Bedingungen zu betrachten, der für die tropischen Hochgebirgsbereiche charakteristisch ist.

Wenn ein Vogel mehrere Lebensstätten zu seiner Existenz benötigt, dann muss er sich notwendigerweise mit gewisser Regelmässigkeit zwischen diesen Lebensstätten hin und her bewegen, wie es z.B. viele Tauben und Finken tun, die im offenen Gelände Nahrung suchen, zum Trinken eine Wasserstelle und zum Schlafen Buschgelände oder höhere Bäume benötigen. In Wüsten- und Steppengebieten sind Tageswanderungen dieses Typs meist auffallend, wie z.B. in den Bergsteppenbereichen der Andenabhänge. Die Massenvereinigungen an bestimmten Schlafplätzen, wie man sie bei Reihern, Papageien, Tauben und vielen anderen Vögeln kennt, erfordern oft einen weiten Anflugweg der Einzeltiere. Die Neuweltgeier, besonders der Kondor, unternehmen täglich weite Flüge zur Nahrungssuche, von denen sie zu bestimmten Schlafplätzen zurückzukehren pflegen. In manchen Gegenden wählen die täglich von den Anden zur Meeresküste herabfliegenden Kondore an jedem Morgen denselben Flugweg, so dass man an bestimmten Stellen an jedem Tage zahlreiche Exemplare beobachten kann. Wieder eine andere Form der Tageswanderung findet man beim Guacharo *Steatornis caripensis*, der nachts weit von der Wohnhöhle wegzufliegen scheint, worauf die Fruchtkerne hinweisen, die wir in der Höhle von Ninabamba in Nordwestperu sehr zahlreich fanden. Die dort ansässigen Hirten und Bauern versicherten uns, die betreffenden Früchte nicht aus der näheren Umgebung zu kennen. Eine typische Tageswanderung führt auch zeitweilig die Graumöwe *Larus modestus* durch, deren Brutplätze im Inneren der nordchilenischen Wüsten liegen. Wie Goodall, Johnson und Philippi (1951) berichten, halten sich diese Möwen während der Brutzeit den Tag über am Sandstrand des Meeres auf und fliegen jeden Abend zu den wohl bis 100 km vom Meer entfernten Brutplätzen.

Die peruanischen Guanovögel (*Phalacrocorax bougainvillii*, *Pelecanus thagus*, *Sula variegata* und *S. nebouxi*) brüten und schlafen auf den Guanoinseln und auf den sogenannten "Puntas" (Halbinseln, die durch hohe Mauern künstlich vom Hinterland abgetrennt wurden), und fliegen täglich in langen kettenartigen Formationen zu ihren Fischgründen, die sich oft in beträchtlicher Entfernung vom Lande befinden. Sie führen also typische Tageswanderungen durch, und es scheint, dass es in diesem Falle von diesen bis zum echten jahreszeitlich bedingten Zug nur noch ein kleiner Schritt ist. Dieser

Schritt kann darin bestehen, dass die Vögel ausserhalb der Brutzeit nicht mehr täglich zu ihrem gewohnten Schlafplatz zurückkehren, sondern auf einer anderen ähnlichen Insel oder Halbinsel übernachten. Wie Jordan (1958, 1960) und Jordan und Cabrera (1960) berichten, wandern der Guanokormoran und der Guanotölpel im Küstenmeer von Mittelchile bis Ekuador mit einer gewissen Abhängigkeit von den Jahreszeiten hin und her. Ausserdem führen sie auch noch gelegentlich invasionsartige Sonderwanderungen durch, die vor allem nach Süden gerichtet sind und die mit dem Verschwinden ihres wichtigsten Nahrungsfisches, der Anchoveta *Engraulis ringes*, aus dem oberflächennahen Wasser im Zusammenhang stehen, was in solchen Jahren einzutreten pflegt, in denen der Humboldtstrom abnorm ausgebildet ist. Die Guanovögel zeigen also ein durchaus zugähnliches Verhalten, wenn sie auch noch nicht als echte Zugvögel bezeichnet werden dürfen. Sie sind zur Fortpflanzung auf bestimmte Brutplätze angewiesen und können ausserhalb der Brutzeit sich dann über diejenigen Teile des Küstenmeeres ausbreiten, die ihre ökologischen Ansprüche befriedigen, worauf auch im dritten Abschnitt dieses Kapitels noch näher eingegangen wird.

Vögel, die weit voneinander getrennte inselartige "Mikrohabitats" benötigen, sind, wie schon gesagt, die Besucher von Blumen oder in Blüte stehenden Büschen und Bäumen wie Kolibris und manche Coerebiden. Viele von ihnen, wie *Aglaeactis cupripennis* der andinen Bergsteppen und Bergwälder, oder *Rhodopis vesper* der steppenartigen Biotope des Küstengebietes und des westlichen Andenabhanges pflegen eine Zeitlang denselben Busch oder Baum jeden Tag zur gleichen Zeit zu besuchen, woraus man schliessen kann, dass diese Vögel einen im grossen und ganzen festliegenden Tagesrundflug durchführen. Manche Kolibris erscheinen und verschwinden ausserdem mit dem Aufblühen und Verblühen gewisser Blumen, wodurch der Eindruck einer echten, wenn auch örtlich begrenzten Wanderung entsteht (vergl. Abs. 4 dieses Kapitels).

Eine Gruppe von Lebensgemeinschaften, die sich durch einen beträchtlichen täglichen Wechsel der abiotischen Bedingungen auszeichnen, sind die hochandinen Biozönosen. Während der warmen Stunden des Tages werden hier auch die extremen Stellen wie Hügelkuppen von Vögeln aus tieferen und geschützteren Stellen aufgesucht, wie es z.B. manche Kolibris tun, wie *Coeligena iris eva*. Niethammer (1953) beobachtete in Bolivien, dass *Diuca speculifera* dort eine in entgegengesetzter Richtung verlaufende Tageswanderung ausführt. Er fand einen Schlafplatz dieses Finken in einer Gletscherspalte in 5 300 m Höhe und beobachtete die Vögel bei der Nahrungssuche etwa 600 m tiefer.

Vögel, die mit der jahreszeitlichen Ausdehnung ihrer Lebensgemeinschaft wandern

Es gibt in Peru eine Reihe von Lebensgemeinschaften, deren Ausdehnung mit dem Jahreszeitenwechsel gewissermassen variiert, indem ein Ausdehnungs- und ein Schrumpfungsvorgang miteinander abwechseln. So dehnen sich z.B. die kleinen Gebiete des makrothermen ("tropischen") Regenwaldes an der Westseite der Anden Nordperus und Ekuadors währen der Regenzeit praktisch über grössere Flächen aus, was dadurch geschieht, dass die angrenzenden nur sommergrünen Wälder ihnen durch die Fülle der durch den Regen hervorgerufenen Vegetation ähnlich werden (Chapman, 1926; H.-W. Koepcke, 1961). Vögel, die dem makrothermen Regenwald angehören, können sich dann erheblich ausbreiten, wie wir es bei *Trogon melanurus*, *Platypsaris homochrous* und *Cacicus cela flavicrissus* beobachten können. Als im April 1953 heftige Regenfälle in Nordwestperu niedergingen, veränderten die *Prosopis*-Wälder (vom Grundwasser abhängige Wälder) nach Süden zu bis Olmos (6° S) ihren sonst allgemein savannen- bis buschwaldartigen Aspekt und wurden in mancher Hinsicht einem makrothermen Regenwalde ähnlich. Dieser Eindruck wurde vor allem durch schnellwüchsige und grossblättrige Rankpflanzen wie die Cucurbitacee *Sicyos* hervorgerufen, die Bäume und Büsche z.T. vollständig einhüllten und wie mit frischem Grün bedeckt erscheinen liessen. Vögel, die dort gewöhnlich fehlen oder selten sind, wie *Sporophila luctuosa*, traten häufig auf, ja es wurde sogar der Königsgeier *Sarcorhamphus papa* dort beobachtet.

Ähnliche Verhältnisse findet man auch bei den Halbwüsten und Steppen Nordperus, die nach gelegentlichen Regenfällen ihren Aspekt wesentlich verändern, indem sich die Steppe gewissermassen ausdehnt, weil die angrenzenden Halbwüsten dann zeitweilig steppenartig erscheinen. Für gewöhnlich findet man in diesen Halbwüsten nur wenige Vogelarten wie *Geositta p. paytensis*, *Piezorhina cinerea* und *Burhinus superciliaris*, aber wenn diese Gebiete sich begrünen, dann werden sie von anderen Vögeln besucht, wie *Heliomaster longirostris albicrissa*, *Parula pitiayumi pacifica* oder *Gnathospiza raimondii*. Diese Lebensstätten der regenzeitbedingten Vegetation Nordwestperus sind Beispiele für sich zeitweilig ausdehnende und wieder schrumpfende Lebensgemeinschaften des Flachlandes. Ein entsprechender Fall im Gebirge ist die zeitweilig talabwärts gerichtete Ausdehnung der Bergsteppen am Westhang der peruanischen Anden in Jahren mit besonders starken Regenfällen. Vögel wie *Colibri coruscans*, *Conirostrum cinereum* und *Spinus magellanicus* werden an Stellen angetroffen, an denen sie sonst zu fehlen pflegen.

Diese Fälle zeigen uns die nicht überraschende und auch allgemein bekannte Tatsache, dass jede Art die Tendenz hat, ihre typische Lebensstätte vollständig zu besiedeln. Aber solche "pulsierenden" Ortsbewegungen dürften zu den Anfangsstadien des Vogelzuges gehören.

Arten, die ein geographisch eng begrenztes Brutgebiet und ein ausgedehntes Nahrungsgebiet besitzen

Offenbar sind die im vorstehenden Abschnitt behandelten Ausbreitungserscheinungen den viel auffälligeren Wanderungen anderer Vögel verwandt, wie sie z.B. *Larus modestus* ausführt, die, wie schon in Abschnitt I dieses Kapitels gesagt wurde, in den nordchilenischen Wüsten brütet und sich ausserhalb der Brutzeit an den marinen Sandstranden hauptsächlich nach Norden ausbreitet, wobei sie in geringer Zahl sogar Ekuador erreicht. Diese Möwe ist eine für die Sandstrande im Bereich des Humboldtstromes typische Art, die ein ausgesprochener Nahrungsspezialist ist, indem sie sich fast ausschliesslich von dem Brandungskrebs *Emerita analoga* ernährt (vergl. Koepcke und Koepcke, 1953). Wenn diese Vögel sich entlang der peruanischen Küste nach Norden ausdehnen, dann tun sie nichts weiter, als ihre typische Lebensstätte vollständig besiedeln. Mit dem Aufhören des Massenvorkommens von *E. analoga* nördlich vom Cerro Illescas (6° S) und dem Einsetzen mehr tropischer abiotischer Bedingungen an den Stranden wird *Larus modestus* in Nordperu ein immer seltenerer Vogel.

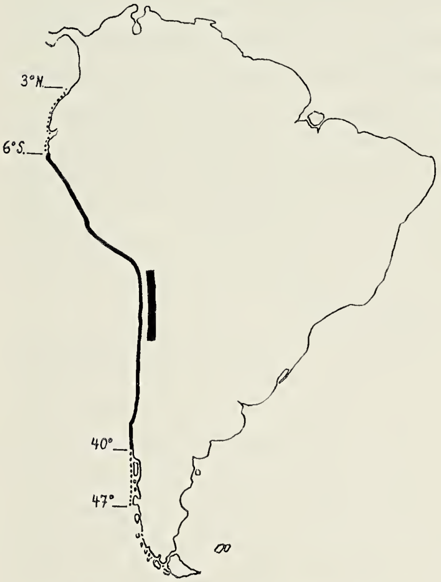

Fig. 1. Verbreitung von *Larus modestus.* Ungefähre Lage des Brutgebietes; Gebiet des gewöhnlichen Auftretens ausserhalb der Brutzeit (zwischen 40° S und 6° S); Gebiete des nur gelegentlichen Vorkommens: zwischen 6° S und 3° N (ausnahmsweise bis Panama) sowie zwischen 40° S und 47° S.

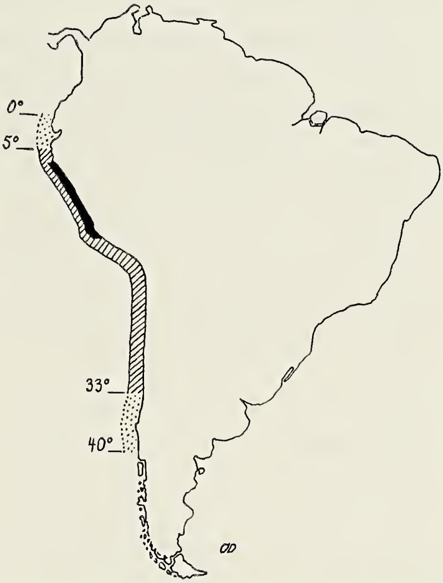

Fig. 2. Verbreitung des Guanokormorans *Phalacrocorax bougainvillii.* Schwarz: Lage der hauptsächlichen Brutinseln und "Puntas"; Schraffiert: Gebiet des Massenvorkommens ausserhalb der Brutzeit (vergl. Text); Punktiert: Gebiete, in denen die Art meist nur in kleinen Flügen oder nur gelegentlich auftritt.

Einen weiteren Fall bilden die Guanovögel der perunanischen Küste, wie schon im ersten Abschnitt dieses Kapitels gesagt wurde. Sie sind gezwungen, hauptsächlich im Bereich der mittelperuanischen Küste zu brüten, weil besonders in diesem Teil der vom Humboldtstrom beeinflussten westamerikanischen Küste geeignete Inseln vorhanden sind. Von den Brutstätten ausserhalb dieses Kerngebietes ist die des Guanokormorans auf der Insel Pupuya in Chile besonders bemerkenswert. Die Guanovögel müssen deshalb auf Inseln brüten, weil die durch Füchse (*Dusicyon*) und eiersammelnde Menschen bedingten Störungen eine erfolgreiche Brut auf dem Festlande normalerweise unmöglich machen. Nur an den schon erwähnten durch hohe Mauern abgesicherten Halbinseln, den sogenannten "Puntas" können die Vögel seit einiger Zeit nun auch auf dem Festland in Massen brüten (vergl. Schweigger, 1959). Ausserhalb der Brutzeit breiten sich die Guanovögel über alle Teile des benachbarten Küstenmeeres aus, soweit wie sie Nahrung und die ihnen zusagenden ökologischen Bedingungen finden, und beides finden sie in dem gesamten Gebiet des durch sein grünes Wasser gekennzeichneten kalten Humboldtstromes zwischen Mittelchile und Nordperu, und zum Teil auch noch bis Ekuador. Nur in diesen Gewässern gibt es die gewaltigen Mengen von *Engraulis ringens*, an deren Vorhandensein die Guanovögel weitgehend gebunden zu sein scheinen. Das bedeutet, dass auch die normalen Wanderungen der Guanovögel als ein periodisches Ausfüllen der für sie typischen Lebensstätte aufgefasst werden müssen.

Es ist sicherlich berechtigt, die Wanderungen mancher Zugvögel als ein ähnliches periodisches Ausfüllen ihres Nahrungsbiotops aufzufassen. Die einzigen Biotope, die sich über weite Teile der Erde von Norden nach Süden in ganz oder doch fast zusammenhängenden Beständen erstrecken, sind das freie Wasser des Meeres und die Lebensstätten des Meeresufers. Diese Tatsache macht es verständlich, dass gerade die Arten, die diesen Lebensstätten typisch sind, zu weltweiten Wanderungen neigen (viele Sturmvögel, manche Seeschwalben und Limicolen), soweit sie nicht wie *Larus modestus* oder die peruanischen Guanovögel an ganz spezielle Verhältnisse angepasst sind.

Vögel, die von einem Biotopbestand zu einem anderen gleichartigen hinüberwechseln indem sie Lebensstätten überfliegen, die für sie untypisch oder feindlich sind

Im immergrünen Regenwald des Amazonasbeckens kann man nur relativ wenige Landvögel beobachten, die mit einer gewissen Regelmässigkeit grössere Flüsse überfliegen. Neben solchen Vögeln, die schon zum Nahrungserwerb viel und weit fliegen müssen wie Segler, Schwalben, Nachtschwalben und manche Raubvögel, sieht man hauptsächlich solche Arten die Flüsse überfliegen, die sich zu Trupps zusammenschliessen und in einem begrenzten Gebiet umherwandern wie es vor allem Papageien, Tukane, Stärlinge und Tangaren (vergl. II) tun. Wie diese Beispiele zeigen, handelt es sich zum überwiegenden Teil um Bewohner der Baumwipfel oder des Waldrandes. Die meisten der zahlreichen Arten von Formicariiden, Pipriden und viele Cotingiden und Tyrannen sieht man nie einen breiten Fluss überfliegen. Diese Vögel sind ganz an das Leben im dunklen Waldesinnern angepasst und nicht nur die freie Wasserfläche eines Flusses, sondern schon dessen Uferbiotope (offener Cecropienwald, Gramineenbestände, schwimmende Pflanzendecken, Steilufer, Sandbänke usw.) werden von ihnen gemieden, ja sogar eine Strasse mit zu beiden Seiten abgeholztem Waldstreifen kann für manche Arten ein Hindernis bedeuten. Die schon erwähnten aus *Cranioleuca*, *Leptasthenura* usw. zusammengesetzten Trupps, die häufig in den andinen Bergwäldern angetroffen werden, sieht man des öfteren von einem Waldstück zum anderen herüberwechseln, während andere Vögel derselben Wälder wie *Scytalopus unicolor* oder *Ochthoeca albidiadema* dies nach unseren Beobachtungen nicht zu tun pflegen.

Diese Beispiele zeigen, dass die Fähigkeit, fremdartige oder lebensfeindliche Lebensstätten zu überfliegen, nur ganz bestimmten Arten zukommt. Diese Fähigkeit gehört aber zu einer der Voraussetzungen zur Durchführung weiter Wanderungen, denn selbst solche Arten, die über weite Strecken gleichartig beschaffene Lebensstätten bewohnen, müssen kleine andersartige Biotopbestände überspringen können, wie z.B. wandernde Strandvögel, die Flussmündungen und Strecken von Felsufer überfliegen.

Vögel, die in solchen Lebensgemeinschaften leben, in denen sich die ökologischen Eigenschaften mit dem Wechsel der Jahreszeiten ändern, oder die zeitweilig verschwinden

Eine Lebensgemeinschaft, die zeitweilig vollständig verschwindet, sind die flachen Sand- und Geröllbänke in grossen Teilen des Amazonasflachlandes, die währen der Regenzeit, in der das Wasser in Peru 8 bis 12 m steigt, überflutet werden. Nur zwei Vögel sind in Peru eng an diese Sand- und Geröllbänke gebunden: die Nachtschwalbe *Chordeiles rupestris* und der Regenpfeifer *Charadrius collaris.* Die erstere tritt währen der Hochwasserzeit auch in solchen Teilen des amazonischen Flussystems auf, wo Sand- und Geröllbänke überhaupt fehlen. Sie setzt sich dann auf anderen Untergrund. Wir haben bisher keine Hinweise, dass dieser Vogel besondere Wanderungen ausführt. Der Regenpfeifer dagegen scheint weiter flussaufwärts zu wandern oder sogar in gewisser Anzahl das Amazonasflachland zu verlassen. Goodall, Johnson und Philippi (1951) bezeichnen *C. collaris* als einen gelegentlichen Besucher der chilenischen Küste.

Die beiden weissen Reiher *Casmerodius albus egretta* und *Leucophoyx t. thula*, sowie *Mycteria americana* und *Jabiru mycteria* sind auf denselben Sandbänken des Amazonasgebietes während des Wassertiefstandes häufig und werden, wenn das Wasser steigt, zum Teil an den kleinen Nebenflüssen und auch im Andenbereich angetroffen. Besonders *Casmerodius* wird dann häufig am Ufer der hochandinen Seen gefunden, währen *Leucophoyx* dort in geringerer Zahl auftritt und *Mycteria americana* nur ausnahmsweise so hoch hinaufgeht. Der Jabirú, *Jabiru mycteria*, überfliegt sogar gelegentlich die Anden und wird dann an der pazifischen Küste gefunden (eine Beobachtung von Arequipa, und zweimal bei Mejía, Südperu, gesehen). Ein anderer im Amazonasflachland häufiger Wasservogel ist der Kormoran *Phalacrocorax b. brasilianus*, der dort in grossen Kolonien brütet und der ebenfalls zeitweilig an den hochandinen Seen (in deren Bereich er zwar auch Brutvogel ist) in grösserer Anzahl auftritt als für gewöhnlich. Es ist anzunehmen, dass die Kormorane zur Hochwasserzeit im Amazonasgebiet nur schwer genügend Fische erbeuten können, weil dann dort das Wasser trübe und tief ist und viele Fische sich in die inneren Teile der überfluteten Wälder begeben. In diesem Zusammenhang muss auch eine Angabe Taczanowskis (1884) Seite 62 erwähnt werden, nach der im Tal von Huayabamba (Nordperu) die dort in der Regenzeit zeitweilig auftretenden Teiche von *Colymbus dominicus*, *Querquedula cyanoptera*, *Oxyura ferruginea*, *Phalacrocorax brasilianus*, *Casmerodius albus* und *Leucophoyx thula* besiedelt werden.

Einen anderen noch nicht ganz geklärten Fall stellt die Andenmöwe *Larus serranus* dar, die sich in gewisser Weise entgegengesetzt zu verhalten scheint, wie die genannten Wasservögel der Urwaldflüsse, indem sie in der Punazone des Hochandengebietes brütet und während des Südwinters zum Teil zur Pazifikküste herunterkommt.

Die Fälle, in denen nicht die ganze Lebensgemeinschaft verschwindet, sondern sich nur einer ihrer ökologisch bedeutsamen Faktoren ändert, sind zahlreich. So besuchen fruchtfressende Vögel manche Gebiete nur dann, wenn dort gewisse Früchte reif sind. *Ara militaris* z.B., der im ostandinen Bergland zuhause ist, tritt an der Westseite der Anden im Wald von Taulis (Nordperu) nur zur Reifezeit bestimmter Früchte auf. Die isolierte Lage dieses Waldgebietes erfordert es, dass diese Aras grössere Strecken des andinen Punagraslandes überfliegen müssen.

Für Kolibris und manche Coerebiden sind manche Blüten ein entscheidender ökologischer Faktor. So führen z.B. die vier Kolibriarten der mittel- und südperuanischen Küste *Rhodopis vesper*, *Myrtis fanny*, *Amazilia amazilia* und *Thaumastura cora* regelmässige Wanderungen zwischen den Flussoasen und den Lomasgebieten der sonst wüstenhaften Küste durch. Die Lomas sind Gebiete mit einer zeitweilig auftretenden zartblättrigen Nebelvegetation, deren Existenz durch das vom kalten Humboldtstrom bedingte Klima ermöglicht wird. Kolibris sind in den Lomasgebieten nur dann häufig, wenn diese grün sind und einem Blütenmeer gleichen, und die meisten von ihnen verschwinden wieder, wenn die Lomas trocken werden und grösstenteils einen halbwüstenartigen Charakter annehmen. Einen ähnlichen Wechsel der Lebensgemeinschaften führen auch noch andere Vögel durch wie z.B. *Zonotrichia capensis peruviensis* und *Volatinia jacarina peruviensis*, die zum Brüten in die Lomas kommen. Ausser den zwischen Lomas und Flussoasen hin und her wandernden Arten gibt es zahlreiche Arten, die in einer oder in beiden Lebensgemeinschaften Standvögel sind. Standvögel der Lomas sind z.B. *Asthenes cactorum* und *Geositta crassirostris*, die den Flussoasen fehlen, während *Zenaida asiatica meloda* und *Crotophaga sulcirostris* zu den typischen Arten der Flussoasen gehören, die den Lomas fehlen. Ausserdem sind auch einige Standvögel beiden gemeinsam, wie *Speotyto cunicularia nanodes* und *Troglodytes musculus audax*. Die Ursache des verschiedenen

Verhaltens der soeben genannten Arten ist in ihren verschiedenen ökologischen Ansprüchen zu suchen; so leben die als Standvögel Genannten in solchen ökologischen Nischen, die vom Jahreszeitenwechsel noch am wenigsten betroffen werden.

Der intensive Jahreszeitenwechsel in den Lomagebieten der peruanischen Küste und die Tatsache, dass die meisten Lomas durch breite Wüstenstreifen sowohl von den Flussoasen als auch von den Regensteppen des westlichen Andenabhanges gut isoliert sind, macht diese Gruppe von Lebensgemeinschaften zu einem Objekt, das zum Studium der Initialphasen der Entwicklung des Vogelzuges besonders gut geeignet ist.

Die im obigen Text als Einwanderer in die Lomas genannten Arten kommen aus den mehr oder weniger benachbarten Flussoasen, die zwar keinen ausgeprägten Jahreszeitenwechsel besitzen, aber zu derselben Küstenlandschaft der Feuchtluftwüsten (vergl. Koepcke und Koepcke, 1953) gehören wie die Lomas und nur einen anderen Oasentyp darstellen. Es wandern aber auch Arten von den Bergsteppen des westlichen Andenabhanges in die Lomagebiete ein. Diese Bergsteppen zeigen, wie M. Koepcke (1954) und H.-W. Koepcke (1961) bereits näher ausgeführt haben, einen den Lomas in gewisser Weise ähnlichen Gesamtaspekt und zum Teil auch miteinander vergleichbare Lebensgemeinschaften. Beide Gebiete pflegen aber durch einen breiten Streifen von Extremwüste von einander getrennt zu sein und liegen auch in verschiedener Höhe über dem Meer. Die Lomas reichen meist nicht höher als 1 000 m und liegen an der Küste, während die viel weiter landeinwärts befindlichen Bergsteppen vor allem zwischen 1 500 und 3 000 m Höhe liegen. Von besonderem Interesse ist ferner die Tatsache, dass die Lomagebiete immer dann grün sind, wenn die Bergsteppen Trockenzeit haben und umgekehrt. Die Nebelzeit an der Küste liegt in Mittelperu zwischen Mai und Oktober, und die Regenzeit im Gebirge fällt in die Monate November bis März.

In bezug auf ihr Wanderverhalten kann man die Vögel, die den Bergsteppen des westlichen Andenabhanges und den Lomas gemeinsam sind, in verschiedene Gruppen einteilen. Standvögel, die nur in den Lomas und in den Bergsteppen vorkommen, sind die schon erwähnten *Geositta crassirostris* und *Asthenes cactorum*. Andere Arten, wie *Psilopsiagon aurifrons* und *Spinus magellanicus* sind im gesamten Gebiet der Westseite der Anden von Mittel- und Südperu verbreitet und wandern in diesem Gebiet nach Art von Strichvögeln umher. Weitere Vögel wie *Colibri coruscans* und wahrscheinlich auch *Phrygilus alaudinus bipartitus* und *Catamenia analis*, die in den Flussoasen selten sind oder dort ganz fehlen, scheinen nur zwischen Lomagebieten und Andenabhang hin und her zu wandern.

Der Regenpfeifer *Oreopholus ruficollis* ist in Peru nur vom Küstengebiet und von den Hochanden bekannt. Er brütet regelmässig in manchen Lomagebieten und erscheint am Brutplatz zu Beginn der Nebelzeit in Trupps. Über ihre Herkunft ist nichts Näheres bekannt. Es müsste durch das Beringungsexperiment festgestellt werden, ob diese Vögel ständig im Küstengebiet bleiben oder zwischen Hochanden und Küste hin und her wandern. Eine nicht weniger bemerkenswerte Art ist der Höhenläufer *Thinocorus rumicivorus cuneicauda*, der z.B. in den Lomas von Lachay (Küste von Mittelperu) in beträchtlicher Anzahl brütet. Auch die Höhenläufer erscheinen am Brutplatz schon kurz vor der Nebelzeit und sind dann in grossen Schwärmen bis zu 2 000 Exemplaren vereinigt. Es ist nicht bekannt, wo sich die Hauptmenge dieser Vögel ausserhalb der Brutzeit aufhält. Da sie nicht in den Anden vorkommen, ist es möglich, dass sie im Küstengebiet umherwandern. Ausserdem werden die Lomas auch von echten Zugvögeln besucht, wie von der chilenischen *Muscisaxicola macloviana mentalis.*

Die echten Zugvögel tun im Grunde genommen dasselbe, wie die zwischen den Bergsteppen des westlichen Andenabhanges und den Lomagebieten der Küste hin und her wandernden Arten, wenn auch ihre Wanderungen viel weiter führen. Auch sie verlassen eine Lebensstätte, in der infolge des Jahreszeitenwechsels ungünstige Lebensbedingungen eintreten und wandern durch Überfliegen lebensfeindlichen Geländes in eine ähnliche Lebensstätte ein, die einen entgegengesetzten Jahreszeitenwechsel besitzt, d.h. die gerade dann optimale Lebensbedingungen bietet, wenn die erstgenannte ungünstige bekommt. Die echten Zugvögel brüten also ganz ähnlich wie die zum Brüten in die Lomas einwandernden Arten in Lebensgemeinschaften, die ihren Aspekt grundlegend mit den Jahreszeiten wechseln, und in vielen Fällen führen ihre Wanderungen sie zu ähnlichen Lebensgemeinschaften, die sich auf der entgegengesetzten Halbkugel der Erde befinden können, wo der Jahreszeitenwechsel für gewöhnlich entgegengesetzt verläuft, oder (in den eigentlichen Tropen) ganz fehlen kann. Auch das Wechseln zwischen einer Lebensstätte mit Jahreszeitenwechsel und einer solchen ohne diesen finden wir an der peruanischen Küste auf kleinstem Raume wieder, indem auch dort gewisse Arten zwischen Lebensgemeinschaften mit Jahreszeitenwechsel (Lomas) und solchen ohne einen solchen (Flussoasen) hin und her wandern. Wenn wir den Vogelzug unter diesem Blickwinkel betrachten, dann erscheint das Studium der Lomasvögel von einiger theoretischer Bedeutung.

IV. ZUGVÖGEL, DIE NACH PERU KOMMEN

Nach unserer gegenwärtigen Kenntnis sind 106 Arten, das sind 7,3% der rund 1 450 bisher aus Peru bekannten Vogelarten, als wirkliche Zugvögel zu betrachten, die nicht in Peru brüten. Ein Viertel dieser Zugvögel kommt vom Süden und die übrigen aus dem Norden. Die einzigen bisher bekannten Fälle von Vögeln, die in Peru brüten und regelmässig über die Landesgrenzen hinaus wandern, sind die schon in Kap. III, 2 behandelten Guanovögel.

Zugvögel aus dem Süden

Ein von Süden kommender Einwanderer, der schon in Kap. III. behandelt wurde, ist die Graumöwe *Larus modestus.* Die einzigen weiteren möwenartigen Vögel, die ausser dieser Art noch von Süden kommen, sind *Catharacta skua chilensis*, die in Feuerland brütet und an der pazifischen Küste nach Norden bis Mittelperu wandert, und *Sterna hirundinacea*, die zwar auch noch in Südperu brütet, aber auch von Chile her nach Norden zu wandern scheint. Ausser einer Reihe von Sturmvögeln dürften keine weiteren Meeres- oder Küstenvögel bekannt sein, die von Süden her nach Peru kommen. Von den bisher aus Peru bekannten 24 Arten von Sturmvögeln (Tubinares) sind 17 Zugvögel aus dem Süden. Beringungsergebnisse scheinen bei den nach Peru wandernden Arten bisher nur von *Macronectes giganteus* vorzuliegen. Chilenische und peruanische Wiederfunde zeigen, dass diese Art weit wandert und sogar von den zu Neuseeland gehörenden subantarktischen Inseln zur Westküste Südamerikas kommt. Andere Arten, die man als Brutvögel bisher nur bei Neuseeland fand, sind die gelegentlich an der peruanischen Küste erscheinenden *Diomedea cauta salvini*, *D. bulleri* und *Puffinus bulleri*. Die meisten übrigen von Süden nach Peru kommenden Sturmvögel brüten zirkumantarktisch, nur *Pterodroma cookii defilippiana*, *Fregetta grallaria segethi* und *Puffinus creatopus* brüten auf den der chilenischen Küste vorgelagerten Inseln (Juan Fernández etc.).

Es gibt nur verhältnismässig wenige Landvögel, die vom südlichen Südamerika nach Peru wandern. Mit Ausnahme der Schwalben *Atticora cyanoleuca patagonica* und *Progne modesta elegans* sind es nur Tyrannen. Unter diesen sind fünf Arten von *Muscisaxicola*, die im Andenhochland und im Küstengebiet wandern und *Pyrocephalus r. rubinus*, der von Argentinien aus in das Amazonasgebiet einwandert, besonders bemerkenswert.

Zugvögel aus dem Norden

Drei Viertel der aus Peru bekannten Zugvögel sind nördliche Arten. Vier von diesen kommen von den Galapagos-Inseln, nämlich *Diomedea irrorata*, *Oceanodroma ph. phaeopygia*, *Creagrus furcatus* und zum Teil auch *Sula dactylatra granti*. Auch aus Mittelamerika und dem südlichen Nordamerika scheinen hauptsächlich nur Meeres- und Strandvögel nach Peru zu kommen wie *Oceanodroma m. melania*, *Thalasseus elegans*, *Rynchops nigra*, *Pelecanus occidentalis* und *Fregata magnificens*. Die grosse Mehrzahl der nach Peru wandernden nördlichen Zugvögel kommt jedoch aus dem hohen Norden. Die meisten Zugvögel der gemässigteren Breiten Nordamerikas überwintern dagegen bereits in Mittelamerika und im nördlichen Südamerika. Dadurch wird die Regel bestätigt, dass die am weitesten im Norden brütenden Zugvögel am weitesten nach Süden zu wandern pflegen.

Es dürfte von einigem Interesse sein, kurz zu schildern, in welchen Lebensstätten die aus dem Norden nach Peru kommenden Zugvögel überwintern. Im Hochandengebiet finden wir hauptsächlich Wasser- und Ufervögel, die dort für gewöhnlich nicht in grossen Verbänden auftreten. Alle dort festgestellten Arten kommen auch an der Küste vor. Man beobachtet in den Hochanden vor allem *Pluvialis dominica*, *Steganopus tricolor*, *Actitis macu* *laria* sowie einige *Erolia*- und *Tringa*-Arten. Ausserdem findet man im Hochandenraum einige Raubvögel wie *Buteo swainsoni, B. platypterus, Pandion haliaetus carolinensis, Falco peregrinus anatum,* die ebenso wie die Ente *Querquedula discors* und der Stärling *Dolichonyx oryzivorus* auch an der Küste und zum Teil auch im Amazonasflachland überwintern.

In den immergrünen tropischen Regenwäldern des Amazonasflachlandes treten als Zugvögel hauptsächlich Passeres auf, wie *Tyrannus tyrannus, Nuttallornis mesoleucus,* Arten von *Myiochanes* und *Empidonax, Vireo olivaceus, Wilsonia canadensis, Dendroica aestiva* sowie *Turdus ustulata swainsoni* und *T. minima aliciae.* Alle diese Arten kommen niemals oder doch nur sehr selten in das Küstengebiet. Andere Arten dagegen, wie *Chaetura pelagica, Dolichonyx oryzivorus* und *Hirundo rustica erythrogastra* überwintern sowohl im Amazonasgebiet als auch an der Küste.

Es ist erstaunlich, dass man im Amazonasgebiet nur sehr wenige Arten von Wasser- und Ufervögeln als Überwinterer antrifft. Die einzigen Limicolen z.B., die regelmässig in diesem Gebiet überwintern, sind *Actitis macularia, Tringa solitaria, T. flavipes* und *Erolia melanotos.* Eine der Ursachen dieser Erscheinung dürfte darin liegen, dass die Strande und Sandbänke in grossen Teilen dieser Region während der Hochwasserzeit (die sich zum Teil mit der Überwinterungszeit deckt) überschwemmt werden, so dass diese Vögel im Amazonasgebiet nicht ihre typische Lebensstätte finden. Ausserdem bildet für viele Limicolen die Meeresküste eine Leitlinie beim Zug, die nicht in das Amazonasgebiet führt. Die vier vorstehend genannten Scolopaciden sind Beispiele für Vögel, die in Peru ausserdem noch im Hochandengebiet und an der Küste überwintern. *Actitis macularia* ist ein Vogel, der sogar in nahezu allen Uferlebensgemeinschaften auftritt, denn man sieht ihn nicht nur an Flüssen und Seeufern, sondern auch an Salzlagunen, kleinen Tümpeln in der Wüste und auch an allen Meeresufer-Biotopen wie Felsufer, Geröllstrande, Mangrovebestände etc. Ausser den wenigen Limicolen sind nur noch zwei weitere an aquatische Lebensstätten gebundene Zugvögel aus dem Amazonasflachland Perus bekannt: der Fischadler *Pandion haliaetus carolinensis,* der wie *Actitis* ein Ubiquist ist und in fast allen Teilen Perus vorkommt und der Scherenschnabel *Rynchops nigra,* den man auch an der Meeresküste regelmässig antrifft. Es ist bemerkenswert, dass keine Möwe und keine Ente das peruanische Amazonasgebiet regelmässig als Winterquartier aufsuchen. Diese Armut an Wasser- und Ufervögeln, welche in das überaus wasserreiche Amazonasbecken ziehen, ist auch deshalb bemerkenswert, weil dort eine Anzahl von endemischen an das Wasserleben angepassten Vögel existieren (*Heliornis, Dendrocygna, Cairina, Anhinga, Phaetusa, Hoploxypterus,* Eisvögel u.s.w.).

Für Landvögel wird die Wanderung im perunanischen Küstengebiet sicherlich durch die grossen Wüstenstrecken erschwert. Dies mag ein Grund dafür sein, dass hauptsächlich nur gute Flieger, wie *Chaetura pelagica, Hirundo rustica erythrogastra* und *Falco peregrinus anatum* an dieser Küste entlang wandern und Mittelperu erreichen oder noch weiter nach Süden gehen. Der Icteride *Dolychonyx oryzivorus* scheint der einzige Landvogel zu sein, der seine Nahrung nicht im Fluge erbeutet und der dennoch in grösserer Anzahl regelmässig im Küstengebiet um Lima auftritt.

Ein ganz anderes Bild zeigen die Wasser- und Ufervögel, von denen nicht weniger als 47 von Nord- und Mittelamerika kommende Arten an der peruanischen Küste gefunden werden. Viele von ihnen überwintern in den nordperuanischen Mangrovesümpfen und in den Mündungsgebieten der grösseren Küstenflüsse Nordperus. Aber eine beträchtliche Zahl, nämlich 30 Arten, ziehen regelmässig wenigstens bis zur mittel- und südperuanischen Küste, manche gehen sogar bis Südchile. Einige Arten treten in jedem Jahr äusserst zahlreich auf, wie *Larus pipixcan*, die z.B. bei Pisco in Riesenansammlungen bis zu etwa 100 000 Exemplaren gesehen wurde und sich nach Magenuntersuchungen dort hauptsächlich von Anchovetas, *Engraulis ringens*, ernährt. Ein anderer Wintergast, der in jedem Jahr an der peruanischen Küste ebenfalls in Massen auftritt, ist der Sanderling, *Crocethia alba*, der in grossen Trupps (bis zu tausenden von Exemplaren) an den marinen Sandstranden überwintert. Die Sanderlinge ernähren sich an der peruanischen Küste hauptsächlich von dem Brandungskrebs *Emerita analoga*, der, wie oben schon ausgeführt wurde, die ausschliessliche Nahrung der Graumöwe *Larus modestus* darstellt. Da aber *L. modestus* gerade dann in Chile brütet, wenn *Crocethia alba* in Peru überwintert, sind diese beiden Vögel keine Nahrungskonkurrenten. Die Fortpflanzungszeit von *Emerita analoga* fällt ausserdem noch gerade in die Zeit der Abwesenheit ihres Hauptfeindes *Larus modestus*, so dass die Sanderlinge an allen Stranden grosse Mengen von jungen *Emerita* (die ausgewachsenen können ihrer Grösse und Härte wegen von *Crocethia* nicht gefressen werden) vorfinden, wenn sie nach Peru kommen. Das bedeutet, dass die Sanderlinge gerade in denjenigen Monaten die peruanische

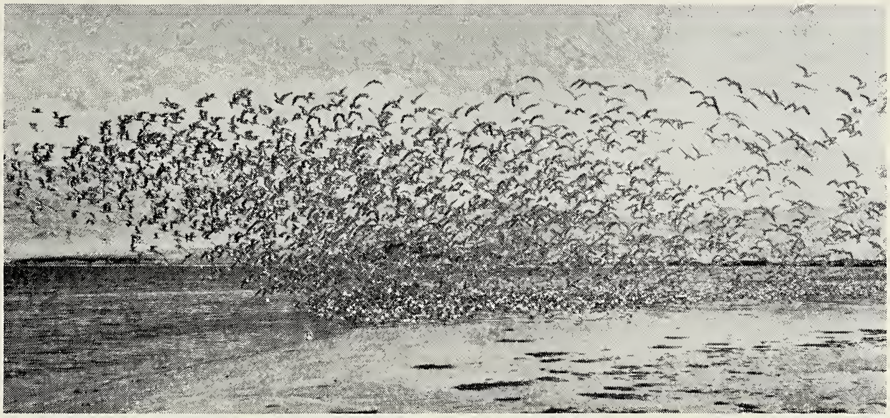

Fig. 3. Massenvorkommen von *Larus pipixcan* am Strand bei Laguna Grande (südlich von Pisco, Mittelperu).

Küste in Massen besuchen, wenn das Nahrungsangebot dort für sie besonders gross ist.

Die vorstehenden Ausführungen zeigen, dass es in Peru eine Menge interessanter den Vogelzug betreffender Fragen zu klären gibt. Es ist zu erwarten, dass ein gründlicheres Studium des Wanderverhaltens der einzelnen Arten, vor allem bei ausgiebiger Anwendung der Beringung, weitere bedeutsame Ergebnisse bringen wird.

SUMMARY

Problems of Bird Migration in Peru

There are about 1,450 known species of birds in Peru with some 2,200 subspecies. As one would expect in a tropical country, the majority of Peruvian birds are permanent residents. The permanent residents are subdivided into the following categories:

A. Birds that live always in one life community;
  a. Birds with a home range of small size, normally only as wide as the distance that the voice carries;
  b. Birds with a larger home range that exceeds the distance that the voice carries;
  c. Birds that join in flocks, with each other or with other species, in the nonbreeding season and traverse a relatively vast but well-defined territory;
B. Birds that depend on small "insular" habitats (such as flowering bushes or trees) which are scattered over a relatively large area;
C. Birds that depend on two or more different life places (as when the breeding and sleeping places are widely separated from the feeding grounds).

As a result of local environmental change, such as those indicated in *B* and *C* and also those brought about by regular fluctuations of local conditions, some birds have developed the habit of moving daily from one place in the habitat to another in a systematic fashion. There are also birds that wander in correspondence with the occasional or seasonal extension, or the shrinking, of the life community in which they live.

Some species do not occupy all the feeding areas available to them during the breeding season, because they are confined to a narrow breeding zone; but when the breeding season ends, they spread out and occupy at least a part of this larger area. Examples of such species are the Peruvian guano birds and the Gray Gull (*Larus modestus*). This last group brings us to those birds that migrate into continuous and world-wide distributed life communities (many petrels and shorebirds).

There exist life communities in Peru that disappear temporarily with seasonal changes (such as sandy banks in the Amazonian flat land, and lagoons in steppes). Birds that inhabit these niches must at times be able to occupy another life place or to move to another locality where these niches still exist. Sometimes not all of the life community disappears but only one of its ecological factors (certain fishes in the Amazonian drainage, flowers, fruits, etc.), so that birds that depend on such a factor must wander. There are many birds that never are seen to overfly communities that are strange or dangerous to them (such as rivers or areas without vegetation); however, other birds do so with regularity. This ability can be considered to have great importance in the development of true migration.

Migrating birds, in a more advanced sense, are species that go from a life community that has a marked seasonal change (as the "lomas" or areas of fog-vegetation of the Peruvian coastal desert) to a nearby one that does not change (river valleys of the Peruvian coast), or to one that has a complementary seasonal change (rain-steppes of the western slope of the Peruvian Andes).

In principle, the true migrating birds follow the same practice as those mentioned above. Most of them also inhabit life communities that fundamentally change their type with the seasons, but in order to find appropriate habitats they may move great distances, flying even from one hemisphere to the other.

The migrants from the south that come to Peru consist principally of shore- and

seabirds, such as the Gray Gull and numerous Tubinares; only a few landbirds are known, i.e. swallows (*Atticora cyanoleuca patagonica* and *Progne modesta elegans*) and some tyrant flycatchers.

In comparison, the northern migrants are more numerous. These may be subdivided into the following groups: (a) migrants from the Galapagos Islands, (b) migrants from Central America and from the southern part of North America, and (c) migrants from the northern part of North America. The three principal geographical zones of Peru (coastal region, high Andes, and Amazonian drainage) shelter different compositions of species of northern migrants.

In Peruvian birds nearly all kinds of migration occur; taken together, these comprise a series or gradation from the simplest to the most complex.

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Weather Factors Initiating Migration

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The following contribution summarizes my conclusions regarding the weather facts initiating migration over eastern England and the southern North Sea, based on radar studies (Lack, 1960*a*, 1962, 1963, and *in prep.*; also Lack and Eastwood, 1962). It considerably corrects my earlier conclusions based on the work of others (Lack, 1960*b*). Radar gives a nearly complete picture of migration, except for birds flying low and for bird echoes obscured by extensive rain. The quantitative data relate to the frequency and density of each movement, the density of bird echoes being assessed on an arbitrary scale, which depends partly on the height of flight, so comparative differences are accepted only when very large. Over the area studied, the commonest movements are eastward in spring and westward in autumn, but movements in both directions occur in every month. Southward movements, although commonest in autumn, likewise occur in every month, and northward movements have been recorded in most months but are hard to study in this area.

For all movements in late summer and autumn, the factor with the greatest influence was the wind direction, birds normally traveling in greatest numbers with a wind blowing from within 45° of directly behind their normal heading; but some movements occurred against the wind, primarily when it was light. On the eastward movements in spring, more birds set out with following than opposing winds, but the difference was proportionately much smaller than in autumn (although not absent, as I formerly claimed; Lack, 1960*a*, 1960*b*), and the birds often left against stronger winds. The difference may be adaptive, and correlated, at least in part, with the danger of drift in autumn, when about half the population consists of juveniles, whereas in spring the migrants are returning to a known goal.

In midwinter, the situation was different again, practically all movements being recorded with a more or less following wind. At this season, the birds evidently have a nearly equal tendency to fly east or west (and other populations, north or south), and the direction of the wind determines which will occur. This fits the ecological situation, easterly or northerly winds bringing ice or snow to the feeding grounds, and westerly or southerly winds a thaw.

With following winds, the speed of the wind had no apparent influence. With opposing winds, there was more migration with light than strong winds, the difference being proportionately much greater in autumn than spring. (In midwinter, virtually no migration occurred against the wind.)

Atmospheric pressure probably had no direct influence. Although most westward and southward movements occurred in anticyclones, and most east-

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ward ones in somewhat (but not very) disturbed weather, these differences were primarily, if not entirely, due to other associated weather factors.

At all seasons, there was more migration in clear than cloudy weather, but this might have been due partly to rain. All of the occasionally disoriented movements occurred with full overcast; but on many occasions when the nearest weather station recorded full overcast, migrants were oriented, although they might have been flying either above the overcast or in a clear patch.

Temperature had no apparent influence in June and July. In autumn, most southward and westward movements occurred when it was cold, but contrary to popular and my own earlier belief (Lack, 1960*b*), this was evidently due solely to the association of cold with northerly and easterly winds, respectively, and not to temperature as such. The same held for nearly, if not quite, all the "hard-weather movements" in midwinter, those southward occurring with winds from between the northwest and northeast but not from the southeast, however cold, and those westward with winds from between the northeast and southeast but not from the northwest, however cold. In autumn and winter, wind direction presumably acts as the main "signal" for departure, but this means in fact that most southward and westward migration occurs when it is cold. In spring, after full allowance for wind direction, temperature had a marked direct influence on the eastward departures, especially in March and April, but to some extent in February, more migration occurring when it was warmer. This is presumably correlated with the timing of breeding in relation to the ecological conditions.

The above findings refer to the southern North Sea area, and primarily to passerine species and Lapwings (*Vanellus vanellus*). Preliminary results from the Outer Hebrides (S. L. B. Lee, *in prep.*) show that, in this area of autumnal storms, Icelandic passerine migrants depart much more freely with strong crosswinds and against fairly strong head winds than do the same species in Norfolk in autumn. In spring, on the other hand, they depart almost entirely with following or light winds. Both differences are probably adapted to the local weather and local geography, as discussed in the work cited.

SUMMARY

Wind direction had a paramount influence on migration in midwinter, a very strong influence in autumn, and a moderate influence in spring, most movements occurring with a wind within 45° of directly behind the birds. Wind speed had no influence with a following wind, but there was more migration against light than against strong head winds, especially in autumn and to a lesser extent in spring. Most westward and southward movements occurred in anticyclones, and most eastward movements in somewhat, but not very, disturbed weather, probably because of other associated weather factors. There was more migration in clear than cloudy weather. Tempera-

ture had a marked influence on the eastward departures in spring, which were commoner when it was warm, but the tendency for most autumn and "hard-weather" movements to occur in cold weather is wholly explicable through the influence of following winds.

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The Astronomical Bases of "Nonsense" Orientation

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The strongly marked, season-through tendency of Slimbridge-caught Mallard (*Anas platyrhynchos*) to fly northwest on release has been described by Matthews (1961). The function of such "nonsense" orientation is still obscure. It seems to be unrelated to social needs for maintaining the flock, as it is shown by ducks released in groups or in sight of the roosting area (Matthews, 1962). Mallard populations with southeasterly nonsense orientations have been found in southern England and in Sweden (Matthews, 1963). Thus, explanations seeking to relate nonsense orientation to northward dispersal of young birds must be rejected. The mixing of populations during migration may lead to an apparent lack of orientation, and hence Mallard caught at Peakirk, Northamptonshire, can be used for experimentation only in August and September. The Slimbridge, Gloucestershire, population seems to be relatively unaffected by foreign "contamination" and provides an excellent opportunity to examine the astronomical bases of the orientation. There is the particular advantage that the birds' behavior in free flight can be examined, uninhibited by confining walls or distorted by unavoidable shortcomings of an apparatus.

The experiments that follow were carried out at five release points with birds that were initially captured as follows:

Release Point	*Point of Capture*		
	Location	*Bearing*	*Distance (miles)*
Shobdon	Slimbridge	149°	40
Madley	Slimbridge	137°	28
Coln St. Dennis	Slimbridge	254°	24
North Witham	Peakirk	120°	18
Deeping St. Nicholas	Peakirk	187°	6

In all cases the birds were released individually and followed to vanishing point before the next bird was released. Arrangements for capture, retention, transport, and release were as detailed by Matthews (1961).

THE ROLE OF THE SUN

The bearings of ducks released under heavy, lowering overcast (experiments M.30 at Shobdon 15 April 1960 and M.41 at N. Witham 22 September 1960) were found to be scattered around the compass rose (Fig. 1). However, other features of the sky besides the sun are blotted out. Overcast which obscured the sun but allowed, to the human eye, its approximate location did not seriously disrupt orientation. This suggests that the sun really is the important feature in the sky. A method of measuring the thickness as

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well as the extent of cloud cover was needed. The photographic method of von Frisch et al. (1960) was rather too refined for our needs. Moreover, it was concerned with the detectability of the actual sun position, whereas general compass directions may be gauged from the uneven lighting of the clouds over the sky as a whole. The technique that is now being employed with ducks is one of taking photometer readings on the calculated sun position and at 30° intervals around the sky at the same elevation. An alidade-mounted matching photometer, capable of measuring brightness over ½° of sky with a range of a million to one, is used for this purpose. The results are encouraging but as of this time not complete enough for a definitive statement.

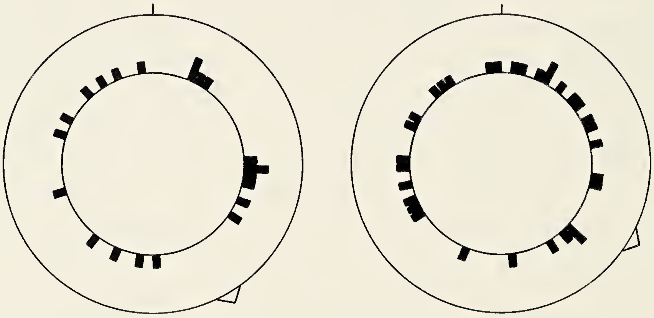


Fig. 1. Lack of orientation of Mallard released by day under thick overcast. Left: Slimbridge birds; right: Peakirk birds. The bearing at which each bird was lost to sight is represented by a 5° block. Home direction is indicated by the arrowhead on the outer circle. North point is uppermost.

During the course of one such cloudy release (experiment M.62 at Madley 13 January 1961), conditions arose that provided a natural experiment by moving the sun's apparent position. Twelve birds had been released under cloud that permitted development of a normal orientation mainly between north and west (Fig. 2, white blocks). Then followed thickening cloud accompanied by random departures (not shown), and rain forced a halt. Eventually, as the frontal system moved through, a break in the clouds appeared low in the northwest. The sun, completely cloud-obscured, was now setting and a bright red flush ran around to the opening crack. To human eyes it looked exactly as if the sun had just set there. The few remaining birds released at this time apparently interpreted the phenomenon in this way, for they gave a consistent fan to the northeast instead of the northwest (Fig. 2, black blocks). The suggestion is very strong that orientation is by the sun's position.

One could wait a long time for such conditions to be repeated, and with free-flying birds one cannot manipulate the sun's position in space with mirrors. The alternative is to change the sun position in time by manipulating the "clocks" of the birds. A considerable amount has been done in this way by Hoffmann (1960) with caged birds and by Schmidt-Koenig (1961*a*) with "homing" pigeons. The same technique was used of confinement in an artificial day of the same length but moved 6 or 12 hours out of phase with the normal day. Twenty Mallard at a time were confined in a room 10 ft by 9 ft, with a pitched ceiling rising to 15 ft. Food, water, and bathing facilities were provided, and the birds were then disturbed as little as possible. The room was not soundproof, but a background noise was provided by water pumps running day and night. Two 250-watt floodlights were projected upward to give diffuse illumination, and outside light was largely prevented from entering, although the nature of the roof resulted in occasional small leaks. The isolation from outside conditions was thus by no means complete; but, as will be seen, it was sufficient to make the birds accept the imposed rhythm. Birds remained in good condition for a week under these circumstances, but some deterioration was apparent by 10 days; and if suitable weather conditions had not occurred by then, that particular batch was abandoned. Following the above authors, a minimum treatment of 4 days was aimed at for a 6-hour shift, and 7 days for a 12-hour shift. Control birds originally captured at about the same date were kept in outdoor aviaries during the experimental incarceration.

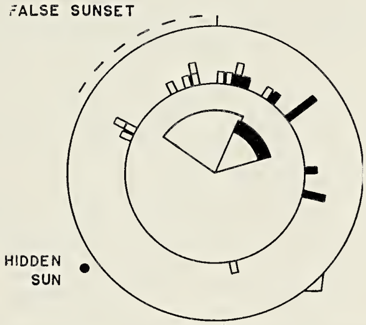


Fig. 2. A natural sun-shifting experiment. White blocks: directions taken by 12 birds released under sky permitting normal orientation; black blocks: directions taken by 9 birds released later when a crack in the cloud cover gave a false sunset effect (broken lines in diagram) in the northwest. The central fans summarize the mean deviations of the two groups from their respective medians.

The effects of such treatment on the birds released in sunny conditions and at times when the true and false days overlapped are summarized in Table 1. The medians of birds with their clocks forced 6 hours out of phase are swung through approximately a right angle left (–107°) or right (+95°) of the controls, according to whether the artificial day was in advance of or behind the normal day (Fig. 3). These releases were at the same point as that in Fig. 2, and the similarity in the effect of shifting the sun's "position"

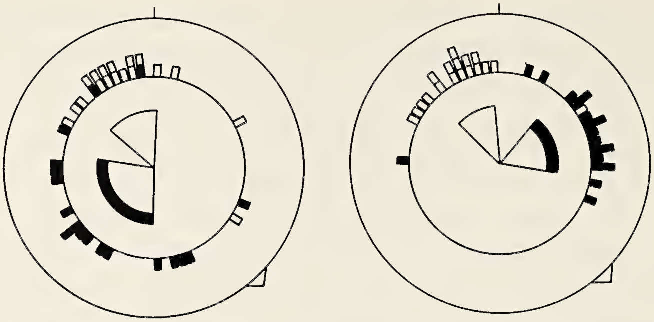


Fig. 3. Reorientation after treatment to shift the birds' "clocks" 6 hours fast (left, above) or slow (right, above) when released under the sun.

to the right with that of holding the "time" back by 6 hours is striking. When the time shift was 12 hours, the consequent orientation was nearly reversed (–150°) as will be seen from Fig. 4.

These results are in accord with the Mallard using the sun as a reference point to determine their nonsense orientation, varying their angle according to the time of day. There is a marked parallel with the results obtained by Schmidt-Koenig (1961*a*) with pigeons he supposed were showing homeward orientation. The inference, already drawn by Matthews (1961) that such pigeons were in fact showing nonsense orientation, receives further support.

With the present data we can do little to resolve the vexed question as to whether the sun position in azimuth alone is concerned, as Schmidt-Koenig and his colleagues would hold, or whether there is a "sun altitude correlated factor," as demonstrated in fish by Braemer (1960). The fact (Table 1)

TABLE 1.—RELEASES AT MADLEY UNDER SUN IN THE PHYSIOLOGICAL DAY AFTER CLOCK-SHIFTING TREATMENT

Treatment . . .	6 Hours Advanced	6 Hours Retarded	12-hour Shift
Ref. no.	M.105	M.102	M.161
Days treated	7	4	7
Date released	5 Oct. 1961	22 Sept. 1961	14 Apr. 1962
Wind	S.1	S.1	NE.3/2
Time (GMT)	08.11–10.54	12.58–15.49	15.52–18.21

Group . . .	Control	Experimental	Control	Experimental	Control	Experimental
No. of bearings	18	18	18	18	19	19
Median[a]	337°	230°	335°	070°	317°	167°
Deviation[b]	26°	49°	20°	30°	29°	61°
In sight[c]	2m.40s.	4m.00s.	3m.05s.	4m.00s.	2m.45s.	3m.05s.
30 sec/final[d]	30°	59°	36°	42°	36°	76°

[a] Median of the final bearings.

[b] Mean deviations of the final bearings from the median.

[c] Mean time from release to vanishing point in 16 × 40 binoculars.

[d] Mean difference between the individual's bearing at 30 seconds after release and at vanishing point.

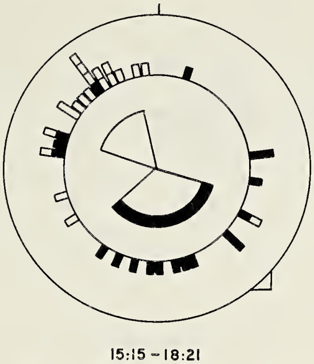


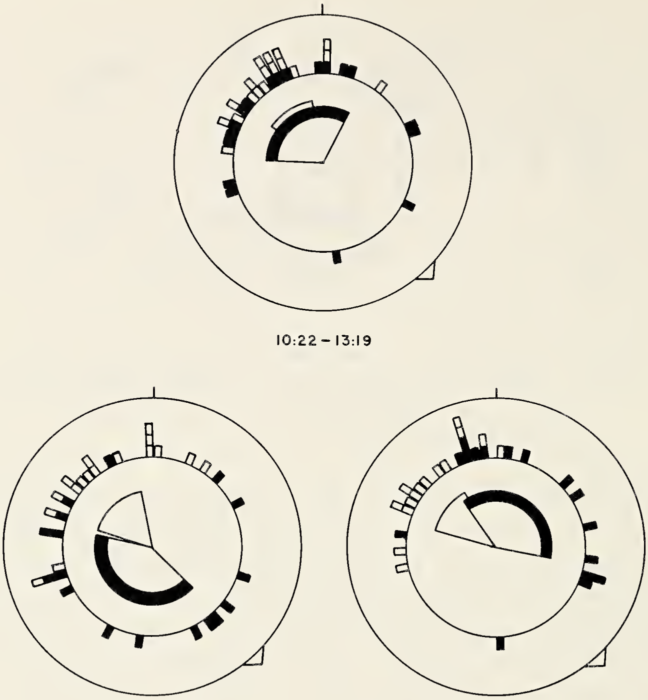
Fig. 4. Reorientation after a 12-hour "clock" shift when released under the sun during the birds' physiological day.

that the experimental birds show twice as much scatter about their median as do the controls could simply be due to the individual "clocks" being reset by differing amounts. That the experimentals remained longer in sight and followed a more devious track (as shown by the difference between 30-second and final bearings) would seem to indicate some added uncertainty, which might be due to the sun being at the wrong height or moving in the wrong direction. Unfortunately, in high summer, when the greatest altitude differences and the greatest amount of overlapping between artificial and real days occur, Mallard are in poor condition if not flightless.

Another matter on which there is a conflict of evidence, and an apparently genuine one, concerns the problem of where animals "think" the sun goes at night. Schwassmann (1960) quite rightly stresses that the question is really whether the orientational rhythm dictating a varying angle to the sun position continues through the night or unwinds. It is nonetheless easier to visualize the problem in terms of whether animals react "as if" the sun is north or south at midnight. It can be investigated by releasing birds subjected to

Table 2.—Releases at Madley under Sun in the Physiological Night of the Experimental Birds after 12-hour Clock-shifting Treatment

Ref. no.	M.164		M.110		M.162	
Days treated	7		9		7	
Date released	2 May 1962		21 Oct. 1961		24 Apr. 1962	
Wind	SSW.1		SSW.½		NE.1	
Time (GMT)	08.20–10.13		10.22–13.19		13.33–15.45	
Group . . .	Control	Experimental	Control	Experimental	Control	Experimental
No. of bearings	17	17	18	18	15	16
Median	317°	208°	328°	330°	307°	033°
Deviation	31°	74°	22°	57°	23°	68°
In sight	3m.20s.	4m.45s.	2m.00s.	3m.20s.	4m.25s.	4m.50s.
30 sec/final	49°	76°	15°	40°	68°	75°



10:22 – 13:19

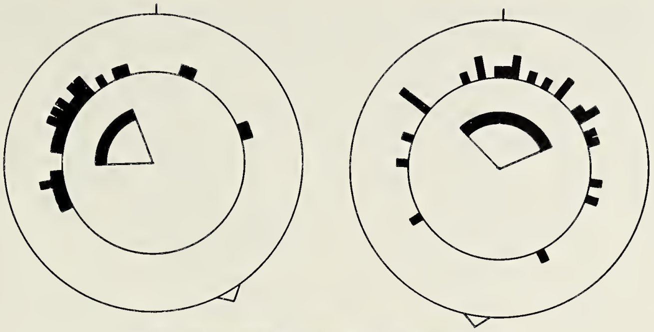
08:20 – 10:13

13:33 – 15:45

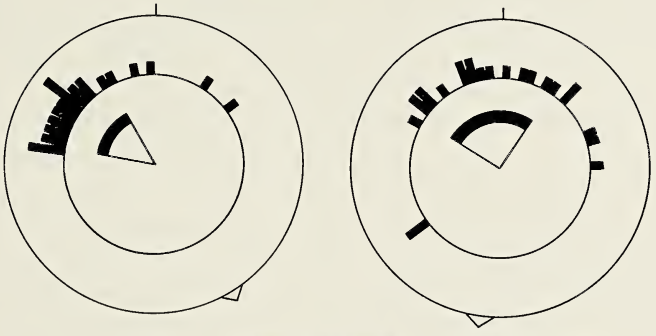
Fig. 5. Orientation after a 12-hour "clock" shift when released under the sun during the birds' physiological night.

a 12-hour shift at times when their clocks tell them it is night, although the sun is actually above the horizon. Two sets of predictions can then be made. Birds reacting "as if" the sun runs on through north should give a reversed (i.e. southeast) orientation no matter what time of the real day they are released. Birds reacting "as if" the sun runs back through south should vary their orientation according to the real time of release. In the morning it should be southwest, around noon northwest, and in the afternoon northeast. Results that have been thus far accumulated are summarized in Table 2 and Fig. 5.

It was obvious that the birds, on release, were somewhat confused by the situation. Like Tweedledee, they seemed to find it odd to see the sun shining in the middle of the night. Many shook their heads repeatedly in flight. Quite a few initially adopted a wholly unusual mode of flight, hovering with the body nearly vertical for 10 or more seconds. Most flew normally after a while, but the spread of bearings about the median was great compared with the controls, and wavering from the 30-sec bearing was more pronounced. The results are thus not so clear cut as would be desired. The release around noon/"midnight" gave fairly unequivocal results: After the same treatment (for a longer period), which had reversed the orientation of



(A) BEARINGS AFTER 30 SECONDS (B)



(A) FINAL BEARINGS (B)

Fig. 6. Orientation, under starlit skies, of Mallard from (A) Slimbridge, (B) Peakirk.

birds released during their physiological day (Fig. 4), these birds headed mainly northwest. The forenoon and afternoon releases had such a wide scatter that further tests are needed before final conclusions are drawn. But their tendencies are definitely intermediate between northwest and southeast, respectively southwestward and northeastward. Therefore, as far as they go, the results favor the second hypothesis, of the sun running backward (or the rhythm unwinding) during the night.

This is in accord with the evidence obtained by Schmidt-Koenig (1961*b*) with two caged, direction-trained pigeons and indicates that both these species have a mechanism similar to that in certain arthropods (*Velia*, *Talitrus*, *Talorchestia*) and different from that in fish and bees (sun running onward). The situation may well be different in ducks which actually experience a 24-hour sun movement above the Arctic Circle, as Hoffmann (1960) has shown with Starlings (*Sturnus vulgaris*).

THE ROLE OF THE STARS

Mallard are very convenient experimental birds in that, unlike pigeons, they fly equally well by day and night. Bellrose (1958) devised an ingenious means of following duck at night and found that they showed orientated flight (16 bearings) when only stars were available. Using Bellrose's technique of attaching a light to the leg, an extensive series of night observations have been made. A modification has been to attach the bulb (1.25 v, 0.25 amp, 11 mm round) to the 2-inch battery (1.5 volt) by 1 inch of insulated wire soldered at right angles. The light is thus held clear of the bird's body and is not obscured when the bird turns toward the observer. The attachment weighs 10 g, around 1 percent of the body weight, and clearly is no encumbrance. On release of the bird, the light oscillates for a few seconds but steadies as the bird adjusts to the unaccustomed weight; thereafter the light on its steady course has a close resemblance to a "sputnik." It burns for somewhat under 10 minutes, ample time for observation of this type of orientation. The battery is attached along the leg by means of paper tape that softens when wet so that the bird is shortly freed of the attachment.

Nonsense orientation is as well marked and immediate under the stars as by day. Fig. 6 illustrates two typical releases with Mallard of two different stocks (experiments M.61 at Shobdon 11 January 1961 and M.92 at Deeping 11 September 1961). Only 30 seconds after release, there is already a marked orientation, which sharpens with time to the vanishing point. We may compare orientation statistics of ducks released under stars without any experimental treatment with those for releases under the sun in similar weather at the same places (Table 3). There appears to be nothing to choose between the two sets of data in the spread of the final bearings or the rapidity with which they are adopted. A small proportion of ducks work their way back and are recaptured. We now have 17 cases in which the same individual has been released both under stars and under the sun, in a different place on the second occasion. The pairs of final bearings were:

Stars	231	265	266	278	296	305	307	309	319
Sun	330	306	353	299	332	297	011	021	045

Stars	322	330	335	339	342	003	030	038
Sun	333	320	313	010	313	328	296	236

The differences between the two bearings average 53°. For another 54 individuals similarly released twice at different places, both times under the sun, the differences between their bearings average 52°. The 17 individual birds on their star release were actually less time in sight, 2m.45 vs. 3m.10, and showed less wavering, 30 sec/final 46° vs. 60°, than they did on their sun release. It is thus clear that the individual Mallard can use sun orientation *and* star orientation with equal case.

When there is thick continuous cloud blotting out the stars (experiment M.117 at Madley 15 November 1961), the vanishing points are at random (Fig. 7, left), but it may be that the birds are better equipped to deal with marginal conditions than we are. The release recorded in Fig. 7, right (M.64 at Madley 16 February 1961) was carried out with stratus overcast sufficient to cut out the stars to the human eye except for a few dim ones immediately overhead. Yet there is a nonrandom scatter. However, in this case there was

TABLE 3.—ORIENTATION STATISTICS ON DUCKS RELEASED UNDER STARS WITHOUT ANY EXPERIMENTAL TREATMENT and THOSE FOR RELEASES UNDER THE SUN IN SIMILAR WEATHER AT THE SAME PLACES

		Stars	Sun
NO. OF DUCKS RELEASED	Madley	58	57
	Coln	55	52
	Shobdon	27	29
	North Witham	25	28
	Deeping	16	19
EXPERIMENTAL RESULTS	No. of bearings	181	185
	Median	329°	319°
	Mean deviation	37°	35°
	In sight	3m.00s.	3m.20s.
	30 sec/final	51°	50°

a light (Force 2) southerly wind and this may have been sufficient to cause the apparent northerly tendency.

A central question in star orientation is whether the birds take up an angle to the azimuthal position of one or more stars or whether compass directions are determined from the alignment of patterns of stars (as we do ourselves). The star sphere apparently rotates through 360° in the course of a year, so that the same stars are not in the same position at the same solar time throughout the year. Only stars close to the celestial pole remain visible at night the year through, the others in some months rise above the horizon only during daylight hours. This movement of the star sphere is conveniently recorded by the bearing of the First Point of Aries (the point at which the ecliptic crosses the celestial equator). Night releases have now been carried out over much of the year, in September (25 bearings), October (33), November (16), December (35), January (51), February (20), March (37), and May (32). These final bearings are plotted against the Greenwich Hour Angle of Aries in Fig. 8. This shows plainly that final bearings remain con-

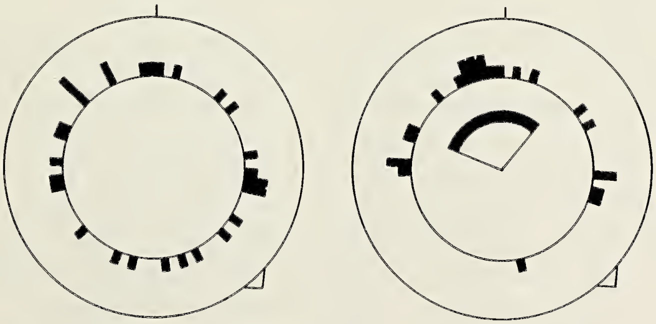


Fig. 7. Lack of orientation when stars were covered by thick overcast (left); apparent orientation with thin overcast (right).

centrated between north and west despite the apparent shift of the stars and the emergence and disappearance of constellations that are not circumpolar.

It can be argued that this result makes it less likely that orientation is with reference to the position of certain stars in azimuth. If noncircumpolar stars are used, information on a succession of different stars would have to be available to the bird. On the other hand, circumpolar stars, being often near the zenith, are particularly unsuitable for azimuth measurement (involving downward projection to the horizon). An essential element in orientation in azimuth is time measurement, so "clock" shifting offers a test. A series of experiments in which birds were subjected to 6-hour and 12-hour shifts were carried out and are summarized in Fig. 9 and Table 4. The treatment was the same as for those releases under the sun summarized in Table 1 and Fig. 4, and the 6-hour-shift birds were released at the same place. The first 12-hour shift had to take place at Coln because of weather conditions and was even then incomplete. No less than five other attempts at this experi-

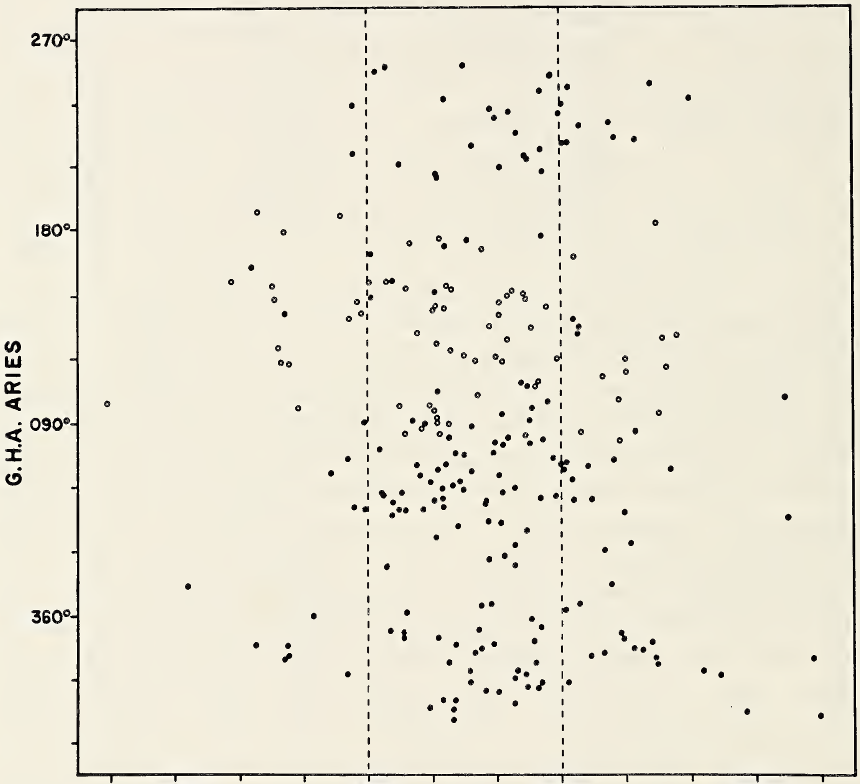
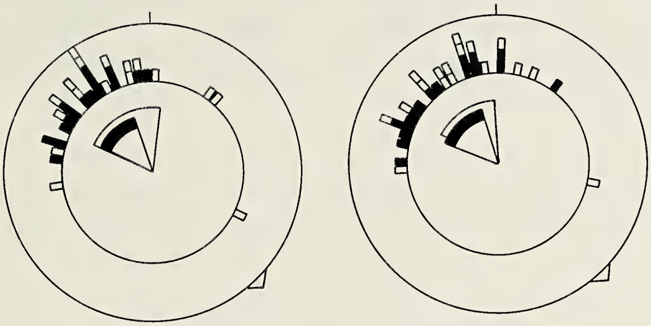


Fig. 8. Night orientation through the seasons. Solid circles: stars only; open circles: stars and moon.

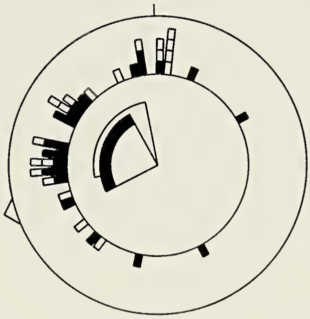
ment were frustrated by weather, and the joint data for two releases under not wholly satisfactory conditions have to be given. The comparison between controls and experimentals is, however, perfectly valid.

Put baldly, "clock"-shifting treatment, which produces predictable re-



6 HOURS FAST

6 HOURS SLOW



12-HOUR SHIFT

Fig. 9. Absence of reorientation after 6-hour and 12-hour "clock" shifts by birds when released under the stars.

TABLE 4.—RELEASES AT MADLEY (107, 126) AND COLN (113, 153) UNDER STARS AFTER CLOCK-SHIFTING TREATMENT

Treatment . . .	6 Hours Advanced		6 Hours Retarded		12-hour Shift	
Ref. no.	M.107		M.126		M.113/153	
Days treated	6		6		8 and 7	
Date released	11 Oct. 1961		13 Dec. 1961		4 Nov. 1961 5 Mar. 1962	
Wind	Calm		SW. ½		NW.⅔	NW.1
Time (GMT)	19.55–23.00		22.58–01.49		21.54–01.59	
Group . . .	Control	Experimental	Control	Experimental	Control	Experimental
No. of bearings	17	16	17	17	20	23
Median	332°	320°	328°	318°	305°	288°
Deviation	36°	23°	29°	26°	45°	44°
In sight	3m.15s.	3m.00s.	3m.10s.	2m.45s.	3m.00s.	2m.50s.
30 sec/final	49°	50°	47°	43°	58°	61°

orientations by day, has no effect whatsoever on orientation under the stars. The time-shifted birds showed rather less spread about their medians, which differed little from those of the controls. Further, the experimentals did not remain longer in sight or show more initial uncertainty than did the untreated birds. This was particularly remarkable in the 12-hour-shift birds, which had perforce to be released in their physiological day (overlap periods fell within twilight, which has been rigorously avoided in night releases). Some, to judge from the path of their "sputnik," did helicopter at first but soon got under way.

We are forced to the conclusion that the time element does not enter into star-compass orientation, that measurement of the movement of certain stars in azimuth is not the concern of these birds. From this it does not seem possible to escape the implication that the birds are finding their compass direction by reference to the orientation of the star *patterns*, possibly using the same constellations as we do ourselves. Whether this is so is a matter for further investigation, which will necessarily be long-term, being dependent on the forecast appearance of slow-moving banks of cloud at appropriate times. One point on which the present conclusions bear concerns the controversy over Sauer's (1957, 1960) claim that caged warblers, presented with a planetarium sky in advance of normal, reacted by fluttering westward as if to correct for a longitudinal displacement to the east. It still seems that the evidence presented is insufficient. But Walraff's (1960) counter-suggestion, that the birds are reacting to the advanced sky "as if" its clock was slow, and so deviating in azimuth to the right of the normal direction, can no longer be entertained.

THE ROLE OF THE MOON

Sauer (1957) and later workers on the night orientation of caged migrants are in agreement that the presence of the moon merely confuses the birds, which become positively phototactic to it or to the light it throws on the wall of the cage. However, Papi (1960) has provided solid evidence of moon-compass orientation in the crustacean *Talitrus*.

A fairly limited number of nonexperimental releases of Mallard have been made at night with a half to full moon as well as the stars. The indications are that the presence of the moon does not aid orientation and may actively hinder it, possibly by making the stars less easy to see. Comparable orientation statistics to those for sun-only and star-only releases earlier in Table 3 are:

	No. of Bearings	*Median*	*Deviation*	*Time in Sight*	*30 sec/Final*
Stars + Moon	68	308°	45°	2m.50s.	69°

The spread of bearings about the median was considerably greater and the final bearings differed more widely from the initial bearings. The fact that

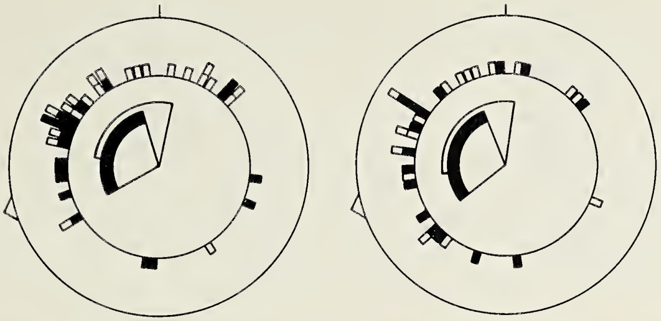


Fig. 10. Absence of reorientation after 12-hour "clock" shifts when released under the stars and moon. Left: moon rising; right: moon setting.

the birds were in sight for rather less time is probably only due to the "sputniks" being less visible on a bright moonlight night.

Again clock-shifting experiments can help to provide an answer, since an orientation with regard to the moon position would require a time factor. Birds were subjected to a 12-hour shift as heretofore and released under star-plus-moon conditions. One possible complication was suggested by the earlier finding that the sun-orientation mechanism reacted "as if" the sun ran back through south during the night. It was thus possible that the mechanism would lock on to the moon as a sun substitute when the birds were in their physiological day. With a last-quarter moon rising and releases from about midnight on, the moon and the "sun" will be in the same sector of the sky. With a first-quarter moon setting, the moon and "sun" would be in different sectors. These two conditions were therefore selected, and the results summarized in Fig. 10 and Table 5. The experimental birds gave a scatter but little different from the controls and certainly no general re-orientation nor any noticeable difference between the two moon-phase con-

TABLE 5.—RELEASES AT COLN UNDER STARS AND MOON AFTER 12-HOUR CLOCK-SHIFTING TREATMENT

Lunar Phase . . .	Last Quarter Rising		First Quarter Setting	
Ref. no.	M.113/128		M.149	
Days treated	8 and 7		10	
Date released	4 Nov. and 27 Dec. 1961		14 Feb. 1962	
Wind	NW.$\frac{2}{3}$	NE.1	N.$\frac{3}{2}$	
Time (GMT)	23.21–03.29		00.18–02.47	
Group . . .	Control	Experimental	Control	Experimental
No. of bearings	22	20	17	16
Median	325°	292°	315°	285°
Deviation	47°	51°	53°	53°
In sight	2m.30s.	2m.00s.	2m.40s.	2m.30s.
30 sec/final	68°	50°	83°	56°

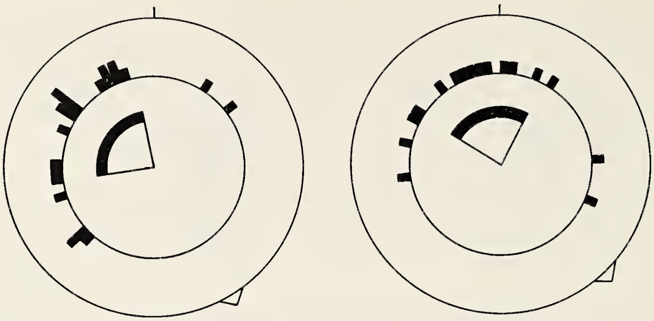


Fig. 11. Orientation with moon + stars (left) and "moon-only" (right) conditions.

ditions. Although the birds were in their physiological "day" when released at night, the moon is visible in the true day at such times and would provide an effective overlap. It is not necessary, therefore, in these instances to consider how a moon-orientation mechanism would operate when the moon is below the horizon! We may content ourselves with the present conclusion that where star-orientation information is available it is used, whether or not conflicting moon-orientation information is also available.

To resolve the matter completely requires a series of experiments in "moon-only" conditions. These are provided when stratus cloud is sufficiently dense to blot out the brightest stars and yet still permit the moon to be visible as a disc. It is remarkable how seldom such conditions occur at the right time of the night and moon phase *and* are accurately forecast by the meteorological-information service. The requirement of having birds in a suitable stage of clock-shift increases the odds against a successful experiment. Eventually, however, the tests will be made. Bellrose (1958), considering birds released under "moon-only" conditions, concluded that his Mallard showed no moon orientation. Only one release under "moon-only" conditions has been possible in the present series. It is shown in Fig. 11 (right), compared with a moon + star release in Fig. 11 (left). This one instance would suggest that, in the absence of other astronomical information, Mallard can still pick up their nonsense orientation from the moon position. But no firm conclusion should be drawn yet, although on the face of it such orientation should not be very difficult to credit.

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SUMMARY

"Nonsense" orientation in Mallard is determined during the day with reference to the sun's position. This is shown by a natural experiment in which the sun's apparent position was shifted and by experimental treatment that shifts the birds' "clocks" through 6 or 12 hours. Mallard subjected to a 12-hour shift and then released during their physiological night orientate "as if" the sun runs backward through south.

Orientation under the stars is as well marked and as immediate as by day. Individual birds are able to use both sun and star orientation apparently with equal ease. Orientation is possible throughout the season, despite the apparent shift of the stars and the emergence and disappearance of constellations. Shifting of Mallards' "clocks" does not affect their star orientation at all. It is inferred that directions are obtained with reference to the patterns of stars, not to the position in azimuth of individual stars.

The presence of the moon does not apparently assist orientation by the stars. "Clock"-shifting experiments indicate that any information available from the moon is ignored in favor of that from the stars. First indications are, however, that when stars are not available orientation with reference to the moon may be possible.

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Visible Diurnal Migration in the Sudan

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The present paper is a first report on studies of visible diurnal migration undertaken in the vicinity of Khartoum, mainly referring to the flyway effect of the river Nile.

During a period of 2 months (12 February to 12 April 1961), visible diurnal migration was studied at the junction of the White and the Blue Nile, west of Khartoum. Daily observations were carried out for at least 8 hours (except 31 March to 2 April, illness). The time of observations alternated, on 1 day beginning at dawn and continuing until 2 P.M., the next day beginning at 10 A.M. and ceasing just after dark, and so on. Every observed migrating bird was recorded. The time was given in periods of 10 minutes. In that way I obtained a sequence of observations, which offered material for different studies on the migration. Complementary observations were undertaken in the desert surroundings. Geographical names and the position of the observation point are shown in Fig. 1.

NUMBERS RECORDED FOR DIFFERENT SPECIES

Within the Sudan about 185 species of Palaearctic migrants are recorded. Some of them occur in small numbers and at scattered localities, others occur in immense numbers and gather in special habitats. A small fraction, about 15 species, are only found in the coastal area at the Red Sea.

The birds that are most suited for a study of the flyway effect of the river Nile are those known to occur in large numbers as winter visitors in different inland parts of eastern and southern Africa, e.g. in the Sudan and farther south. To be suitable, they must also be mainly day migrants and known to react to topographical details of the landscape. Of the 46 species indicated in the handbooks (Bannerman, 1953; Cave and Macdonald, 1955; Mackworth-Praed and Grant, 1952–62; Roberts, 1957) as being common or abundant nonbreeding visitors to the Sudan and eastern and southern Africa, I obtained numerical data on 38. The figures shown below refer to the numbers obtained during my observations; i.e. birds migrating northward between 12 February and 12 April within the observation section given in Fig. 1. Species marked with asterisks were observed to follow the river course more strictly than those not so marked.

*_Pelecanus onocrotalus_	465	*_A. querquedula_	15,260
*_Ardea cinerea_	580	*_A. acuta_	14,900
*_A. purpurea_	159	*_A. clypeata_	5,630
*_Nycticorax nycticorax_	71	_Aythya fuligula_	—
(*)_Ciconia ciconia_	15,580	*_Ay. nyroca_	40
*_Plegadis falcinellus_	4,160	*_Anas_ sp.	16,300
*_Anas crecca_	436	_Falco naumanni_	64

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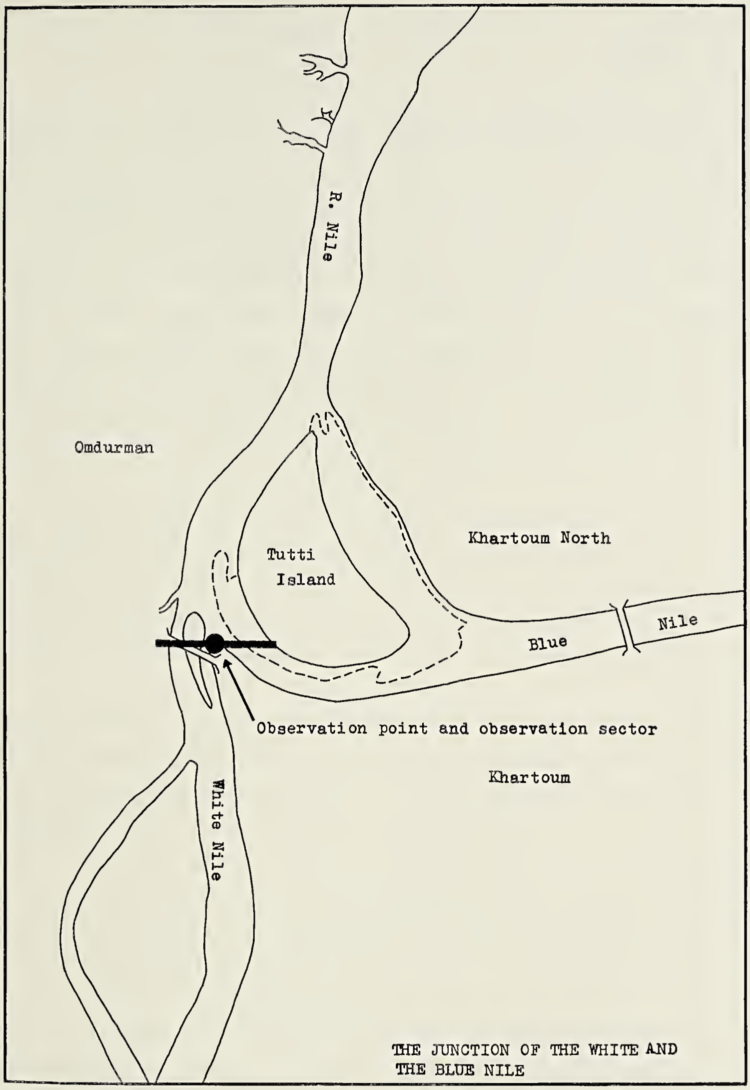

Fig. 1. Location of study area.

Grus grus	630	**Larus fuscus*	416
Anthropoides virgo	141	**Chlidonias leucopterus*	1,070
Charadrius dubius	41	**Ch. hybrida*	80
Ch. alexandrinus	—	**Gelochelidon nilotica*	314
Ch. asiaticus	—	**Hydroprogne tschegrava*	15
**Limosa limosa*	423	*Streptopelia turtur*	6,180
Tringa hypoleucos	—	*Apus apus*	43
Tr. nebularia	9	*A. pallidus*	—
Tr. stagnatilis	—	*Merops apiaster*	288
**Calidris minuta*	9	*M. superciliosus*	100
**C. temminckii*	1	*Calandrella brachydactyla*	22
**Philomachus pugnax*	35,640	*Hirundo rustica*	460

Delichon urbica	51	*A. cervinus*	23
**Riparia riparia*	5,760	*Motacilla alba*	76
Anthus campestris	12	*M. flava*	361
A. trivialis	—	*Emberiza caesia*	—

BEHAVIOR PATTERNS CONNECTED WITH THE RIVER FLIGHT ZONE

In general, the effect exerted by details of the landscape upon the behavior of migrating birds is to a great extent dependent on their flight altitude. Birds migrating at a high altitude are, in general, less influenced by ecological conditions of the landscape than those migrating at a low altitude.

This general rule was illustrated by some of my observations. All of the above birds recorded in very large numbers, except *Ciconia ciconia*, migrated at a low to moderate altitude, normally below about 250 ft. The large numbers of *Ciconia ciconia* are remarkable. This species was a high migrant, sometimes so high that it was impossible to watch a single bird without a binocular.

From my observation point, I had good opportunities not only to watch for birds migrating just over the river and along its sides, but also (by binocular) to keep parts of the desert area around Omdurman under observation, as well as parts of the wooded section of western Khartoum. Figures obtained during the latter observations are not included in the above numbers.

However, I did not note any migration over the desert area around Omdurman, nor did I prove any migration (if some rare exceptions are disregarded) during excursions in the desert surroundings of Khartoum concerning species marked by asterisks in the preceding list. They all followed the river course.

Streptopelia turtur, *Merops apiaster*, *M. superciliosus*, *Hirundo rustica*, and *Delichon urbica* were observed migrating over the green parts of Khartoum as well as along the river. They seemed to be as attracted to the wooded belt bordering the river as to the river itself.

From an ecological point of view, the herons, ducks, waders, gulls, terns, and even the Sand Martin are bound to water. I did not note any tendencies among these "water birds" to broaden their migration front to correspond to the wooded parts. They all strictly followed the river.

Among migrating ducks, ibises, and some other species, I often observed a behavior apparently connected with their strong dependence on the river. I found this behavior especially among migrating flocks of *Plegadis falcinellus*, *Anas querquedula*, *Larus fuscus*, and *Philomachus pugnax*. The flocks always arrived along the White Nile in their northward-directed flight. At the junction of the Niles (cf. Fig. 1), some flocks turned to the east, following the Blue Nile instead of continuing along the main river. Most of these flocks arrived at the Blue Nile after having crossed the small point of Mograns Park. They faced a river system at a right angle both to their original flight direction and to the river system (White Nile) that they had just left. In this situation the flocks were deviated to the east.

When watching the subsequent behavior of *Anas querquedula* and *Philomachus pugnax,* I noticed that they followed the Blue Nile half a mile or sometimes more. Then obviously a conflict between their tendency to fly along the ecologically favorable river valley (but in a false direction) and their need to take up their original northward direction released a special behavior. The birds descended at a more or less steep curve. The strong unity of the flock was dissolved. The single birds sideslipped down along their median axis. Some meters above the river surface they rose again, and the flock gathered. Then the flock often continued its flight in the normal, original direction, across Tutti Island and/or Khartoum North toward the main Nile. Sometimes, however, it turned to the west toward the junction or to the White Nile (especially *Anas querquedula*), from where it continued to the north. The flocks of *Plegadis falcinellus* and *Larus fuscus* simply turned to their normal flight direction without any special behavior.

Philomachus pugnax deserves comment for behavior not found in any other bird. Large numbers of *Philomachus* were seen flying to the north mainly from late afternoon until dusk, e.g. 4,880 on 25 March, 5,650 on 27 March. After a day with such a strong northward movement, there was often a strong southward movement during the succeeding morning (e.g. 2,950 on 24 March, 1,300 on 28 March). The nature of these movements was not fully studied. However, it seemed as if a feeding behavior might be involved, but obviously most birds flying to the north continued their flight as a true migration.

I could not see that either *Calandrella brachydactyla* or *Anthus campestris* were attracted to the Nile. However, resting flocks (large numbers of the former species) and single specimens were regularly observed in arid fields, often far from the river.

Grus grus seemed to migrate away from the river, although some flocks were observed to follow the Nile Valley. From the flight directions of observed crane flocks, one may assume that the bulk of Sudan-wintering cranes probably passed west of the Nile on their northward migration. From the flight directions of observed flocks of *Anthropoides virgo,* I infer that this crane, on the other hand, probably migrated mainly to the east of the Nile.

The two passerines mentioned above (*C. brachydactyla* and *A. campestris*) are quite numerous as resting birds in certain parts of the Khartoum area. The two crane species are very numerous along the White Nile, and flocks containing 10,000–20,000 specimens have been observed not far to the south of Khartoum. These facts strongly suggest that the relatively small numbers of these species actually observed migrating along the Nile were atypical of the migratory behavior of these species in this region.

Aythya fuligula, Charadrius alexandrinus, Tringa hypoleucos, T. stagna-

tilis, *Apus pallidus*, *Anthus trivialis*, and *Emberiza caesia* were extremely rare as resting birds in the Khartoum surroundings.

THE FLYWAY EFFECT OF THE NILE VALLEY

The migration across the Sahara and the effect of the Nile Valley upon migrating birds have been discussed in several papers (cf. e.g. bibliography in Kullenberg, 1956, and Moreau, 1961). However, the discussions are mostly based on scattered observations made by chance. No continuous observations (covering the whole migration period or the larger part of it) have been carried out. The present study is an attempt to fill this gap. To get undisputable facts, however, it would have been desirable to have simultaneous observations at several points at the same time, i.e. in the desert as well as along the river valley. Furthermore, it would, of course, have been most desirable to use radar observations, during the daytime as well as at night. However, this has not yet been possible.

The geographical conditions of northern Africa are dominated by the vast desert that, under the names of the Sahara, the Libyan, and the Nubian deserts, extends from the western to the eastern coasts of the continent.

Some parts of the desert are more favorable to birds than others from an ecological point of view. In the east, the Nile Valley offers favorable ecological conditions, which have no counterpart in other parts of the desert area. The south-to-north course of the river forms a favorable migration zone connecting the tropical belt with the eastern Mediterranean area. The geographical character of the valley, however, is not the same in all parts of the river course. Very arid conditions are found in Upper Egypt and in Nubia. Here, the Nile Valley often is not more than a stream, with no vegetation at all along its sides, and sand dunes or cliffs extend almost to the waterline. Rains do not occur or occur very rarely.

In the Khartoum area, the favorable zone along the river edge is broader. After the rains (rainy season: July–August), the plains along the river are covered with grass, agricultural plants, and other temporary vegetation. In spring, however, after months without precipitation, the vegetative zone is narrow. Where no irrigation is maintained, only few drought-resistant plants and trees are seen. The contrast between the narrow vegetation belt along the river zone, with irrigated gardens, etc. on the one hand and desert plains on the other, is very pronounced in spring. Therefore, the spring affords good opportunities to study migration behavior connected with the flyway effect of the Nile.

As we know the ecological requirements of many birds involved in this migration and also their relative abundance in different parts of Africa, we may expect certain trends in their general occurrence and behavior. That a bird species is reported to be a common or abundant visitor to eastern Africa, however, does not always mean that it is common in all ecologically satisfactory places. Thus, several species did not occur in the Khartoum area in the numbers expected, neither as resting birds nor as observed migrants. For example, *Motacilla flava*, with several subspecies, is known to occur in huge concentrations in the spring at Entebbe at the Victoria Nyanza in Uganda and in the Fayum south of Cairo in Egypt (Meinertzhagen, 1954). One would expect to find a strong migration along the Nile Valley connecting these two areas. My observations did not confirm this presumption. Other examples could be given. If these trends are general or only refer to the situation in the spring of 1961, we still do not know.

Concerning the frequency of different migrants at my observation point, however, we may presume that:

a) The very high frequency of some of the species presented above is due to the effect of the river. These species obviously migrate on a narrow front in the actual area. There is no evidence that a possible broad-front migrant of the Khartoum area should give very high figures at the observation point.

b) The low frequency of some birds, on the other hand, is due either to a low dependence upon the effect of the river (migration on a broad front in the Khartoum area) or to a generally low frequency in the Khartoum area. An explanation of the low figures for night migration requires for many species—e.g. *Grus grus*, *Hirundo rustica*, *Delichon urbica*, *Motacilla flava*—an opposite behavior to that known for their migration in Europe, where these species are known as day migrants.

SUMMARY

From the data above, we find that the Nile Valley attracts different kinds of migrating birds. It is impossible to say whether or not the frequency obtained in my observations is the same from year to year. But obviously the Nile Valley forms a great flyway out of Africa for many Eurasiatic migrants. However, we also find birds that ignore the favorable migration zone. Taxonomically, the species observed to follow the Nile form a heterogeneous group. Most of them, however, are ecologically attached to water biotopes, although some exceptions occur.

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La Migration de *Sylvia borin* concernant particulierement l'Italie

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La migration des oiseaux en Italie a été étudiée par des ornithologistes italiens, sur la base du registre des captures provenant de plusieurs importantes installations fixes. Pendant la période des dernières trente cinq années, Dr. A. Toschi, Dr. A. Duse, et moi-même avons pu rédiger un calendrier de la migration d'été et d'automne pour plusieurs espèces dans le nord de l'Italie. Je rappelle aux chercheurs que nos travaux ont été publiés par le Laboratoire de Zoologie de l'Université de Bologne et aussi en partie dans la *Revue Italienne d'Ornithologie*. Le travail que je présente en l'occasion de ce Congrés concerne *Sylvia borin*.

D'abord, je tiens à remercier l'Ing. Eugenio Mandelli de "l'Associazione Uccellatori Italiani" qui a mis aimablement à ma disposition les données relatives à la période 1941–61.

S'il est difficile de trouver des enregistrement de captures journalières de *S. borin*, néanmoins j'espère contribuer à la connaissance, encore défectueuse, de la migration de cette espèce. Je compléterai mon travail par quelques données remarquables de *S. borin* baguées. Pour l'étude analytique de *S. borin*, j'ai suivi une méthode analogue à celle employée depuis 1930 par les ornithologistes italiens mentionnés ci-dessus. Cette méthode a été suivie aussi par M. Gerard de Crousaz dans un travail très intéressant sur "La Migration d'automne des Motacillidés aux cols de Cou-Bretolet" pendant les années 1958–60, publié dans *Sammelbericht der Schweiz, Vogelwarte Sempach*, 1959–60. La période en considération pour la station de Mandelli, située près de Bergamo (45°41′ N, 9°40′ E), est 1941 à 1961, à la exception de 1945 et 1948 quand les travaux de cette station ont commencé en retard. Le total journalier des captures du 19 août au 8 octobre m'a permis d'illustrer (Fig. 1) le déroulement complet de la migration de *S. borin*.

Ce graphique nous montre un calendrier fidèle de la migration, avec un maximum entre le 4 et 11 septembre et, avant cette période, un fort passage vers la fin d'août. Voici les jours pendant lesquels on a enregistré le plus grand nombre de captures:

1941: 4 septembre
1942: 28 août
1943: 6 septembre
1944: 10 septembre
1946: 9 septembre
1947: 28 août–5 septembre
1949: 6 septembre
1950: 29 août
1951: 8 septembre
1952: 29 août
1953: 9 septembre
1954: 29 août
1955: 2 et 20 septembre
1956: 5 et 6 septembre
1957: 6 septembre
1958: 31 août et 14 septembre
1959: 1 septembre
1960: 9 septembre
1961: 6 et 19 septembre

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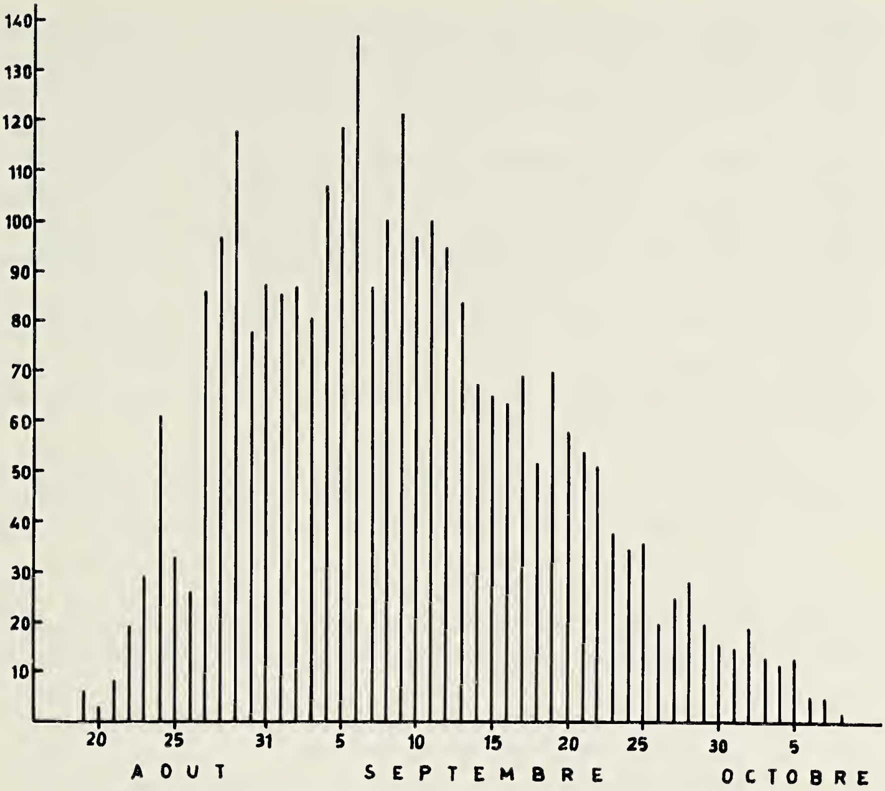

Fig. 1. Le déroulement complet de la migration de *Sylvia borin*.

Il est peut-être intéressant d'observer que le beau temps est favorable à la migration de *S. borin*; il a fait beau pendant les jours indiqués à l'exception du 2 septembre 1955 (temps variable), du 1 septembre 1959 (nuageux), et du 9 septembre 1960 (variable).

Les captures annuelles ont été plus ou moins abondantes, phénomène commun, d'ailleurs, à toutes les autres espèces. Les années de captures abondantes ont été plus nombreuses que celles de captures pauvres. Les captures ont été abondantes en 1942, 1944, 1947 (239 captures), 1949 (292 captures), 1950, 1951, 1954 (191 captures), 1955, 1956 (223 captures); pauvres en 1946 (81 captures), 1952, 1953 (95 captures), 1960 (80 captures).

Il est opportun de compléter ce travail par les données les plus intéressantes des reprises de *S. borin*, déduites d'après ce que quelques auteurs ont dejà publié (Rydzewski, Novak, Moltoni, et Drost), d'après plusieurs comtes-rendus des stations de baguage d'Helsinki, Bruxelles, Sempach et d'après les signalations obtenues des directeurs des stations de Stockholm, Göteborg, Paris, et Zool. Bologna.

REPRISES EN ITALIE

Les individus bagués repris en Italie proviennent pour le plus grand nombre du nordest: on connaît une dizaine d'individus bagués en Finlande, 6 en

Suède; et un nombre infèrieur en Allemagne, France, Tchécoslovaquie, Pologne, Hollande, et Suisse. Parmi les reprises ont peut citer les suivantes: près de Messina le 5 septembre 1954 (n° 102941 Praha bagué le 22 mai 1954); près de Salerno le 10 septembre 1939 (n° 471386 Rositten, Allemagne) et encore près de Salerno le 27 août 1948 (n° 51429 N. Leiden, Hollande); à Naples le 3 septembre 1955 (n° HU 2938 Paris bagué le 9 juillet 1955). Ces reprises, enregistrées dans le sud de l'Italie exactement pendant la période correspondant au maximum du passage remarqué à la station Mandelli (Nord Italie), nous montrent qu'il n'y a pas de différence sensible dans la migration entre le Nord et le Sud de l'Italie quoique la distance soit de 700 km et quoique les conditions de climat soient très differentes. On peut remarquer aussi que presque tous les individus de *S. borin* bagués en Finlande ont été repris en Italie.

Le baguage conduit par "l'Associazione Italiana Uccellatori" qui a son siège à Bergamo, mais qui a aussi plusieurs stations, nous fera savoir dans l'avenir si les *S. borin* baguées dans l'Italie du Nord se dirigent vers le sud, ou vers l'ouest ou le sudouest, (c'est-à-dire les côtes du midi de la France ou l'Espagne), direction suivie par la plupart des passeraux qui traversent en automne l'Italie du Nord. La plupart des individus repris en Italie pendant la migration d'automne ont été bagués dans le nord de l'Europe à l'époque de la nidification.

DIRECTION DE LA MIGRATION

Les directions suivies par *Sylvia borin* vers ses quartiers d'hivernage sont intéressantes. Les reprises énumérées ci-dessous nous montrent mieux que n'importe quel commentaire que plusieurs individus bagués en Allemagne, Danemark, Hollande, et France se dirigent vers le sudest, tandis que d'autres bagués en Allemagne, Finlande, Suède, France, Suisse, Tchécoslovaquie, et aussi dans des pays plus à l'est, se dirigent vers le sudouest (direction suivie par le plus grand nombre des oiseaux de l'Europe). Les trois premières reprises dans la liste ont été reportées par Rydzewski, qui a recueilli beaucoup de données sur les reprises d'oiseaux bagués dans les îles de la Méditerranée.

Pour la direction sudest on peut lister:

Helgoland	juv.	bagué	27. 6.1933	Dalbersdorff, Allemagne		51°12′ N, 17°44′ E
898140A		tué	26. 8.1933	Larnaca, Ile de Chypre		34°55′ N, 33°39′ E
Helgoland	pull.	bagué	30. 5.1934	Burg, Allemagne		52°17′ N, 11°52′ E
8085637		repris	16.10.1934	Famagusta, Ile de Chypre	ca.	35°09′ N, 34°00′ E
Varsovie	pull.	bagué	28. 5.1938	Sporyaz, Pologne		49°41′ N, 19°13′ E
G98464		tué	19.12.1938	Cattavia, Ile de Rhodes		35°56′ N, 27°47′ E
Mus. Paris		bagué	17. 9.1958	La Tour du Valat, France		43°30′ N, 4°30′ E
SA8739		tué	7.10.1958	Mazara del Vallo, Sicile		37°39′ N, 12°36′ E
Z. M. Denmark	ad.	bagué	21. 9.1939	Bornholm, Danemark		55°02′ N, 15°00′ E
960971		tué	29. 9.1939	Blato Korcula, Yougoslavie	ca.	42°57′ N, 17°08′ E
Mus. Leiden		bagué	10. 6.1948	Weesp. Gosi, Nord Hollande		52°18′ N, 5°03′ E
51429		repris	27. 8.1948	Cava de'Tirreni, Italie	ca.	40°40′ N, 14°40′ E

Mus. Paris		bagué	9. 7.1955	Armentières, Nord France	50°41′ N, 2°53′ E
HU2938		tué	3. 9.1955	Naples, Italie	40°50′ N, 14°15′ E

Pour la direction sudouest on peut lister, parmi de nombreuses reprises, les suivantes:

Praha		bagué	11. 6.1952	Plzen, Tchécoslovaquie	49°45′ N, 13°23′ E
M215859		repris	avril 1953	Akropong, Côte d'Or	6°00′ N, 0°03′ W
Mus. Paris	ad.	bagué	19. 9.1957	Oessant, Finistère, France	48°28′ N, 5°05′ W
JE0094		trouvé mort	6.10.1957	Jerez de la Frontiera, Cadix, Espagne	36°41′ N, 6°08′ W
Helgoland		bagué	1. 9.1960	Helgoland, Allemagne	54°11′ N, 7°55′ E
9841690		trouvé mort	9. 9.1960	Monchanin, France	46°46′ N, 4°30′ E
Helsinki		bagué	25. 8.1954	Signilskar, Ile Aland, Finlande	60°12′ N, 19°22′ E
67961		repris	19. 9.1954	Piombino, Italie	42°55′ N, 10°30′ E
Stockholm	pull.	bagué	25. 6.1947	Halsingborg, Suède	56°05′ N, 12°45′ E
ZD4656		contrôlé	2. 9.1947	Ygos St. Saturnin, Landes, France	43°58′ N, 0°43′ W

VITESSE DE MIGRATION

Parmi les nombreux résultats que l'on peut obtenir grâce au baguage, ceux qui concernent la vitesse des déplacements sont certainement des plus intéressants.

En voici quelques-uns qui montrent que *S. borin* bagué à l'époque de la migration se déplace très rapidement vers les quartiers d'hivernage. L'individu mentionné le premier a parcouru presque 400 km par jour.

Stockholm	bagué	18. 9.1955	Orebro, Narke, Suède	59°17′ N, 15°13′ E
Z. A. 9050	tué	22. 9.1955	Palazzolo sull'Oglio, Italie	ca. 45°40′ N, 9°50′ E
Rositten 659366	bagué	26. 8.1942	Windenburg Post Kinten, Ostpreussen, Allemagne	55°17′ N, 21°13′ E
	tué	2. 9.1942	Segusino di Treviso, Italie	ca. 45°50′ N, 12°00′ E
Rositten 471386	bagué	6. 9.1939	Windenburg Post Kinten, Ostpreussen, Allemagne	55°17′ N, 21°13′ E
	tué	10. 9.1939	San Giungano di Salerno, Italie	ca. 40°37′ N, 14°29′ E
Helgoland 9672637	bagué	6. 9.1958	Helgoland, Nordsee, Allemagne	54°11′ N, 7°55′ E
	tué	16. 9.1958	Pescia, Italie	ca. 43°56′ N, 10°55′ E
Helgoland	bagué	1. 9.1960	Helgoland, Allemagne	54°11′ N, 7°55′ E
9841690	trouvé mort	9. 9.1960	Monchanin, France	46°46′ N, 4°30′ E
Helsinki 67961	bagué	25. 8.1954	Signilskar, Ile Aland, Finlande	60°12′ N, 19°22′ E
	tué	19. 9.1954	Piombino, Italie	42°55′ N, 10°30′ E

TENDANCE A RETOURNER AU PAYS D'ORIGINE OU DE NIDIFICATION

De nombreuses reprises confirment cette tendance chez *S. borin*. Le Dr. Novak en signale un nombre remarquable dans son travail sur la migration des espèces du genre *Sylvia* baguées en Tchécoslovaquie, publié en 1959. Il mentionne que 5 oiseaux sont retournés pour 3 ans, 2 pour 2 ans, et 13 pour un an. Un individu bagué en juin en Suède est retourné dans la même région à la fin de mai de l'année suivante. Un autre, bagué à Armentières, France (nº N. Paris H.V. 5254), le 14 mai 1956 y est revenu le 28 avril 1957; un autre, bagué à Arendonk, Belgique (nº 16 A.9394, Bruxelles) le 26 juillet 1957 y est revenu le 6 juillet 1958. En Suisse, un oiseau est revenu deux ans plus tard au mois de mai 1942, à l'endroit où il avait été bagué; un autre après un an en 1944; et un individu bagué en juin 1940 est revenu au site du baguage en mai 1942 et avril 1943.

Nos connaissances sur les lieux d'hivernage sont très limitées ainsi que Novak l'a montré en 1959. Dr. Drost fournit d'importantes données sur les quartiers d'hiver des espèces du genre *Sylvia* dans un article qui m'est arrivé après avoir fini ce travail.

Parmi les individus trouvés dans leurs quartiers d'hiver, notons les suivants:

le nº 98464 Varsovie (déja cité) bagué "pull." en mai 1938 en Pologne, tué à l'île de Rhodes le 19 décembre 1938;

le nº M.215859 Praha (déja cité) bagué en juin 1952 en Tchécoslovaquie, repris sur la Côte d'Or en avril 1953;

le nº E.34148 Praha, bagué "juv." le 11 juin 1940 à Novà Hut'u Niz'bora (Tchécoslovaquie), repris le 17 novembre 1941 à Bogdum (Cameroun);

le nº 392004 Sempach, bagué le 11 mai 1957 à Kloten/Zh (Suisse), repris le 29 novembre 1960 à Sanlucar Barrameda (Cadix), Espagne;

le nº 8737914 bagué le 30 juin 1953 à Schkeuditz-Leipzig, Allemagne, tué le 14 février 1955 près de Ogwashi Uku (Benin City), Nigeria.

Le Dr. Drost (Vogelwarte Helgoland) a mentionné une autre reprise en décembre en Espagne (provenance Suisse). Les deux individus repris en Afrique Equatoriale Occidentale ont parcouru plus de 6.000 km.

J'ai remarqué qu'en ces dernières années la Suisse, la France, et la Finlande ont remarquablement intensifié le baguage des Fauvettes des jardins (*Sylvia borin*); je souhaite donc que l'intelligent travail que développent en ces nations MM. Dr. Schifferli, R.-D. Etchécopar, et G. Nordstrôm donnera bientôt des résultats très importants.

A mon avis il faudrait que les stations de l'Europe du Nord baguassent un plus grand nombre d'individus quand la migration été-automne a déja commencée.

SOMMAIRE

L'article ci-dessus présente un calendrier des captures journalières de *Sylvia borin* à une station de baguage située près de Bergamo, Italie septentrionale, pour la période de sa migration d'été, pendant la période 1941–61. Les reprises en Italie des oiseaux bagués dans d'autres stations Européennes sont mentionnées, ainsi que la direction des migrations, la rapidité des mouvements, et la tendance qu'ont les oiseaux à retourner à leur lieu de nidification.

Migration and Population Dynamics of American Coots in Western North America

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The American Coot (*Fulica americana*) is a widespread breeder in North America, nesting at least locally throughout much of the continent and wintering primarily in California, Mexico, and states bordering the Gulf of Mexico (Fig. 1 and 2). Hunting regulations place this aquatic rail along with the ducks and geese as "waterfowl." In certain parts of the United States, the coot is rather important in the total kill of waterfowl taken by hunters. However, in many sections this species is considered unsporting and not as palatable as most ducks and geese. Kiel and Hawkins (1953) and Burton (1959) have stressed the importance of the coot in the Mississippi Flyway and presented data relative to its kill, winter status, annual mortality rate, age composition, and distribution in this region of particularly heavy hunting pressure.

This paper deals primarily with the distribution and mortality of the American Coot as based upon recoveries of birds banded west of the Mississippi River and the eastern borders of Minnesota and Manitoba. An attempt has been made to relate these findings with the bird's breeding biology as described in recent studies (Sooter, 1941; Gullion, 1954; Kiel, 1955; Ryder, 1958 and 1961).

The U.S. Fish and Wildlife Service, particularly Walter F. Crissey and

Fig. 1. Breeding range of the American Coot. Fig. 2. Wintering range of this species.

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Allen J. Duvall, has been most cooperative in making available information relating to over 6,000 recoveries from approximately 85,000 coots banded throughout North America. These coots were banded by 209 permittees. The author gratefully acknowledges these individuals and agencies, especially the California Department of Fish and Game (P-R Project 30-R), the Louisiana Wildlife and Fisheries Commission, the Oregon State Game Commission, and the Utah Fish and Game Department.

Fig. 3. Generalized locations of direct and indirect recoveries of American Coots banded in Oregon and Saskatchewan. Total recoveries involved: Oregon, 175; Saskatchewan, 158. (Encircled numbers show percentage of recoveries by location; *T* = trace, less than 1 percent.)

Financial assistance was received in the form of grants from the Colorado State Legislature, Colorado State University Research Foundation, and the Society of the Sigma Xi and RESA Research Fund.

MIGRATION

Coots nest most abundantly in the so-called "duck factory" of the northern Great Plains States and the Prairie Provinces of Canada. Local concentrations also occur in the Great Basin, particularly around Great Salt Lake and on such federal refuges as Tule and Clear lakes in California and Lower Klamath and Malheur in Oregon. According to U.S. Fish and Wildlife Service waterfowl surveys (Crissey, 1961), the highest breeding populations of coots during the past 10 years have been in Saskatchewan (a breeding-population "index" of over 300,000 in 1956). Since 1956 there has been a

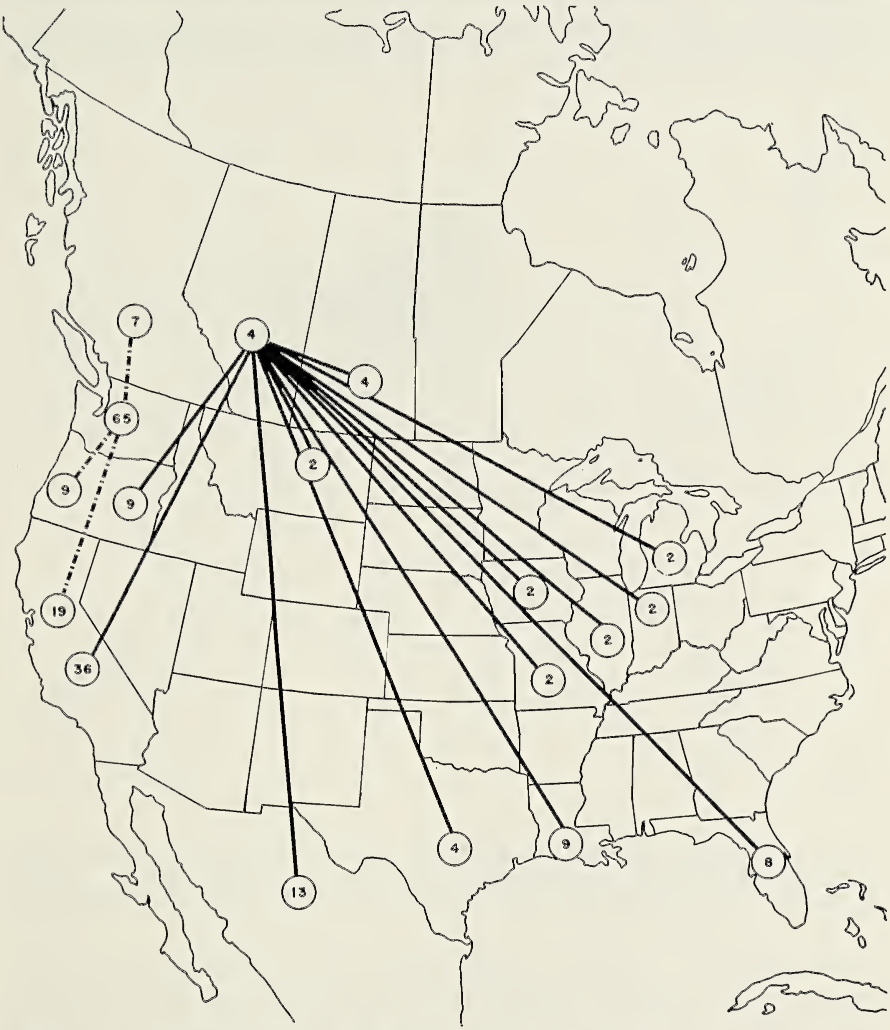

Fig. 4. Generalized locations of direct and indirect recoveries of American Coots banded in Washington and Alberta. Total recoveries involved: Washington, 58; Alberta, 53. (Encircled numbers show percentage of recoveries by location.)

marked decline in most nesting areas. In 1959–61, coots were more abundant in Alberta than in Saskatchewan.

Based upon banding recoveries, it may be said that coots breeding in the Prairie Provinces seem to migrate southward along many routes (probably a broad front), but in general those from Alberta go mainly to California and western Mexico, whereas those from farther east largely go to more easterly wintering grounds, such as eastern Mexico, Texas, Louisiana, and Florida (Fig. 3, 4, 5, and 6). There seems to be no clear-cut distinction of flyways. For example, 9 percent of the recoveries from coots banded in Alberta have been in Louisiana and 8 percent in Florida, while 10 percent of the recoveries from Saskatchewan have been in California.

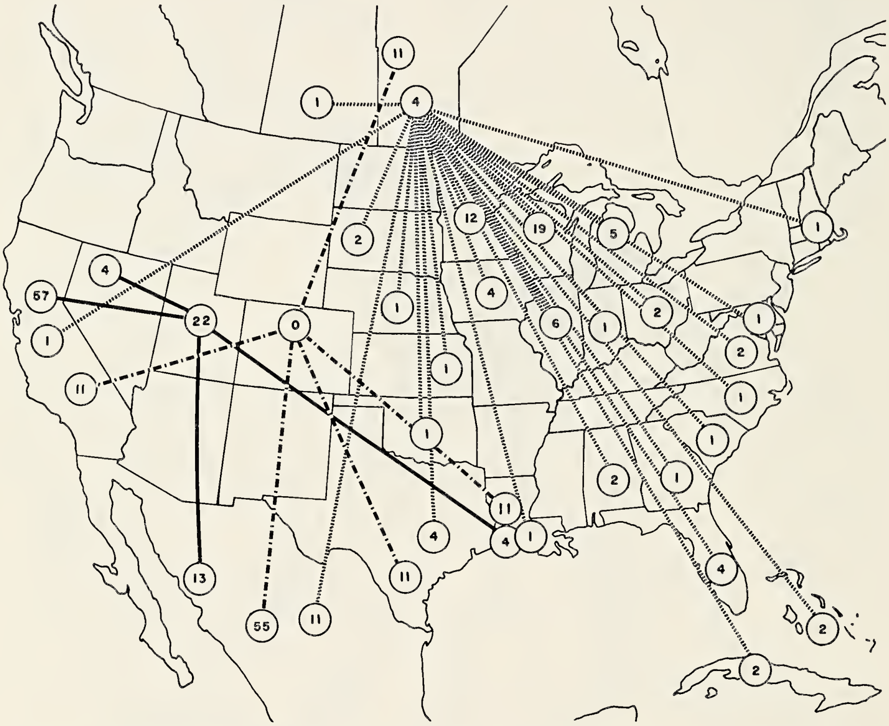

Fig. 5. Generalized locations of direct and indirect recoveries of American Coots banded in Utah, Colorado, and Manitoba. Total recoveries involved: Utah, 23; Colorado, 9; Manitoba, 104. (Encircled numbers show percentage of recoveries by location.)

A word of caution should be interjected regarding the use of recoveries as a means for understanding this species' migration. Most coots are reported from areas where shot coots are saved or at least examined. In many parts of the West, coots are shot merely for a "warm-up" and not retrieved (Ward, 1953; Ryder, 1958).

There does, however, seem to be a marked tendency (see Table 1) for coots from the eastern breeding grounds to winter in eastern Mexico (especially the states of Vera Cruz and Tamaulipas), while those from more western breeding areas are more likely to winter in western Mexico (primarily in Sinaloa and Jalisco).

Some banded coots from breeding grounds in western North America have been recovered as far south as Guatemala, Cuba, the Bahama Islands, and Honduras. Apparently, coots from more southern breeding grounds migrate farther south, e.g. 32 percent of the coots banded in Iowa and 10 percent of those banded in Missouri were recovered in Cuba. Perhaps these particular coots nested in Iowa or Missouri, but it is more likely that they came from the southern edge of the main breeding grounds farther north.

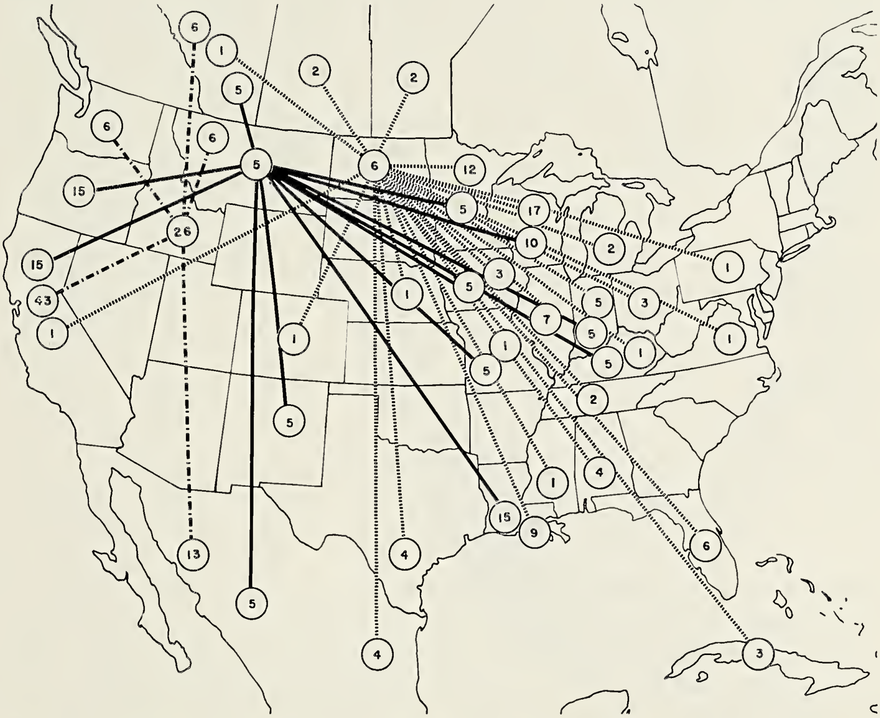

Fig. 6. Generalized locations of direct and indirect recoveries of American Coots banded in Idaho, Montana, and North Dakota. Total recoveries involved: Idaho, 16; Montana, 20; North Dakota, 132. (Encircled numbers show percentage of recoveries by location.)

Coots banded in states and provinces bordering the West Coast seem to be largely resident or at best to migrate only short distances to warmer valleys and coastal areas. Coots wintering in Louisiana apparently come from a vast breeding area ranging from the Yukon Territory to Ontario and the East Coast southward, greatest numbers seemingly coming from Saskatchewan and the northern plains states (Fig. 7).

Coots reared in the Great Basin winter primarily in California with lesser

TABLE 1.—MEXICAN RECOVERIES OF COOTS BANDED IN WESTERN NORTH AMERICA

Where Recovered in Mexico . . .	WEST COAST		EAST COAST		INTERIOR	
Place of Banding	No.	Percent	No.	Percent	No.	Percent
Alberta	6	10	–	–	–	–
California	23	38	1	4	1	6
Colorado	5	8	–	–	–	–
Idaho	2	3	–	–	–	–
Iowa	–	–	1	4	–	–
Louisiana	1	2	–	–	–	–
Manitoba	2	3	5	18	2	13
Montana	–	–	1	4	–	–
Minnesota	1	2	4	16	2	13
Missouri	1	2	2	7	1	6
Nebraska	1	2	–	–	–	–
Nevada	1	2	–	–	–	–
New Mexico	3	5	–	–	1	6
North Dakota	3	5	2	7	–	–
Oklahoma	–	–	4	15	–	–
Oregon	3	5	–	–	–	–
Saskatchewan	5	8	5	18	7	44
South Dakota	–	–	2	7	1	6
Utah	2	3	–	–	1	6
Wyoming	1	2	–	–	–	–
Totals	60	100	27	100	16	100

numbers going to western Mexico, although a few birds wander as far east as Louisiana (Fig. 5 and 6).

Throughout their range, coots are probably night migrants (Sooter, 1941; Ward, 1953), usually moving south ahead of most species of ducks, but in the West, at least, after such migrants as the Blue-winged Teal (*Anas discors*) and the Pintail (*Anas acuta*). In the spring, coots are rather late migrants compared to most ducks. Little seems to be known regarding the height and speed at which coots migrate or whether they fly in flocks. Apparently they fly in loose aggregations, keeping in contact with one another by calling (Hochbaum, 1955:173–174). Ward (1953) noted that coots called more during their spring migration than in the fall. Both in Manitoba (Ward, 1953) and in Utah (Ryder, 1958), there is evidence that males and nonbreeders congregate on larger bodies of water late in the summer and perhaps move southward ahead of the females and young.

MORTALITY

Mortality rates of the American Coot were obtained by constructing life tables, such as described by Hickey (1952). Due to fire damage and the subsequent necessity to reconstruct its records, the banding office of the Fish

Fig. 7. Generalized locations of direct and indirect recoveries of American Coots banded in California and Louisiana. Total recoveries involved: California, 1,586, including 92 in that state; Louisiana, 1,960, including 85 in that state. (Encircled numbers show percentage of recoveries by location.)

and Wildlife Service was unable to provide the numbers of coots banded by years and locations. Consequently, it was not possible to employ Haldane's (1955) method to correct mortality estimates for bandings that are too recent

TABLE 2.—DYNAMIC LIFE TABLE BASED UPON RECOVERIES OF 2,325 COOTS OF ALL AGES BANDED IN WESTERN NORTH AMERICA

"Age Interval" in Years (x)	Number Found Dead (d_x)	Alive at Start of Year (l_x)	Mortality Rate (q_x)
0–1	1,322	2,325	56%
1–2	542	1,003	54
2–3	244	461	53
3–4	99	217	46
4–5	47	118	40
5–6	35	71	47
6–7	13	36	
7–8	10	23	
8–9	8	13	
9–10	3	5	
10–11	1	2	
11–12	1	1	
Totals and mean	2,325	4,255	55%

to provide data for the entire life span. Thus, rates computed from recent bandings are undoubtedly biased (probably too low). Although, to some degree, age and sex of coots can be determined in the field, comparatively few of the recoveries analyzed were of coots for which either age or sex was specified. Therefore, little information was obtained regarding differential mortality by age or sex. All of my computations are based on a "recovery year" of 1 August through 31 July.

TABLE 3.—COMPARATIVE MEAN ANNUAL MORTALITY OF AMERICAN COOTS BASED UPON BAND RECOVERIES

Area Where Banded	Total Recoveries in Samples	Age Group	Annual Mortality in Percent
Western North America	2,325	All	55
Western North America	240	Adult	61
Western North America	501	Young	83 (1st year 88; 60 thereafter)
Western North America	112	"Local"[a]	83 (1st year 87; 65 thereafter)
California	604	All	53
Louisiana	871	All	47
Oregon	104	All	62
Saskatchewan	129	All	70
North Dakota	118	All	72
British Columbia, Washington, Alberta	105	All	66
Manitoba, Minnesota, South Dakota	218	All	78
Prairie Provinces, the Dakotas Minnesota, Iowa, and Illinois	139	Adult	57 ± 6[b]
	174	Juvenile	79 ± 4[b]

[a] Banded as young birds, out of the nest but at the time of banding incapable of flight.

[b] From Burton (1959).

A mean annual mortality rate of 55 percent was obtained for 2,325 coots known to have been shot or otherwise found recently dead when recovered (Table 2). This rate is considerably lower than most that have been computed for similar (all ages) samples for specific banding areas. These other rates ranged from 47 to 83 percent (Table 3). The lowest rate (47 percent) was based upon 871 coots banded in Louisiana prior to March 1951. In fact, all but four were banded earlier than 1942. The longest reported interval from banding to recovery for all records examined was less than 12 years (a coot banded in Oregon on 20 October 1934, and recovered in Mexico on 1 December 1945).

Therefore, for the period from 1920 to 1942, the Louisiana mean annual mortality rate is probably quite reliable and representative for coots after they have survived at least one fall migration. Mortality for coots in more northern areas in recent years seems to be higher. However, most "all age" samples in Table 3 are probably somewhat biased by containing a higher proportion of young than the Louisiana sample.

Coots identified as young or "local" when banded had a much higher mean annual mortality rate than those recorded as adults when banded (83 compared to 61 percent). However, after a first-year mortality rate of 88 and 87 percent, respectively, for young and locals, these birds had 60 and 65 percent average annual mortality rates in subsequent years.

In general, the American Coot seemingly has a higher average annual *mortality rate* than most dabbling ducks and, at least in some areas, as high as those thus far calculated for such declining species as the Redhead and Canvasback (Table 4).

In contrast, Chattin (1954) showed that the direct *recovery rate* for the coot in the Pacific Flyway (1.6 percent) was only about one-tenth that of most ducks (Mallard 10.6 percent, Redhead 14.4 percent). Elder (1955) cited a 4.1 percent cumulative recovery rate for 3,201 coots banded, compared to 14.5 percent for 259,986 Mallards and 12.8 percent for 12,987 Redheads. I obtained 2.9 percent direct and 3.8 percent cumulative recovery rates from 475 coots banded in Utah in 1956. These lower coot recovery rates are evidence that fewer coots are retrieved than ducks, although the actual mortality rates of the two groups are comparable.

In fluoroscope studies, Elder (1955) found coots had only about one-tenth the incidence of imbedded body shot as ducks, and concluded that coots are low in body shot for four reasons: (1) They migrate at night; (2) they raft in open water; (3) many move south just ahead of the hunting season; and (4) like the teal, coots are more likely to be downed by one shot-pellet than larger ducks. Thus, he concluded that the incidence of body lead was not as reliable an indicator of hunting pressure on coots as on ducks. Elder also mentioned that coot vulnerability to hunting is not properly indicated by band recovery rates, probably since ". . . many hunters do not bother to pick up coots they have killed."

TABLE 4.—COMPARATIVE COOT AND DUCK MEAN ANNUAL MORTALITY RATES CALCULATED FROM BAND-RECOVERY DATA

Species	AV. ANNUAL MORTALITY RATES (%)			Authority
	All Ages	Adults	Young	
American Coot (*Fulica americana*)	55	61	83	This study
Mallard (*Anas platyrhynchos*)	58[a]	38–55	55–75	Calculated by Keith (1961) from Van Den Akker and Wilson (1949) and Ryder (1955); Hunt et al. (1958)
Pintail (*Anas acuta*)	44[a]	50	—	Calculated by Keith (1961) from Van Den Akker and Wilson (1949); Sowls (1955) after Munro (1944)
Redhead (*Aythya americana*)	77[a]	55	70	Calculated by Keith (1961) from Van Den Akker and Wilson (1949); Hickey (1952)
Canvasback (*Aythya valisineria*)	70	52	77	Geis (1959)
Gadwall (*Anas strepera*)	52[a]	—	—	Calculated by Keith (1961) from Van Den Akker and Wilson (1949)
American Widgeon (*Mareca americana*)	54[a]	—	—	Calculated by Keith (1961) from Van Den Akker and Wilson (1949)
Shoveler (*Spatula clypeata*)	58[a]	—	—	Calculated by Keith (1961) from Van Den Akker and Wilson (1949)
Green-winged Teal (*Anas carolinensis*)	48[a]	—	—	Calculated by Keith (1961) from Van Den Akker and Wilson (1949)
Blue-winged Teal (*Anas discors*)	57	—	—	Bellrose and Chase (1950)

[a] Includes survivors of botulism.

TABLE 5.—CAUSES OF DEATH REPORTED FOR COOTS BANDED IN WESTERN NORTH AMERICA

Cause	Number	Percent
Shot	1,950	80.5
Found dead	344	14.3
Traps (other than banding)	55	2.3
Predators	29	1.2
Accidents (drowned, hit obstacles, etc.)	29	1.2
Weather	8	0.3
Botulism	6	0.2
Totals	2,421	100.0

CAUSES OF MORTALITY

Of 4,721 recoveries of coots banded west of the Mississippi, about half were trapped and released alive in subsequent banding operations or reported as recovered in some manner that might have involved release and further life ("found injured," "entangled in nets," etc.). At least 2,421 recoveries were terminal, i.e. resulted in death of the banded coots. Most were lost to hunting ("shot" category in Table 5 and probably many of those in the "found dead" category). Other causes of death are listed in Table 5.

These reported causes of mortality are just a few of those affecting coots *after* banding. Known and possible decimating factors affecting adult coots, their eggs, and young are summarized by Ryder (1958 and 1959).

DYNAMIC POPULATION MODELS

From personal experience and a review of the literature, certain data are available from which to theorize on the population dynamics of the American Coot. The extremes of these statistics (as well as arbitrarily selected norms) are summarized in Table 6.

Table 6.—Natality and Mortality Statistics for the American Coot

(Authority in parentheses; this study unless otherwise noted)

Type of Statistic	Minimum	Maximum	Assumed Current Norm
Eggs laid per clutch	6.1 (Sooter, 1941)	10.2 (Smith, 1956)	8.8 (Ryder, 1961)
Hatching success	41% (Anderson, 1957)	97% (Kiel, 1955)	91% (Ryder, 1961)
Young fledged per pair	1.9 (Sooter, 1941)	5.7[a] (Ryder, 1958)	4.8[a] (Ryder, 1961)
First-year mortality	79% (Burton, 1959)	88%	83%
Annual mortality after first year	47%	65%	55%

[a] Includes second broods, which apparently occur in the southern part of the American Coot range.

From these gain-and-loss statistics, a population model (Table 7) can be devised representing the number of adults and their offspring surviving from one nesting season to the next. Use of the most limiting population statistics results in a rapidly declining population that drops from an assumed 200 breeding birds one spring down to 70 the next. Those statistics that permit maximum survival result in a second-season population of 221. Those that I assume to be "normal" yield a declining population that may either be in error or perhaps truly represents the existing trend in continental coot populations—a steady decline. U.S. Fish and Wildlife Service breeding-ground and winter inventories suggest a decline since the mid-1950's.

Table 7.—Theoretical Dynamic Population Models for the American Coot Based upon Initial Population of 100 Pairs

(See Table 5 and text for details)

Type of Statistic	MINIMUM REPORTED PRODUCTIVITY AND SURVIVAL		MAXIMUM REPORTED PRODUCTIVITY AND SURVIVAL		ASSUMED CURRENT NORM	
	Adults	Young	Adults	Young	Adults	Young
Start of first nesting season	200		200		200	
Eggs laid		(610)		(1,020)		(840)
Eggs hatched		250		990		810
Losses prior to fall migration[a]	–10	–60	–2	–420	–4	–330
Population at start banding year	190	190	198	570	196	480
Annual mortality	–124	–186	–89	–458	–88	–399
Population at start of second nesting season	66	4	109	112	108	81
Total adults and young	70		221		189	
General trend of population	Declining rapidly		Increasing		Declining slowly	

[a] Hypothetical for adults. Young, based upon fledging rates.

SUMMARY

The American Coot breeds mainly in the northern Great Plains States and in the Prairie Provinces with local concentrations elsewhere, particularly in the Great Basin. Based upon an analysis of 4,721 recoveries of banded coots, it appears that this species migrates southward over a variety of routes more or less on a broad front. Coots that breed in the eastern Prairie Provinces and plains states winter largely in Louisiana and eastern Mexico, whereas those from more western nesting grounds winter mainly in California and western Mexico. Apparently, coots from more southern nesting regions are more likely to winter as far south as Central America and the Caribbean.

Mean and annual mortality rates were computed as follows: 55 percent for all age samples, 61 percent for coots banded as adults, and 83 percent for those banded before their first migration. The latter birds experience first-year annual mortality rates of 87–88 percent, and 60–65 percent in years thereafter. Although somewhat biased too low, these rates seemed higher than those for most dabbling ducks. A dynamic population model based on statistics assumed to represent current norms suggests that the population is now slowly declining.

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Migration Habits of Golden Plovers

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According to Larson (1955), the subfamily Charadriinae originated in the tropics or subtropics, from whence some representatives eventually ranged north into the Boreal Region. Johansen (1956, 1958) points out that the common ancestral form of the Golden Plover probably lived in the Alpine Zone of the east Asian mountains and might have shown the following evolutionary steps during the glacial period: Some birds avoided the glaciers by moving west along the border of the tundra toward Europe. There, after geographical isolation from the Siberian ancestral form, *Pluvialis apricaria* probably speciated during an interglacial period; later it split into the two subspecies *apricaria* and *altifrons*. Another branch of the ancestral form probably moved eastward into the Bering Sea refuge, and expanded westward as *P. dominica fulva* after the glaciers receded. *P. d. dominica*, the main element of this branch, might well have spent the last period of glaciation in the Alaskan refuge, from which it subsequently invaded the arctic regions to the east. In postglacial times *P. apricaria* (*altifrons*) expanded eastward and met *P. dominica* (*fulva*), by then specifically distinct.

Today the two species occupy the boreal circumpolar region with the exception of Greenland, where only occasional stragglers are reported from the eastern and southern sections. The most interesting range expansions are now taking place in western Siberia; the breeding ranges of *P. a. altifrons* and *P. d. fulva* now overlap. The two species seem to have remained separated, as they occupy different biotic communities (Johansen, 1956, 1958, 1960). However, Voous (1960) reported possible hybridization between the two. Whether this new development will result only in a few exceptional and locally restricted hybrids, or will reunite the two species on a new evolutionary level, thereby terminating their speciation, which has probably lasted 10,000 years or longer, is a question of frequency and time.

One may expect the present migratory patterns of the Golden Plover to reflect the historic movements of their ancestors. Field observations and the few recoveries of banded birds support this view (to be discussed in detail in a separate paper). For example, birds from northern Russia, the northern mountain range of the Urals, and the lower Yenisei River have been reported wintering in Holland. Their fall migration reflects the movements of their ancestors at the beginning of the glacial period. Birds of the North American subspecies breeding in the northern districts of Alaska are believed to migrate eastward in fall across northern Canada and to turn

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[1] Dedicated to Professor Dr. Rudolf Geigy, Director of the Swiss Tropical Institute at Basel, Switzerland, in honor of his 60th birthday.

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south when they approach the meridian of Newfoundland. This eastward movement also reflects the population's earlier range expansion. Whether or not the north–south components of the Golden Plovers' migrations were established under preglacial, glacial, or postglacial influences is difficult to determine. While the preglacial northward movement of the earliest ancestors of the Golden Plovers is probably of great significance in relation to the origin of their migratory movements, the glacial and postglacial south–north movements doubtlessly enforced, re-established, and modified the original pattern.

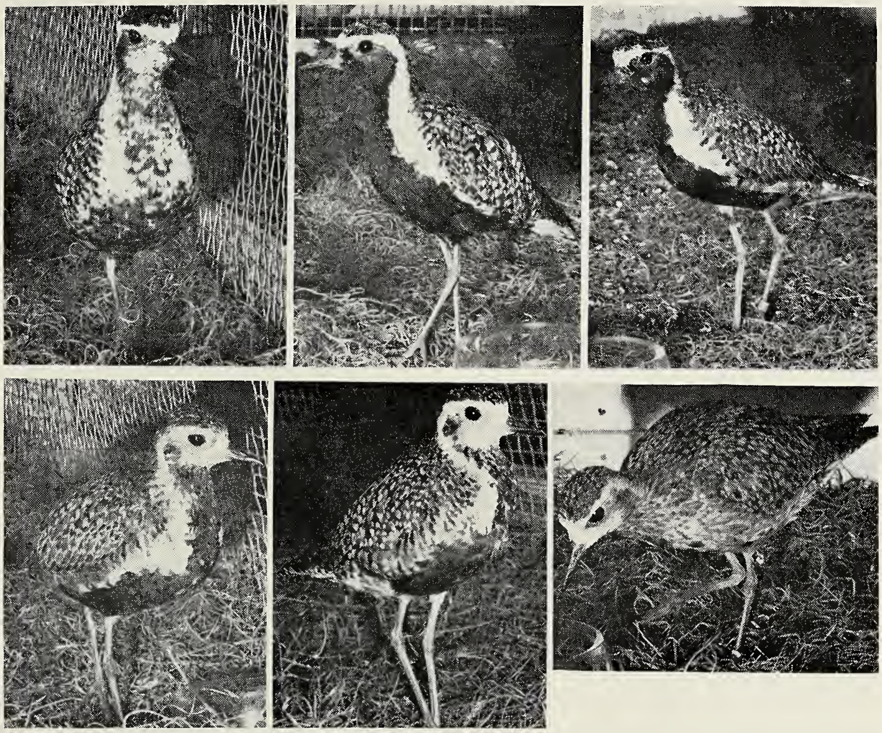


Fig. 1. Some of the hand-raised birds at various stages of their summer molt on 29 July 1962. Upper row, left to right: RB ♂; Gl ♂; LB ♂. Lower row, left to right: RL ♀; RD ♀; LW ♀.

The purpose of the current investigation is to analyze migratory patterns and orientation abilities in Golden Plovers. For a first approach, ten birds of *P. d. fulva* were obtained from a location as close as possible to the Siberian ancestral home of the Golden Plovers. In the summer of 1960, I collected and hand-raised the ten birds at Boxer Bay on St. Lawrence Island, Bering Sea (Sauer, 1962). From the Bering Sea area, *P. d. fulva* seems to migrate essentially southward, with few deviations to the east or the west. This leads the birds across the Pacific Ocean toward the Hawaiian Islands, the Marquesas Islands, and the Low Archipelago.

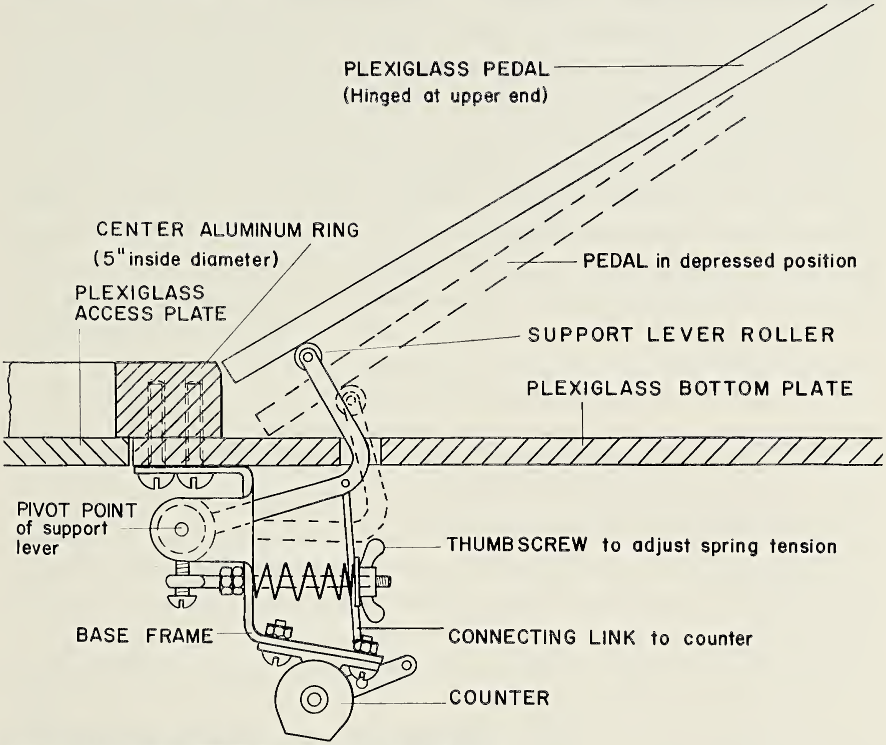
The ten birds, 2 years old at the time of this writing, are still in captivity and in excellent health (Fig. 1). They have shown migration restlessness and molted in natural sequence, and are still being used in experiments. The experimental work has been greatly favored by the tameness of these hand-raised birds. They readily display their motivation-specific instincts with a minimum amount of disturbing activation, even in the presence of a human observer and under the unnatural experimental conditions. One can rely, therefore, on the quality of the migration restlessness of these birds much more than on that of wild-caught adult birds in a similar experiment. The latter often develop internal conflicts and motivations, mainly fear and escape, that interfere with or influence their migratory activity and condemn the experiment to failure.

A second reason for using hand-raised birds is the desirability for a clear experimental situation. These ten individuals never experienced natural migration. They never "learned" a migratory route by flocking with experienced travelers, nor could they have become imprinted on a flyway. Thus, if learning is involved in their migration, the existence of geographical imprinting can be tested by experimental geographical displacements or by an experimental arbitrary setting of their internal clocks, provided that these exist and that they could be shifted. Where the birds hatched at Boxer Bay on St. Lawrence Island, they were exposed to the natural sky, and one could expect their internal clocks to be in phase with the local time. Prior to their first migratory period, the ten birds, ranging from 24 to 46 days of age, were taken on 22 August in a skin boat to Gambell on St. Lawrence Island. From here they were flown on 28 August via Nome, Anchorage, Fairbanks, Seattle, Denver, and Chicago, to Madison, Wisconsin. In February 1961 they were flown to San Francisco. In Gambell, as well as during their travels, the birds were prevented from seeing the sky.

EXPERIMENTAL METHOD

In order to provide an experimental basis for a comparative study, 6 (in San Francisco, 4) of the birds were kept in light-controlled rooms both with and without climatic controls. The day–night and annual rhythms acting upon these birds were kept in phase with the natural conditions that would have influenced them at and between the two localities of Boxer Bay, St. Lawrence Island, and Honolulu, Hawaii. Therefore, daily and annual cycles were induced in phase with those to which birds of this subspecies may be exposed in nature. For a few experiments in Madison, Wisconsin, these birds were exposed for short times to the natural sky (to be discussed in a separate paper). The 4 birds of the second group (in San Francisco 6 individuals) were kept under the local conditions of Madison and later of San Francisco. They could see at least a part of the natural sky during day and night.

During their migratory periods, the migratory restlessness and directional tendencies of the ten birds were recorded in an experimental cage designed for these nonperching waders (Fig. 2). The circular cage, 35 inches in diameter, with an opaque wall of a double layer of heavy black felt, and topped with either a plexiglass plate or chicken wire painted flat black, has a radial arrangement of 16 sloping pedals hinged at their upper, peripheral margin, and pressure-sensitized mechanically. The mechanical counting device, which eliminates electronics and heavy gear, was developed for field work in desolate places as well as in the laboratory. The pressure of each lever supporting a pedal and working on a microcounter can be



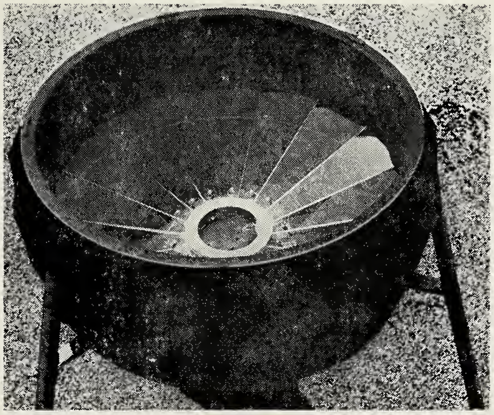


Fig. 2. The experimental cage.

Left: Overall view with plexiglass cover in place.

Above: Cross section of a single unit of the counting device.

adjusted by a spring so that a bird of a given range of weight can walk up, down, or across the pedals without operating the counters. To produce a count, the bird has to apply the impulse of a takeoff or a landing on one pedal. These movements are shown in the diagrams.

The cage is designed to test a single bird at a time. The activities of each bird inside the cage are quickly checked, for a plexiglass base allows observation from below the cage either directly or photographically. During the experiments, a light-proof black felt prevents light from shining into the cage through the bottom plate. Each bird is put into and removed from the cage through the central platform. When activated to migrate, the birds prefer to stand on the sloping pedals facing the opposite side of the cage, and to fly to or across the central platform. Typically, a bird oriented northward would stand on the "south pedal." Its takeoff would register on the "south pedal." Characteristically, then, for every northward "flight" there are three possible outcomes. Two counts would be recorded on the "south pedal" when the bird lands on the same pedal. No landing will be registered when the bird flies to the central platform. Its landing will be recorded on the "north pedal" when it flies across the central platform. Afterwards, a bird that has left its starting point would walk back to this area and prepare a new takeoff. With northward-oriented flight intentions, the number of registrations on the "north pedal" (as a possible landing site) cannot be greater than the number of registrations on the "south pedal" (preferred takeoff site).

In the diagrams, each of the 16 outward-oriented sectors, with N on the top of the diagrams, shows the registration of the microcounter belonging to the pedal opposite this sector. Consequently, the degree-reading in the diagrams shows the true azimuths of the oriented activity of the inward-facing birds, plus a negligibly small percentage of back azimuths. The latter are the result of these occasional flights of highly activated birds across the center platform. They are concentrated on the vectors opposite those of the preferred directions if they are at all present. They mean little for the outcome of an experiment, but their significance is that they reflect an enforcement of the size of the mode and will be considered so in a statistical analysis. Each bird has shown its own individual, small rate of overshooting the central platform with increased activity.

All the birds have given a remarkable display of their migratory activity in this unnatural situation. Each quickly perceives the interior dimensions of the cage, turns or moves calmly, often exhibiting some pendulum movements, and finally faces a particular direction. Then, after showing repeated flight intentions, it takes off and lands again, thereby operating the recording device. Usually the birds repeat this performance again and again, showing a preference for one or more directions depending on varying environmental influences and their internal motivations.

As Golden Plovers normally migrate in flocks, a single bird in the experimental cage may show less activity than might be expected under natural conditions. A tape recorder playing the flight notes of Golden Plovers through a loudspeaker centered below the cage definitely increased the birds' activities. Cage and loudspeaker were rotated and set up at various localities to eliminate possible directional cues. The numbers of the 16 microcounters were read before and after each experiment. During an experiment under the natural sky, wind speed and cloud cover were repeatedly recorded.

The experiments in San Francisco during 1961 had to be confined to the diurnal phase of the plovers' migration, because on the few cloudless nights commercial searchlights scanned the sky constantly, which so disturbed the birds that experimenting with them was futile. The experiments were carried out on the flat roofs of the California Academy of Sciences. The Morrison Planetarium of the Academy was also used for some tests in the course of this study.

RESULTS AND DISCUSSION

During the spring of 1961, 76 experiments involving 124 hr and 50 min of recording were performed, and during the fall of 1961, 83 experiments involving 125 hr and 02 min of recording. The seasonal migratory periods were strictly defined and of limited duration. The peaks of migratory restlessness appeared in the second half of May and in the second half of September. The onset of migration seemed to be much more sharply defined than its end, which showed fluctuations in the intensity of the activity, possibly caused by the birds' inability actually to migrate to their seasonal goals.

Typical examples of the results obtained from the birds in the two experimental groups are shown in the accompanying vector diagrams. For their evaluation, the Great Circle tracks connecting Boxer Bay, Madison, San Francisco, and Honolulu (Fig. 3) were selected as a system of reference. The figures in the single sectors, corresponding with the 16-pedal arrangement of the recording device, indicate the number of times the birds pushed the microcounters during their attempts to take off and land. The black arrows outside the diagrams show the mean direction calculated by vector addition.

The internal clocks of the birds in the first experimental group were, to various degrees, as much as 3 hr, 16 min, and 40 sec slow compared to San Francisco local time. Despite these various degrees of shift, the modes of their undisturbed spring migration orientation approached closely the initial course of the Great Circle route from San Francisco to Boxer Bay, which is 327°13′20″ (Fig. 3*a*). This mean was also maintained under complete overcast that left the position of the sun visible (Fig. 4*a*). Winds exceeding 22 knots from west to northwest frequently blew the birds off their course in the apparatus when it was topped with the chicken wire instead of plexiglass. This resulted in markedly decreased activity, but the

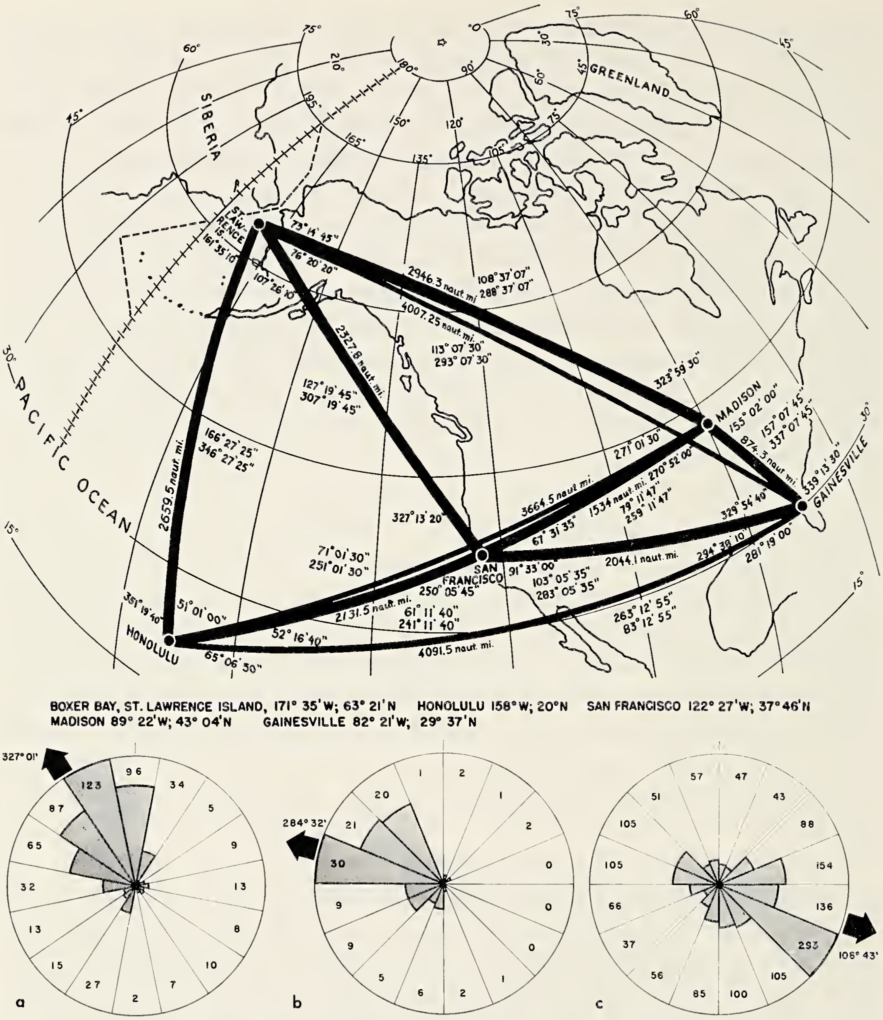


Fig. 3. *Above*: Great Circle tracks from Boxer Bay, St. Lawrence Island. *Below*: Three examples of 1961 spring (*a*, *b*) and fall (*c*) migration at San Francisco.

Explanations: Time in San Francisco Local Meantime (L.M.T.). *C* = recorded counts; *TC* = total counts; *dt-* = difference of the setting of the internal clocks lagging behind L.M.T. Clouds: *ACu* = altocumulus; *Ci* = cirrus; *CiCu* = cirrocumulus; *Cu* = cumulus; *St* = stratus; cloud cover from 1/10 to 10/10; compass bearings mark directions of wind; wind speed is indicated in knots; occ. = occasionally.

(a) LD ♂,	7 June	0815–0945; C:112; clear, 4/10 St Cu; W 5–8, occ. 10–20.
	8 June	1040–1217; C:411; clear, 4/10 Cu, later CiCu; W-NW 10–14, occ. 25.
	9 June	0825–0955; C:23; clear, SW 2–3. TC:546, dt-2h 50m (42°30′).
(b) RB ♂,	13 May	1535–1745; C:56; clear, high Ci; W 10.
	15 May	1440–1650; C:53; clear, W 2–10. TC:109.
(c) LD ♂,	14 Sept.	1324–1453; C:504; clear, 1/10–3/10 St, SW 10–14, 18, W 2–5.
	19 Sept.	1155–1328; C:357; clear, W 1–3, S, occ. SW, 2–4.
	25 Sept.	0920–1050; C:189; clear, W 1–3.
	26 Sept.	0845–1015; C:93; clear, N 2–4.
	29 Sept.	1036–1206; C:190; clear, W 3–6.
	30 Sept.	1348–1524; C:58; clear, W 2–3.
	2 Oct.	1521–1625; C:137; 1/10–5/10 Ci and low St, W-SW 4–6. TC:1528, dt-3h 16m 40s (49°10′).

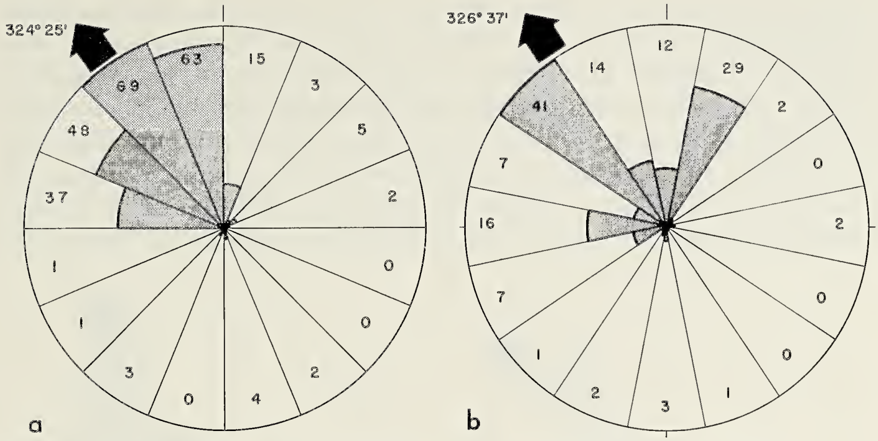


Fig. 4. Spring migration: (a) undisturbed under complete but light overcast; (b) LB ♂, repeatedly blown off course in apparatus when wind exceeded 22 kn, compensates for wind drift.

(a) LB ♂, 17 May 1340–1445; C:253; 10/10 St, position of sun visible, 1440 clearing, SW-W 6–8, occ. 10. dt-2h 20m (35°).
(b) LB ♂, 7 June 1350–1525; C:137; changing St less than 2/10, W-WNW 10–12, occ. 20, W-NW 20–30, occ. 10. dt-2h 50m (42°30′).

birds nevertheless compensated for this drift and maintained a close approximation of the typical mean course (Fig. 4*b*).

Possibly because of the apparatus' limited horizon, small, low clouds drifting in and passing the visual field in an otherwise clear and sunny sky often distracted a bird (Fig. 5*a*). Their distractions on 23 May, which caused them to deviate to 355° at various times during the day (Fig. 5*b* and *c*), are more difficult to explain, unless the birds were frightened by an increasing number of low-flying aircraft that day.

During daytime experiments under an increasingly cloudy sky, which ob-

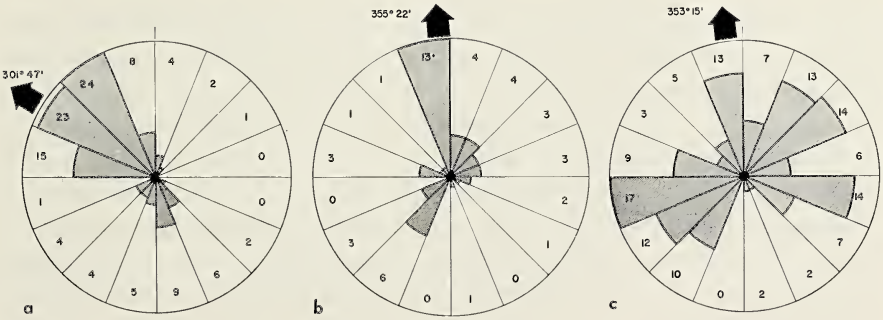


Fig. 5. Disturbed spring migration: (a) by small low clouds swiftly passing the visual field; (b) and (c) possibly by low-flying aircraft.

(a) LB ♂, 17 May 1445–1555; C:108; clear, few drifting St, W 4–5, occ. 10. dt-2h 20m (35°).
(b) LD ♂, 23 May 0920–1058; C:45; clear, NW 6–10. dt-2h 20m.
(c) LB ♂, 23 May 1345–1600; C:134; clear, W-NW 10–22. dt-2h 20m.

scured the sun so that a human observer could at best only roughly estimate its approximate position, these birds of group 1 lost their initial orientation toward their seasonal goal. Their bearings showed an orientation based on an assumed azimuth position of the sun according to the setting of the birds' internal clocks (Fig. 6*a* and *b*). In this situation the birds obviously failed to navigate, i.e. to perform bi-coordinate celestial orientation. The results can be interpreted as an azimuth orientation in which the birds probably neglected the actual altitudinal component of the veiled sun. If the birds refer to the azimuth position of the sun only, a clockwise deviation from their original course is to be expected according to the lag of their internal clock behind local time. These findings explain that the two modes obtained from the birds of the two experimental groups are qualitatively different from each other. They also confirm the view that Golden Plovers migrate by means of visual celestial orientation, that they can estimate time accurately, and that they make use of a bi-coordinate grid figured during daytime by the position of the sun. Exactly what kind of "image" of the sun the birds perceive we do not know, but it may possibly be not in the form of a single "point."

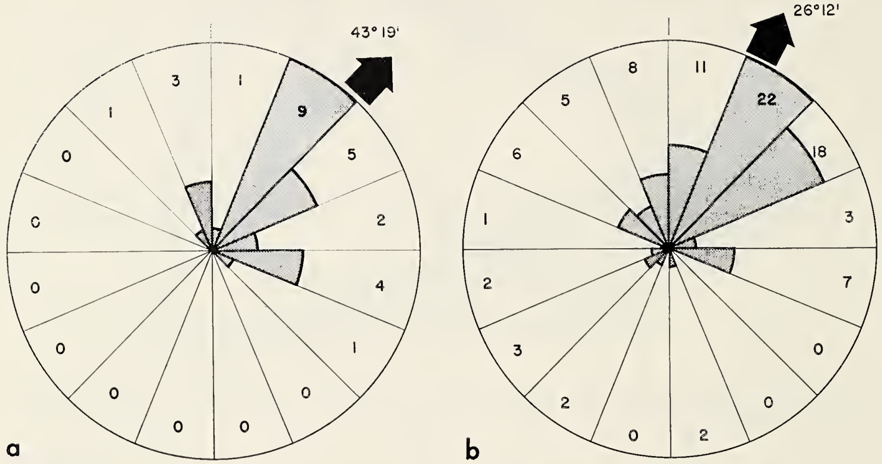


Fig. 6. Spring migration of time-shifted birds under increased overcast. The directional mode deviates clockwise according to the setting of the internal clocks of the birds.
(a) LB ♂, 27 May 1230–1400; C:26; two layers of clouds, ACu and low, moving and brewing Cu, light spot, NW-W-WSW 10–22, W 10–18. dt-2h 20m (35°).
(b) LD ♂, 22 May 1314–1420; C:50; 4/10–6/10 Cu, W-SW-SSW 10–18.
22 May 1420–1520; C:7; 6/10–7/10 Cu, CiCu, SW 10, W 2–4.
26 May 1232–1425; C:33; clear, SW-W-NW 6–8, occ. 12, W-NW 10–20. TC:90, dt-2h 20m.

The birds of the second group, which were exposed to the Madison sky in the fall of 1960, had their internal clocks in phase with San Francisco local time. Their spring orientation at San Francisco approached the Great Circle track leading from Madison to Boxer Bay (Fig. 3*b*).

The birds hand-raised at Boxer Bay must have gone through a sensitive phase during which they became imprinted on that location before their first migratory period. Later, during, and after their first migratory cycle, they must have become imprinted on Madison in a second sensitive phase. That they learned and established a definite pattern of migration between these two positions is suggested by their display of it after their displacement to San Francisco. The fall experiments showed that the birds' imprinting on their experimentally selected winter quarters was also influenced by their time spent in San Francisco. This leaves doubt as to whether this kind of learning is definitely irreversible. I rather think that the birds are at least in part able to make later adjustments.

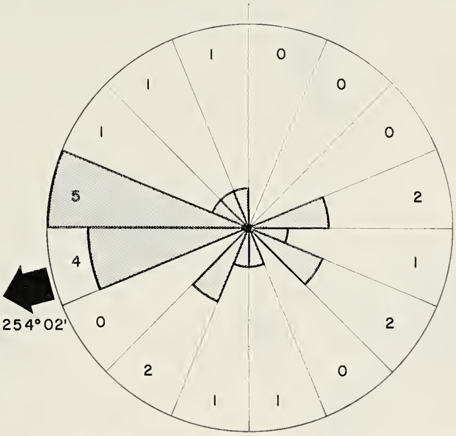


Fig. 7. Spring migration: disorientation and fading of the migratory activity under heavy overcast and absence of sun.

RB ♂, 20 May 1620–1830; C:21, 6/10–10/10, heavy overcast, sun below artificial horizon, SW-W 1–4.

These results indicate that Golden Plovers do not possess an "inborn" knowledge of their birthplace nor a mystic inertial ability to "home" to that place under any conditions. Nor is it reasonable to think that they must have a rigid, hereditarily fixed flight pattern between their breeding and wintering grounds. These patterns are more likely learned by imprinting. It is most probable that under natural conditions a genetically determined, species-specific migratory range is individually modified and conditioned by external environmental influences. As small as the hereditarily determined range for possible modifications may be, it seems to be a factor of enormous adaptive value in these transoceanic migrants.

With increasing heavy cloudiness, the initial orientations of the Golden Plovers from both groups gave way to a broader scatter. Under heavy overcast, as well as in the late afternoon when the sun was below the artificial horizon of the cage, the birds lost their initial seasonal orientation (Fig. 7). They first drifted westward (in fall eastward) and, after a short scattering

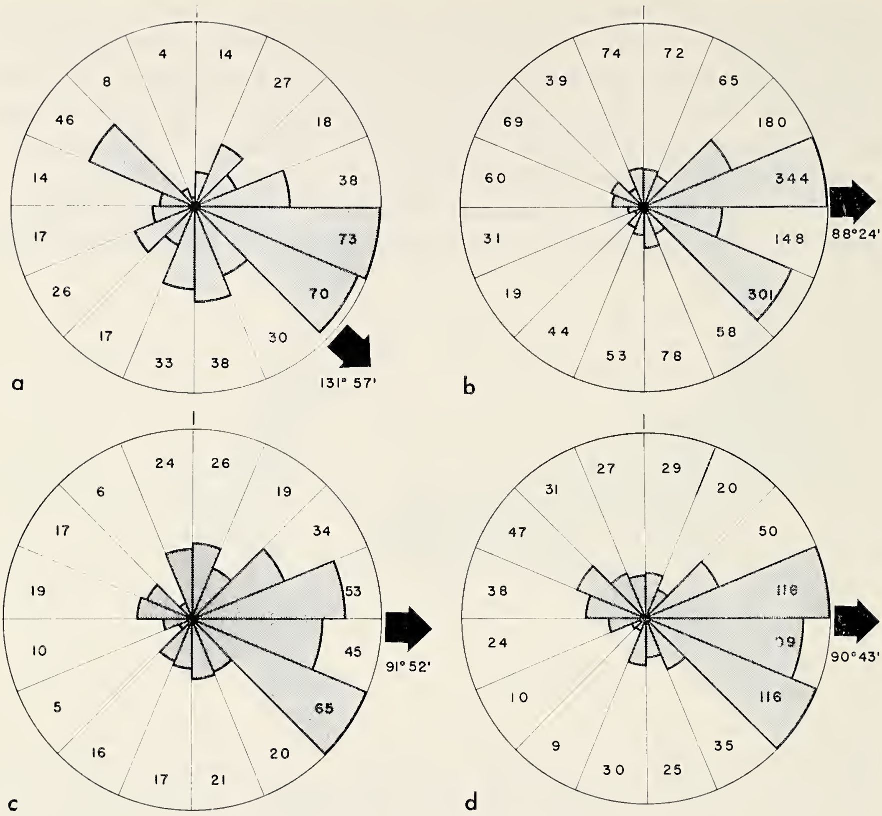


Fig. 8. Fall migration: (a) emphasis on south vectors resulted from repeated noon flights to the shaded area of the cage; (b) directional mode parallels the course Boxer Bay–Madison; (c) and (d) deviations toward east under heavily clouded skies.

(a) RL ♀,	14 Sept.	1153–1320; C:29; clear, 1/10–7/10 fast-moving clouds, SW-W 10–14.
	19 Sept.	1023–1148; C:105; clear, W 1–3.
	25 Sept.	1055–1231; C:85; clear, W 1–3.
	26 Sept.	1152–1316; C:45; clear, N 2–4, W 1–3.
	27 Sept.	1016–1141; C:90; clear, 4/10–10/10 thin St, W 0–2.
	29 Sept.	1207–1339; C:60; clear, W 3–6, W 2–4.
	30 Sept.	1211–1344; C:59; clear, W, occ. SW 0–2, W 2–3. TC: 473, dt-3h 16m 40s (49°10′).
(b) LL ♂,	30 Sept.	0851–1025; C:360; clear, N-NNW 0–4.
	2 Oct.	1035–1205; C:314; clear, 7/10 Ci, W 0–2.
	3 Oct.	1030–1203; C:241; 4/10 ACu, ASt, W 1–4.
	4 Oct.	1453–1619; C:522; clear, fog from W, W 8–12.
	9 Oct.	1006–1136; C:198; clear, NW 1–3, W 2–4. TC:1,635.
(c) LD ♂,	15 Sept.	1420–1550; C:338; changing 5/10–10/10, heavy overcast, light spot, SW-NW 4–6, SW 10–16.
	28 Sept.	1030–1200; C:59; 10/10 heavy overcast, SW-S 2–5, SW-W-NW 10–16. TC:397, dt-3h 16m 40s (49°10′).
(d) LL ♂,	27 Sept.	1529–1650; C:462; scattered ACu, 10/10 heavy, W 6–8.
	28 Sept.	0855–1025; C:244; 10/10 heavy, ACu, ASt, St, SW 2–5. TC:706.

with no directional preference, they consistently terminated their migratory activity. I do not want to add a new mystery to those that have been introduced lately into the analysis of bird orientation, but these drifts when the sun disappeared, to the west in spring and toward the east in autumn, were consistent, and the spring drift of the Golden Plovers under a sunless sky, especially in the late afternoon, resulted in a vector closely approaching the Great Circle route to Honolulu from San Francisco where the experiments were performed. This was the only time the birds ever displayed a clear orientation toward their "natural" wintering grounds; it lasted only a short time and is not statistically significant.

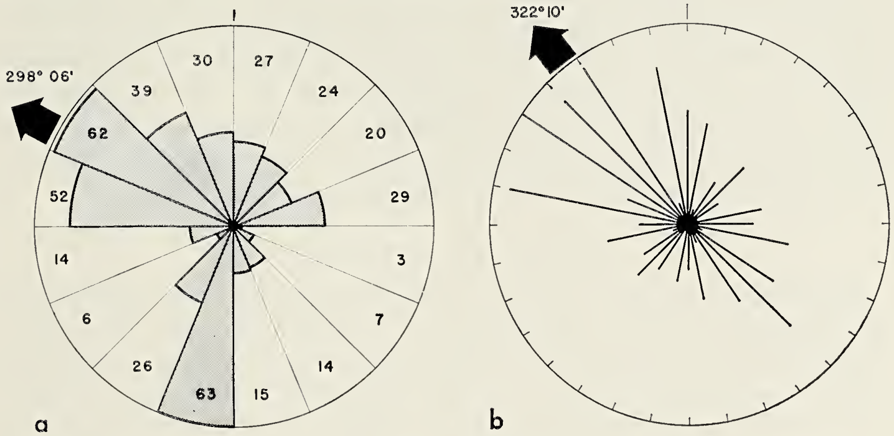


Fig. 9. Nocturnal migration during spring: (a) distraction by searchlight from southerly direction; (b) planetarium experiments, $P =$ setting of the planetarium sky.

(a) LL ♂, 11 May 1920–2340, C:307, clear, 2020 small cloud passing, NW 14, occ. 19–20.
12 May 1920–2330, C:124, clear, NW 0–15. TC:431.

(b) LB ♂, 20 May 2115–2222, P:2000, 20°N; dt-2h 20m, C:634.
21 May 2340–0030, P:2150, 20°N; dt-2h 20m, C:526.
28 May 2120–2220, P:1930, 20°N; dt-2h 20m, C:372. TC:1,532.

The means of the autumnal orientation of the birds in San Francisco were back azimuths of the spring modes. If these are projected from Boxer Bay, the autumnal courses of the birds of group 1 aimed toward San Francisco (Fig. 3*c*); deviations toward the south occurred on warm days during the noon hours, when the birds repeatedly flew into the shaded area in the south section of the cage (Fig. 8*a*). The directional means of the locally adjusted birds of group 2, when projected from Boxer Bay, led to Madison, Wisconsin (Fig. 8*b*). Heavy overcast masked the results obtained from the birds of both groups; both responded with eastward flights (Fig. 8*c* and *d*), thereby reversing the mode they displayed during spring in the same situation (see above).

The few results obtained under a clear night sky and under the planetarium sky correspond essentially with those of the daytime experiments. Although the plovers proved able to compensate for the distraction caused by a single searchlight (Fig. 9*a*), several in operation, as usually happened on clear nights, confused them utterly. More experiments need to be done in a planetarium, although the few tests, made by personal observation with a circular cage containing a flat plexiglass bottom (Fig. 9*b*) and with the automatic-recording system, confirmed the findings under the natural sky.

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SUMMARY AND CONCLUSIONS

Experiments involving 250 hours' recording of the migratory restlessness of ten hand-raised Pacific Golden Plovers (*Pluvialis dominica fulva*) were carried out at San Francisco in a circular cage with an automatic recording device. It was concluded that: (1) The birds migrate both day and night by means of visual celestial orientation obtained from the visible sun and the stars. (2) Their internal clocks enable them to compensate for the relative movements of the celestial bodies, and to compensate for geographical displacements, provided the birds can detect a difference in time between the setting of their internal clocks and the local time. (3) If the celestial bodies are clearly visible or their position can be accurately located under an overcast, the birds navigate, i.e. refer to a bi-coordinate celestial grid. (4) When the sun is veiled to a certain degree, they do not navigate, but display an azimuth orientation, probably neglecting the altitudinal component of the sun. (5) When the celestial bodies are invisible, as during the experiments in San Francisco, the birds deviate from their seasonal directional mean and drift westward in spring, eastward in fall. This new mode lasts only for a short time and is followed by a short phase of disorientation and the end of migratory activity. (6) The ten Golden Plovers have gone through at least two sensitive phases during which they became geographically imprinted on their breeding and wintering areas. They show an ability to modify their genetically determined pattern of migration by learning, thereby reaching a level of efficiency beyond that of pure instinct. I regard this as of great adaptive value, and as probably the evolutionary key to their mastery of the flight across some 2,000 miles of trackless Pacific Ocean.

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Vom Zug der Buchfinken (♂ ♂ und ♀ ♀) *Fringilla coelebs* in der Schweiz

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Im untern Wallis, am obern Beginn des Val d'Illiez besitzt die Schweizerische Vogelwarte seit 1958 eine alpine Fang- und Beringungsstation. Sie befindet sich auf dem Col de Bretolet auf 1930 m Höhe. Ihr Unterhalt wird aus Mitteln des Schweizerischen Nationalfonds zur Förderung wissenschaftlicher Forschung finanziert. Auf dieser Vogelzugsstation konnten bis zum Herbst 1961 rund 25 000 Buchfinken gefangen und beringt werden. Nach Gefiedermerkmalen wurde nicht nur das Geschlecht, sondern auch das Alter bestimmt. Die täglichen Fangzahlen an ♂ ♂ und ♀ ♀, an adulten und juvenilen Buchfinken dürfen als repräsentativ für die Gesamtzahl der über den Pass ziehenden Buchfinken betrachtet werden. Ein möglicherweise unterschiedliches Verhalten zwischen ♂ ♂ und ♀ ♀ und zwischen Jung- und Altvögeln musste sich in den Zahlenwerten der täglichen Fangergebnisse widerspiegeln. Von diesen so zahlreich auf dem Durchzug beringten Buchfinken erhielten wir genügend Fundmeldungen, um über das Winterquartier und—wenn auch nicht mit derselben Genauigkeit—auch über Herkunft und Brutgebiet der fremden Buchfinken orientiert zu sein.

Im Winter 1961–62 untersuchten wir zusammen mit Mitarbeitern der Vogelwarte das Zahlenverhältnis der Geschlechter der in der Schweiz verbliebenen Buchfinken. Über 7 800 Buchfinken wurden im Gebiete des Jura, des schweizerischen Mittellandes und der Alpen gesondert nach ♂ ♂ und ♀ ♀ gezählt. In verdankenswerter Weise erhielten wir zudem aus Polen, der Tschechoslovakei und Deutschland Angaben über das Geschlechtsverhältnis der dort überwinternden Buchfinkenbestände. Auf einer Reise Ende Januar 1962 nach Südfrankreich konnten wir die Verhältnisse in diesem Gebiete des eigentlichen Buchfinken-Winterquartiers aus eigener Anschauung kennen lernen. Zusammen mit den Fang- und Ringfundergebnissen vom Col de Bretolet und der übrigen Schweiz bildet dieses Beobachtungsmaterial die Grundlage für unsere Untersuchung.

Ähnlich wie im übrigen Mittel- und Nordosteuropa ist der Buchfink auch in der Schweiz Teilzieher, d.h. einige der Brutvögel ziehen im Herbst nicht weg. Der im Winter in der Schweiz verbleibende Anteil ist aber recht gering. Er dürfte 5 Prozent nicht übersteigen; möglicherweise liegt er bedeutend tiefer und, je weiter nach Nordosten, desto kleiner wird dieser Anteil. So wissen wir, dass in den zur Brutzeit verhältnismässig dicht von Buchfinken besiedelten schweizerischen Bergwäldern diese Vögel im Winter oberhalb 1 400 m ganz fehlen. Nur in den Dörfern werden einige wenige angetroffen. Im Unterschied dazu finden wir Buchfinken in kleineren Schwärmchen im

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Mittelland und in niederen Lagen des Jura, auf Äckern und Feldern mit etwas Unkrautbewuchs. Doch sind auch hier die Winterbestände im Vergleich zur Brutzeit sehr klein. In der Schweiz überwintert auch eine bescheidene Anzahl fremder, aus dem NE zugewanderter Buchfinken, was mit 2 Ringfunden belegt ist.

Die zur Brutzeit (16. April—15. September) nestjung, juvenil oder adult beringten Buchfinken überwintern in Südfrankreich und weiter südwestwärts bis nach dem südlichen Spanien. Sie halten sich im Winter im ähnlichen Raume auf wie die zahlreich durch die Schweiz wandernden, fremden Buchfinken (siehe Abb. 1), scheinen aber etwas weniger weit zu ziehen als die fremden Durchzügler. Doch sind die Funde zu wenig zahlreich um hierüber sicher Bescheid zu wissen (siehe Abb. 2).

Abb. 1. Funde aus dem Winterquartier und dem Weg dorthin von Buchfinken, die zur Brutzeit (16. April bis 15. September) in der Schweiz beringt wurden.

Fig. 1. Winter recoveries of Chaffinches ringed as breeding birds in Switzerland.

Die Brutgebiete der durch die Schweiz ziehenden Buchfinken reichen über Deutschland, die Tschechoslovakei und Polen bis weit nach Russland hinein (östlich Moskau).

Die meisten Winterfunde stammen aus Südfrankreich, wo die Rhone-Ebene eine ausserordentlich starke Anziehungskraft auf die Buchfinken ausübt. Sie halten sich dort zu einem grossen Teil in den sanft ansteigenden Rebbergen, in den Zwergobstkulturen und den Reisfeldern auf, wo sie sich von Unkrautsämereien und verlorenen Reiskörnern ernähren. Ein grosser Teil aber zieht weiter südwestlich über die Pyrenäen und überwintert in Spanien, hinunter bis an die Südspitze der iberischen Halbinsel; wohl als Ausnahme dürften die beiden Funde, je einer von den Balearen und aus Algier, betrachtet werden. Es ist aber interessant zu wissen, dass gelegentlich Buchfinken auch das Mittelmeer überfliegen. Beim Fund von den Balearen handelte es sich um ein adultes ♀, beim Fund aus Algier um ein adultes ♂.

Deelder (1949) weist daraufhin, dass die skandinavische Buchfinken-Population, die teilweise durch Holland wandert, Unterschiede im Zugverhalten zwischen ♂♂ und ♀♀ zeigt. Währenddem viele ♀♀ bis nach Irland gelangen, verbleiben viele ♂♂ in Holland oder England zurück. Deelder schliesst deshalb auf einen bei den ♀♀ stärker ausgebildeten Zugimpuls, der sich unter anderem darin äussert, dass die ♂♂ grössere Hemmungen haben, das Meer zu überfliegen als die ♀♀.

Abb. 2. Funde von Buchfinken, die im Herbst auf dem Col de Bretolet während des Durchzuges beringt wurden. Die Funde aus dem NE fallen ins Brutgebiet der durch die Schweiz ziehenden Buchfinken (auf dem Col de Bretolet und in der übrigen Schweiz beringt) und die Funde aus dem SW markieren Winterquartier und Weg zu ihm. Sie stammen alle aus der Winterszeit, die unmittelbar der Beringung folgt.

Fig. 2. Winter recoveries of Chaffinches ringed as migrating birds on the Col de Bretolet in autumn. The recoveries in the northeast include Chaffinches that had been ringed in other parts of Switzerland.

Die in der Schweiz auf dem Col de Bretolet durchziehenden Buchfinken zeigen diesen Unterschied nicht. So deckt sich die Zugrichtung für alle 4

Gruppen vollkommen. Die Mittelwerte der Entfernung vom Beringungsort liegen für 3 Gruppen (♂♂ juv. und ad. und ♀♀ juv.) nahe beisammen. Nur die adulten ♀♀ zeigen eine schwache Tendenz etwas weiter zu ziehen. Doch ist dieser Unterschied statistisch nicht gesichert. Der mittlere Entfernungsunterschied zwischen den beiden Extremwerten (♀ ad. und ♀ juv.) misst etwa 180 km. Die mittlere Zugstrecke vom Brutort bis zum Winterquartier (berechnet aus den Funden vom Brutgebiet ca. 1 000 km bis auf den Col de Bretolet und etwas mehr als 500 km weiter bis zum Winterstandort) darf mit etwa 1 500 km angenommen werden. Der beim ♀ ohnehin statistisch nicht gesicherte Entfernungsunterschied von 180 km dürfte im Hinblick auf die Gesamtzugstrecke mehr oder weniger bedeutungslos sein. In jedem Fall dürfen wir nicht ganz allgemein von einem stärkeren Zugimpuls beim ♀ sprechen.

Abb. 3. Richtung und Entfernung der Funde vom Beringungsort (Bretolet). Mittelwerte wie sie aus Abb. 2 hervorgehen, aufgegliedert nach den 4 Gruppen: ♂♂ ad., ♂♂ juv., ♀♀ ad., und ♀♀ juv.

Fig. 3. Average values of directions and distances of Chaffinches on the Col de Bretolet ringed and recovered in the same migration season.

Unterschiede zeigen sich zwischen diesen 4 Gruppen im zeitlichen Ablauf des Durchzuges. Um die Frage abzuklären haben wir die Zahlen der täglich auf dem Col de Bretolet 1959 und 1961 gefangenen Buchfinken nach Alter und Geschlecht gesondert und in Zeiteinheiten von je 7 Tagen (= 1 Woche), angefangen vom Beginn der Zugzeit, zusammengefasst. Auf diese Weise war es möglich, äussere, den Fang und Durchzug beeinflussende Faktoren auszugleichen. Von den so erhaltenen Wochenwerten errechneten wir die Prozentzahlen der von der Gesamtzahl einer jeden Gruppe durchzogenen Buchfinken und transformierten sie in Probits (Schwarzenbach, 1960; Documentia Geigy, 1955). So erhalten wir für jede Buchfinkengruppe eine Gerade, die sich vergleichen lässt. Da wir die Fangaktion auf dem Col de Bretolet jeweils 1–2 Wochen vor dem eigentlichen Zugende abbrechen mussten, liegen die Probitwerte für die letzte 7. Woche etwas rechts ausserhalb der Geraden, was aber bedeutungslos sein dürfte.

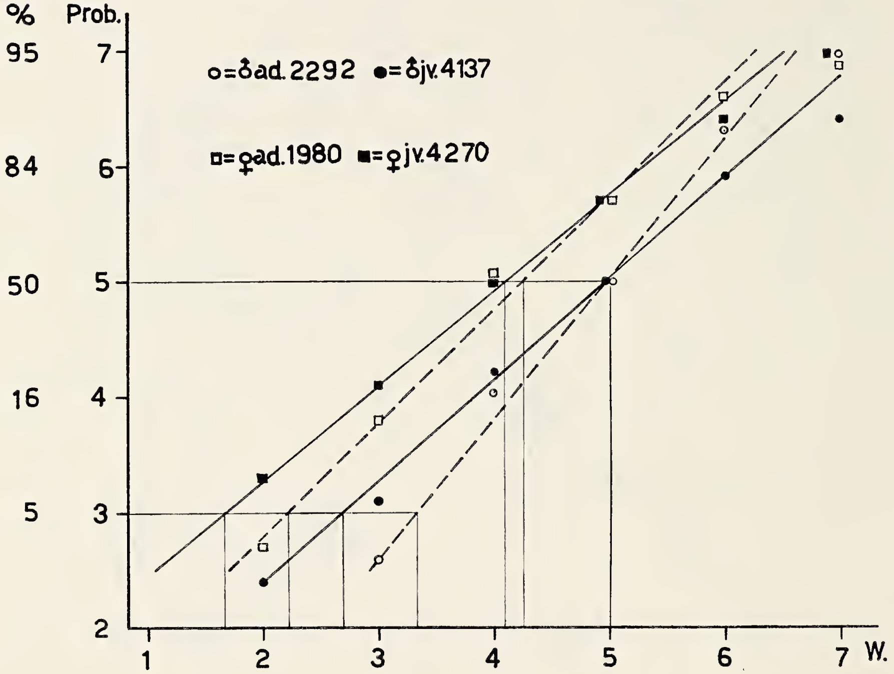

Abb. 4. Verlauf des Buchfinkenzuges auf dem Col de Bretolet als zeitliche Funktion, aufgegliedert nach Alter und Geschlecht. Probittransformation. Die Geraden wurden nach Augenmass durch die Punktschar gelegt. *W* = Anzahl Wochen nach Zugbeginn.

Fig. 4. Chaffinch migration as a function of time for males and females, adults and juveniles. Probit transformation of percentage figures. *W* = number of weeks after start of migration.

Der Durchzug der Buchfinken auf dem Col de Bretolet beginnt um Mitte September. Zuerst erscheinen die jungen ♀♀, von denen am Ende der ersten Zugwoche bereits 5% durchgezogen sind. Es folgen 4 Tage später die alten ♀♀, 7 Tage später die jungen ♂♂ und schliesslich 11–12 Tage später die alten ♂♂. Die Hälfte aller ♀♀ ist zu Beginn der 4. Woche, und 5 Tage später ist die Hälfte aller ♂♂ durchgezogen. Währenddem die jungen ♀♀ mindestens 5½ Wochen benötigen bis 95 Prozent von ihnen durchgezogen sind, ist diese Zeit für die alten ♂ ♂ auf 3⅔ Wochen zusammengedrängt. Die beiden andern Gruppen liegen zwischen diesen beiden Extremwerten.

Unsere Erhebungen über die zahlenmässige Zusammensetzung der Geschlechter des Buchfinken zur Winterszeit nordöstlich von Südfrankreich zeigen ein recht einheitliches Bild. Die ♂ ♂ sind überall im Verhältnis von etwa 3 : 1 in der Überzahl. Und zwar gilt dies von Grenoble in Frankreich bis nach Polen. Erst südlich von Lyon, im untern Rhonetal, beginnt das Geschlechtsverhältnis sich dem Verhältnis 1 : 1 zu nähern. Im Rhone-Delta fanden wir die ♀ ♀ sogar leicht in der Überzahl.

Abb. 5. Die Zahlen bedeuten den ♂-Anteil des durch Probezählungen festgestellten Buchfinkenbestandes zur Winterszeit. Diese Probezählungen umfassen für die Schweiz 7 880 Buchfinken, für Frankreich 2 500 und je 100–500 für die einzelnen Zahlen im NE der Schweiz und für Polen 14 Buchfinken.

Fig. 5. The percentage of males in wintering Chaffinch populations.

Es stehen sich also zwei Feststellungen gegenüber, die sich auf den ersten Blick zu widersprechen scheinen; denn wir fanden auf dem Col de Bretolet kein Überwiegen der ♀ ♀, trotzdem von Grenoble bis nach Polen hinein die ♂ ♂ stark in der Mehrzahl zurückbleiben und überwintern. Unsere Zählungen im Winter haben uns und viele Feldornithologen im Ausland überzeugt, dass vom gesamten Bestand der brütenden Buchfinken nur ein verschwindend kleiner Teil überwintert, der das Geschlechtsverhältnis der Durchzügler nur unbedeutend oder gar nicht zu beeinflussen vermag.

Der in Holland (Deelder, 1949) für die skandinavische Buchfinken-Population festgestellte zahlenmässige Unterschied zwischen den beiden Geschlechtern dürfte deshalb wohl in bezug auf Entfernung und Richtung für die südöstlich davon gelegene Buchfinken-Population nicht generell bestehen, oder er wird doch nur von einer ganz verschwindend kleinen Zahl von ♂♂ gezeigt, die in etwas grösserer Zahl als die ♀♀ im Brutgebiet überwintern. Dagegen bestehen auch für die von uns untersuchten Buchfinken Unterschiede im zeitlichen Verlauf des Durchzuges, indem die Jungvögel über eine längere Zeit ziehen als die Altvögel, sie beginnen den Zug einige Tage vor den Alten und beenden ihn auch später. Auch ziehen die ♀♀ früher als die ♂♂ und befinden sich noch auf dem Zug, wenn die ♂♂ bereits durchgezogen sind.

SUMMARY

Sex and Age of Chaffinch Migrants in Switzerland

The main winter quarters for Swiss Chaffinches and those migrating through Switzerland extend from the lower Rhone Valley south of Lyon to the southern parts of Spain and Portugal (Fig. 1 and 2). The breeding areas for foreign Chaffinches migrating through Switzerland extend in the northeast as far as Poland and northwestern Russia (Fig. 2).

There are no significant sex and age differences involved in the length and direction of Chaffinch migration in Switzerland, in marked contrast to the Scandinavian population (Deelder, 1949).

The migration of juvenile Chaffinches is spread over a longer period than that of the adults. Both juvenile and adult ♀♀ start their migration a little earlier in the season than the ♂♂; after the start of the migration season, we find first the juvenile ♀♀, followed at intervals of 3–4 days by adult ♀♀, juvenile ♂♂, and adult ♂♂ (Fig. 4). These differences are statistically significant. The figures are obtained from 12,750 Chaffinches caught on the Col de Bretolet during the autumn migration of 1959 and 1961. These birds showed a sex ratio of nearly 1 : 1, which appears to disagree with the fact that the sex ratio of Chaffinches wintering in their breeding areas in Switzerland and northeastward is 75 percent ♂♂ and only 25 percent ♀♀. However, this discrepancy is not significant, as the number of nonmigrants is relatively small (less than 5 percent). It is impossible to generalize, therefore, or to postulate a stronger migratory impulse for the ♀♀ Chaffinches of our region, as has been suggested for the Scandinavian population.

More detailed investigations are needed before we can be certain that the different results obtained from analysis of the migration behavior of Scandinavian and Swiss Chaffinch populations are real or apparent.

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On the Northwestern Migration Divide of the White Stork

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It has been known for more than 50 years that the storks of western and central Europe by-pass the Mediterranean: They fly around either flank. There are, therefore, two populations, the habitats of which probably border upon each other at a "migration divide." Bird ringing has provided the necessary data to prove the existence of such a migration divide, and has enabled us to trace its course. At the beginning, our knowledge was quite incomplete, and it was not until 1953 that a somewhat detailed first description could be given (Schüz, 1953). During the 9 years that have elapsed since that time storks have also been systematically ringed in areas that had heretofore escaped investigation, so that we are now in a position to make quite an accurate statement as to the course of the migration divide. If, though, this course is still doubtful in some areas, it is because the distribution of storks is—today more than in former times—interrupted by wide gaps, or their numbers are so small that recoveries cannot be expected in some areas.

A migration divide must not be imagined as a sharp dividing line that strictly separates localities with different autumn-migration directions. There is, rather, a mixed zone, in which different autumn-migration directions are found, i.e. the "mixed migration-divide area." Where within this area autumn migration in southwesterly and southeasterly directions counterbalance each other, a "migration-divide ridge" can be recognized. As we move from this ridge to the west, incidences of migration into a southeast to south sector diminish more or less quickly, and the same is true in respect to incidences of southwest migration in the area east of the ridge.

The course taken by the migration-divide ridge can be seen in Fig. 1. It begins at the northern edge of the Alps and crosses Bavaria from south to north, west of the 11th degree of longitude, first along the river Lech, then north of the Danube, following the rivers Rednitz and Regnitz. There we enter a zone where the number of storks diminishes greatly, merging into a gap in distribution. Beyond the gaps, we can again scan the migration behavior of the stork in the western part of the Halle district. We think we can recognize the ridge somewhere in the Kyffhäuser Mountains (approximately 51°25′ N 11°05′ E). From here it turns sharply west-northwest or northwest along the southwestern edge of the Harz Mountains and the Weser Hills. From here the ridge continues in a westerly direction to the area north of Osnabrück, about through 52°20′ N 8° E, ending in the Netherlands, approximately at Kampen, 52°30′ N.

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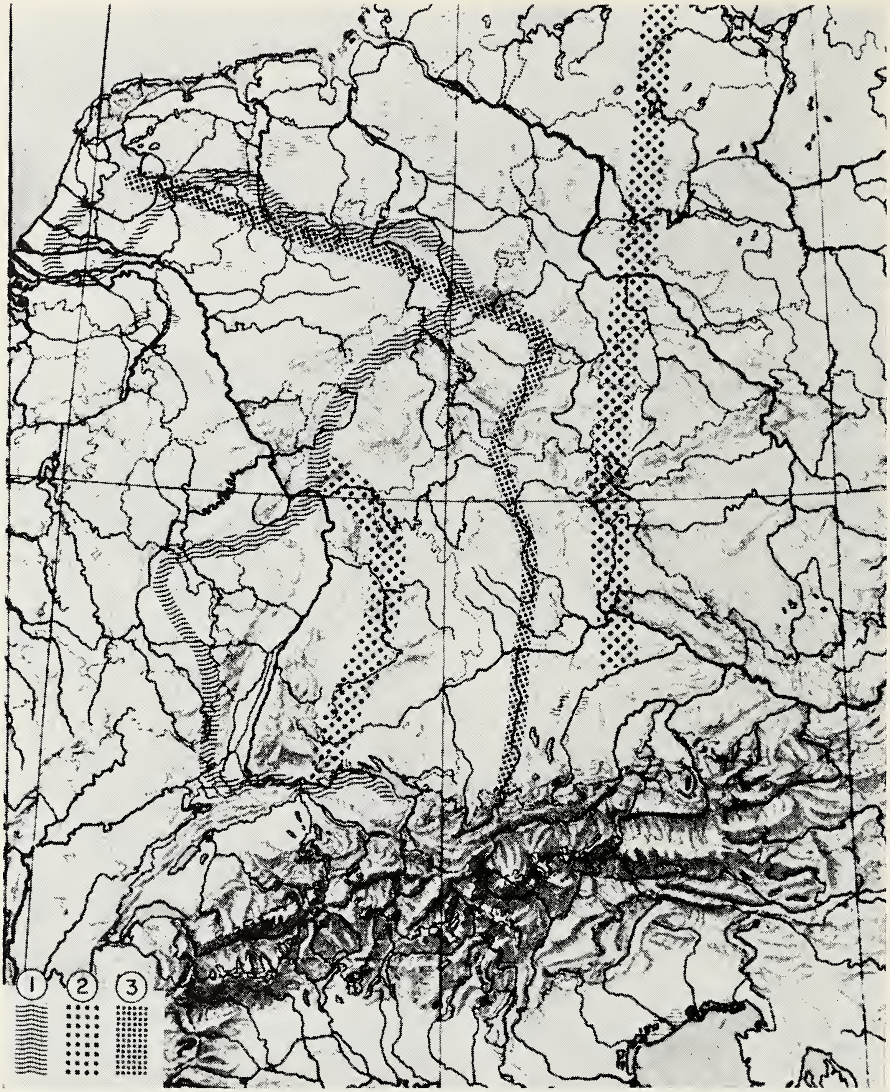

Fig. 1. The northwestern migration divide of the White Stork.

1. Western nesting boundary of the species in central Europe, 1961.
2. Approximate western and eastern boundary of the "mixed migration-divide area."
3. Approximate "migration-divide ridge."

The question arises as to how far in width the migration-divide area that adjoins the ridge extends. To the west, the position is as follows: The storks inhabiting either side of the Black Forest clearly belong to the southwest migration area; the same holds true for the storks in Hesse. Then follows a large gap in distribution. Beyond it, the southern border of the mixed migration-divide area coincides with the southern edge of the distribution area in the southern Netherlands. In the eastern parts of the mixed area, incidences of southwest migration in autumn occur as far as eastern Bavaria, the western parts of the March of Brandenburg, and Mecklenburg. It is, however, almost impossible to draw a proper border line in this region and, even beyond the outlined border of the mixed area, recoveries of ringed storks have been made that would indicate, as rare exceptions, migration on the west route, for example from the isle of Rugen to western Switzerland. It is chiefly among older storks that such deviations occur. A number of facts seem to indicate that sometimes storks of western and eastern origin meet in their winter quarters and that a few individuals can be "displaced," meaning that they join storks of the "wrong" population. This may be true in the case of a stork from Alsace, found in Northern Rhodesia on 14 March at the end of its first year of life.

Another characteristic of the mixed migration-divide area is that quite a few storks from this area cross the Alps, so that their autumnal route takes them, for instance, to Italy, where, unfortunately, most of them are killed. These intermediate recoveries have given rise to the question of whether one is entitled at all to speak of a pronounced migration divide, or whether it is simply a question of an extensive dispersion. However, this interpretation has not found much approval, in view of the fact that the number of these intermediate recoveries is relatively small.

The significant problem concerns the factors that bring about the divergence of migration directions. It should be remembered that young storks, when fledged, stay for another 4 or 5 weeks at their native place and will return to their parental nests in order to rest. A few will, however, leave their native place prior to setting out on their migration route. As a rule, young storks depart before their parents. So it would appear that the adult storks lose touch with the young ones before their departure. It is, however, possible that some adult storks mingle with the flights of young storks, so that these old birds might be able—on the strength of experience previously gained—to determine the route or at least the direction. This significance of social migration can be considered to be proved by the well-known migration experiments carried out by the Bird Research Institute at Rossitten. The result of these experiments was, in brief, that nestlings that had been hatched in East Prussia, i.e. far east of the migration divide, and were taken to the Rhineland, west of the migration-divide ridge, selected the southwest route, when released at the normal time and thus had a chance to join their fellow storks of the new homeland. However, if they were retained and migration delayed, so that they had no opportunity to join western storks, they then set out predominantly in southeast to south-southeast directions (Schüz, 1951).

It also seems very probable that environmental factors influence the direction in each individual case. Among edaphic factors, for example, it is obvious that, alternatives given, a biotope is preferred that offers advantages in respect to rest and food. Therefore, an open river valley with meadows will be more attractive than a mountainous or wooded area. In fact, many a clue seems to indicate that the Lowlands of the Upper Rhine, situated between two wooded mountains, i.e. the Black Forest and the Vosges, exercise such an influence on migrating storks, e.g. those from Hesse. Storks that are virtually destined for southwest migration follow the whole southern part of this valley almost as far as the region around Basle, and will only then turn to the "scheduled" westerly component and migrate through the Burgundian Gate.

Abiotic factors, varying with locality and time, may also be significant. The stork is, as is well known, highly dependent on efficient up-currents (mostly thermal currents); this character undoubtedly accounts for the fact that, as a result of natural selection, storks by-pass the Mediterranean. Furthermore, the stork is sensitive to rainy weather, partly because of the absence of upwinds under such conditions, partly because of the weighting of the plumage by moisture. While the departure is, therefore, highly dependent on fine weather, upwind conditions and the possibility of drift may also be important factors to the individual stork for selecting its route. The high significance of drift is a proven fact.

Thus, no doubt social and ecological factors concur to determine or co-determine the direction in each individual case. The question is, however, to what extent they are actually decisive for the selection of direction. In this respect, experimenting with storks is very difficult. However, Gustav Kramer (cf. summary, 1961) and others have shown for the Starling (*Sturnus vulgaris*) and other migrants, as well as for the nonmigrant Rock-pigeon (*Columba livia*), that specific directions are determined with the assistance of the sun's azimuth and an "internal clock." It has not yet been decisively proved, but it can hardly be doubted that this ability applies to migrant birds in general, and there is nothing to indicate that the stork is an exception.

Essentially, two questions arise. First, with what accuracy do storks adhere to the angle of migration? It would be hard to prove sufficiently that only a general tendency to migrate to the south exists. The Rossitten stork experiments go far to prove that a relatively accurate angle can be kept. Secondly, where does the knowledge of this angle originate? Is it a secondary process, a process of an engraving of the route on the memory, as might happen during the first migration, for instance, under the guidance of an experienced fellow migrant? Or is the knowledge of the migration angle genetically fixed? In my opinion, the result of the stork experiments carried out at Rossitten seems to support this view, although it must be admitted that these storks were transplanted as nestlings and not in the egg stage. One might, therefore, object that the little nestlings had an opportunity to engrave on their minds impressions at their native place, and that the autumn migration to the southeast of these East Prussian storks from the area of the western population might be explained as a kind of correction of the transplantation to the west, on the basis of an engraving of coordinates that had taken place in the nest. If one thinks this over, the assumption of an innate angle of autumn migration, which differs in the two populations, seems no less likely.

The particular complication in the case of the stork is that, as is well known, storks change their angle of migration at least once, perhaps even more often. This applies particularly to the storks that fly over the southeasterly course. This, as is now well known, involves deviation of the course from southeast to south at the Gulf of Iskenderun, a fact which, as far as I can see, escapes explanation simply by cogent ecological reasons.

In this respect, the stork is, in an astonishing and particular way, fitted into a large-scale topographical structure in a vast sector of the earth, an adaptation that is both expedient and serves the survival of the species. This is obviously the result of the coming into being of distinct populations with pronounced specialized behavior by means of natural selection.

The European populations vary specifically not only with respect to selection of migratory direction but also with respect to factors of population dynamics, such as breeding maturity and number of young storks. We are at present trying to find out to what extent the migration divide also constitutes a boundary line between groups differing in population-dynamic factors. Some clues seem to indicate that this is so, but further data are required. If it should turn out that the migration-divide ridge is also a boundary line between populations that differ with respect to factors conditioned by ecological facts, then it could be considered as certain that the stork as a species arrived in Europe from the southwest as well as from the southeast and that the migration-divide ridge is the line where the two immigration groups meet.

It can be assumed that in addition to this migration divide in central and northwest Europe there are others in northwest Africa, the European part of Russia, and in western Asia. As very little is known about these divides, it would be desirable and worthwhile to investigate this problem. I cannot deal, either, with migration divides with respect to other birds, such as are known to exist in the United States and Canada, where some species migrate toward the Atlantic as well as toward the Pacific, indicating that some kind of migration divide can be expected to have developed in the central parts of the habitat. Our American colleagues are more qualified than I am to enlarge on this subject.

In any case, the problem of migration divides brings up essential problems, not the least of which involve physiological populations or races. Thus, we are dealing with a particular subject in "The New Systematics."

SUMMARY

European *Ciconia ciconia* leaving in fall migrate for the most part either to the southeast or the southwest. The ringing data disclose a migration divide from the Alps (Bavaria) to Kampen (Netherlands). There is a "migration-divide ridge" and a "mixed migration-divide area." The migratory direction can be determined by guidance and learning from experienced birds, by other external factors, and probably also by an innate ability in each population to select a certain direction given by the sun and an "internal clock."

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Orientation Experiments with Northern Waterthrushes Wintering in Venezuela

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This paper reports the results of a series of homing experiments carried out with color-banded Northern Waterthrushes (*Seiurus noveboracensis*) that were wintering in the Botanical Garden of the Universidad Central de Venezuela in Caracas. The experiments are part of a project initiated in April 1956, during which more than 300 Northern Waterthrushes have been banded.

Early in the program it was established that, as winter residents, individuals of this species maintain definite territories in which they spend most of their time and which they defend vigorously against intraspecific intrusion. Further, those birds that returned in subsequent years occupied the same territory of their previous residence.

The birds were captured with mist nets. Each individual was netted with the specific intention of catching that individual. Their ground-foraging habits and strong territoriality made that not only possible but necessary, even with transients for they, too, established territories for the period of their stay.

In the homing experiments, the birds were transported from the trapping point (their territory) to the release points in individual paper bags with no means of observing their surroundings during the trip.

The first experiment was made 16 January 1960. One resident from the previous season and two first-year residents were released at a small ravine about 10-km airline distance east of the Botanical Garden. The old resident returned to its territory in 8 or 9 days. Two weeks after release neither of the other two had returned. This was suggestive; one old resident returned, two new residents so far failed to return.

I repeated the experiment, this time with three new residents, release being made 31 January at the same place. When by 14 February none of the five new residents had returned, I made a careful check of the area of release and found that one bird from the first release had taken up a territory about 100 m upstream from the point of release and one from the second release had established itself about 200 m downstream. Both were still present in their new territories when last visited on 20 March. The others could not be found.

The next season (1960–61) I released six more first-year residents at the same 10-km distance. The releases were made on 8, 15, and 22 January. None of these returned to the Botanical Garden. On 5 and 9 February a

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patrolling of the release area disclosed that four of them were still present; by 25 February only two could be found.

Meanwhile, I had proceeded with the program of releases at more distant points. Two residents from the previous season were trapped late in the afternoon of 1 January 1961 and released early the next morning at the edge of an artificial irrigation lake about 65-km airline distance southwest of the Botanical Garden. One returned in approximately 10 days. The other was back in 12 days.

Another resident from the previous season was released at sea level, across the Coastal Andes range, at a point about 25 km airline northwest of the Botanical Garden. Release was made 8 January; the bird was back in its territory 12 days later.

In the season 1961–62, only one old resident returned from the North, so no further long-distance experiments were performed. To improve the chances of having the maximum number of old residents with which to work during the coming season and thus continue long-distance releases to points several hundred kilometers distant, none of the new residents in the Botanical Garden were disturbed except for some short-distance experiments. However, to see if attractiveness of the point of release could have been a factor in the failure of the first-year birds to return to the Botanical Garden, three new residents from the original point of release 10 km east were caught and set free in the Botanical Garden, one on 16 December 1961, another on 4 February 1962, and the third on 17 February. The first took up a territory in the Botanical Garden and was still present on 21 April. The other two did not remain to reside in the Botanical Garden. Neither did they succeed in returning to the ravine from which they had been taken, as disclosed by several careful checks there.

In reviewing results up to the present, we find that of four old residents released at points from 10 to 65 km from their winter territory, *all* returned, while of 14 new residents released 10 km from their territories, *none* returned. The statistics are admittedly few but they are 100 percent consistent.

To determine if it might be lack of attachment to territory that could explain the homing failure of first-year residents, I made a number of releases of new birds at points from 500 to 1,200 m from their territories, most of them at about 1,000 m, and at various times between September and March during several seasons. All birds of resident status returned to their territories and even some of obvious transient status returned to their temporarily established territories before eventually resuming their journey. (Northern Waterthrushes begin to arrive in the study area in early September. Transients may remain in the area for several days or several weeks, as I have learned from six seasons' work with banded birds. Birds that remain to become first-year winter residents do not arrive in the area until after mid-October. Since there are practically no exceptions to this, unbanded birds arriving during September and early October may be assumed to be transients, even before their departure confirms this status.)

The territories of residents may vary from a compact 400 sq m in crowded areas to a sprawling 5,000 sq m in years of light population pressure or where the area is ecologically unsuitable to support a bird in a smaller area. It may even be a disjoint series of small clumps of vegetation stretching over 200–300 m. There is some extraterritorial supplementary foraging, and most birds venture abroad in search of water since few of the territories have a constant water supply. I have seen individuals as much as 400 m from their territory for purposes of bathing and drinking. They probably have no need to venture farther than that.

Local orientation is well known, and probably no one would question that it is based on visual recognition of landmarks learned during the birds' daily experiences. Birds released 1,000 m or so from their territories would need a minimum of random searching before finding some visual clue that permitted their quick orientation and return to territory, and they were usually back in a day or less, although some recently arrived individuals required longer.

Another obvious order of orientation is long-distance orientation. Although these first-year residents had not yet shown their possession of this faculty except in the sense that they had flown southward in fall migration, it is difficult to believe that all of these 14 randomly picked birds should have lacked it.

In thinking of reasons for the failure of first-year residents to home from the 10-km distance, it occurred to me that the conditions are unique: This is one of the only two possible *natural* situations where homing experiments could be performed on migratory birds that had not yet had the experience of *leaving* the territories being considered as "home." The other would be to work with juveniles before they departed from whatever territories they established after becoming independent from their parents.

Since the first-year winter residents apparently lacked neither attachment to territory nor ability to return from distances short enough to permit their finding orientation marks that they had learned, and since one may assume that they also did not lack innate long-distance orientation ability, I conclude that these birds apparently lacked only one thing: the experience of orientation to intermediate distances near their present home.

Since 4 out of 4 old residents showed that they did possess this orientation and 14 of 14 new residents apparently lacked it, it seems to me that this ability is learned. But presumably, these 14 new residents would normally be able to orient back to the area of their youth, so they must possess such orientation with respect to that area. Thus, besides being learned, it appears that this orientation is learned at or about the time the bird is departing.

I have referred to this as intermediate-distance orientation. Perhaps it is actually the learned part of long-distance orientation supplementing that which is innate; but whatever is learned it appears to refer only to the home area from which the bird is departing. What the bird learns on its first trip south does not enable it to orient to its new winter home if artificially removed from it; but having once flown north from the winter territory, the bird—even if artificially removed—is thereafter able to return to this winter home.

Author's Note: Since presenting the above paper at the Congress, there has come to my attention a review (*Auk* 79:511) of H. Löhrl's 1959 paper (*J. Ornithol.* 100:132–140). Working with young flycatchers (*Ficedula albicollis*), Löhrl took nestlings from one place, reared them in another, and released them before normal fall migration in a third place 90 km south of the rearing locality (approximately the other of the two possible conditions of inexperience mentioned earlier in my paper). A significant number returned the next spring to the area of release. "It is postulated that the important factor may be the bearings taken by the young bird just as it starts southward in the fall migration; these bearings are used when the bird returns the next spring.—W.J.B."

Although Löhrl's work partially antedates mine, I was unfamiliar with it. Our conclusions, drawn independently from work at opposite poles in the birds' life cycles, are essentially the same.

SUMMARY

Seiurus noveboracensis establishes winter territories in Venezuela of 400 to 5,000 m^2. When 4 adult and 14 first-year resident birds were experimentally moved 10–65 km away, only the adults returned. It is postulated that this orientation ability is learned at the time the first-year birds start northward in their spring migration.

Factors Concentrating Fall Migrants at an Alpine Pass

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It has long been recognized that the spectacular concentration of fall migrants at some Alpine passes resulted from a combination of geographical and meteorological factors (Sutter, 1955). But it is only in recent years that this phenomenon has been studied in more detail, especially after the creation of the Alpine Ornithological Station at the col de Bretolet above the village of Champéry in Valais, Switzerland. The research at the station is supported by a grant from the "Fonds national suisse pour la recherche scientifique" and undertaken in collaboration with the Schweizerische Vogelwarte Sempach.

In Europe, extensive studies on weather and migration, concerning mostly coastal movements, have been carried out in Fenno-Scandia (Svärdson, 1953; Nisbet, 1957), in Holland (van Dobben, 1953), and the British Isles (Snow, 1953; Lack, 1960*b*). In central Europe, several workers have accumulated many data, but comparatively little is known about this area because their results have not yet been published. Until recently, the biggest gap in our knowledge concerned the role of the Alps in continental migration. The importance of the research at the Alpine station at Bretolet in this connection is obvious. A general report on the work at Bretolet prior to 1958 was written by Godel and de Crousaz (1958), and yearly reports for the period 1958–60 have been published by Vuilleumier (1959), G. de Crousaz (1960), and Ph. de Crousaz (1961).

The purpose of this paper is to analyze some of the geographical and meteorological factors affecting fall migration at the col de Bretolet, and to describe how these factors, combined with the Alpine barrier, influence the migration pattern in southwestern Switzerland (Fig. 1).

The Swiss Val d'Illiez divides into two valleys, one leading to the col de Bretolet and the other to the col de Cou, both of which provide passes into the French Val de Morzine. Lying east-northeast–west-southwest between two mountain ranges (the summits of which lie at 2,400 m to the north and at more than 3,000 m to the south), the passes are at an altitude of 1,925 m above sea level (6,315 ft). A more detailed description of Cou–Bretolet can be found in Godel and de Crousaz (1958:97).

Two main techniques were used to record the migration: (1) banding (57,642 birds of 104 species between 1953 and 1961); and (2) quantitative observations on diurnal migration.

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GEOGRAPHICAL FACTORS

After comparing the volume of migration on the Swiss Plateau and elsewhere in the Alps (see especially the papers by Benoit, 1953; Burnier, 1953; Desfayes, 1950; Géroudet, 1959*b*; Strahm, 1953; and Sutter, 1955) two conclusions are apparent. First, visible diurnal migration is heavier at Cou–Bretolet than at any other place in the Alpine range studied so far (except perhaps the Maloja, Sutter, 1954), and second, migration is as intense, if not quite as diverse, at Cou–Bretolet as at a number of localities of the Plateau.

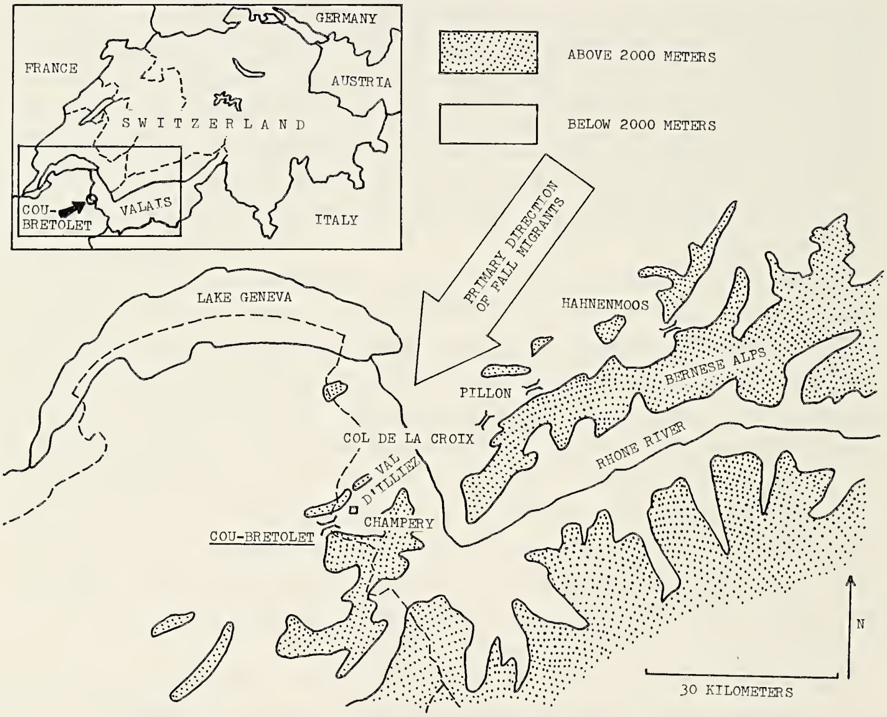

Fig. 1. Southwestern Switzerland.

As early as 1953, Géroudet (as cited in Sutter, 1954:125) expressed the opinion that the strong migration at Cou–Bretolet could be explained by the geographical situation of the passes. Migrating at various elevations above the Plateau, birds fly easily over the pre-Alps (which culminate at about 2,400 m and constitute no barrier) and are diverted from their southwesterly heading (*sensu* Lack and Williamson, 1959) by the high Bernese Alps. They then fly parallel to the Bernese range, concentrating in the area lying between the pre-Alps and the Bernese Alps, are redirected to their original direction in the Val d'Illiez, and eventually arrive at the passes of Cou–Bretolet.

If Géroudet's hypothesis is correct, the volume of migration in the northern foothills of the Bernese Range should be smaller than at Cou–Bretolet, and the birds migrating through this area should later be found at Cou–Bretolet. Observations at the passes of Hahnenmoos (Benoit, 1953; Strahm, 1953), Pillon, and La Croix indicate that the first assumption is probably right. Two recoveries of banded birds tend to support the second: Two Great Tits (*Parus major*) banded at the passes of Hahnenmoos and Pillon in 1961 were recaptured a few days later at Bretolet.

Glutz von Blotzheim (1960) believes that the above explanation is also corroborated by the very small spring migration in the Cou–Bretolet area. At this time of year, there is no channeling effect and birds are scattered over the Alpine range. Indeed, the few April excursions at Cou–Bretolet have revealed the scarcity of migrants there. For example, G. de Crousaz, J. van de Poll, and I saw only some Fringillidae and Motacillidae on the move on 3 April 1960.

The present data certainly suggest an influence of geographical factors in the fall at least in this part of the Alps, but it should be confirmed by a detailed analysis of quantitative observations at the various passes.

METEOROLOGICAL FACTORS

It is well known that weather factors have a strong influence upon migration. In southwestern Switzerland, there are two basic weather patterns impinging upon the regularity of the autumn migration: (1) a relatively stable anticyclonic situation, interrupted by only a few depressions, which results in a steady increase in the numbers of migrants to a peak in October; and (2) a rapid succession of depressions with brief periods of fine anticyclonic weather, which in turn results in rushes of migrants, causing an irregular migration pattern. These two patterns were clearly demonstrated at Cou–Bretolet during the fall migration periods (from mid-August to late October) in 1958, 1959, and 1960.

The fall of 1959, when the weather was dry and moderately windy, was an example of the first. This stable anticyclonic condition with light easterly winds was only occasionally interrupted by the passage of depressions from the Atlantic. The lows, the fronts of which brought comparatively little precipitation, resulted in rather unimportant variations in the overall migration pattern. The movement started in the middle of August, increased in intensity to its peak in the first third of October, and decreased thereafter.

In 1958 and 1960, on the other hand, the weather was characterized, particularly in October, by a faster succession of Atlantic depressions. Their fronts produced abundant precipitation and left only very short intervals of fine anticyclonic conditions. The migration was frequently delayed at Cou–Bretolet during the cyclonic influence and released after the return of anticyclonic situations.

In 1958, for example, we witnessed very little migration during the passage of the cold front of a depression from the British Isles between 4 and 7 October. On the eighth, warm anticyclonic air was brought to continental Europe from the Mediterranean. The counts revealed an immediate increase in the numbers of migrants: 4,350 Chaffinches (*Fringilla coelebs*), only 322 on the 7th; 1,135 Linnets (*Carduelis cannabina*), against 42; 800 Hirundinidae, none the previous day. The increase was even more marked on the 9th (15,200 *F. coelebs*), and the 10th (13,600 *F. coelebs*); but with the arrival of another cold front on the 11th, migration decreased dramatically and was extremely reduced for the next 10 days. It should be noticed that the main peak of migration did not occur immediately, but 48 hours after the reestablishment of an anticyclonic situation. This was observed on a number of occasions.

The majority of passerines reach their seasonal peaks during such anticyclonic conditions, a situation similar to that in the lowlands of Scandinavia (Nisbet, 1957). After a detailed analysis of the migration of the Motacillidae, de Crousaz (1961) concluded that their response to weather is identical to that of other species only when the cyclonic disturbances are of relatively long duration, as in 1958 and 1960. But if the cyclonic weather is of short duration (1–3 days), the numbers of wagtails (*Motacilla* spp.) and pipits (*Anthus* spp.) do not show the increase witnessed in other species, and their numbers remain low after the return to anticyclonic situation. Furthermore, when a depression is approaching, a time when most species diminish in numbers, the Motacillidae actually increase. This difference in migratory behavior has apparently been recorded only at Cou–Bretolet (G. de Crousaz, 1961).

Migration is more intense with clear or partly clouded sky and light to moderate westerly or southwesterly winds. With the same cloud cover but easterly or northeasterly winds (downwinds), migration becomes extremely reduced through the passes. Géroudet (in a footnote in Godel, 1957) suggested that the movement then takes place at a much higher altitude. There are a few observations of birds at very high elevations in the Alps: *Motacilla flava thunbergi* at 3,500 m on the Jungfraufirn in August 1932 (Meylan, 1933); several Motacillidae (*Motacilla flava*, *M. alba*, *Anthus spinoletta*, *A. trivialis*) in spring and fall at altitudes between 3,213 and 3,820 m (G. de Crousaz, 1961); *Falco tinnunculus*, hirundines, *Carduelis carduelis*, *C. cannabina*, *Fringilla coelebs*, and *Prunella modularis* in the Alps of Valais between 3,000 and 3,550 m in April (de Crousaz, 1955); *Oriolus oriolus* on the summit of the Finsteraarhorn (*in* Glutz von Blotzheim, 1962); and hirundines in the High Alps of Valais (D'Arcis, 1939). Despite these observations, it is not yet certain whether or not a regular high-altitude movement occurs with easterly winds. Such migration would not be surprising in view of the high-altitude movements of the Chaffinch with following winds over Holland (Deelder, 1949), and especially in view of the reports of hirundines migrating high with a following wind in the Engadin (Sutter, 1952) and the

Pyrenees (Lack and Lack, 1953). Rain and fog result in a marked decrease of the volume of migration. When such weather prevails for a long period, there are sometimes irregular rushes of birds. They occurred, for example, during the continuously inclement weather from 12 to 21 October 1958, when as many as 9,270 *Fringilla coelebs*, 740 *Carduelis spinus*, 440 *C. cannabina*, and some other species passed in a few hours on the 15th.

Overcast sky, rain, fog, decrease in temperature, and westerly winds accompanying a low of westerly (Atlantic) origin are unfavorable to migration at Cou–Bretolet, while fine weather (clear or lightly clouded sky), and usually higher temperature and easterly winds, corollaries of anticyclonic conditions over central Europe, are favorable to migration. This tendency for more migration in anticyclonic than cyclonic weather has been shown to take place elsewhere in Europe (Lack, 1960*a*).

At Cou–Bretolet, anticyclonic conditions can be characterized either by cold easterly to northeasterly winds (bise) or by an increase of temperature quickly following cold. Movements are less conspicuous with easterly winds, but in both cases a strong migration occurs. Although it is not known yet whether or not migration is actually more important with following or opposite winds, the above observations suggest that wind (and perhaps wind direction?) may have more influence than temperature on migration in the Cou–Bretolet area. The recent conclusion of Lack (1963), that "wind-direction is the factor of paramount importance" in the initiation of fall migration, is therefore of particular interest.

Since the foehn wind is a characteristic meteorological event in the Alps, its effect upon migration is worth describing, especially because almost no reference to it can be found in the literature.

In 1958, a mass migration of Hirundinidae (*Hirundo rustica* and *Delichon urbica*) involving tens of thousands of birds was observed in the last three days of September. Géroudet (1959*a*) accounted for this movement as follows. On 28 September, central Europe was under the influence of anticyclonic conditions, which moved to the east, together with the Atlantic low. At Cou–Bretolet the weather was fine with southwesterly wind, and more than 20,000 hirundines passed. The next day the cold front of the depression reached France. At Cou–Bretolet, the weather changed during the day and the foehn blew over the summits from the south, forming typical clouds. About 25,000 hirundines were estimated to be moving through the passes from 6:45 A.M. to 5:30 P.M., but at 11:20 A.M. a second flow of migrants was seen to move through at about 2,300–2,400 m altitude. This simultaneous movement, which continued until at least 2 P.M., included a considerable number of birds—perhaps 20,000–30,000. On the 30th, the cold front, accompanied by rain, arrived in western Switzerland, while the foehn situation remained well established in the Alps. The foehn clouds characterized the tops of mountains in the Cou–Bretolet area, where rain, a drop in temperature, and a fast drop in barometric pressure were indicative of the cold front.

The swallows and martins continued their migration throughout the day at both altitudes. The higher group showed fluctuations in intensity with spectacular peaks: 19,000 birds from 8 to 8:15 A.M.; 58,000 from 4:15 to 5 P.M. An estimated 300,000 birds passed through the area on that day. On 1 October, there was no hirundine migration.

Géroudet thought that this mass movement could be explained as follows: The swallows and martins flew into a narrowing "meteorological channel" (constituted by the foehn wind on one side and the advancing front of the depression on the other), superimposed on the topographical channel described earlier.

Similar high-migration tracts in foehn conditions were also recorded in 1960, during the first week and on 14 October (40,000 birds estimated on that day).

COMBINED EFFECTS OF GEOGRAPHICAL AND METEOROLOGICAL FACTORS

These have been summarized by G. de Crousaz (1961): The importance of the Alps as an obstacle varies according to the altitude at which birds fly when they meet the Alpine range, and the altitude in turn is very dependent on the meteorological conditions. Birds migrating high do not concentrate at the passes, and they probably cross the range on a broad front. Birds flying very low are the ones most affected by the diversion line of the Bernese Alps; as they ascend the slopes they meet other migrants. This results in the concentration at the altitude of Cou–Bretolet, associated with the diversion. When weather factors modify the flight altitude, these may cause either concentration at the passes or dispersion above them. Therefore, the numbers of migrants obtained by the counts may be quite misleading and give an inadequate image of the migratory movement across the entire range. As stated by G. de Crousaz (1961:80): ". . . the passage of a species at Cou–Bretolet may decrease if the birds fly higher, although there might be more individuals crossing the Alps; inversely, the numbers may increase at Cou–Bretolet if a species flies lower, even though fewer birds are migrating over the range."

De Crousaz's explanation implicitly admits that variations in the intensity of migration at Cou–Bretolet are due to differences in the flight altitude of the birds, i.e. when a concentration is observed, birds fly lower, and when less migration is observed, birds fly higher (in a broad front over the Alps). This might well be true, but actually is only an incomplete description of what happens. Neither de Crousaz nor other authors working on Alpine migration have taken into account the possibility of drift (as defined by Lack and Williamson, 1959).

As mentioned above, the migration is more conspicuous with westerly than with easterly winds, and the Bernese Alps act as a line of diversion on migrants. With westerly winds, birds flying over the Swiss Plateau may be drifted toward the Bernese range, hence the concentration in the funnel of

Cou–Bretolet. In other words, both a lateral displacement and the influence of a diversion line act at the same time. With easterly winds, on the other hand, birds may be drifted away from the Bernese range (this could be a downwind-directed drift), and as a consequence there is no concentration at the passes. In this case, it is quite possible that birds increase their flight altitude (cf. Kramer, 1931; van Dobben, 1953, cited by Lack, 1960*a*). They may very well disperse in a broad front over the Alps, but this dispersion is better explained by drift than just by a change in altitude.

SUMMARY

The high density of fall migration at Cou–Bretolet in southwestern Switzerland is believed to be due in part to the high Bernese Alps, which act as a diversion line, promoting a concentration of migrants heading toward the Val d'Illiez and the passes of Cou–Bretolet.

Cyclonic weather is unfavorable to migration. At the approach of a depression, most migrants—but not the Motacillidae—decrease in numbers. The return to fine anticyclonic weather is followed by an increase in the volume of migration that reaches its peak about 48 hours after the cyclonic influence has gone. After a cyclonic disturbance of short duration, the Motacillidae react in a different way from that of the other birds and their numbers remain low.

Migration is more conspicuous with westerly than easterly winds. Birds fly higher with easterly (following) winds. Since the temperature can be either warmer or colder after the return of anticyclonic weather, this factor does not seem to be as important as the wind. Wind direction may be the main factor regulating the fall migration of birds each year in this part of the Alps.

In certain foehn conditions, the combination of topographical and meteorological factors produces spectacular concentrations of hirundines at Cou–Bretolet.

The image of migration at Cou–Bretolet is a result of both topographical and weather conditions, and does not necessarily give a true sample of the total migration through this part of the Alpine range. Drift may account for the differences of volume of migration: With easterly winds, birds would fly high and in a downwind-directed drift, so that there is no concentration at the passes; with westerly winds, lateral displacement and concentration of migrants along the diversion line of the Bernese Alps produces the intense movements at Cou–Bretolet.

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Ermittlung und Aussagewert der Verweildauer zugdisponierter Vögel

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Laboratoriumszoologen untersuchen, was die Tiere zu leisten vermögen, Feldzoologen, was sie wirklich tun. Eine spezielle Aufgabe der Feldornithologie ist das Studium des Verhaltens der Vögel während des Zuges. Bei genauer Analyse dieses Verhaltens zeigt sich, dass die Vögel in der Zugperiode tatsächlich nicht immer täglich ziehen, sondern dazwischen Tage, Wochen oder Monate verweilen. Die Verweildauer, in Tagen ausgedrückt, kann sogar die Zahl der Zugtage eines Individuums bedeutend übertreffen. In den Darstellungen des Vogelzuges kommt das zu wenig zur Geltung. Hier sollen deshalb einige Ergebnisse über Verweildauer ziehender Vögel verschiedener Ordnungen bekanntgegeben und die Ursachen der Verweildauer erörtert werden. Die Resultate stammen hauptsächlich aus dem Ismaninger Teichgebiet bei München, das für derartige Untersuchungen besonders günstige Voraussetzungen bietet. Diese Seenplatte entstand im Jahre 1929 und umfasst beinahe 9 qkm fast stehender Gewässer. Vorher waren hier kultivierte Moorwiesen.

Das Material lässt sich unter Umständen durch reine Feldbeobachtung gewinnen. Einzelne sehr seltene Durchzügler kann man, oft unter Berücksichtigung der Kleider, identifizieren, Gruppen mit einiger Sicherheit an der Individuenzahl. Am Ammersee südwestlich von München sah ich z.B. am 2. und 23. Oktober 1961 vier Kiebitzregenpfeifer (*Pluvialis squatarola*) am gleichen Platz, woraus man auf eine Verweildauer von 3 Wochen schliessen kann. Manchmal erlaubt ein auffallendes traditionelles Verhalten Folgerungen in Hinsicht auf die Herkunft und Verweildauer. So überwintern in München seit vielen Jahrzehnten Hunderte von Lachmöwen aus Nordosteuropa. Sie ernähren sich zu dieser Jahreszeit an den städtischen Gewässern. Im März aber wimmelt es auf einmal in der ganzen Stadt einige Wochen lang von Lachmöwen (*Larus ridibundus*), die weitab vom Wasser an Häusern um Futter betteln. Zweifellos handelt es sich hier um eine durchziehende Population, die dieses bei uns nicht übliche Verhalten sich in einer anderen Stadt, wahrscheinlich der Schweiz, angewöhnt hat und zu uns mitbringt. In Zürich und Genf werden die Möwen an den Häusern gefüttert und haben sich längst an diesen Winterlebensraum angepasst. Das sicherste Mittel, die Verweildauer zu bestimmen, ist natürlich die individuelle Kennzeichnung der Vögel mit Aluminium-, Kunststoffarbringen usw. Unsere Erfahrungen sprechen dafür, dass der dazu notwendige Fang im allgemeinen das Zug- und Rastverhalten nicht oder höchstens vorübergehend beeinflusst, wenn man die nötige Vorsicht walten lässt.

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Unter den Aussenbedingungen, die das Rasten veranlassen, spielt das Nahrungsangebot die grösste Rolle. Die an organischen Stoffen reichen Schlamm- und Wasserflächen des Ismaninger Teichgebietes ermöglichen Limikolen und Schwimmvögeln wochenlanges Verweilen. Die meisten dieser Durchzügler rasteten vor 1929 hier entweder gar nicht oder in nicht nennenswerter Zahl. Je nach Wasserstand und Jahreszeit zählen wir auf den knapp 9 qkm jetzt bis zu 18 000 Schwimmvögel (Anatiden und Blässhühner = *Fulica*) (Wüst, 1962), 945 Bruchwasserläufer (*Tringa glareola*) und 1 060 Kampfläufer (*Philomachus pugnax*), die sich hier gleichzeitig mit Nahrung versorgen. Durch Beringung und Wiederfang wurde als Verweildauer festgestellt beim Bruchwasserläufer (*Tringa glareola*) bis 20 Tage im Juli, beim Flussuferläufer (*Actitis hypoleuca*) bis 29 Tage im August/September, beim Zwergstrandläufer (*Calidris minuta*) bis 8 Tage im September und beim Eisvogel (*Alcedo atthis*) bis 12 Tage im September/Oktober. Die enorme Produktion an Insekten führt sogar während der Brutzeit zu Schlechtwetternahrungsflügen von Mauerseglern (*Apus apus*), die sich dann zu Zehntausenden im Gebiet konzentrieren und aus mindestens 185 km Umkreis stammen (Wüst, 1962).

Rastplätze werden aber auch dadurch attraktiv, dass sie Deckung, Ruhe und Schutz vor Feinden bieten. So besass das Erdinger Moos, an dessen Rand Ismaning liegt, von jeher ergiebige Äsungsplätze für Gänse. Aber erst seit sich das Speicherseebecken mit Wasser gefüllt hat und dadurch Gänse zum ungestörten Rasten und Schlafen einlud, fanden sich zunächst zögernd und unregelmässig kleine Verbände von Saat- und Blässgänsen (*Anser fabalis* und *A. albifrons*) ein. Heute verweilen hier mit grosser Zuverlässigkeit alljährlich etwa 80–240 Saatgänse, obwohl sie in den Gewässern selbst keine Nahrung finden und täglich Dutzende von Kilometern fliegen, um zu ihren Äsungsplätzen und zurück zu gelangen (Wüst, 1961, 1962). Sie schlafen jede Nacht und ruhen auch tags einige Stunden auf der Wasserfläche schwimmend ausser Schussweite. Der Einzug beginnt frühestens Mitte September. Die Saatgänse erscheinen in kleinen Gruppen von der Grösse einer oder mehrerer Familien, die sich erst im Ismaninger Teichgebiet zu einem grossen Pulk zusammenschliessen. Dieser Vorgang währt ungefähr 3–4 Wochen; oft kommt Ende November nochmals ein Schub. In der Mitte des Winters gehen die Saatgänse ziemlich auf einmal ausser Landes, wohin, ist unbekannt. Nach 1–2 Monaten treffen sie neuerdings ein, verweilen wiederum etwa 2 Monate, um uns zur Wende März/April Richtung Brutheimat zu verlassen. Sicher hat sich hier auf Grund der vom Menschen vor 33 Jahren geschaffenen Landschaftsverhältnisse eine Tradition eingespielt. Es ist anzunehmen, dass jährlich gewisse erfahrene Leittiere, die den Ismaninger Speichersee kennen, die Führung dorthin übernehmen. Gänse werden ja ziemlich alt und besitzen hervorragende Lernfähigkeit. Auch ihr Verhalten beim Eintreffen am Platz des regelmässigen Verweilens spricht für individuell erworbene Ortskenntnis.

Offenbar spielt auch die Landschaftsphysiognomie beim Aufsuchen der Rastplätze und bei der Verweildauer eine Rolle. Schellenten (*Bucephala clangula*) sind auf waldige oder eingeschnittene Ufer geprägt. Dies scheint mir der Grund dafür zu sein, dass sie auch während des Zuges Gewässer mit waldigen, bergigen Ufern entschieden bevorzugen. So tritt die Schellente auf den Isarstauseen unterhalb von Landshut und vor allem auf den Innstauseen unterhalb von Rosenheim, wo wenigstens stellenweise Wald an das Wasser heranreicht, in bedeutend höherer Dominanz auf als am offen daliegenden Ismaninger Speichersee (Bezzel, 1961). Nahrungsökologische Gründe scheinen hier keinen Ausschlag zu geben. Umgekehrt haben Lachmöwen einen gewissen "Widerwillen" gegen von Wald und steilen Ufern eingeschlossene Gewässer und bevorzugen zum Verweilen deutlich weite, freie Flächen.

Bekanntlich hat das Zugverhalten erbliche, also innere Voraussetzungen. Der Zugtrieb ist mit den beiden anderen Phasen des Jahresrhythmus, der Fortpflanzungs- und der Mauserphase, verknüpft. Die drei Perioden verzahnen sich ineinander. Von der hormonal gesteuerten Zugdisposition, der Grobeinstellung, unterscheidet man zweckmässig die von Auslösern abhängige Feineinstellung, die Zugstimmung (Schüz, 1952). Letztere kommt nur auf Grund der inneren Zugbereitschaft, gewöhnlich unter bestimmten äusseren stimulierenden Reizen zustande. Einzelne Individuen, die den Zusammenhang mit Verbänden ihrer Art verloren haben und zu lange verweilten, die also einerseits nicht mehr durch Artgenossen in Zugstimmung gebracht werden, andrerseits angesichts üppiger Nahrungsbedingungen über die Jahreszeit der herbstlichen Zugunruhe hinausgerieten, versuchen zu überwintern. Teilweise erstmals in Bayern oder Deutschland beobachteten wir im Winter und dann stets einzeln folgende Limikolen: Dunkler Wasserläufer (*Tringa erythropus*), Grünschenkel (*T. nebularia*), Flussuferläufer (*Actitis hypoleucos*), Alpenstrandläufer (*Calidris alpina*) und Kampfläufer (*Philomachus pugnax*). Da der Herbst hier oft mild verläuft, der Winter aber erst im Januar/Februar mit Strenge einsetzt, dürften solche Überwinterungsversuche in 500 m NN normalerweise scheitern. Sie führen jedenfalls nicht zur Anbahnung eines in dieser Richtung neuen Zugverhaltens, zu keiner Verlagerung winterlicher Rastplätze. Die wenigen Aussenseiter verfallen der Ausmerze.

Verschiebungen geographisch und mengenmässig grossen Ausmasses hatte das Ismaninger Teichgebiet dagegen insofern zur Folge, als sich hier eine umfangreiche Mausererpelstation für verschiedene Anatidenarten entwickelte (Bezzel, 1959). Die ♂♂ der Enten trennen sich bekanntlich während der Brutzeit von den ♀♀ und suchen im Sommer Mauserplätze auf, an denen sie einesteils in Ruhe die Wochen ihrer Flugunfähigkeit verbringen können, andernteils genug zu fressen finden. Beide Bedingungen erfüllt das Ismaninger Teichgebiet. Besonders klar bahnte sich die Tradition, hier zu mausern, bei den Tafelerpeln (*Aythya ferina*) an. Schon im zweiten

Jahr des Bestehens der künstlichen Gewässer, im Sommer 1930, fanden sich 57 ad. (♂ ♂) ein, im Juni 1931 hatten sie sich auf 110 verdoppelt, im Juni 1932 waren es 275, im Sommer 1933 über 1 000, 1934 mindestens 4 000. Bei dieser Grössenordnung blieb es dann etwa, bis sich das Ende 1958 in Kraft getretene Jagdabkommen mit Verlängerung der Schonzeit für Enten und völliger Befriedung des grösseren Teils vom Ismaninger Teichgebiet auswirkte. Im Sommer 1960 wurden dann 6 200 und im Sommer 1961 sogar 9 500 bis 9 600 ad. Tafelenten, hauptsächlich ♂ ♂ , gezählt. Auch Reiher- (*Aythya fuligula*) und Kolbenenten (*Netta rufina*) entwickelten unerwartet frequentierte Mausererpelstationen mit wochenlanger Verweildauer. Die Enten wandern dann nach beendeter Vollmauser im Spätsommer ab, bevor der herbstliche Entenzug voll in Gang kommt. Dieses Phänomen kannten wir in Süddeutschland früher zu keiner Zeit. Geändert hat sich aber nicht das angeborene Verhalten jener Tauchenten, sondern das ökologische Gefüge ihres Lebensraumes. Sie stellten sich rasch auf die Änderung um. Es wäre interessant zu wissen, wo diese Erpelmassen vorher zur Mauserzeit verweilten. Jedenfalls füllte sich die im Jahre 1929 geschaffene ökologische Nische, nach der sichtlich starker Bedarf bestand, in wenigen Jahren bis zur Sättigung auf und wurde zum wochenlangen regelmässigen Mauserquartier von maximal 10 000 Erpeln, die sich hier auf Grund ihrer Erfahrung aus einem Raum kontinentalen Ausmasses ein Stelldichein geben. Wenig später, Juli bis September, konzentrieren sich bis zu 534 Schnatterenten (*Anas strepera*) beiderlei Geschlechts zum Zweck ihrer traditionellen Sozialbalz. In diesem Falle scheint mir die gesellige Brautschau der Anlass des alljährlichen wochenlangen Verweilens zu sein.

Zum Vergleich der Verweildauer von Frühjahr und Herbst besitzen wir noch kein statistisch genügend gesichertes Material. Immerhin spricht es nicht gegen die Annahme, dass die Vögel auf dem Wegzug länger verweilen als auf dem Heimzug. Beim Schilfrohrsänger (*Acrocephalus schoenobaenus*) ergaben 6 Wiederfänge im April/Mai eine maximale Verweildauer von 9 und eine durchschnittliche von 4 Tagen; 14 Wiederfänge von Juli bis September eine maximale Verweildauer von 12 und eine durchschnittliche von ebenfalls 4 Tagen (Springer, 1960, und unveröffentlichte Ergebnisse). Einzelne Teichwasserläufer (*Tringa stagnatilis*) verweilten nach blossen Beobachtungen zwischen April und Juni jeweils mindestens 3 Tage (Wüst, 1960), im August einmal wenigstens 10 Tage.

Wahrscheinlich besteht die Regel, dass zugdisponierte Vögel um so rascher die Rast abbrechen, je grösser der Verband von Artgenossen ist. So verweilten im Mai/Juni 18 Löffler (*Platalea leucorodia*) einen Tag, 3 Löffler (2 ad., 1 juv.) mind. 3 Tage, 2 Exemplare 3 Tage und 1 ad. Löffler 17 Tage. Irrgäste halten es unter Umständen sehr lange aus. Einzelne Zwergscharben (*Phalacrocorax pygmaeus*) verweilten 200 Tage (September bis April) und 151 Tage (Juli bis Dezember), eine Gruppe von 9–12 Zwergscharben blieb rund 125 Tage (November bis April) (Wüst, 1960).

Das gleiche gilt für Tiergartenflüchtlinge. Für solche notierten wir folgende Verweildauern: Flamingo (*Phoenicopterus r. ruber*) etwa 45 Tage; Kuhreiher (*Ardeola ibis*) etwa 180 Tage; Brandente (*Tadorna tadorna*) mindestens 65 Tage; Nilgans (*Alopochen aegyptiaca*) etwa 31 Tage und Graugans (*Anser anser*) im Anschluss an Saatgänse (*A. fabalis rossicus*) etwa 180 Tage. Es handelte sich um voll flugfähige Tiere, die einen gesunden Eindruck machten.

Wenn man nach Altersklassen aussortiert, hat man den Eindruck, dass juv. Exemplare durchziehender Gäste länger verweilen als ad. Doch können wir zu diesem Punkt noch nicht mit Zahlen aufwarten.

Zweifellos aber steht die Entfernung vom Zugziel oder vom Ort des Aufbruchs in Korrelation mit der Neigung zu verweilen. Ein hervorragendes Beispiel dafür sind die beiden schwarzweissen Fliegenschnäpper, deren ökologische Ansprüche identisch sind. Der Trauerschnäpper (*Ficedula hypoleuca*) rastet alljährlich als Durchzugsgast im April/Mai und wiederum von Juli bis Oktober zahlreich im Ismaninger Teichgebiet. Trotz intensiver Nachsuche entdeckten wir indessen während der vergangenen 33 Jahre noch nie einen Halsbandschnäpper (*Ficedula albicollis*), obwohl, ja gerade weil die nächsten Brutplätze nur etwa 3 km entfernt sind. In der Nähe des Nistreviers kann der Halsbandschnäpper nicht mehr rasten, es zieht ihn mit elementarer Gewalt in dieses hinein. Die Verweildauer des Halsbandschnäppers ist nahe dem Brutplatz absolut null. In so krasser Form ist uns der Magneteffekt engbegrenzter Brutplätze von Zugvögeln noch nirgends bekannt geworden. Dagegen sah und hörte ich den Halsbandschnäpper schon zweimal ganz unerwartet in den wenigen Bäumen des Neusiedlerseeufers rastend.

Strandläufer (*Calidris*) ziehen mit Vorliebe an Meeresküsten entlang, wohl nur zum Teil quer durchs Binnenland. An dem nur knapp 100 km von der Nordsee entfernten Dümmer verweilen Vögel dieser Gattung in geringerer Anzahl, unregelmässiger und kürzer trotz günstiger Biotope als im Ismaninger Teichgebiet, das tief im Binnenland Mitteleuropas liegt. Das mutet zunächst paradox an, findet aber leicht seine Erklärung: Kurz hinter dem Meeresstrand haben es die Vögel noch nicht nötig zu verweilen. Im küstenfernen, inneren Kontinent aber wirken die wenigen geeigneten Rastplätze auf die inzwischen ermüdeten und hungrigen Strandläufer wesentlich einladender zu ergiebiger Unterbrechung der Wanderung.

Eine genauere Analyse der durchschnittlichen Verweildauer der einzelnen Vogelarten und -populationen würde wahrscheinlich auf weitere Verbreitung zwischenzugartigen Verhaltens hinweisen, als bis jetzt angenommen wurde. Ökologisch-faunistische Arbeiten sollten mehr denn bisher zur Veranschaulichung der Biotope und zur Charakterisierung des Verhaltens der Gäste dieser Biotope zahlenmässige Angaben über die Verweildauer enthalten. Schliesslich ist solches Material als exakte Grundlage für Massnahmen der Vogelhege im Sinne des Naturschutzes unentbehrlich.

SUMMARY

During migration, birds often stay in certain areas for a long time. The length of stay, which can be determined by various methods of field ornithology, depends on both ecological factors and individual disposition. Important factors are food, cover, landscape, possibilities of joining other birds, direction of migration (whether fall migration or homeward migration), sex, age class, and distance from destination or starting place. Further and more detailed studies of the length of stay are necessary both for conservation purposes and for the clarification of the underlying causes.

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Evolution within the Psittaciformes

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CONTENTS

INTRODUCTION

Two aspects of evolution within the order Psittaciformes are treated here: Firstly, some consideration is given to the influence of social behavior, and secondly, phylogenetic relationships are discussed. Various degrees of development of social behavior occur in this order, and it seems likely that this attribute has been subject to natural selection and has changed adaptively. The converse, too, seems likely, that evolutionary success has depended on the kind and level of social behavior. As no studies of this facet of the biology of the order are available, and because of its relevance to the taxonomy of the group, the present results are published.

The taxonomy of the group has proved difficult in the past, over half the species being placed in a single subfamily (Table 1) by Peters (1937). More recently certain groups have been carefully examined. Condon (1941) and Cain (1955) have reviewed the platycercines, and Moreau (1948) and Dilger (1960) have studied the genus *Agapornis*. Brockway has made an ethological study of *Melopsittacus undulatus* (1962), and the head-scratching behavior and its distribution has been analyzed (Brereton and Immelmann, 1962). The general ecology of all species in northern New South Wales has been undertaken by Brereton and Sourry (1959) and Brereton (MS) with these things in mind, and after an examination of some of the older literature, a more satisfactory taxonomic arrangement of the order seemed possible. This is considered in the second part of the paper. In general, the nomenclature used for genera and species is that of Peters (1937). However, *Cacatua* and *Eclectus* are used rather than *Kakatoe* and *Lorius*, and *Barnardius* has been retained as recommended by Condon (1941) and Cain (1955). Rather than follow Cain, *Eunymphicus* is used in preference to its being placed in synonymy with *Purpuriecephalus*, even though they do appear very closely related. Suggestions for superfamily and family names, largely following Salvadori, appear in the text and in Table 5 (to be presented later). When family names are used in this paper, it is in the sense of Table 5, while subfamily names are in the sense of Peters (1937).

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SOCIAL BEHAVIOR AND EVOLUTION

Breeding Structure and Population Regulation

Any study of the evolution of a group is incomplete without some knowledge of the social behavior and breeding structure, and manner of population regulation of the evolving elements within the group. As in all such studies, this aspect of the evolution of the Psittaciformes is imperfectly known. Nevertheless, I wish to make a short report here on a study of this nature for one species, and to consider these preliminary results against our sketchy knowledge for other forms.

A detailed study of the biology of the Eastern Rosella (*Platycercus eximius*) has been in progress for the past 4 years at the University of New England, New South Wales, by means of capture–recapture methods, field observations, and cage studies. In summary, the seasonal changes are these. In autumn, during the day, small parties of 4–8 individuals feed on the ground, or fly to trees to rest or avoid danger. In the evening they roost in the outer foliage of shrubs or trees in flocks of about 25 individuals. In winter they feed in larger groups of 25–30 individuals, but the groups sometimes reach much larger size, even up to several hundred birds. In early spring the birds again occur in smaller units, and now spend much of their time in patches of woodland where large eucalypts occur with suitable holes for breeding. These small groups of about six birds are probably family parties. This relationship holds throughout the 2–3 months during which the search by the parents for a suitable nest hole continues, and for the period up to the beginning of fledging. At this point, the ties with the juveniles become more tenuous. Immediately after fledging, a second brood is often started, and during some weeks of this time the male feeds the fledglings. During this period it is extremely difficult to determine exactly what happens, but by autumn the typical groups have 4–8 birds. It seems likely that population adjustment occurs during this period, probably by the "budding off" of earlier broods which sometimes join others to form nonbreeding flocks.

The results of the capture–recapture study indicate that adults live typically more than 4 years and probably much longer, but most of the juveniles disappear within the year. The trapping shows no movement between the three colonies studied, which are 5 miles apart, and each of which consists of about 30 individuals. As trapping is only possible in the winter, it is not known how much gene flow occurs between colonies; but it may be very small, as pairs appear to remain together throughout the year and from year to year, although only two pairs have been followed in any detail so far.

The Eastern Rosella has 19 known calls, determined by field observations and tape recordings of caged birds. These are: 1 generalized alarm, which may bring up to 20 individuals to the calling bird; 1 flight alarm; 8 post-flight, by which individuals appear to maintain association; 5 having to do with agonistic displays; 3 very quiet or "murmuring"; and 1 food-begging. Plumage pattern is almost the same for different age groups and sexes, but the female and juveniles are duller. The latter also have a band of white dots on the gray background under the wing, while males lack this band and are densely black in this region. This character is universal for the platycercines. In the platycercines in general, the central four tail feathers are almost equal in length and dark in color, while each of the four lateral feathers on each side has its distal portions white or paler in color. This pattern becomes conspicuous when the tail is splayed, as in certain agonistic behavior. The tail of the platycercines is less splayed in flight than that of the loriines or pezopoporines, and its function is therefore more epigamic than aerodynamic.

Courtship feeding is restricted in *Platycercus eximius*, *P. adscitus*, and *P. elegans*, and courtship preening has never been observed. This is in sharp contrast with the related genus *Psephotus*, where courtship feeding and preening occur freely. Another behavioral point of distinct difference lies in the fact that *Platycercus* holds food in the foot, while *Neophema bourkii* and *Psephotus haematonotus* have never been seen to do so.

From the foregoing sketch we see that the breeding unit is highly sedentary and is composed of established pairs while the juveniles spend a comparatively short time with this group. We have no knowledge of what happens to them, but we do know that no ringed individuals have moved from one of our known colonies to another. It is assumed that they move away (they may account for the flocks of juveniles that are found in the winter at times), and it is further postulated that, in general, it is they who maintain "pressure" at the distributional boundary of the species. These are the individuals that may succeed in colonizing new and sometimes distant habitats, and that tend to exploit new niches in old habitats. If they are successful in any of these activities and if they are genetically isolated from their parent colonies, they are incipient new species. This, of course, is not the only way a sedentary species of parrot may speciate. If some form of climatic or geographical change breaks up the range, sedentary species are apt to undergo speciation, especially if the regions isolated are rather different from one another. On the other hand, a nomadic species may continue to range over the whole area, jumping from one isolate to another. Even where such a species lives in very tight colonies, it will show little morphological variation, because the environmental effect will be the same for all colonies. I will now consider degrees of social behavior and nomadism in more detail in connection with speciation.

Social Behavior in Sedentary and Nomadic Species

Individuals of *Platycercus eximius* are not seen singly but in groups of various sizes. Much of their behavior appears to be coordinated so that individuals act with the group. They are seen feeding, flying, resting, roosting, and bathing together. If a wild bird is caught and held in the hand, it gives the generalized alarm call which may bring 20 or 30 other individuals to the site. In the relative vastness of the local environment it seems unlikely that these associations are accidental, especially when we recatch birds at the same place over and over again, often together. This coordination of activities, and even defense of a captured individual, requires communication between individuals, and frequently ability to recognize individuals. These signals may be given visually and/or audibly.

TABLE 1.—SUMMARY OF GENERA, SPECIES, AND SUBSPECIES OF ORDER PSITTACIFORMES[a]

Subfamily	Genus	Species	Subspecies
Strigopinae	1	1	0
Nestorinae	1	3	1
Loriinae	14	58	84
Micropsittinae	1	6	13
Cacatuinae	4	16	30
Psittacinae	58	248	319
Totals	79	332	447

[a] Modified from Peters (1937) according to Cain (1955) and Dilger (1960). *Lathamus* and *Nymphicus* are also moved to Psittacinae.

Most birds that fly in large flocks (e.g. the brush-tongue parrots [Loriinae, Tables 1 and 2], *Cacatua galerita, C. roseicapilla, Nymphicus,* many waders, ibis, Black Swans, etc.) show—while in flight—little or no difference in the plumage of males, females, and juveniles. Every individual gives and receives the same signal in the flock. The plumage of *Platycercus eximius* is like this, showing only the small sex and age differences noted above, although this species does not make long flights, nor does it fly in tight and orderly formations. In both these respects it is like most members of the Platycercidae. However, in the genus *Psephotus* the sexes are often markedly different in plumage pattern, although courtship preening is very extensive. This similarity in the plumages of most platycercines suggests that social coordination is important even though it may not be closely connected with flock flight. It may allow the juvenile males to move with the parental group for a longer period, even after sexual maturity is reached, thus contrasting with some members of the Alisteridae and Palaeornithidae, which have very marked differences in male and female plumage. According to aviculturists' reports, mature males of *Alisterus* and *Aprosmictus* are very intolerant of one another, rivals being killed if kept in the same cage (see also Vane, 1961). Several males and females of *Platycercus eximius* may be kept in the same cage, although they will not develop into breeding condition if this is done.

The degree to which a pair of parrots will tolerate another pair of their species nearby varies greatly from species to species. Within the genus *Cacatua* we find species in which pairs nest close together, even in the same tree (e.g. *C. sanguinea, C. roseicapilla*), while *C. leadbeateri* pairs are always distant. In the development of various calls, there are also wide differences both between families and between species.

It is difficult to define social behavior and to decide if one species is more or less social than another. Sociality coordinates behavior when group behavior is more advantageous than individual behavior; thus, all sexually reproducing animals have some behavior which we shall call social behavior because it involves the coordination of two or more individuals. From this low level, development progresses to a point where nearly all activities are coordinated. Although this gradation in the degree of sociality makes it difficult to compare this attribute of species, it is both an interesting and an important subject for investigation within an evolutionarily related group of animals.

Table 2 represents an attempt to evaluate sociality in a single index for a group of parrots from northern New South Wales. The ecology and behavior of these birds are fairly well known. All manifestations of sociality so far recognized, involving more than the coordination of the parental pair, have been listed and subjectively scored. The sum of these values gives a crude measure of sociality. If the results are examined, a number of points emerge.

In the first place, there is a tendency to homogeneity within families (as listed later in Table 5), although this is far from absolute, as is shown in the genus *Cacatua*. Next is the correlation of high sociality scores in nomadic species, pointing to an evolutionary correlation of increased sociality with this way of life:

Type	*No. of Species*	*Range*	*Average*	*Subspecies per Species*
Nomadic	2	100	100	0.75
Migratory–nomadic	2	76–83	79	0
Sedentary–nomadic	3	76–80	78	1.0
Sedentary	6	37–67	51	1.6

The biological significance of this result is not hard to see for desert and honey-eating forms. On the other hand, it is not clear why the score should be so relatively high for sedentary species, unless it is an adaptation to population regulation (Brereton, 1959). Perhaps sedentary species regulate in one of two ways: (a) by being solitary and widely spaced, or (b) by

TABLE 2.—CORRELATION OF SOCIAL CHARACTERS WITH FLOCK MOVEMENT IN SOME PARROTS OF NORTHERN NEW SOUTH WALES

Genus or Species	Movement	PLUMAGE		Partner Preening	Courtship Feeding	Winter Roosting	Winter Feeding	Summer Nesting	Summer Feeding	Flight Flock Call	Feeding Call	Total Score
		Sex	Fledgling									
Trichoglossus spp.	Nomadic	10	10	10	10	10	10	10	10	10	10	100
Glossopsitta spp.	Nomadic	10	10	10	10	10	10	10	10	10	10	100
Calyptorhynchus spp.	Sedentary nomadic	7	7	10	10	10	5	5	5	10	10	79
Cacatua galerita	Sedentary nomadic	10	10	10	0	10	10	6	10	10	0	76
C. leadbeateri	Sedentary	10	10	10	0	5	10	2	2	8	0	57
C. sanguinea	Sedentary nomadic	10	10	10	0	10	10	10	10	10	0	80
C. roseicapilla	Sedentary	10	10	10	0	7	10	7	3	10	0	67
Alisterus spp.	Sedentary	0	2	0	8	5	8	3	3	8	0	37
Aprosmictus spp.	Sedentary	0	2	0	8	5	10	5	5	8	0	43
Psephotus spp.	Sedentary	0	2	10	10	7	10	7	4	10	0	60
Platycercus spp.	Sedentary	7	2	0	6	7	7	3	4	3	1	40
Melopsittacus	Migratory nomadic	7	6	10	10	10	10	10	10	10	0	83
Nymphicus	Migratory nomadic	5	5	10	0	10	10	8	8	10	0	66

grouping and reducing the potential increase of the group. On the other hand, it may be the result of a formerly nomadic way of life.

It is now possible to compare the differences in subspeciation and the ability to colonize new habitats.

Evolutionary Change and Social Behavior

In Table 2 is summarized the number of additional subspecies per species for parrots of different indices of sociality. The nomadic and migratory–nomadic species fall below the sedentary species in this regard, although the samples are very small. The sample size can be augmented by the addition of some nomadic and sedentary species the sociality index of which we do not know, but which we can guess at from their taxonomy and ecology. In Table 3 a number of such nomadic and sedentary genera for continental Australia are given, together with the number of species and additional subspecies. The less social forms appear to have produced twice as many subspecies as the social forms. If (excluding *Nymphicus*) we consider the cockatoos for continental Australia, according to the species (10) and subspecies (20) listed in Peters (1937), we again find the sedentary (less social) species forming more subspecies: sedentary–nomadic, 1.6 subspecies per species; sedentary, 3.0 subspecies per species. A similar finding for some Australian passerines was obtained by Keast (1961), although nothing is known of their levels of sociality.

TABLE 3.—COMPARISON OF CAPACITY OF SOCIAL AND SEDENTARY SPECIES TO FORM SUBSPECIES ON THE AUSTRALIAN CONTINENT

Type	Genus	No. of Species	Additional Subspecies	Ratio Additional Subspecies per Species
SOCIAL (NOMADIC) SPECIES	*Trichoglossus*	1	3	
	Psitteuteles	1	0	
	Glossopsitta	3	0	
	Opopsitta	1	2	
	Melopsittacus	1	0	
	Nymphicus	1	0	
	Totals and ratio	8	5	0.6
ASOCIAL (SEDENTARY) SPECIES	*Purpureicephalus*	1	0	
	Barnardius	2	6	
	Platycercus	6	11	
	Neophema	6	3	
	Psephotus	5	6	
	Totals and ratio	20	26	1.3

Having considered the differences in subspeciation in sedentary and nomadic parrots on the continent of Australia, it is useful to compare the degree of subspeciation for those genera of the Loriinae and Psittacinae that occur in three or more of the regions—Wallacia, Australia, New Guinea, and the Pacific. The data are presented in Table 4. For Wallacia there is again more subspeciation in the sedentary forms, but not for Australia and New Guinea. The apparent anomaly in the case of Australia comes about as a result of the fact that those members of the Psittacinae that occur in Australia *and* outside the continent are recently acquired rain-forest and wet-forest forms. New Guinea also is anomalous, perhaps because it easily accepts colonizing species of loriines from Wallacia but does not do likewise for sedentary species. Loriines as nomadic social species do not have efficient forms of interspecific interaction as they do not defend a specific area, while sedentary forms, which even exclude members of their own species from adjacent colonies, may be very efficient at denying colonization to other sedentary forms.

TABLE 4.—THE NUMBER OF SPECIES AND ADDITIONAL SUBSPECIES IN LORIINAE AND PSITTACINAE OCCURRING IN THREE OR MORE OF THE REGIONS WALLACIA, AUSTRALIA, NEW GUINEA, AND THE PACIFIC

Subfamily and Genus	WALLACIA		AUSTRALIA		NEW GUINEA		THE PACIFIC	
	Sp.	Subsp.	Sp.	Subsp.	Sp.	Subsp.	Sp.	Subsp.
LORIINAE[a]								
Chalcopsitta	2	1			4	4	1	0
Trichoglossus	2	10	1	3	1	3	2	1
Psitteuteles	2	3	1	0	1	0		
Domicella	5	4			2	5	2	2
Charmosyna	4	4			7	9	5	0
Opopsitta	2	3	1	2	2	8		
Totals	17	25	3	5	17	29	10	3
Subspecies per species	1.5		1.7		1.7		0.3	
PSITTACINAE[a]								
Lorius	1	8	1	0	1	0	1	1
Geoffroyus	1	11	1	0	2	4	2	2
Aprosmictus	2	1	1	1	1	0		
Alisterus	1	4	1	1	2	3		
Totals	5	24	4	2	6	7	3	3
Subspecies per species	4.8		0.5		1.2		1.0	

[a] As used by Peters (1937).

The markedly lower level of subspeciation on Pacific islands should be noted. This is likely to be the result of their comparatively recent colonization (cf. Mayr, 1940; Darlington, 1957). Both Wallacia and New Guinea are very rich in species of Loriinae, each having more species than the rest of the world put together. Beyond reasonable doubt, these two regions are the center of origin of this group. Unfortunately, we cannot deduce what proportion of this richness is the result of isolation by sea, and what proportion is the result of some form of isolation in New Guinea. We can, however, deduce that the Loriinae are good at colonizing distant unsaturated islands, for they are as common in the Pacific as the Psittacinae, a condition that we should not expect, as there are only 58 species of Loriinae against about 100 species of equally well-situated Psittacinae. Nomadic social species would be expected to be good colonists, as they should arrive at distant places in flocks, while sedentary species should often arrive individually. Thus, we may tentatively conclude that nomadic social species do spread more easily than sedentary species, but do not speciate as easily as do sedentary forms.

A POSSIBLE PHYLOGENY OF THE PSITTACIFORMES

The Characters Studied

During the latter part of the nineteenth century a good deal of comparative internal anatomy was done on the Psittaciformes by Garrod (1873*a*, 1873*b*, 1874, 1876), Forbes (1879, 1880), Mivart (1895, 1896*a*, 1896*b*), Parsons and Beddard (1893), Thompson (1899), Mudge (1902), and Beddard (1898) in an effort to establish a phylogeny of the order. The final arrangement of the internal anatomists proved to have very little appeal, perhaps because the intuition of the naturalists, or their "feeling for the group," led them to mistrust an arrangement that brought into the same subfamily the large flightless *Strigops* of New Zealand and the small lovebird *Agapornis* of Africa; likewise, *Nestor* did not seem to fit well with *Ara* and *Psittacus*. Salvadori's classification (1891, 1905) based almost entirely on external characters was much more satisfactory. Nevertheless, the findings of internal morphologists, especially those of Thompson (1899) on cranial osteology, showed up a number of important weaknesses in Salvadori's scheme, especially in his families Conuridae, Pionidae, Psittacidae, and Palaeornithidae. Thus, with confidence in both camps undermined, Peters (1937) had little choice but to neglect very largely the divisions resulting from the two divergent viewpoints and to place (Table 1) all the doubtful species in one subfamily (Psittacinae). It accounts for 75 percent of all the species in the order. Boetticher (1959) rearranged the order very largely on external features, but his arrangement does not agree well with that presented here. Brereton and Immelmann (1962) recently found that the Psittaciformes contained both over-wing and under-wing head-scratching behavior, and that for the Loriinae and Cacatuinae the character was consistent, while groupings for the Psittacinae tended to be related to zoogeographical divisions. Some of the anomalous species such as *Amoropsittaca*, *Psilopsiagon*, *Bolborhynchus*, and *Forpus*, which alone among the known neotropical forms scratch over the wing, required further study. Thompson (1899) stated that the neotropical species *Pionites* and *Graydidascalus* were considerably different from other neotropical species in their skull morphology, and that they may have closer affinities with Old World forms. As scratching over the wing appeared to be an Old World character, examination of the cranial morphol-

(Text continued on page 510)

TABLE 5.—A POSSIBLE ARRANGEMENT OF SOME PARROT GENERA AND SPECIES INTO FAMILIES

Explanation of Symbols and Abbreviations Used

Column

1 Temporal fossae: relative development (*1—2—3—4*).
2 Postsquamosal fossae: relative development (*1—2—3—4*), *4* being deepest.
3 Head scratching: *un* = under the wing; *ov* = over the wing.
4 Ambiens muscle: + = present; — = absent.
5 Carotid-artery arrangement:
  ls = right carotid normal in the hypophyseal canal while left is superficial;
  2 = carotids symmetrical, both normal in hypophyseal canal;
  1–2 = left only is present in some genera.
6 Wing shape: *B* = broad or low-aspect ratio; *N* = narrow or high-aspect ratio.
7 Hyoid: *sp* = short parahyal process;
  lp = long parahyal process;
  ar = parahyal arch.
8 Furcula: + = present; — = absent.
9 Oil gland: + = present; — = absent.
10 Auditory meatus: *op* = open; *crs* = crescentic.
11 Orbital-ring development:
  cf = complete; prefrontal process joins postfrontal process;
  cq = complete; prefrontal process joins both postfrontal and squamosal;
  f = orbit incomplete, tends to join postfrontal;
  q = orbit incomplete, tends to join squamosal.
12 Geographic distribution:
  A = Australian
  Eth = Ethiopian
  Nt = Neotropical
  O = Oriental
  a = Australian mainland
  m = Madagascar
  nc = New Caledonia
  ng = New Guinea
  nz = New Zealand
  p = Pacific islands
  w = Wallacia
13 Tail length: *l* = long; *m* = medium; *s* = short.

	Temp. Fossa 1	Postsq. Fossa 2	Scratch 3	Ambiens 4	Carotid 5	Wing Shape 6	Hyoid 7	Furcula 8	Oil Gland 9	Auditory Meatus 10	Orbital Ring 11	Geogr. Dist. 12	Tail Length 13
SUPERFAMILY I: Cacatuoidea													
CACATUIDAE													
Strigops	4	1	un	±	2	B	sp	—	+	op	cf	A-nz	m
Probosciger	4	1	un	—	2	B		+	—	op	cfq	Aa-ng	ms
Calyptorhynchus	4	1	un	—	2	B		+	+	op	cfq	Aa	l
Callocephalon	4	1	un	—	2	B		+	+	op	cfq	Aa	m
Cacatua	4	1	un	—	1–2	B		+	±	op	cfq	Aa-w-p	s
PALAEORNITHIDAE													
Tanygnathus	4	1		—	2			+	+	op	q	O	l
Eclectus	4	1	un	—	2			+	+	op	q	O	s
Prioniturus				—	2			+	+			O-w-p	ml
Geoffroyus	4	1		—	2					op	q	O-ng-a-w	s
Psittacula	4	1	un	—	2	N		+	+	op	q	O	l
Psittinus	2	1	un	—	2	N		+	+	op	cq	O	s
AMAZONIDAE													
Anodorhynchus	4	1	un			B				op	f	Nt	l
Ara	4	1	un	+	ls	B	sp	+	+	op	cf	Nt	l
Aratinga	4	1	un	+	ls	B		+	+	op	cf	Nt	l
Pionites	4	1	un	+	ls	B					q	Nt	ms
Pyrrhura	4	1	un		ls	B					cf	Nt	l
Pionopsitta				—	ls	N		+	+			Nt	s
Deroptyus			un	—	ls	B		+	+			Nt	ms
Amazona	4	1	un	—	ls	B		+	—	op	cf	Nt	s
Brotogeris	3	2	un	—	ls	N		+	—	op	f	Nt	s
Pionus	4	1	un	—	ls	B		+	—	op	cf	Nt	s

TABLE 5.—*Continued*

	Temp. Fossa 1	Postsq. Fossa 2	Scratch 3	Ambiens 4	Carotid 5	Wing Shape 6	Hyoid 7	Furcula 8	Oil Gland 9	Auditory Meatus 10	Orbital Ring 11	Geogr. Dist. 12	Tail Length 13
PSITTACIDAE													
Poicephalus	4	1	un	+	ls			+	+	op	q	Eth	l
Psittacus	4	1	un	+	ls		sp	+	+	op	q	Eth	s
Coracopsis	4	1	un	—	ls			+	+	op	q	Eth-m	m
Psittrichas	4	1		—	ls			+	+	op	q	A-ng	l
Prosopeia	4	2		—	ls			+	+	op	q	A-p	m
SUPERFAMILY II: Platycercoidea													
NESTORIDAE													
Nestor	1	4	ov	+	ls	B	ar	+	+	crs	q	A-nz	m
LORIIDAE													
Trichoglossus	2	4	un	—	2	N	ar	+	+	crs	q	Aa-p	l
Vini	2	4		—	2	N		+	+	crs	q	A-p	m
Chalcopsitta	2	4	un	—	2	N		+	+	crs	q	A-ng-w	l
Eos	2	4		—	2	N	ar	+	+	crs	q	A-w	l
Domicella	2	4	un			N	ar			crs	q	A-ng-w-p	m
Glossopsittacas	2	4				N				crs	q	A-a	s
MICROPSITTIDAE													
Loriculus	2	3	ov	—	2	N	lp	+	+	crs	q	Aa-w-O	s
Micropsitta	2	3		—	2	N	lp	—	+			Aa-w	s
Agapornis	4	1	ov	—	2	N	lp	—	+	crs	q	Eth	s
ALISTERIDAE													
Alisterus													
scapularis	2	4	ov	—	2	N		+	+	crs	q	Aa-w	l
amboinensis	2	4								op			l
Aprosmictus	2	2	un	—	2	N		+	+	crs	q	Aa-ng	l
Polytelis	1	3	ov	—	2	N		+	+	crs	q	Aa	l
Nymphicus	3	3	ov	—	2	N		—	+	crs	cfq	Aa	l
PEZOPORIDAE													
Melopsittacus	3	3	ov	—	2	N	ar	+	+	crs	cfq	Aa	l
Geopsittacus				—	2	B		—	+			Aa	l
Pezoporus						B						Aa	l
PLATYCERCIDAE													
Neophema	2	3	ov	—	2	B		—	+	crs	q	Aa	l
Psephotus	2	3	ov	—	ls	B		—	+	crs	q	Aa	l
Lathamus	2	3	ov		ls	B	sp	+		crs	q	Aa	l
Eunymphicus	2	3	ov	—	ls	B		+	+	crs	q	A-nc	l
Cyanoramphus	2	3	ov	—	ls	B		—	+			A-nz-p	l
Barnardius	2	3	ov			B				crs	q	Aa	l
Platycercus	2	3	ov	—	ls	B		—	+	crs	q	Aa	l
Purpureicephalus	2	3	ov			B				crs	q	Aa	l
FORPIDAE													
Forpus	3	2	ov	—	ls	N	lp	—	+	crs	q	Nt	s
Amoropsittaca	2	2	ov	+		NB		+		crs	q	Nt	m
Psilopsiagon	2	2	ov	+				+	+	crs	q	Nt	ml
Bolborhynchus			ov	+	ls	N		+	+			Nt	s

ogy seemed important, and preliminary observations did seem to confirm affinities with Old World groups (Brereton and Immelmann, 1962). This has led to a more thorough assessment of the literature on internal morphology, together with the examination of 75 skulls representing 22 genera, and field and cage-bird observations on the ecology and behavior of some Australian species. Seventy-one characters were selected initially as being likely to be helpful; but, owing largely to the patchiness of information, these were reduced to 13. In 56 species, most of the 13 characters were known, and from these data tentative groupings have been constructed (Table 5). The following remarks briefly describe the characters used.

Cranial Osteology.—Thompson (1899) studied the skulls of 54 species drawn from all of the families listed by Salvadori (1891). He paid particular attention to the condition of the orbital ring, temporal fossa, the suprameatal tubercle, the presence or absence of a notch in the squamosal process, and the degree and shape of opening of the auditory meatus. Reexamination of this work confirms its soundness and brings out, in addition, the need for further studies to explain precisely the function of the structures studied. Hofer (1953) explains some changes that have occurred in this region of the psittacine skull, but much remains to be done to explain the function and evolutionary significance of the postsquamosal fossa, which appears to replace the temporal fossa in importance in the superfamily Platycercoidea, as shown in Table 5.

The studies of Mivart (1895, 1896*a*, 1896*b*) on the hyoid apparatus have shown that the Loriinae are characterized by a parahyal arch. All other parrots studied, with the exception of *Nestor* (Mivart, 1896*b*) and *Melopsittacus* (Thompson, 1899), lack this arch. Mudge (1902) followed this up with a study of hyoid musculature embracing species from all the major groups. He deduced a phylogeny from this single group of characters. The hyoid apparatus together with the relative development of the temporal and postsquamosal fossae, the degree of development of the orbital ring, and the degree of opening of the auditory meatus have been selected in this study and, together with other characters, are indicated in Table 5. Column No. 1 and 2 show the relative development of the temporal and postsquamosal fossae, column No. 11 shows the development of the orbital ring.

Head Scratching.—The behavior of head scratching by the foot has been studied and the results for 100 species are reported in Brereton and Immelmann (1962). The relevant results are recorded in column No. 3 in Table 5.

Ambiens Muscle.—The anatomy and distribution of this character are discussed by Garrod (1873*a*, 1874, 1876). The results are shown in Table 5 in column No. 4. *Strigops* gave variable results and is entered as ±. It is clear from the table that presence or absence is not correlated with the manner of head scratching. The ambiens appears to be a relict structure existing in a few neotropical species and in *Nestor* and *Strigops*.

Carotid Arteries.—The arrangement of the carotid arteries varies in this order, as described by Garrod (1873*b*, 1874, 1876). These results are summarized in Table 5, column No. 5.

Wing Shape.—The aerodynamic characteristics of wings, tail, and body features should prove of great usefulness for taxonomic and evolutionary studies. The work on this aspect of the study is not complete, but a number of points can be made. The wing-beat action is highly characteristic in the platycercines, pezoporines, calyptorhynchines, and cacatuines, as sight and motion-picture records easily show. Other features of flying technique are being studied. In the case of the loriines, platycercines, and probably other groups, aspect ratio and wing loading are diagnostic. The amount and manner of slotting are also useful characters (Condon, 1941; Cain, 1955). In Table 5, wings have been simply characterized as broad or low-aspect ratio and as narrow or high-aspect ratio, the necessary data for the calculations being lacking, except for some Australian species.

Furcula.—Garrod (1874, 1876) regarded the presence or absence of the furcula as an important character suitable for determining familial relationships. In the present scheme it is considered to be comparatively plastic, and to have been lost separately in several groups. As is so often the case, our lack of understanding of its function prevents our assessment of its adaptive importance and evolutionary direction. Garrod's results are summarized in Table 5, column No. 8.

Oil Gland.—The oil gland (Table 5, column No. 9) is lacking in *Probosciger*, *Amazona*, *Pionus*, and *Brotogeris* (Garrod, 1876), and it is much reduced in *Cacatua sulfurea* (Beddard, 1898). Two lumbar powder-down patches exist in *C. sulfurea*, *Calyptorhynchus magnificus*, and *Nymphicus*. There are scattered patches in *Brotogeris*, *Coracopsis*, *Amazona*, *Pionus*, and *Psittacus* (Beddard, 1898). This suggests a tendency toward loss of the oil gland, especially in the cockatoos and American parrots.

Zoogeographical Characters.—The distribution of each genus is summarized in Table 5, column No. 12. The regions recognized follow Darlington (1957).

Tail Shape and Length.—Some data in the literature permit the calculation of the ratio of tail to wing and total length, but this is not universal. Until skins and specimens can be measured in a standard way, it seems better to record the tail here as either long, medium, or short. The tails of parrots may fall into a number of categories according to length and graduation. The tail has both an aerodynamic and social releasing function (e.g. in *Platycercus*), and further study will no doubt greatly increase the value of this character.

Arrangement of the Group

The suggested arrangement of the order Psittaciformes into families on the basis of the study of 56 of the 79 genera is shown in Table 5. It is stressed that this is a tentative arrangement, the usefulness of which will be determined by further work, especially in behavior and also, it is hoped, in egg-albumen studies.

Two major divisions or superfamilies are postulated, based on (1) a major change in the skull involving at least three conspicuous characters and (2) the method of head scratching. In the first superfamily, which might be called Cacatuoidea, the temporal muscle is large and runs in a well-developed fossa, the skull is long, the auditory meatus tends to be widely open and square in shape, and head scratching is under the wing. The postsquamosal fossa tends to be greatly reduced. *Strigops* approaches the stem features for this superfamily. In the other superfamily, which might be called Platycercoidea, there is a great development of the postsquamosal fossa, reduction or loss of the temporal fossa, marked forward growth of the posterior boundary of the auditory meatus, generally giving the meatus a crescentic shape, and a strong tendency to head scratching over the wing. *Nestor* is a stem-like animal for this group. In more advanced forms, the deep flange of the squamosal has been eroded away to display the head of the quadrate, and in so doing to produce the notch stressed by Thompson (1899) as a platycercine character.

The type from which these two groups arose had the ambiens muscle, and it is still present in *Nestor*, and frequently so in *Strigops*. However, in more advanced forms it is rarely present.

Symmetrical carotids are also taken as an ancestral character, and *Strigops* and many species in the allied families possess this character. In the Platycercoidea several families also possess symmetrical carotids. The change from symmetrical carotids to the superficial condition of the left appears to have occurred a number of times, and a similar conclusion is necessary for the loss of the ambiens muscle and the development of a full orbital ring, as in the Cacatuidae and Pezoporidae. Similarly, this scheme requires the independent evolution of scratching over the wing for the family Amoropsittidae if its affinities are not truly with the Platycercoidea.

To summarize, it is postulated that an ancestral group existed with the following characters: deep temporal fossa, scratching under, ambiens muscle, symmetrical carotids, broad wings, short parahyal process, furcula, oil gland, open auditory meatus, and incomplete orbital ring with prefrontal tending to join postfrontal.

At some early point in the past history of these parrots, a trend developed which gave rise to narrow wings, deep postsquamosal fossa, parahyal arch, a crescentic-shaped auditory meatus, and a tendency for the prefrontal to join the squamosal. The tendency to scratch over the wing was strong, and it developed in 6 of the 7 families. This division took place before the ambiens muscle was totally lost, and the symmetrical carotids had all become asymmetrical. Such a phenomenon is not difficult to envisage, for the platycercines today have the potential to produce two diverging lines, one with symmetrical carotids and two scalloped primaries (*Neophema*), and the other with the *ls* carotid condition of Table 5 and five scalloped primaries (e.g. *Platycercus*).

The genus *Agapornis* is close to this intermediate condition, having marked affinities with the Cacatuoidea in its deep temporal fossa, but also having definite signs of a crescentic auditory meatus and scratching-over behavior; it is best considered in the Platycercoidea. However, *Agapornis* appears to resemble *Psittinus*, and *Psittinus* resembles *Psittacula*, which could never be forced into the Platycercoidea. Yet *Agapornis* resembles *Loriculus* in many ways (Dilger, 1960). If we place *Agapornis* in the Platycercoidea, it is the only species there with a deep temporal fossa, and the only member of this superfamily in the Ethiopian region. On the other hand, if we place it in the Cacatuoidea, it is the only one with over-wing scratching in that assemblage. *Agapornis* therefore may stand close to the division of the two superfamilies. A rather similar anomaly occurs with *Alisterus*; *A. scapularis* is typical, but *A. amboinensis* has virtually an open type of auditory meatus. This species would repay further study (see also Vane, 1961). In the same family Alisteridae, there is another interesting problem in *Aprosmictus*, which scratches under the wing and has a less marked postsquamosal fossa than *Alisterus*. Perhaps this family is close to the point of division. Attention should also be drawn to the inclusion of *Nymphicus* in the family Alisteridae. This genus is usually placed near *Cacatua*, partly because it is crested, but probably chiefly because the orbital ring is complete as in the cockatoos. However, the crescentic shape of the auditory meatus and the platycercine type of postsquamosal fossa, together with scratching over, suggest that its correct position is with the Platycercoidea. It is difficult to know where it should be placed within the superfamily. It is possible that it is closer to the Pezoporidae, especially the genus *Melopsittacus*, but considerably more work is required before these genera and *Geopsittacus* and *Pezoporus* can be confidently assessed and arranged.

The Platycercidae present much firmer ground. As Table 5 shows, the family includes *Neophema*, *Psephotus*, *Lathamus*, *Eunymphicus*, *Cyanoramphus*, *Barnardius*, *Platycercus*, and *Purpureicephalus*. Doubt has always existed about the rightful place of the Swift Parrot (*Lathamus discolor*), but there is no need for this doubt. The species lacks the parahyal arch of the loriines and has a typical platycercine hyoid (Mivart, 1896*b*). In its way of scratching and its carotid arteries, it is platycercine and not loriine. Forbes (1879) states that it is platycercine in pterylosis, beak, nostrils, cere, feet, skull, pelvis, feathering around the eye, and rounded remiges. It also possesses the wing spots and tail markings of *Platycercus* discussed below. On the other hand, the tongue has a brush of hairs; also, its nomadic or migratory movement in following the blossoming of trees, the red markings around the head, and its noisiness in feeding and in flock flight are all loriine features. Such features must be shown to be homologous in detail with those of the Loriidae before they can be weighed against the clear-cut platycercine characters. Further, I cannot consider *Lathamus* as a stem animal for both the Loriidae and the Platycercidae, for the evolution of symmetrical from asymmetrical carotids seems unlikely.

Aside from what has already been said of platycercine characters, it is important to discuss five further points. In the first place, this group is unified by features of the tail: The four central rectrices are almost equal in length, and the lateral ones are paler at the distal end, so that when the tail is splayed a distinct pattern is formed. Secondly, homologous behavior is seen in the tail wobble, tail splay, beak clatter, and in-flight wing retraction. A third feature is the occurrence of a linear series of spots under the wing in juveniles and females (Condon, 1941). Fourthly, a well-developed tendency exists for a wing of low-aspect ratio. This is associated with a tendency to increase in length of the seventh and eighth primaries relative to the ninth and tenth, and to increased slotting through emargination of the seventh and sixth primaries in addition to the ninth and eighth, which are emarginated in the Alisteridae and Pezoporidae, but not the Loriidae. Finally, the Platycercoidea are found exclusively on the Australian mainland and Pacific islands.

The precise origin of the Platycercidae cannot be easily shown. The family has affinities with the Pezoporidae, Alisteridae, and Loriidae in a number of ways. It would take up too much space to consider this in detail here, but a number of aspects should be briefly mentioned. In *Neophema* we find equal carotids as in the three families mentioned, while the wing action and shape are like those of the Alisteridae and Pezoporidae. Certain agonistic behavior patterns are less developed than in *Platycercus*, *Psephotus*, and *Barnardius*. *Eunymphicus*, which Cain (1955) has merged with *Purpureicephalus*, is clearly close to the *Platycercus* (sensu stricto) group. It seems possible that *Lathamus* and *Cyanoramphus* are fairly close, for the general markings are similar, and their tails are less well developed than other platycercines. The social nomadic behavior and tail shape of *Lathamus* may be homologous with those of the Loriidae, and it may therefore be a primitive platycercine, in spite of its *ls* carotid condition. If such is the case, the sedentary asocial ways of the platycercines may have evolved from nomadic social ones.

In attempting further to see the origin of the Platycercidae, we must take account of the Pezoporidae. The linear series of marks under the wing in the juveniles and females of the Platycercidae is a character occurring in the Pezoporidae. In *Melopsittacus*, *Pezoporus*, and probably *Geopsittacus*, this character is found in all individuals. In *Nymphicus* it is lost in the males, as in the Platycercidae. In a number of genera of the Loriidae this linear series is also seen in every individual, while there are genera where it is not found at all, and others in which it occasionally occurs. The relationship with the Pezoporidae can be seen in still other ways. The movement of the auricular feathers forward to obscure the lower beak occurs markedly in the

Pezoporidae (also the Cacatuidae), and is also seen to some degree in the Platycercidae. Webber (1948) noted that in *Pezoporus wallicus* the covering of the lower mandible by the auriculars helped the bird to merge with the grassy habitat when it "froze." None of the Pezoporidae hold food in the foot. This appears so also in *Polytelis*, although *Alisterus* and *Aprosmictus* will hold freely. The ground-feeding "grass parrots" have relatively long tarso-metatarsi and slender feet, while the tree-feeding and climbing forms have shorter tarso-metatarsi and larger feet. Both types occur in the Platycercidae, for *Neophema* and *Psephotus* do not climb and do not hold food in the foot, in contrast to the remainder of the family. Thus, in the Platycercidae we see genera related in various ways to other families, yet they hold together well. This appears to be further evidence for claiming that these families have a similar origin. Two of the families, Pezoporidae and Loriidae, are highly social, one being adapted to gathering seeds in arid grassland, and the other to getting honey from the blossom of trees and shrubs. It was perhaps the nomadic seed-eaters that found a way via grassland across the Antarctic Continent to South America, to produce there the family Forpidae.

On the point of going to press, the author became aware of an excellent paper on the classification of the Psittaciformes by Dr. René Verheyen: "Analyse du potential morphologique et projet d'une nouvelle classification des Psittaciformes" (1956), Institut royal des Sciences naturelles de Belgique 32:1–54. The general similarity of the two arrangements is remarkably close, although the characters used are to a large degree different.

The Enigma of "Platycercines" in South America

The final question that must be considered is the correct position of the Amoropsittidae. This family of four known genera has the characteristics of an advanced family of the Platycercoidea, and in this respect it is thoroughly anomalous zoogeographically. As a South American family, it is surrounded by the species of a family so numerous that they account for over half of the species listed by Peters (1937) in his subfamily Psittacinae. Two hypotheses are tenable: Either the platycercine type has arisen twice, or platycercines have made their way to South America comparatively recently. They show some signs of primitiveness in their retention of the ambiens and furcula, the limited development of the postsquamosal fossa, and their narrow wings. The skull of *Amoropsittaca* is very similar to that of *Neophema.* They occur from Central America to southern South America, generally in the higher parts of the Andes. Very little appears to be known of their ecology and behavior and, unfortunately, they are rarely found in aviaries. If further work proves their affinity with the Platycercoidea, there is presented the interesting problem of how they came to South America; on the other hand, if they evolved from the Cacatuoidea in South America, this is a most remarkable case of parallel evolution.

SUMMARY

The population and general ecology of *Platycercus eximius* is briefly considered. Its degree of sedentariness and social behavior is then compared with other Australasian parrots and an index of sociality is established. This is used in comparing the ability of social and asocial forms to colonize "unsaturated" habitats and to form subspecies.

The second part of the paper presents a re-arrangement of the genera of the order based on skull characters, head scratching, ambiens muscle, carotid arteries, wing shape, hyoid apparatus, furcula, oil gland, auditory meatus, orbital ring, zoogeography, and tail length. The order is divided into two superfamilies: Cacatuoidea and Platycercoidea. The Cacatuoidea includes families in the Australasian, Oriental, Neotropical, and Ethiopian regions. All the Platycercoidea occur in the Australasian region except for one family, which occurs in the Neotropical region.

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Evolutionary Trends in Nest Building by the Weaverbirds (Ploceidae)

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Among the external constructions built by animals, the nest of a bird is a classical example. Despite the central importance of nests in the life of birds, only very secondary consideration has generally been given by ornithologists to the study of nests, or caliology, compared with other aspects of avian biology. The weaverbird family (Ploceidae) would appear to be eminently suited for a comparative study of nests and nest building, since the weaverbirds build a greater variety of nests than does any other family of birds. Many years ago, Chapin (1917) used variations in nest form in his classical article on the taxonomy of the Ploceidae, and our reading of this article first acquainted us with the varied and elaborate assortment of nests constructed by this predominantly African family. More recently, Sálim Ali (1931), Friedmann (1930), Skead (1947, 1954, 1956, 1959), Morel and Bourlière (1956), Collias and Collias (1959*a*), Crook (1960), and Immelmann (1960) have described the nests of certain weaverbirds in some detail.

Our own studies have been in large part devoted to a comparative study of weaverbird nests and nest building as an example of the evolution of complex behavior patterns, and were made possible by a grant from the U.S. National Science Foundation. The field work for this project was conducted in various parts of Africa—central, eastern, and southern—over a 1-year period during 1956–57. In the course of this study we were advised and aided in many ways by Dr. and Mrs. James P. Chapin, as well as by many friends and colleagues in America, Europe, and Africa.

In general, our results are in close agreement with Chapin's classification of the Ploceidae, published in some detail in 1954, and we have used his taxonomy as a reference point.

FORM OF THE NEST

The dome of the nest is one of the most salient features of the Ploceidae, which is very largely a tropical family. The great majority of small birds in the North Temperate Zone build open, cup-shaped nests, or else nest in holes; domed nests are quite exceptional among small birds north of the tropics. In contrast, a domed nest is typical of many families of small, tropical birds having altricial young, and apparently helps provide some protection against the high predation, excessive rainfall, and extreme solar intensity of tropical areas (Collias and Collias, 1959*b*). Both the heating effect and the ultraviolet component of the sun's rays may be involved. Because of their normally high body temperatures, birds are quite resistant to such high air temperatures as are normally encountered in their environments. Small,

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naked nestlings would be expected to be more sensitive to ultraviolet than older birds covered with feathers. There may be 5–10 times more ultraviolet in tropical than in temperate areas (Goody, 1954), but the possible importance of this factor in the ecology of tropical birds does not seem to have attracted much attention. Recently, Skutch (1961) has pointed out that, as a rule, only birds that have roofed nests, or breed in enclosed spaces, sleep in their nests when not incubating or brooding young. Such a habit should furnish protection against both predators and weather. The weaverbirds typically breed during the rainy season, often in relatively exposed sites, and the roof of the nest would, of course, then help shelter the female and nestlings from the rain.

Of the subfamilies of weaverbirds, the Plocepasserinae, Passerinae, and Bubalornithinae appear to form one closely related assemblage; the Estrildinae, Viduinae, and Sporopipinae form another. The Ploceinae, or true weavers, are most nearly related to the Plocepasserinae.

We have confirmed the main characteristics of the nests in different subfamilies of Ploceidae, as previously described by Chapin (1917, 1954), Friedmann (1950), Moreau (1960), and others: the simple, nonwoven (Delacour, 1943; Morris, 1958) nest with side entrance typical of the weaver-finches (Estrildinae and Sporopipinae), the loosely constructed, feather-lined nests of the sparrows (Passerinae), the thorny covering of the nest in the buffalo-weavers (Bubalornithinae), the two-hole, compactly thatched nests of the typical sparrow-weavers (Plocepasserinae), and the woven nests of the true weaverbirds (Ploceinae). The Viduinae are nest parasites and ordinarily build no nest of their own. The stages in the possible evolution of the parasitic habit in weaverbirds have been recently described in a book by Friedmann (1960).

Our observations were made with special reference to the finer details of nest construction and to the mode of building of nests. Only one subfamily, the Ploceinae, can be truly said to weave the nest. We have been impressed by the similarity of the nest and nest building of the Sporopipinae to that of the Estrildinae, and by the primitive distinctness of the nest and nest building, relative to other Ploceinae, of *Amblyospiza albifrons*, the Grosbeak Weaver.

The sequences in nest building, i.e. what could be called the "ontogeny" of a nest, may be used to furnish clues to the phylogenetic relations of different types of nests.

In the more primitive weaverbirds the nest is begun as a cup or platform, before the dome is added, and this sequence suggests that a cup nest, rather than a domed nest, was the original and primitive type of nest built by the ancestors of the Ploceidae. The nest is typically begun as a simple platform or bowl to which the roof is later added in the Estrildinae, Sporopipinae, and Passerinae. The nest is started as a crescent or inverted arch, later roofed over and a hole left at either end, in the Plocepasserinae (except in the highly specialized nest of *Philetairus*) and *Dinemellia*, more primitive of the two genera of buffalo-weavers (Bubalornithinae). In the Ploceinae the nest is typically begun as a crescentic footrest, or sling, and the roof of the nest is generally started before the floor of the brood chamber, thus forming an initial ring. The initial footrest becomes the threshold of the entrance to the brood chamber. In *Amblyospiza*, however, the initial footrest is followed by building of the cup-shaped bottom of the brood chamber before the roof is added, as was noted by Roberts (1953) and confirmed by Crook (1960) and by ourselves.

Fig. 1. Variations in nests of weaverbirds: *A—Dinemellia dinemelli*; *B—Plocepasser mahali*; *C—Pseudonigrita cabanisi*; and *D—Philetairus socius.*

Fig. 1 and 2 illustrate some of the main types of weaverbird nests with photographs from nature of fresh nests, and Fig. 3 summarizes the main trends of evolution of nests in the Ploceidae, as deduced from observation of different stages in nest building and from comparison of nests of different species. The nests and building of the nest in some two dozen selected and representative species were studied by us in some detail in Africa, and in addition nests of many other species were also examined both in the field and at various museums.

By definition, no bird classified as a member of the Ploceidae has a cup-shaped nest. Semidomed nests are present in some Ploceidae that nest within enclosed spaces, e.g. the House Sparrow (*Passer domesticus*). But when this species nests in the open in branches of trees, as is well known, it builds a completely roofed, i.e. domed, nest. A domed nest with two entrances at either end is typical of *Plocepasser* among the sparrow-weavers. Presumably the second hole, which is plugged up in brood nests, functions as an escape hatch in case birds sleeping in the nest are surprised by a predator. In *Pseudonigrita*, another genus of sparrow-weaver, the two entrances open at the bottom of the nest, and it seems reasonable to assume that this more ventral position of the nest openings gives an added measure of protection from predators approaching along the branches of the colony tree.

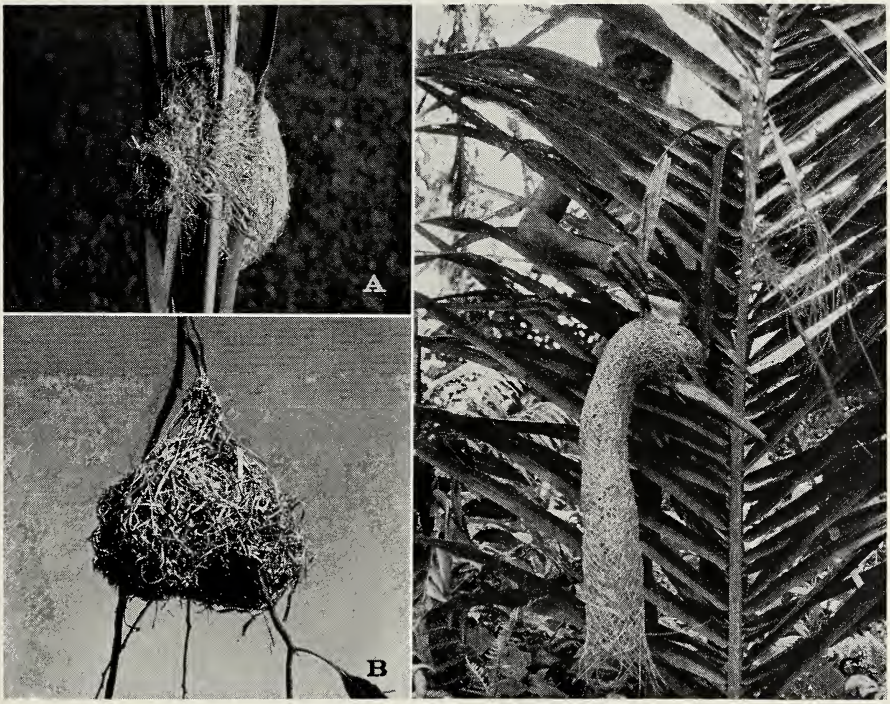

Fig. 2. Additional variations in nests of weaverbirds: *A—Amblyospiza albifrons*; *B—Textor velatus*; and *C—Malimbus cassini.*

The combination of insect associates and thorny trees is of frequent occurrence in certain weaverbirds inhabiting arid country and may well have been important to the evolution of greater gregariousness and of a compound nest. In Kenya we found three colonies of the Grey-capped Social Weaver (*Pseudonigrita arnaudi*) in which the nests were grouped into physically contiguous masses of up to nine nests. Two of these colonies were in ant-gall acacias occupied by hundreds of ant colonies. In contrast, we saw scores of colonies of this weaverbird in acacia trees that lacked ant galls and in only one of these trees were the different nests in physical contact, and in most instances there were only a few nests in each tree. Colonies of the South African Social Weaver (*Philetairus socius*) may also be associated with noxious insects, such as ants or wasps.

The giant compound nest of *Philetairus* has a dome-shaped communal roof that seems to have made unnecessary the function of an extra escape hole, and the numerous brood chambers in the underside of the nest mass each have only one opening to the exterior. *Philetairus* is often classified as a member of the Plocepasserinae. Similarly in the Bubalornithinae, the outer shell of twigs, often thorny twigs, gives an added measure of security against predators and helps to make possible a high degree of gregarious breeding.

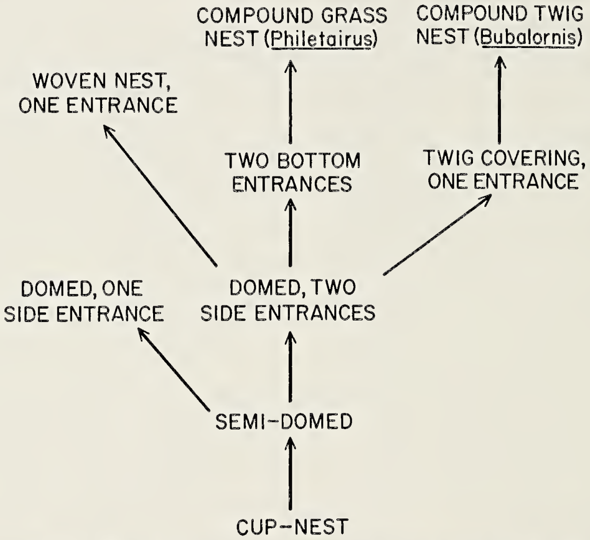

Fig. 3. Main trends in evolution of nest building in the weaverbird family (Ploceidae).

Domed nests placed in trees tend to evolve pensile attachment (from the roof), ventral entrance, and entrance tube, presumably protections against an approach from above by arboreal snakes (Van Someren, 1956; Pitman, 1958) and other predators. All of these features, which may be discerned even in some Plocepasserinae, are enhanced by the origin and evolution of weaving, and reach their culmination in the Ploceinae (Fig. 4). It would seem that the strength conferred on the walls by a woven construction aids the further evolution of the protective features mentioned above.

In contrast, nests of the Ploceinae having a side entrance, as in *Amblyospiza*, *Ploceëlla*, *Euplectes*, and *Coliuspasser*, are often to be found in marshy vegetation, slung between vertical stalks of reed grass or other herbaceous plants, and hence subject to the approach of nonavian predators from below.

Some of the detailed variations in nest form within the Ploceinae are characterized below in the form of a key. The materials used vary with species and habitat, but nest form appears to be quite consistent in different genera of weavers. There is evidence that entrance tubes have been evolved in at least two different ways in the Ploceinae (Fig. 4). Thus, in African species, the nest is retort-shaped, the entrance tube forms a more or less acute angle with the brood chamber below at the site of attachment; and even before the tube is added, the entrance is ventral in position. In contrast, the inner attachment of the entrance tube in Asiatic *Ploceus* forms an obtuse angle with the bottom of the brood chamber, enhancing the erect oval appearance of the brood chamber. In the Asiatic species *Ploceus manyar,* the entrance tube may be either present or absent in different nests with eggs, and the entrance to the nest may be either more or less lateral in position, or else at the bottom of an entrance tube. It is possible that the African retort-type nest has undergone a rotation to bring the originally lateral entrance to a ventral position, whereas Asiatic *Ploceus* seems to have retained the original erect positioning of the nest.

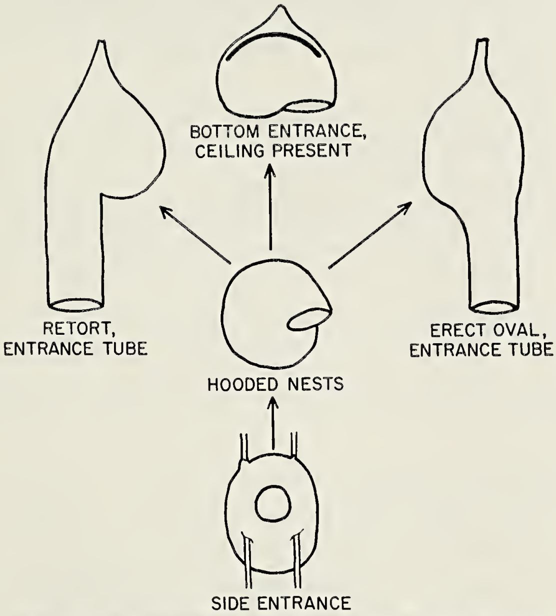

Fig. 4. Principal stages in evolution of nest form in the true weaverbirds (subfamily Ploceinae).

The special ceiling that characterizes the typical *Textor* nest is a nonwoven or thatched lining of the upper half of the nest. This ceiling may be composed of grass heads, acacia leaves, short, broad sections of grass leaf, or other materials. Its function is not clear, although it may help to shed rain.

Species of *Textor* with nests of grass-head ceilings are to be found especially in arid or semiarid savanna (e.g. *vitellinus, rubiginosus, velatus*), while species of *Textor* in which the ceiling consists of broad sections of grass leaf blade or of fair-sized dicot leaves are more likely to be found in more forested areas of frequent and abundant rainfall (e.g. *aurantius*, *nigerrimus*, and some races of *cucullatus*).

Our key (Table 1) to nests of the genera of Ploceinae is tentative in view of the present inadequacies of our knowledge, but nevertheless we feel that it is worth presenting as a summary and as a guide and stimulus to further work. A few genera, for which we have not personally been able to examine nest examples, have been omitted (e.g. *Symplectes* and *Melanoploceus*). When more is known of the manner in which the nest is built in all the ploceine weavers, it will be possible to have a more definitive key to the nests. The key presented here is based on completed nests, as judged by the presence of eggs or nestlings.

In general, those genera in the first part of the key have a side entrance to the nest and usually comprise granivorous inhabitants of marsh and grasslands, e.g. *Amblyospiza*, *Ploceëlla*, *Euplectes*, and *Coliuspasser*. In the second half of the key are included some genera of insectivorous forest species that nest in trees, and have nests with a well-developed entrance tube, i.e. *Hyphanturgus*, *Phormoplectes*, and *Malimbus*. The genus *Textor*, with a ventral entrance and little or no development of an entrance tube, contains more species than any other genus of Ploceinae. Some textors nest in trees in savanna and cultivated lands while others are to be found in marshes. Even those species of *Textor* in arid country are often to be found nesting near water.

In the preceding key, *Foudia sakalava* and other Madagascar fodies are well separated from each other, because the nests are very different from each other and because the grouping of *sakalava* and (e.g.) *F. madagascariensis* in the same genus is probably an artificial arrangement (R. Moreau, pers. comm.). The latter species might be a primitive member of the euplectine line (J. P. Chapin; R. Moreau, pers. comm.).

In addition, we have in the key removed *Icteropsis pelzelni*, *Textor luteolus*, and *T. intermedius* from immediate association with the rest of the genus *Textor* and allied them with *Hyphanturgus*. The reason for this change from customary groupings is that in their nests and behavior, insofar as known, these three species not only bridge the gap between *Hyphanturgus* and other textors, but more closely resemble the genus *Hyphanturgus*. Thus, the nest resembles that of *Hyphanturgus* and differs from that of other textors in the absence of a ceiling, in the use of palm strips or plant fibers for lining the floor of the nest, in the frequent use of materials other than grass or palm-leaf strips in the construction of the outer shell, and in the relatively long entrance tube (in *luteolus* and *intermedius*). The eggs are white, as a rule, in these three species, whereas in all other textors where eggs have been recorded they are generally colored and often spotted, or if white they are generally also spotted. *Hyphanturgus melanogaster* and *H. nigricollis* sometimes have white eggs (Chapin, 1954), again suggesting a close relationship

TABLE 1

*Tentative Key to Nests of the Genera of True Weaverbirds (*Ploceinae*)*

I. Nest chamber longest in its vertical axis, and (excepting typical *Ploceus* of Asia) with side entrance; no special ceiling present.

  A. Crudely woven, with loose loops projecting from surface of nest; walls relatively thick; side entrance.

    1. Outer shell built of heterogeneous materials (excluding *Foudia sakalava*) .... *Foudia*

    2. Outer shell woven from strips of grasses or similar materials.

      a. Nest relatively large; entrance near middle of side and small for the bird .... *Amblyospiza*

      b. Nest small; entrance high up on one side of nest .... *Ploceëlla*, *Brachycope*

  B. Weaving of nest relatively good.

    1. Walls relatively thick, floor of egg chamber typically not lined with grass heads; nest typically pensile and often having an entrance tube and ventral entrance; Asia .... *Ploceus*[a]

    2. Walls relatively thin, nest with a side entrance and generally slung between upright herbaceous stems and as a rule lined with fine, soft grass heads.

      a. Lower lip of entrance with an inner shelf .... *Quelea*[b]

      b. No inner shelf; walls of nest very thin .... *Euplectes*, *Coliuspasser*

II. Nest chamber longest in its horizontal axis, and (excepting *Othyphantes*, which has a special ceiling) with a bottom entrance.

  A. Nest attached by a single rope-like suspension; few or no grass heads in bottom lining; Madagascar.

    1. Short suspension; nest loosely woven of heterogeneous materials .... *Foudia sakalava*

    2. Long suspension; nest better woven of more uniform materials .... *Nelicurvius*

  B. Nest attached in various ways but not by a rope-like suspension; African.

    1. Entrance relatively small.

      a. Special ceiling present; entrance tube short or absent; nest generally lined with grass heads over floor.

        (1) Side entrance; crudely woven .... *Othyphantes*

        (2) Bottom entrance .... *Textor*[c]

      b. Special ceiling absent; entrance tube often well developed; nest generally not lined with grass heads.

        (1) Nest not lined with lichens.

          (a) Nest small (including *Icteropsis* [*Sitagra*] *pelzelni*, *Textor* [*Sitagra*] *luteolus*, and *Textor* [*Sitagra*] *intermedius*) .... "sitagrine" weavers

          (b) Nest larger .... *Hyphanturgus*

        (2) Nest lined with lichens .... *Phormoplectes*[d]

      c. Special ceiling present; with well-developed entrance tube; nest of coarse materials bound together by alternately reversed windings .... *Anaplectes*

    2. Entrance relatively wide (generally 6.5 cm or more inside diameter); special ceiling poorly developed or absent; little or no use of alternately reversed winding in the nest .... *Malimbus*

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[a] Systematic status of *P. megarhynchus*, with coarsely woven nest and a side entrance, is in doubt (Ali and Crook, 1959).

[b] Nests of *Q. quelea* and *cardinalis* seen but not that of *erythrops*.

[c] Excluding *T. luteolus* and *T. intermedius*.

[d] Based on *P. insignis* and *preussi*; nests of *angolensis* and *dorsomaculatus* still unknown.

between the genus *Hyphanturgus* and these three small, textor-like or sitagrine weavers. Of special significance, also, is the fact that in *Textor luteolus* (Bannerman, 1949; Chapin, 1954), and in the *Icteropsis pelzelni* that we observed at Entebbe, both male and female incubate. We have found no record of a male of any other species of the genus *Textor* incubating; moreover, Skead (1954) and Van Someren (1956) have observed incubation by the male of *Hyphanturgus ocularius*. The three small weavers—*pelzelni*, *luteolus*, and *intermedius*—also resemble each other closely in plumage color. Finally, the food of the three species in question, like that of species of *Hyphanturgus*, consists mainly of insects. The bill of *Icteropsis pelzelni*, as in *Hyphanturgus*, tends to be relatively slender, at least in some races. In contrast, most other textors include a considerable proportion of grain in the diet, and their bills are frequently relatively thick (cf. Chapin, 1954).

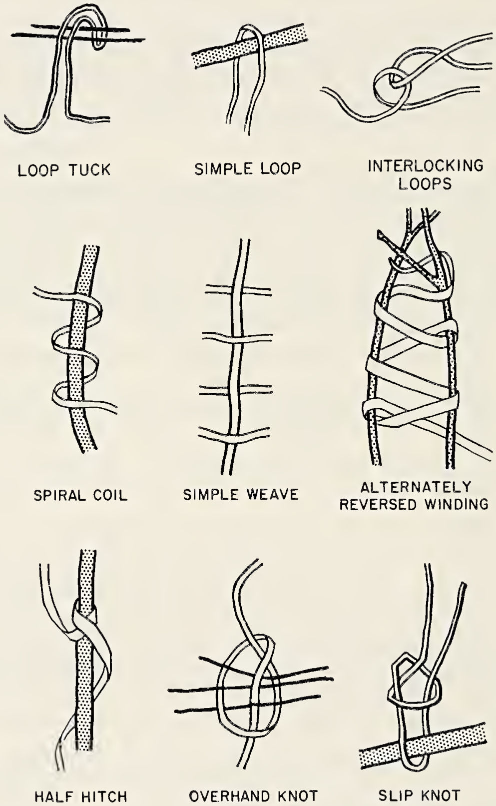

Fig. 5. Types of stitches and fastenings used by different weaverbirds (Ploceinae).

Whether or not *Icteropsis pelzelni*, *Textor luteolus*, and *T. intermedius* should be removed from the genus *Textor* and placed in a genus by themselves and called *Sitagra* (the generic name that seems to have priority, cf.

Sclater, 1930), combined with *Hyphanturgus*, or used as a reason for uniting *Hyphanturgus* and *Textor* is a matter that might be settled after more complete observations on behavior of these various species; to some extent the solution is at present a matter of opinion and convenience.

WEAVING OF THE NEST

The weaving of suspended nests in the Ploceinae appears to have arisen under moist open-habitat conditions, since apparently all Ploceinae use green flexible materials in making their nests, as we have observed in some two dozen representative species in the field. In contrast, we have observed that most nonploceine weavers of arid country thatch rather than weave their nests by pushing stiff, dry grass stems into the nest mass. The Ploceinae pull as well as push nest materials through the interstices of the nest in a systematic organized way. True weaving is characterized by interlocking loops of flexible material, but knots other than "hitches" are quite rare, although they do occur. Various presumptive and illustrative stages in the evolution of weaving can be recognized (Fig. 5): (1) a partially woven nest with some simple loops as in *Foudia madagascariensis*; (2) the whole nest woven largely of simple loops often tucked in as such (*Amblyospiza*); (3) emphasis on coiling in addition to loop-backs (*Quelea quelea*); (4) nest a mass of very loose, interlocking loops with some advanced stitches present (*Othyphantes baglafecht stuhlmanni*); (5) much use of systematic alternation in the direction of component materials (*Textor cucullatus*); (6) greater compactness of weaving with few loose loops (*Hyphanturgus ocularius*); and (7) regular arrangement of crossing strands into a pattern like the warp and woof of human weaving (*Malimbus cassini*). There has been a trend from irregularity to regularity of pattern, from loose to close weaving, and from coarse to fine stitches, the culminating stages being best exemplified by Cassin's Weaver (*Malimbus cassini*), the changes presumably aiding the nest to retain a firm, well-rounded form (Fig. 6). In some cases there has also been an evolutionary change from a thick-walled to a thin-walled woven shell, presumably furnishing sufficient strength with greater economy of materials and effort.

Coincident with these changes and improvements in the types of stitches used went an improvement in the nature and flexibility of the materials used, from grass stems with leaves and flowering or seed-bearing heads still attached, to the use of long individual strips torn from the leaves of grasses or palms. One of the most general correlations of nest materials with habitat among the Ploceinae is the use of grass stems in the woven outer shell of the nest, seen in many species of dry country, whereas Ploceinae from moist, open habitats, such as marshes, riverbanks, and cultivated country generally use strips torn from leaves of grasses, sedges, palms, and the like.

Specialization in the use of different materials for weaving is much more marked in forest weavers than in those of open country. Thus, almost all species of bishop birds and whydahs, whose nests we have seen, used strips of grass or sedge leaf, or grass stems, for the outer shell of the nest, and lined the interior of the nest with soft grass tops. In general, grasses are much less available in mountain forest and in rain forest than in savanna or cultivated country. Forest-inhabiting weavers use such materials as are generally available in forest habitats: tendrils, vines, lichens, and stems of compound leaves. Different species of forest weavers may specialize in different materials, this specialization being well seen, for example, in different species of *Malimbus*. In some instances, species from different genera of Ploceinae have evolved convergently toward use of similar materials for nest construction. Thus, tendrils are used for all or much of the outer shell of the nest in *Hyphanturgus alienus*, *Malimbus coronatus*, *Phormoplectes insignis*, *Symplectes bicolor*, and *Melanoploceus tricolor*.

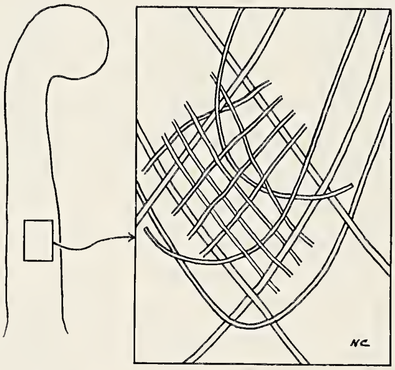

Fig. 6. Details of the weaving in a portion of the entrance tube in a nest of Cassin's Weaver (*Malimbus cassini*).

In many Ploceinae the male builds the outer shell of the nest, and selection from among such nests by the female must be an important force in the evolution of weaving. By watching color-banded individuals of the Village Weaver (*Textor cucullatus*), we discovered that, if no female accepts the nest of a given male within about a week, the male then tears down this nest and builds another in its place (Collias and Collias, 1957). One male may build two dozen nests in the course of the breeding season, each nest generally being destroyed by the owner in favor of a renewed model, until a female signalizes her acceptance of the nest by starting to line it with soft grass heads.

SUMMARY

The roofed or domed nest typical of the weaverbirds (Ploceidae), as well as of many other families of tropical birds with altricial young, helps to provide protection against the high predation, excessive rainfall, and intense solar radiation of tropical areas. Evolution of gregarious breeding in relative security from predation culminated in compound nests, such as those of *Bubalornis* and *Philetairus.*

The form of the nest is generally consistent in different genera of weaverbirds, but the materials used vary greatly with species and even with habitat in the same species. Weaverbird nests placed in grass or in herbaceous, marshy vegetation generally have a side entrance. Weaverbird nests in trees tend to evolve a pensile attachment from the roof, a ventral entrance, and an entrance tube; all of these features help to protect the nest from certain predators, especially those that make their initial approach from above the nest, and all are enhanced by a woven construction to the nest.

The weaving of nests appears to have evolved under moist, open-habitat conditions, together with the birds' ability to pull flexible, green grasses through the nest, instead of merely pushing through stiff, dry grass stems, as do many weavers of semi-arid or arid country, which thatch rather than weave their nests. Weaving is characterized by interlocking loops of flexible materials, and is restricted among weaverbirds to the subfamily Ploceinae. There has been a trend from loose to close weaving, from coarse to fine stitches, and from irregularity to regularity of pattern, the culminating stages being best exemplified by Cassin's Weaver (*Malimbus cassini*), which builds one of the most finely constructed nests of any bird.

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Behavioral Isolating Mechanisms in the Family Anatidae

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The ducks, geese, and swans present a host of species-recognition and isolating-mechanism problems that are equaled by few other groups of birds. As a family, the Anatidae have provided the greatest number of interspecific hybridization records of any avian family (see Gray, 1958, and Johnsgard, 1960*a*) both in captivity and under natural conditions. A surprising number of these hybrids have proved to be fertile, even when obtained between what appear to be well-marked genera. This remarkable capacity for hybridization indicates that isolating mechanisms must be operating effectively if species are to retain their integrity under natural conditions. Since genetic isolation is practically absent in the Anatidae, other isolating mechanisms must, of course, have evolved to take their place. Of these, the most significant appear to be behavioral differences and various morphological (plumage and soft-part) specializations that are usually associated with these behavioral differences. A comparative behavioral study of the Anatidae was undertaken from 1959 to 1961 at The Wildfowl Trust, in England, where I was able to observe in life 125 out of the approximately 140 extant species of Anatidae, including 34 of the 41 genera accepted by the most recent authority on the family (Delacour, 1954–59).

Of the 10 tribes of Anatidae accepted by Delacour (1954–59), all but 1 (Anseranatini), which is monotypic, are characterized by the inclusion of numerous closely related, often sympatric, species. It is, of course, in these groups that behavioral and morphological elaborations associated with pair formation and copulation are most conspicuous, and it is also here where the greatest amount of information regarding the development of isolating mechanisms can be gleaned. The following discussion is subdivided into sections corresponding to the tribes and included genera of Delacour (1954–59), except where results of my studies have suggested certain modifications in his classification (Johnsgard, 1961*a*). As most of the observations given below are my own, I have not resorted to frequent citation to support them. Where terms refer to ritualized displays, the first letter of these terms has been set in capital letters.

SUBFAMILY ANSERANATINAE

Tribe Anseranatini

The Magpie Goose (*Anseranas semipalmata*) stands apart from the rest of the Anatidae in numerous anatomical as well as behavioral respects, and it

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seems unlikely that hybridization with any other species of waterfowl is possible. It is certainly not probable, for in the Magpie Goose copulation occurs on land, which is most unusual in the Anatidae. Furthermore, the associated behavior (see Johnsgard, 1961*b*) is also entirely different from that associated with copulation in the rest of the Anatidae. The Magpie Goose's general behavior is reminiscent less of the true geese and swans (Anserini) than of the screamers (Anhimidae). Copulatory behavior in screamers has not been described, so unfortunately it is impossible to compare them to the Magpie Goose in this respect.

SUBFAMILY ANSERINAE

Tribe Dendrocygnini

The whistling ducks (*Dendrocygna*) are second only to the Anseranatini in their isolation from the rest of the Anatidae, and definite hybrid records have been obtained only for intrageneric combinations among the eight species of *Dendrocygna.* Seven of the species are sympatric with one or more other species, but no natural hybrids have been recorded. In captivity nine hybrid combinations have been obtained, but the fertility of these hybrids is not known. It appears that isolating mechanisms in the whistling ducks include plumage-pattern differences of varying degrees, vocalization differences which are considerable, and relatively less differentiation of visual displays. Each species possesses specific recognition or greeting calls which are distinctive and which, by themselves, could effect species recognition. Although a few species have very similar plumage patterns (e.g. *bicolor* and *arcuata*; *guttata* and *arborea*), such species are allopatric with each other. Visual pair-forming, or "courtship," displays appear to be essentially absent in whistling ducks, and are probably replaced by vocal signals. Unlike the situation in the true geese and swans, there appears to be no behavior functionally related to Triumph Ceremonies.

In their behavior patterns associated with copulation, certain differences are present that might prove effective as isolating mechanisms. Two species (*arborea* and *autumnalis*) copulate on shore or, more often, while standing in shallow water near shore. The others (except possibly *guttata,* which has not been observed in this connection) copulate while swimming. In these former species, precopulatory behavior consists of mutual Drinking movements that do not appear to differ from normal drinking behavior. In the species that tread on water, the precopulatory behavior consists of mutual Head-dipping movements (*bicolor*, *eytoni*, and *arcuata*) or Bill-dipping motions (*javanica*, possibly *viduata*). These precopulatory movements also do not differ markedly from the nonritualized bathing movements of the species.

Postcopulatory displays differ considerably. In the species that perform the precopulatory Head-dipping movements, postcopulatory display is likewise mutual and consists of an energetic Step-dance, during which both birds tread water vigorously and each raises one wing vertically. The Step-dance is lacking in the two species that copulate on shore. In one of these species (*autumnalis*), there is a slight indication of Wing-raising on the part of the male, but in *D. arborea* this is lacking altogether. Although these two species differ greatly in their adult plumage patterns, they have a strong tendency to form mixed pairs in captivity, which is probably a result of the similarities in their copulatory behavior. Likewise, *D. bicolor* has a tendency to hybridize with the species it most resembles in pre- and postcopulatory behavior.

Tribe Anserini

The true geese and swans comprise 21 species which are divided into 5 genera. Genera that include several closely related species are *Cygnus*, *Anser*, and *Branta*. Hybrids have occurred among 18 of the 21 species, and 5 hybrid combinations have been reported from the wild in *Anser* and *Branta*. Eleven hybrid combinations within these 2 genera, and 5 between them, have proved fertile.

Morphological isolating mechanisms in these genera appear to be primarily based on plumage and soft-part coloration in the head and bill areas, whereas the remainder of the body plumage is more uniform among species of *Anser*, *Branta*, and *Cygnus*. Vocalizations are probably important sources of isolating mechanisms in the true geese and in most of the species of swans. Threat displays and preflight movements are relatively uniform within each genus. The greatest behavioral differences in the tribe occur in the form and vocalizations of the Triumph Ceremonies, which appear to be of primary importance in the formation of pairs among geese and swans (Heinroth, 1911). Such ceremonies are present in all the species of true geese and swans except, apparently, the Coscoroba Swan (*Coscoroba coscoroba*). In some species of swans (*Cygnus olor*, *C. atratus*, *C. melanocoryphus*), they consist of mutual weak calling by both birds while lifting the chin and stretching the neck vertically. In the other swans, the calls are much louder and are accompanied by a waving or flapping of the outstretched wings. In the case of geese, the neck is extended more diagonally or horizontally, and there are often thrusting and horizontal or vertical movements of the neck. These movements during the Triumph Ceremony seem designed to bring into full view the head and bill markings of each bird to its mate or potential mate.

Precopulatory behavior in the Anserini is extremely uniform. It consists, in all but one of the species (*Cereopsis novae-hollandiae*), of Head-dipping movements on the part of both birds. In most of the true geese the tail is also strongly cocked vertically, exhibiting the white undertail coverts. Copulation normally occurs while both birds are swimming. In the Coscoroba Swan it can take place while the birds are standing in shallow water, and in the Nene Goose (*Branta sandvicensis*), a terrestrial species, it normally occurs on land, although the precopulatory behavior nevertheless consists of typical Head-dipping movements.

Postcopulatory behavior in this tribe is more variable than precopulatory behavior, and thus is presumably more effective as an isolating mechanism. In the genus *Cygnus* it is surprisingly variable; the postcopulatory displays of *C. atratus*, *C. olor*, and *C. melanocoryphus* appear to differ markedly from one another and from the other swans. In *C. cygnus* and *C. columbianus* the two birds rise in the water with outspread wings, calling in concert. Heinroth (1911) has described how differences in the postcopulatory behavior of these two groups of swans was partially effective in preventing a mating between *C. olor* and *C. cygnus*. In the Coscoroba Swan both birds stretch their necks and hold their heads high, but do not spread their wings. In the true geese (*Anser* and *Branta*) the postcopulatory displays are almost identical in all species; both sexes call with neck vertical, bill pointed upward, and the folded wings lifted or sometimes partly extended. In the aberrant Cape Barren Goose (*Cereopsis novae-hollandiae*), which seems to be a link between the Anserini and the Tadornini, the birds copulate on land after the male has walked around the female, pecking at her back until she assumes a prone position. The two birds perform what appears to be a Triumph Ceremony as a postcopulatory display, which consists of calling mutually while waving their extended necks vertically and repeatedly lifting their folded wings.

SUBFAMILY ANATINAE

Tribe Tadornini

The shelducks and sheldgeese are a group of 15 species divided into 5 genera as the group is constituted here. Only two of these genera (*Chloephaga* and *Tadorna*) are not monotypic, and hybridization has occurred among the species of these genera fairly frequently in captivity. No wild hybrids, however, are known involving shelducks or sheldgeese, and only a few congeneric species are actually sympatric. As in the preceding groups, pair bonds are often relatively permanent, but in at least some of the shelducks it appears that pair bonds are fairly weak and occasionally may be broken (Heinroth, 1911). Thus, "courtship" displays in males are somewhat more elaborate than in the groups already considered, but generally are not so complex and elaborate as in the following tribes.

Correlated with the fact that pair bonds are less rigid and courtship is more conspicuous in this group are the points that the sexes tend to differ to a greater degree in voice, appearance, and behavior. Males of different species tend to vary in these aspects more than do females, which is to be expected in a mating situation where the female "selects" her mate. Thus, isolating mechanisms tend to be concentrated in the male's plumage, vocalizations, and courtship displays, whereas the females of even rather distantly related species tend to be much more similar in these characteristics. Females of all species of this tribe (and most of the remaining tribes) possess the major courtship display termed Inciting (Lorenz, 1951–53), which is readily recognizable after it has been thoroughly studied in any one species.

Homologous male behavior patterns are much less easy to distinguish, but in the present tribe the male vocalizations seem to fall into two fairly distinct categories. Displays associated with single-syllabled, but often rapidly repeated, calls appear to have primarily a threat function. In the genera *Cyanochen*, *Neochen*, *Chloephaga*, and two species (*tadorna* and *radjah*) of *Tadorna*, these male calls are rapid whistling notes, in *Alopochen* they are huffing noises, and in most of the *Tadorna* species they are throaty honks. The same notes, used in association with a rapid vertical Bowing movement of the head and neck, are used as a sexual display in some species of *Chloephaga*. The major sexual display of the males, however, seems to be a 2-syllabled call which is never a whistle and usually is a throaty or belching note. In *Neochen* and some species of *Chloephaga* (*melanoptera*, *poliocephala*), this is accompanied by a Puffing of the plumage and a variable raising of the wings as the bird assumes a High-and-erect posture. In *Tadorna* this posture and call are used as a sexual display in most species (all but *radjah* and *tadorna*). This sexual note differs sufficiently in auditory characteristics in each species so that it could serve as a species-recognition signal in itself without the added factors of specificity provided by male plumage patterns and slight differences in posturing.

As in the true geese, precopulatory behavior appears to be uniform throughout most, if not all, species, although several species have still not been observed adequately. In the species where precopulatory behavior has been seen (most *Tadorna* species, *Chloephaga picta*), it consists of Head-dipping movements performed by both birds either while swimming or while standing in shallow water. In *Tadorna tadorna* the Head-dipping often grades into shallow diving, and the male may Preen-behind-the-wing before mounting. Postcopulatory behavior is relatively uniform in the species where it has been observed. The female begins to call as treading is terminated and before the male releases his hold of her nape. The male calls as he releases her, and assumes a High-and-erect posture for a few seconds, usually lifting the wing farthest from the female. This Wing-lifting is strongly pronounced only in a few species (*Tadorna cana*, *T. tadornoides*), and is barely noticeable in others. There is no Step-dance as occurs in the somewhat similar postcopulatory display of *Dendrocygna*.

It appears, therefore, that isolating mechanisms in the Tadornini may consist largely of vocalizations which may be associated with special male postures. The three species of steamer ducks (*Tachyeres*), included by Delacour (1954–59) in the present tribe, probably should be placed in a separate tribe (Moynihan, 1958). However, so little is known of their behavior that it is not possible to discuss isolating mechanisms in the steamer ducks at the present time.

Tribe Cairinini

The perching duck group consists of 13 species, which are here divided into 10 genera. This collection of almost monotypic genera suggests that the tribe contains few closely related species, and this is corroborated by the scarcity of hybrids recorded among the perching ducks. The only known case of total genetic isolation preventing hybridization between two closely related waterfowl species is found in this tribe, and involves the Wood Duck (*Aix sponsa*) and the Mandarin Duck (*Aix galericulata*) (Yamashina, 1952). Practically all hybrids of perching ducks with one another and with members of other tribes have proved sterile. No natural hybrids are known, and the only case of congeneric sympatry in the tribe occurs between two species of pigmy geese (*Nettapus*).

Sexual dimorphism of voice occurs in all species, and dimorphism of plumage or body size is also found in all species to varying degrees. No species are known to have permanent pair bonds, and pairing either occurs every year or is practically absent altogether. In the genera where pair bonds are weak (*Cairina*, *Sarkidiornis*, and *Plectropterus*), the courtship and copulatory displays are likewise poorly developed. In the other genera (*Pteronetta*, *Aix*, *Callonetta*, *Amazonetta*, and *Chenonetta*), pair bonds are stronger but are probably renewed yearly, and courtship displays tend to be more elaborate. Likewise, male plumages tend to be more complex in pattern and coloration. Although the male courtship displays tend to be numerous, they are mostly derived from simple preening, drinking, shaking, and wing-flapping movements. Male vocalizations are, in most species, various kinds of whistles usually associated with special posturing. Wing patterns in these genera are usually metallic in color and conspicuous, and are exhibited by Preening-behind-the-wing displays. Although these preening displays are performed in essentially the same manner by all species, the unique speculum patterns "flashed" by each species bestow a specificity on the displays that very likely functions as an isolating mechanism.

Precopulatory displays in the perching ducks are, surprisingly, rather variable, which further indicates that the group is not a closely knit assemblage. In at least two species (*Cairina moschata*, *Sarkidiornis melanotos*), it appears that rape of the female is a frequent, if not the usual, situation. Precopulatory Head-dipping occurs in *Amazonetta*; various forms of Bill-dipping or Head-pumping are precopulatory displays in *Cairina scutulata*, *Chenonetta*, *Aix galericulata*, and probably *Pteronetta*; and Bill-dipping occurs in *Callonetta*, *Aix*, *Chenonetta*, and probably *Sarkidiornis*. Perhaps this diversity of precopulatory displays is one reason why hybrids among the perching ducks are so infrequent in captivity. Postcopulatory displays are also very variable. In *Cairina scutulata* the male simply swims rapidly around at random, calling excitedly; in *Aix galericulata* the male swims rapidly away from the female while Turning-the-back-of-the-head; in *Callonetta* the male calls, then turns and Faces the female; and in *Chenonetta* and *Am-*

azonetta the male tends to swim in a circle around the female with the bill held downward and the hindquarters somewhat raised.

It thus appears likely that the visual aspects of male displays and male plumage patterns function in the perching ducks as isolating mechanisms to a greater degree than in the groups previously considered.

Tribe Anatini

This large tribe of approximately 40 species contains 1 major genus (*Anas*) and 4 monotypic genera (*Malacorhynchus*, *Hymenolaimus*, *Merganetta*, and *Marmaronetta*) which appear to have no close relatives. Therefore, the following discussion is entirely devoted to the genus *Anas*, which is an extremely interesting group from the standpoint of isolating mechanisms. Hybridization within this genus is remarkably common, and at least 115 intrageneric hybrid combinations have been recorded among 32 species (Johnsgard, 1960*a*). Of these, at least 39 combinations have produced fertile offspring, and 38 combinations have occurred in the wild. Thus, isolating mechanisms are least well developed in the group, in spite of the fact that courtship displays and male plumages tend to be elaborate and diversified. Since many species in this genus have extremely broad ranges, there tends to be a great deal of sympatry, and nearly all species with breeding ranges that overlap the breeding ranges of numerous other *Anas* species are characterized by having bright male plumages and elaborate courtship displays.

Male courtship displays in *Anas* are exceedingly diversified, although all species do share certain homologous displays. Lorenz (1951–53) was first to study and compare the displays of most *Anas* species, and provided a basis for terminology and comparison of displays in the other species. Displays shared by males of most, if not all, species of *Anas* include Preening-behind-the-wing and Turning-the-back-of-the-head, both of which, by various head-plumage and wing-speculum patterns, very likely function as isolating mechanisms in spite of the uniformity of their performance. Other major male displays include the Grunt-whistle, which occurs in at least 15 species, the Head-up–tail-up, also found in at least 15 species, and the Down–up, found in at least 9 species. A courtship call, or Burp, occurs in most, and probably all, species, but varies greatly in auditory characteristics and associated head movements. It is generally true that closely related species share the greatest number of homologous male courtship displays, but there are several exceptions. Often two sympatric species of *Anas* perform several homologous displays but, by various kinds of differences in display combinations, or "linkages," rather markedly different optical and auditory effects are produced. Secondly, some species normally lack displays that are present in closely related forms, and evidence that such displays have been lost secondarily is provided by (1) the rare occurrence of the display in otherwise normal individuals, and (2) the occurrence of the display in hybrid combinations where both parental forms lack the display. There are several examples of both these situations in *Anas*. Examples of the first include the Common Mallard (*A. platyrhynchos*), Common Pintail (*A. acuta*), and Bahama Pintail (*A. bahamensis*) when they sometimes perform independent Bridling, the Brown Pintail (*A. georgica spinicauda*) occasionally performing the Head-up–tail-up, and the Falcated Duck (*A. falcata*) rarely performing the Down–up. The Common Pintail and Brown Pintail also often perform a very rudimentary version of Nod-swimming. Lorenz (1958) has cited examples of the occurrence of displays in hybrid combinations, and his student W. van de Wall (pers. comm.) has studied other cases as well.

Cases of incipient secondary loss of displays may be observed in certain island races of *Anas* that lack contact with other congeneric species. Thus, the Laysan Island race of the Common Mallard (*A. platyrhynchos laysanensis*) has practically lost the Down–up display from its repertory. This display occurs in rudimentary form so rarely that it comprises only about 5 percent of the total major displays, whereas in the continental race it usually constitutes from one-third to one-half of the major displays. The other displays are performed in a much less exaggerated fashion than in the continental race. The same is true to lesser degrees in other island races, such as the Hawaiian Mallard (*A. platyrhynchos wyvilliana*), Kerguelen Pintail (*A. acuta eatoni*), and South Georgia Pintail (*A. georgica georgica*). The fact that these races retain any of their male displays is an indication that intraspecific male competition for mates is partially effective in retaining the male secondary sexual characteristics of the species.

The relatively facile genetic control of male courtship displays, indicated above, and their evident importance as isolating mechanisms make it dangerous for the behaviorist to judge evolutionary relationships solely on the basis of male displays. Fortunately, female displays are less subject to these kinds of variation, and so studies of variations, in the form of female Inciting and other kinds of sexual behavior as well as vocalizations, are more useful for judging intrageneric relationships in *Anas*. Females of most, if not all, *Anas* species uniformly have Decrescendo calls, but the auditory quality and number of notes in these calls vary considerably and very likely act as species- or individual-recognition signals.

Precopulatory behavior in *Anas* is remarkably uniform in all the species where it has been observed, and the mutual Head-pumping behavior is one of the best behavioral characterizations of the genus. Postcopulatory behavior is more variable, but in all species studied the male calls one or more times by Burping or Bridling, then often either Faces the female or Turns-the-back-of-the-head toward her. Bridling, followed by Nod-swimming, are the male postcopulatory displays of all the mallard-like ducks.

It thus appears that isolating mechanisms in *Anas* are based primarily on male plumage or soft-part features and the associated courtship displays that exhibit these features. Male vocalizations are almost always associated with particular courtship postures and, together with morphological features, further enhance the specificity of these courtship displays. The frequency of hybridization in the genus appears to be the combined result of the great amount of natural sympatry, the relatively close relationships of all the species of *Anas*, and the very uniform precopulatory behavior of all the species in this genus.

Tribe Aythyini

The pochards comprise a group of 16 species that are world-wide in distribution. Fifteen of the species might be called "typical" and are included in the two genera *Aythya* and *Netta*. The other is the monotypic and extinct genus *Rhodonessa*, which is neither a typical pochard nor a typical dabbling duck, but rather seems to constitute, with *Marmaronetta*, a link between the two tribes. It is clear from hybrid evidence that the Anatini and Aythyini are very closely related tribes, and some intertribal hybrids have even proved fertile (Johnsgard, 1960*a*). Within the tribe, 14 species have been involved in interspecific hybridization, of which at least 6 combinations have produced fertile offspring. Twelve hybrid combinations have occurred in the wild, indicating that isolating mechanisms are not completely effective in this tribe.

Male plumage patterns in the pochards are somewhat less variable than in the dabbling ducks, with head and bill colors apparently being of greatest importance as morphological species-recognition signals. Male vocalizations tend to be soft, with sharp whistles almost absent, but they nevertheless vary sufficiently among species so that most, if not all, species can be readily recognized by their courtship calls. Unlike the genus *Anas*, males of almost all species studied perform displays that are not only recognizably homologous but also extremely similar in form. Two of these displays, the Head-throw and the Sneak postures (Hochbaum, 1944), are primarily visual displays with which vocalizations are usually associated. Two others, the Kinked-neck Call and Coughing, are primarily vocalizations and are accompanied by less-pronounced body movements (Johnsgard, unpublished MS.). In two species (*Aythya australis* and *A. nyroca*), the Kinked-neck Call is often repeated in fast succession several times. As in the genus *Anas*, males of most and probably all species have Preening-behind-the-wing and Turning-the-back-of-the-head displays that are performed in the same way but exhibit different morphological features. In the Head-throw and Sneak displays, different species vary in the rapidity and the degree of exaggeration of these movements, and these quantitative rather than qualitative differences in display form are possibly of significance in species-recognition systems. A Nodding-swim, similar to Nod-swimming in *Anas*, is performed by males of several but not all species.

As in the genus *Anas*, females of all species are very uniform in their behavior. Inciting behavior is similarly performed by all species and constitutes the major female courtship display. Two male displays, the Headthrow and Kinked-neck Call, are also performed by females of a few species. Females of many species Preen-behind-the-wing as a sexual display.

Precopulatory behavior in the pochards is slightly more variable than in the dabbling ducks. In only one species (*Netta rufina*) does mutual Head-pumping behavior occur; in others only the male performs Head-pumping (*Aythya australis, A. baeri*), and in two (*Netta peposaca* and *N. erythropthalma*) this is performed only by the female. Males of all species perform Bill-dipping and Preening-dorsally movements as precopulatory displays, but only in some species are such movements performed by females as well. Postcopulatory displays are, however, extremely uniform in all the pochard group. In all species of *Netta* and *Aythya* studied (as well as in *Marmaronetta*), the male utters a single courtship call after he releases the female, then swims quickly away in a rigid Bill-down posture.

Behavioral isolating mechanisms in the pochards thus appear to be primarily dependent upon auditory and quantitative visual differences in homologous male courtship displays, and to a smaller extent upon differences in precopulatory displays.

Tribe Mergini

The sea duck tribe, which here includes the eiders (see Johnsgard, 1960*b*), contains 20 species (including 2 extinct species) that are primarily of Northern Hemisphere distribution. Four of the 8 genera are monotypic, but the others contain from 3 to 7 species each. Most species tend to be maritime in distribution, at least during the winter period, and there is considerable sympatry of ranges. Ten species have been involved in intratribal hybridization, and 8 hybrid combinations have been reported among wild birds. These have all involved the polytypic genera *Melanitta, Somateria, Bucephala,* and *Mergus*. Since members of this tribe are rarely bred in captivity, there are very few hybrid records stemming from this source.

This tribe, more than any other tribe in the Anatidae, can be characterized by possessing an extreme degree of sexual dimorphism in plumage, voice (and associated tracheal structures), and displays. Some of the most bizarre male plumage patterns and complex male courtship displays are found among these species, and, as a result, species often appear to be much more distantly related to one another than is probably actually the case. Thus, although practically every species of eider, scoter, and merganser has been placed by some taxonomists in monotypic genera, the bases for such genera have been the male secondary sexual characters that very likely act as isolating mechanisms to prevent hybridization among these closely related forms.

Male courtship displays among the sea ducks are so diverse that it is difficult to point out definite homologies even among such closely related species as the goldeneyes (*Bucephala*) and mergansers (*Mergus*). McKinney

(1961) has even found qualitative differences in the male courtship displays of two races of the Common Eider (*Somateria mollissima*). These elaborate (and relatively effective) behavioral isolating mechanisms led Myres (1959) to conclude that the sea ducks are "ancient and/or polyphyletic," but it seems more likely to me that they are, in fact, monophyletic and that the species are relatively well isolated from one another. Arguments in favor of a monophyletic origin have been presented elsewhere (Johnsgard, 1961*b*).

Behavioral isolating mechanisms are not limited to male courtship displays but may also be found in variations of female behavior patterns. Female Inciting is found in most, if not all, species but varies in form to a somewhat greater extent than is true of the preceding tribes. Except for the Inciting and warning notes, females of all species except eiders tend to be relatively silent. Male courtship calls are very diverse, and nearly every species may be readily recognized by its male courtship note alone.

Only a few unifying behavioral characteristics link all the members of this tribe. The most significant of these is the fact that females assume a Prone posture when soliciting copulation, and may remain in this posture for periods of several minutes. In some genera both sexes normally perform ritualized Drinking before this Prone posture is assumed, whereas in other genera no mutual preceding displays have been observed. Before mounting the female, the males of apparently all species perform various ritualized behavior patterns which may or may not differ markedly from normal comfort movements, and the composition, form, and in some cases the sequence of these movements appear to be of primary importance as isolating mechanisms. These precopulatory male displays are, however, much more conservative than are male courtship displays and provide the best behavioral evidence for judging relationships among genera. These displays include Preening-dorsally or Preening-behind-the-wing, Bill-dipping, and ritualized Drinking, Bathing, and Shaking ("Upwards-stretch" of Myres, 1959). In some species mounting is always immediately preceded by the Upwards-stretch, whereas in others it is always preceded by ritualized Preening-behind-the-wing. Ritualized approaches to the female occur in *Polysticta* and two species of *Bucephala*.

That isolating mechanisms might even operate during treading is suggested by the fact that males of several species of sea ducks vigorously Flick-the-wings (Myres, 1959) varying numbers of times while mounted, producing a drumming noise which very likely has signal value. Postcopulatory displays in the sea ducks are relatively variable. In some species (*Polysticta, Bucephala, Mergus cucullatus*), the male retains hold of the female's nape for several seconds, causing the birds to Rotate (Myres, 1959) about a point, before releasing her. The male may then perform one of its courtship displays (*Melanitta perspicillata*, *Polysticta*, *Somateria*) or may Steam away, while often performing lateral Head-turning movements (*Somateria, Polysticta, Bucephala, Mergus cucullatus*).

Tribe Oxyurini

The stiff-tailed ducks are relatively poorly studied from every standpoint, and it is not possible to discuss isolating mechanisms with any degree of assurance because of this fact. Of the 9 included species, 3 are in monotypic genera, and the 6 species of *Oxyura* are so distributed geographically that there is very little sympatry of ranges. Only in South America, where *Oxyura jamaicensis ferruginea* and *O. vittata* are partially sympatric with one another and with *O. dominica*, is there any great likelihood of hybridization, and the only possible record of hybridization within this tribe concerns these two former species.

Male plumage patterns vary less in *Oxyura* than in any other group of Anatinae, and likewise bill coloration is identical in all species. What little is known about male courtship displays, however, suggests that marked differences do occur as isolating mechanisms. Males of some and probably all species of *Oxyura* (as well as *Heteronetta* and *Biziura*) have inflatable tracheal or esophageal structures that function as noise-producing organs, and courtship postures seem to have evolved through the utilization of differing means of producing sound from these structures. Female vocalizations in *Oxyura* are rudimentary and, in *O. jamaicensis* at least, seem to consist of only an aggressive squeaking note. The female of this species also appears to lack anything related to Inciting, and her response to male displays is generally overt aggression.

It seems probable that the precopulatory behavior of *Oxyura* is more uniform than the male courtship displays of the various species. In *O. jamaicensis* this consists of Bill-dipping, followed by a rapid lateral Bill-flicking on the part of the male, to which the female's most frequent response is diving. Similar behavior has been described for several other species of *Oxyura*, but it is uncertain if this occurs in precopulatory situations. In the two species (*O. jamaicensis* and *O. australis*) for which postcopulatory behavior has been described, it differs markedly, so that postcopulatory displays may also be potential isolating mechanisms.

ACKNOWLEDGMENTS

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SUMMARY

The family Anatidae is, for the most part, composed of numerous groups of closely related, often sympatric species which frequently have the capacity to produce fertile hybrids. Isolating mechanisms in these species are a combination of morphological (plumage and soft-part) and behavioral char-

acteristics. The relative importance of morphological and behavioral characteristics as isolating mechanisms varies somewhat in the subgroups (tribes) of the Anatidae. In addition, different aspects of behavior may assume varying degrees of importance as isolating mechanisms in these groups. However, it is generally true that vocalizations and male plumages and soft-part features are probably of greatest importance in preventing hybridization between closely related species, and male courtship displays are only slightly less important in this regard. Pre- and postcopulatory displays and female courtship displays are, on the average, less important as potential isolating mechanisms, and so are of greater taxonomic utility in the determination of evolutionary affinities.

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The Use of Bird Calls to Clarify Taxonomic Relationships

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Faber (1929) was the first scientist to demonstrate the significance of animal sounds for systematic studies—using Orthoptera as an example—and in doing so he founded the special branch of bioacoustics.

Although the calls are of great importance in many bird families, they had no major scientific significance—except for ornithological identification in the field—because it was too difficult to describe the calls or even to give an objective representation of them. It is a fortunate coincidence that, at the same time when ethology gained a growing importance in ornithology, a method was developed that made it possible not only to record acoustically and collect the calls of birds but also to fix them optically.

However, it has been shown by several authors (Thorpe, 1954; E. and I. Messmer, 1956; H. and G. Thielcke, 1960) that some species are able to learn a number of components, primarily as regards singing. This considerably weakens the usefulness of acoustical studies for clarifying taxonomic questions. For some species even the species-specific song depends on whether or not the young bird has had a chance to hear other representatives of the same species. Also, quite a number of various other calls do not fit into the species-specific picture when the young birds do not have this learning opportunity.

The most satisfactory method for studying the development of bird calls was used with the birds that Koehler had reared in soundproof chambers by his students Sauer (1954), E. and I. Messmer (1956), and H. and G. Thielcke (1960). Some indications also resulted from experiments by the Heinroths (1926), who took birds from the nest to hand-rear them, so that from that time on they could no longer hear any other birds of the same species.

The Heinroths noticed that their Willow Tits (*Parus montanus*) did not make the sounds that every field ornithologist recognizes as typical of the species. I verified these statements in the following way: On two occasions I took eggs of *P. montanus* into an area where this species does not exist. They were hatched and reared by other *Parus* species until shortly before fledging. It became evident that these Willow Tits uttered many sounds of the foster parents and that species-specific calls in particular were changed to such an extent that they could no longer be used for identifying the bird.

Lately, I. Vilka (1960) in the Soviet Union also put eggs of tits and other birds into the nests of different species. He found that in many cases the song and sometimes the calls of the foster parents were adopted.

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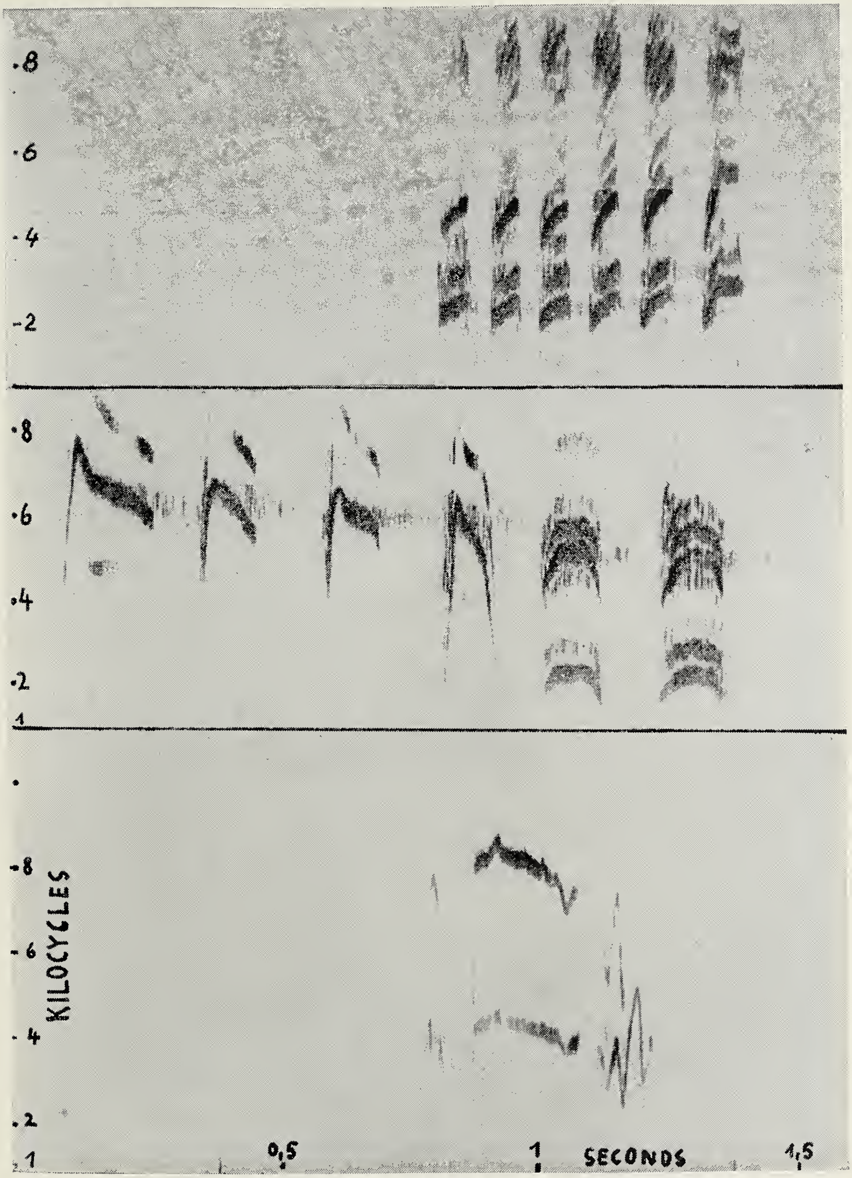

Fig. 1. Dissimilarity in location call of the same genus. Top to bottom: *Parus major*; *P. caeruleus*; *P. cristatus.*

Subsequent to these experiments, the possibility of using bird vocalizations for clarifying taxonomic problems and relationships was greatly restricted for a short time after an objective representation had become technically possible. Of course, it is not possible to rear individual specimens of all species we wish to compare in soundproof chambers in order to determine to what extent their calls are innate or have been learned and adopted later.

Recently, in order to study the influence of adult birds upon the behavior of young birds after fledging, I exchanged the eggs of more or less closely related hole-nesting birds, so that the young birds were reared by foster parents of a different species. All of these young birds gave *one* call in an absolutely species-specific way, namely the *location call*, which all passerines and many other species of birds use after fledging to announce their location at periodic intervals to make it easier for their parents to locate them. Young songbirds could not have learned this call, since they have never heard it. The female of some species has a similar call during the period of courtship feeding.

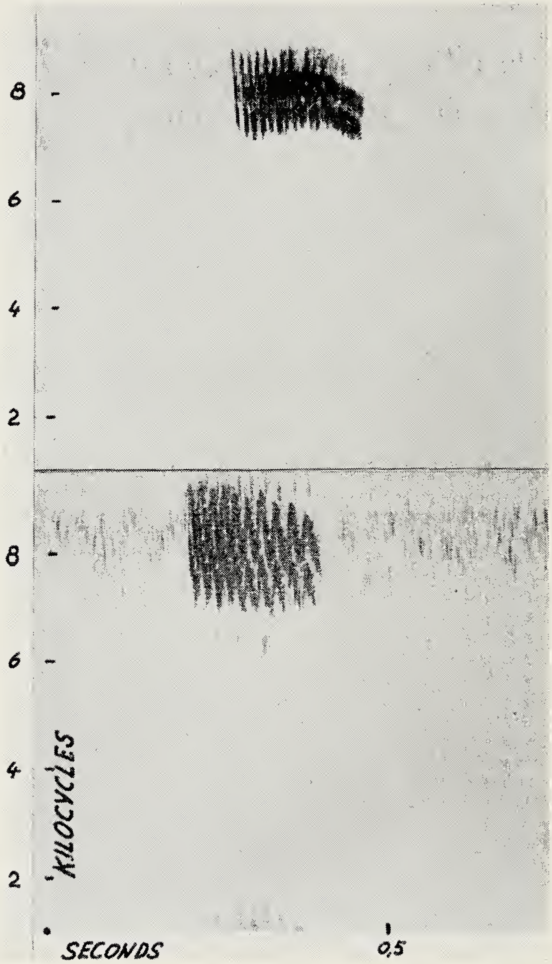

Fig. 2. Similarity in location call between closely related species. Top: *Ficedula hypoleuca*. Bottom: *F. albicollis*.

Except in closely related species, these location calls differ from one another quite considerably—even in the case of species of the same genus. Frequently they differ more markedly than the other calls of the old birds.

The location call of some species of the genus *Parus* (Fig. 1) illustrates this difference. This call shows some fluctuations in its intensity depending on whether or not the young bird is hungry. In nature, most young birds are never quite satisfied, and only rarely are they very hungry, so that not as many fluctuations are noted in the wild as in the case of birds hand-reared in captivity. These fluctuations never change the characteristic elements of the calls.

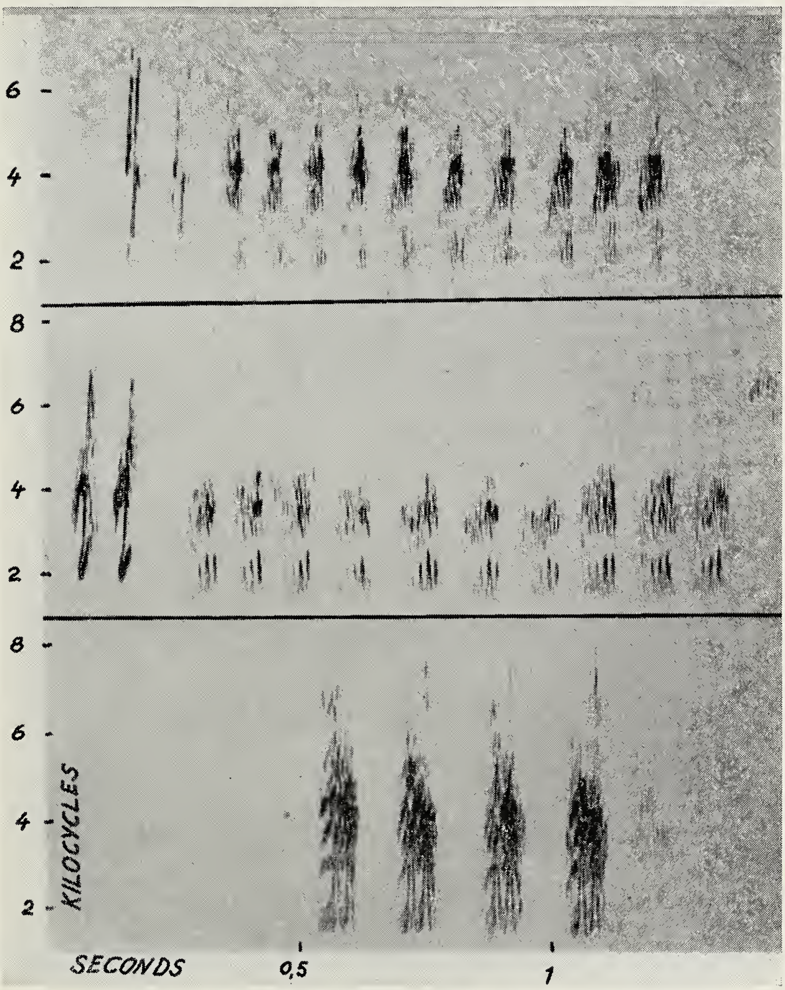

Fig. 3. Alarm calls in two subspecies and one closely related species. Top to bottom: *Parus m. major*; *P. m. nipalensis*; *P. monticolus*.

Of course it was important to study the location calls of closely related species. Two closely related but distinctive species of flycatchers breeding in central Europe, the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*F. albicollis*), have songs and mobbing calls that differ quite considerably while some other calls are very similar. The location calls of these two species, although not distinguishable by ear, can be differentiated through an audiospectrogram (Fig. 2). This shows that the close relationship is reflected by a very similar location call.

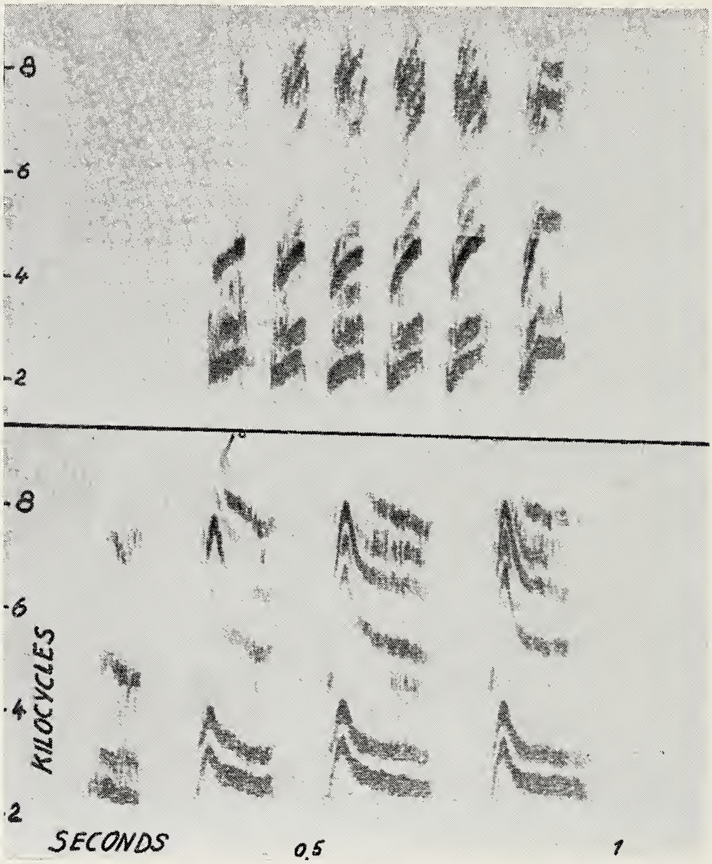

Fig. 4. Location call in closely related species. Top: *Parus major*. Bottom: *P. monticolus*.

Similar observations were made with meadowlarks (*Sturnella*) by Lanyon (1957).

The most common tit species, the Great Tit (*Parus major*), is found all over Europe and Asia in many different habitats. In South Asia, this species is smaller, and the yellow and green colors are replaced by gray. As the subspecies *P. m. nipalensis* is frequently imported through Indian dealers, I had an opportunity to make a comparative study of the two types. The songs of the extreme races *major* and *nipalensis* are very different, but all other calls are practically identical; those of the Indian race sound somewhat weaker in proportion to their smaller bodies. The location call of the two subspecies also shows very few differences.

The Green-backed Tit, *P. monticolus*, which is found only in the Himalayas and on Formosa, is very closely related to the Great Tit but does not hybridize in the border areas, and there is no doubt that this is a good species. Not only is the song very different from that of the Great Tit, but the same is true for all the other calls, e.g. the mobbing calls (I showed a

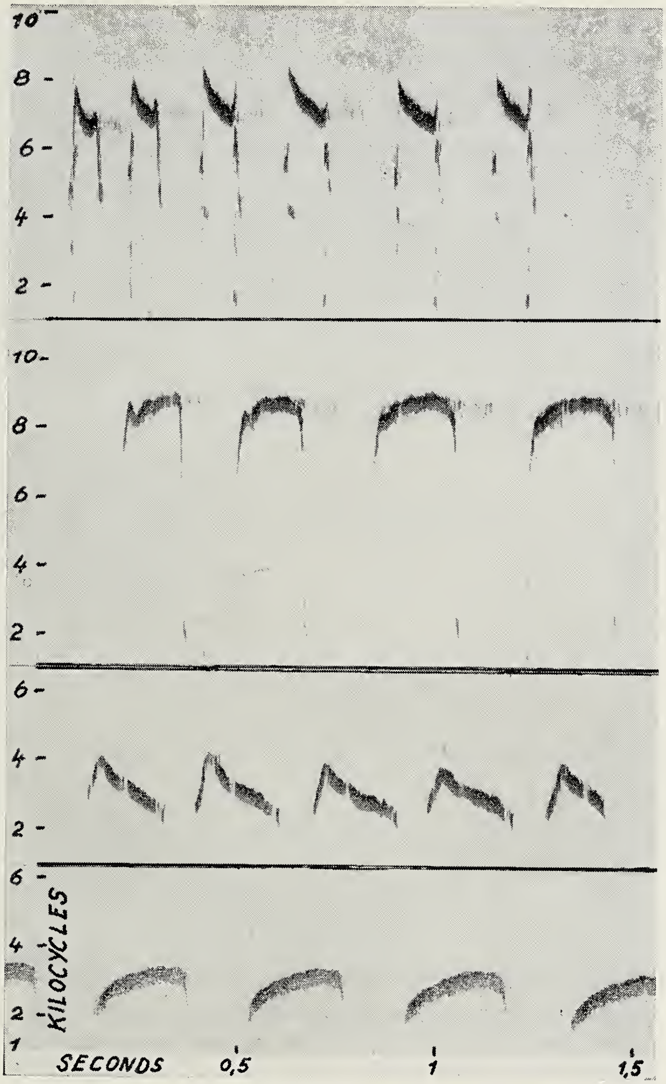

Fig. 5. Location call and song in related species.
Top to bottom: Location call—*Sitta castanea*; *S. europaea*. Song —*S. castanea*; *S. europaea*.

stuffed owl to the birds) (Fig. 3). While the different European and South Asiatic races of *P. major* show a remarkable conformity, the call of *P. monticolus* sounds quite different. *P. monticolus*, which hatched and recently fledged in my aviaries, has a location call which shows a greater similarity to that of the Great Tit than other calls of these two species (Fig. 4). This similarity furnishes proof of the close relationship.

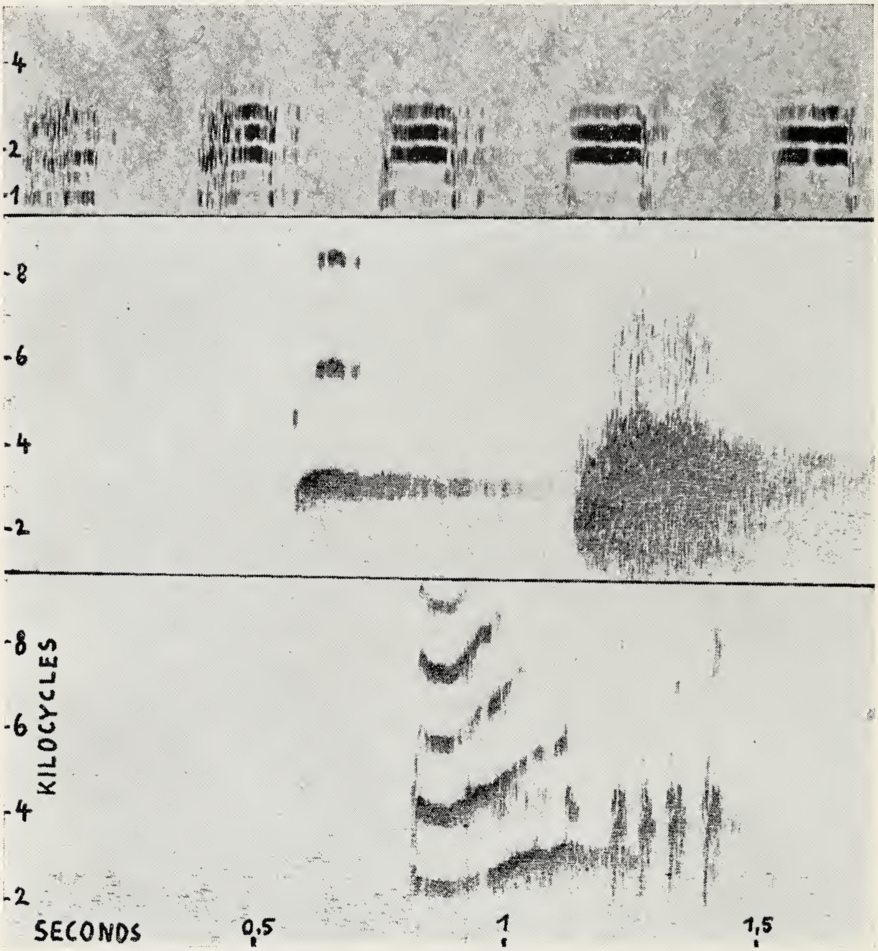

Fig. 6. Dissimilarity of location call in "*Sitta canadensis* group." Top to bottom: *S. canadensis*; *S. whiteheadi*; *S. krueperi.*

A number of forms of the genus *Sitta* are especially problematical in their relationships to one another. *S. europaea* is the species showing the largest regional distribution and the greatest number of different races. It is open to question whether or not the South Asiatic forms with chestnut-brown underparts belong to this species. Some systematists regard these forms as subspecies of *S. europaea*, while others think they are closely related but separate types. Voous and van Marle (1953) say they are "intermediate between a subspecies and a species," while Vaurie (1959) writes that it is "most uncertain whether or not the *castanea* group is conspecific with . . . *europaea*."

As one might expect, the songs of the two *Sitta* groups are rather different from one another. The greatest difference is found in the scolding notes. Although the location call clearly shows the relationship, it just as clearly reveals differences between the songs (Fig. 5). That seems to be one of the arguments speaking against conspecificity of the two groups. Efforts to hybridize the two were successful, but only after great difficulties had been overcome, which were due in no small measure to the "wrong" calls during the mating ceremony.

Just as problematical as the relationship between the *S. europaea* and *S. castanea* groups is the group of the small *Sitta* types that are found at geographically isolated locations and that are also rather different morphologically. However, because of many similarities, they are regarded by some systematists as subspecies of *S. canadensis*. Some calls of three of this group (*Sitta canadensis*, *whiteheadi*, and *krueperi*), which I have studied extensively both in the field and in captivity, showed similarities. However, the dissimilarities were indicated not only by their various calls but also by their completely different location calls. This situation discloses that there has been more extensive differentiation than one would expect in view of their morphological similarity (Fig. 6). I believe that in this case the location call, based on genetically fixed features, is an important argument against these groups being regarded as conspecific.

What I wish to show here is not that location calls are of extremely great importance, but rather, I wish to stress the principle that bird vocalizations are indeed a suitable tool for judging relationships. At least at the *species level*, the collecting and comparing of location calls is likely to lead to discussions that are no less important than those resulting from certain morphological characters.

SUMMARY

Some calls and songs of birds contain learned elements. Experiments with exchanged eggs demonstrated that the young, bred and reared by foster parents of a different species, always gave the location call in the species-specific way. They could not have learned it. The location call is therefore more useful than other calls in taxonomic problems at the species level.

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The Evolution of Manakin Displays

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Something is now known of the behavior of some 25 species of manakins (Pipridae), about one-half of the whole family. Sick (1959) has recently written a general review, and for convenience I have listed in the Appendix the species whose displays have been described, with a summary of their chief characteristics, so far as known. Observations on most of the species are still exceedingly fragmentary. Five are comparatively well known (*Manacus manacus, M. vitellinus, Pipra mentalis, P. erythrocephala, Chiroxiphia pareola*), and it is especially these that I shall use as a basis, admittedly unsatisfactory, for discussion of some general problems concerning the evolution of display in the family. Further observations will certainly modify some of my conclusions.

At the outset it is necessary to define a few terms. All displays in which two or more males are associated together I shall call collective or group displays. It is, of course, in the development of displays of this sort, performed at traditional display grounds, that the manakins are outstanding. Collective displays may be divided into two kinds: lek displays, where the males are clearly rivals, each one occupying his own perch or court, and true communal displays, in which the males take equal parts in a joint performance. Lek displays are characteristic of manakins of the genus *Manacus* and *Pipra*, while the genus *Chiroxiphia* exhibits the supreme examples of true communal displays.

ECOLOGICAL FACTORS IN THE EVOLUTION OF GROUP DISPLAYS

First, we may consider the ecological factors favoring the evolution of group displays performed at permanent traditional display grounds. The chief prerequisite is that the male should be emancipated from nesting duties. In nidicolous birds this is possible only if the female alone is able to incubate the eggs and feed the young, and it is almost certainly because of this that collective displays have evolved, so far as known, only in families that are mainly frugivorous or nectarivorous—the hummingbirds, cotingids, manakins, and birds of paradise—and not in primarily insectivorous families. The reason is surely that fruit- and nectar-eating birds can find food for themselves and their family far more quickly than can insectivorous birds, so that one parent alone can attend the nest. For the same reason, the males can spend a great part of their time at the display grounds, with only short absences to feed. (Our observations, on seven species, showed that male cotingids, manakins, and hermit hummingbirds regularly spend 80–90 percent of the daylight hours on or near their display perches.)

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The emancipation of the male from the nest is made possible by the ability of one parent to attend the eggs and young; it may also be positively advantageous if he is brighter or more conspicuous than the female. Whether sexual dimorphism was evolved in the Pipridae before or after the emancipation of the male is, of course, unknown; but in any case, once the male was dissociated from the nest, sexual selection was, as it were, given its head, and the way was open for the evolution of exaggerated display movements and the accompanying specializations of plumage and structure. At the same time, with the weakening of the pair bond, there must have been a strong selective advantage in polygamy, since those males that fertilized the most females would leave the most descendants.

In this brief and undoubtedly oversimplified argument I have so far taken the small family size for granted. It is not possible to discuss here the significance of the small clutch size of tropical birds, but it may be noted that those tropical forest birds that have communal or lek displays lay clutches of the same size as related species that have no such displays. I agree with Skutch (1949) that, in many tropical forest birds, clutch size is limited by other factors than the ability of the parents to nourish the young.

THE EVOLUTION OF LEK DISPLAYS

The strong sexual selection resulting from the emancipation of the male from nesting duties need not necessarily lead to group displays. Many examples where it has not done so are to be found in the hummingbirds and cotingids, and in the manakins themselves there are species in which the males display well apart from their fellows, within sound but not within sight of each other (*Neopelma, Tyranneutes, Pipra pipra*). But it has led to group displays in several species (*Manacus* and some species of *Pipra*), and the reason why it has done so is not difficult to discern. Once the pair bond has broken down, the coordination between the sexes necessary for successful mating must come to depend increasingly on the female's response to the stimulus provided by the courting male. The two birds may be strangers; there is no opportunity for the gradual overcoming of aggression and fear, as in the process of pair formation, and all must be achieved in a few seconds of highly coordinated mutual activity in which the male plays the leading role. If a group of n males displaying at close quarters has an attractive and stimulating power more than n times as great as that of a male displaying solitarily, any advantage that a male might gain by displaying away from his rivals is lost. Individuals displaying in groups will be more successful in leaving offspring, and the evolution of group displays will follow, unless accompanied by other disadvantages, such as increased danger from predators. It is reasonable to suppose that, in the manakins with lek displays, the stimulus provided by a group of males is in fact greater than that provided by a single male by a factor greater than the number in the group; for the group can advertise themselves much more continuously and effectively than can an individual bird, and, more importantly, the high degree of mutual stimulation between the males results in bursts of display which in impressiveness far exceed anything that the individual bird can achieve.

Yet in practice the group of displaying males has an upper size limit. Certainly in *Manacus* this is often set by the nature of the ground, which is not suitable for more than a certain number of courts, but even with an excess of suitable ground a limit will be set by the distances to which the females must travel to visit the display grounds. If all the males from a large area concentrated at one display ground, a few males setting up a much smaller display ground nearer to the outlying nesting areas would have an advantage over the males at the larger but more distant display ground. From this balance of advantages must result the roughly even dispersion of display grounds throughout the areas of suitable breeding habitat such as is actually found.

At the lek, relations between the males are ambivalent: They are sexual rivals, but at the same time they are drawn together by a strong social bond. Indeed, it is by the balance between these two tendencies that the lek is produced and maintained. At times, when display is slack, the males show their social tendency by sitting together in pairs, often for minutes on end. (In *Pipra erythrocephala*, a male under observation for a whole day spent a total of 3 hours 44 minutes sitting with one or another of his near neighbors.)

THE EVOLUTION OF COMMUNAL DISPLAYS

We may now turn to what is certainly the most advanced stage of group display, true communal or joint displays of males in which each bird plays an equal part, as exemplified especially in the genus *Chiroxiphia*. Again, permanent display perches are used, but these perches appear, at first sight, to be communal property. On them two or, in *C. caudata*, several males perform joint displays either by themselves or in front of a visiting female. As in the lek displays already considered, it seems very likely that the joint performance of two males is more than twice as likely to attract a female as that of a single male. From this point of view we can understand the evolution of joint displays, but they raise their own problems. First, the males must be sexual rivals: What happens when a female comes to the perch ready for copulation? For *C. pareola* in Tobago, observations made by my wife and myself in 1959 provided the answer (Snow, 1963*b*). When a responsive female came to the perch, only a single male was present, and he performed a strikingly different, mainly silent display toward her that culminated in copulation. The sequence occurred several times. Later observations suggested, although I was unable to prove this, that each display perch is in fact "owned" or dominated by a single male, that he attracts neighboring males to dance with him, but when a responsive female is present he is able to keep his neighbors away. The synchronized "cartwheel" dance (Gilliard, 1959), in which two males join, thus presumably represents a preliminary stage in the courtship, the function of which is to advertise the display perch and attract females to it.

If this interpretation is correct, we still have to explain the apparently disadvantageous behavior of the visiting males, which help to enhance the effectiveness of the dominant male's display and get nothing from it themselves. Do these other males also own display perches, to which they attract their neighbors, or do they simply occupy subordinate positions at the dominant bird's court? I attempted to answer this question last year by trapping and color banding the birds in a small area where there were two or three display perches, but my visit proved to be too late in the season, display was slack, and the results were inconclusive. I think it probable that some males own other display perches; and some, especially the younger ones, are subordinate at a dominant bird's court. In either case, behavior is involved which seems disadvantageous to the individual practicing it, and the problem remains.

Coordination between two males has reached such a high degree of perfection in *Chiroxiphia pareola* and related species that one has little clue to the course of evolution leading to this type of display. In *C. pareola* the normal sequence of behavior is that one male (presumed to be the owner of the display perch), sitting 20 or 30 ft up in a tree near the display perch, utters a call that attracts another male to join him. The two then sit side by side, often nearly touching, and utter a series of perfectly synchronized calls. They show absolutely no aggressiveness to one another. After a spell of calling, they may fly down to the display perch, which is only three or four ft above the ground, and perform the joint dance. In species of *Pipra* and *Manacus*, as already mentioned, males with neighboring display perches or courts also spend much time sitting together, usually on some intermediate perch, but they perform no joint activity and are clearly aggressive toward each other; in fact, their very proximity seems to inhibit them from display. In *Pipra* it is very noticeable that they always face away from each other. Thus, an essential step in the evolution of *Chiroxiphia*'s joint displays must have been the breaking down of aggressiveness between neighboring males, in the first instance perhaps on neutral ground between the display perches.

Pipra aureola, which I watched briefly in Surinam last year, shows an interesting condition intermediate between *Chiroxiphia* and other *Pipra* species. Males have their own display perches, 20 yd or so apart, within sound but not sight of each other. Periodically one male would visit a neighbor on his perch, and the two would perform a synchronized, joint display which was no less highly coordinated than that of *C. pareola*. But in this species I never saw neighboring males sitting together midway between their display perches, and I doubt if the present behavior of *P. aureola* provides a parallel with the early stages in the evolution of the behavior of *Chiroxiphia*.

DERIVATION OF THE DISPLAY MOVEMENTS

The final problems I wish to consider are ethological. First, can we discover the evolutionary derivation of the various bizarre, highly stereotyped display movements and postures? Secondly, to what extent can they be homologized between different genera and species in the family? As regards derivation, a few tentative suggestions can be made. The display flight of *Pipra* is almost certainly derived from the male's approach flight to the female preceding copulation. Similarly the "frenzied flutter" in *P. mentalis* and *P. erythrocephala* must be derived from copulation itself. In *P. mentalis* the male lands directly on the female's back (Skutch, 1949); correspondingly, the frenzied flutter takes place as the bird lands. In *P. erythrocephala*, the male lands beside the female and then mounts; correspondingly, the frenzied flutter is performed from a perched position, not on landing after a flight. The side-to-side slide, which is so conspicuous a feature of the displays of *P. mentalis*, *P. erythrocephala*, and *P. aureola*, and a less important element in *Chiroxiphia pareola*, is almost certainly derived from the sidestepping or shuffling movement which is the manakins' usual way of moving along a perch (unlike most passerines, manakins do not hop). The "slide down the pole" of *Manacus* may be similarly derived, but it is also linked with copulation, which is achieved by the male "sliding" down an upright sapling onto the back of the female.

At first, it might appear reasonable to derive the upward jump with fluttering wings, which is an important element in the display of *Chiroxiphia* species and *Neopelma chrysocephalum*, from fighting, but in fact aggression is not expressed in this way in manakins. Fights usually start with one male flying straight at another, the birds may then come to grips and roll together interlocked, or the attacked bird may take flight and a rapid flight-chase ensue. It seems more likely that the upward jump, as well as darting to and fro, and other main elements in the displays, are derived, like the side-to-side slide, from locomotory movements, for which the various ancestral forms were especially well suited by reason of their size, length of wing and of leg, and other bodily proportions. In this connection it is to be noted that manakins take food in flight, and the smaller species have great maneuverability and speed on the wing. The larger species are slower and clumsier in flight. To some extent, these differences must have determined the form their displays have taken. Thus, *Tyranneutes*, a very small manakin with relatively long wings, weighing not more than a large hummingbird, has a display flight in which it moves slowly forward with upright body much like the display of the hummingbird *Phaethornis longuemareus*. Species of *Pipra*, rather larger and also with long wings, are especially agile in flight; when feeding, they pluck berries and change course in the air with amazing rapidity. Correspondingly, rapid flights with sudden changes of course are a prominent part of their displays. *Chiroxiphia* and *Neopelma* are large species relatively heavy for manakins; when displaying, they jump upward only a few inches off the perch, and hang momentarily in the air before descending.

Some homologies between the displays of the different genera and species are clear, but so far they do little more than support conclusions that might be reached on morphological grounds. Within *Pipra*, the displays of *P. erythrocephala*, *P. mentalis*, *P. aureola*, and *P. fasciicauda* all have elements in common, while that of *P. pipra* is very distinct, as is also its color pattern. *P. aureola* is perhaps rather closer to *mentalis* than to *erythrocephala*. Within the group of forms commonly included under *erythrocephala*, *rubrocapilla* from Brazil appears to differ considerably in display from the golden-headed forms, as it does in color. Similarly, in *Chiroxiphia*, the three closely related species, *pareola*, *lanceolata*, and *linearis*, all have rather similar displays, different from that of the morphologically distinct *C. caudata*.

Turning to intergeneric relationships, we may suspect that both *Corapipo* and *Machaeropterus* are related to *Manacus*. Like *Manacus*, the former displays on or near the ground, has a whirring flight, and exhibits its throat feathers, while the latter displays perched on vertical twigs near the ground and produces a mechanical sound with its secondaries. *Manacus* seems not to be close to any other genera whose display is known, resembling *Pipra* only in its rapid flights to and fro between adjacent perches but differing in most other important respects. *Pipra* itself may be closer to *Chiroxiphia* than to any other genus whose display is known; they have in common the type of display perch used, the side-to-side slide, and, perhaps most importantly, a specialized flight to the perch from a distance of several yards. In this connection it may be significant that, as already mentioned, in *P. aureola* pairs of males perform a coordinated joint display analogous to those that are so characteristic of *Chiroxiphia*. Finally, I have suggested elsewhere (Snow, 1961) that, on the basis of its display, *Tyranneutes* may be close to *Neopelma*, a relationship suggested also by their similarity of plumage.

SUMMARY

The group displays of manakins (Pipridae) are divided into lek displays, where the males are clearly rivals, each occupying its own display perch or court, and true communal displays, in which the males participate in a joint performance. It is suggested that emancipation of the male from the nest has been the chief prerequisite for the evolution of such displays; and that they have evolved only in primarily frugivorous or nectarivorous families because such birds can find food for themselves and their families in a very short time, thus allowing the female alone to feed the young and the mate to devote much time to display.

The basic condition for the evolution of lek displays is that a group of n males displaying at close quarters should have an attractive and stimulating power on the female more than n times as great as that of a male displaying solitarily. The implications of this are discussed. The lek is maintained by

a balance between the aggressive and social tendencies of the males. True communal displays result from the breaking down of the aggressive component.

Communal display is best known in *Chiroxiphia pareola*. The joint performance by two males has been found to represent a preliminary phase in the courtship, while copulation itself is preceded by a different display by a single male, presumed to be the dominant bird at the display perch.

The evolutionary derivation of the display movements, and possible homologies between displays of different species and genera, are briefly discussed.

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APPENDIX

Synopsis of Manakin Displays

The order and nomenclature are according to Hellmayr (1929). Species for which calls have been recorded, but no dance or other display, are omitted. Some of these (e.g. *Schiffornis*, *Piprites*) should perhaps be referred to the Cotingidae.

Pipra aureola (Snow, 1963*c*)

Organization: Groups of 2–3 males occupying perches 30–40 yd apart, within sound but not sight; each displaying mainly on its own perch, but also visiting and performing joint display on neighbor's perch.

Display perch: Horizontal twig, 10–30 ft above ground.

Display: Three different calls, two mechanical noises; display flight to perch; rapid sliding back and forth; wing-shivering, with wing-patch displayed.

Pipra fasciicauda (Sick, 1959)
Organization: Two males may display on same perch; no other details.
Display: Display flight to perch; sliding and various other movements and postures.

Pipra mentalis (Skutch, 1949; Snow, unpublished)
Organization: Groups of up to five males occupying perches 7–40 yd apart. Pairs of males frequently sit together midway between their display perches.
Display perch: Horizontal twig or vine, 15–50 ft above ground.
Display: Several calls and mechanical wing-noises; display flight to perch; about-face, backward-slide, and darting back and forth.

Pipra erythrocephala (Snow, 1963*a*)
Organization: Groups of usually 6–12 males occupying perches several yards apart. Pairs of males frequently sit together midway between their display perches.
Display perch: Horizontal twig, 20–40 ft above ground.
Display: Several calls and one mechanical wing-noise; display flight to perch; backward-slide, with wings extended horizontally and then raised at end of slide; about-face, darting back and forth, and upright posture. (Display of *P. e. rubrocapilla* from Brazil differs in several respects, especially in exhibition of markings of under-side of wing [Sick, 1959].)

Pipra pipra (Snow, 1961)
Organization: Two males about 65 yd apart, just within hearing distance.
Display perch: Various perches within a limited area, 18–30 ft above ground; apparently no main display perch.
Display: Slow flapping flight; poorly developed display flight to perch, about-face, and darting back and forth.

Machaeropterus regulus (Sick, 1959)
Organization: Two males perched close together; no further details.
Display perch: Vertical twig near ground.
Display: Whirring or reeling sound; rapid turning to and fro on perch, in head-downward position.

Machaeropterus pyrocephalus (Sick, 1959)
Organization: Two males perched close together.
Display perch: Vertical perch in tree canopy.
Display: Advertising call; flight noise made by wings; rhythmic turning on perch, so rapid that bird becomes blurred; grasshopper-like sound, probably made by secondaries.

Xenopipo atronitens (Sick, 1959)
Organization: 2–3 males within hearing distance of each other; chasing between males, but apparently no collective display.
Display: No special perch; advertising call, with wings hanging and rump feathers raised.

Tyranneutes virescens (Snow, 1961)
Organization: Groups of 2–4 males, 30–50 yd apart, within hearing but not sight.
Display perch: Horizontal twigs, mainly 15–20 ft above ground; several used within a small area.
Display: Advertising call; slow floating flight from perch to perch; head-swinging display with crest raised.

Chiroxiphia linearis (Slud, 1957)
Organization: Coordinated display between pairs of males.
Display perch: Horizontal branch or vine near ground.
Display: Advertising calls; alternate jumping and cartwheel dance performed by two males.

Chiroxiphia lanceolata (Friedmann and Smith, 1955; Snow, unpublished)
Organization: Coordinated display between pairs of males.
Display perch: Horizontal branch or vine near ground.
Display: Advertising calls; alternate jumping by two males.

Chiroxiphia pareola (Gilliard, 1959; Snow, 1963*b*)
Organization: Coordinated display between pairs of males, but one male probably dominant at each display perch.
Display perch: Horizontal or sloping branch or vine near ground.
Display: Advertising calls by single males; synchronized calling, alternate jumping, and cartwheel dance by pairs of males; precopulatory display by single male, with bouncing flight over and across perch and display flight to perch.

Chiroxiphia caudata (von Ihering, 1936; Sick, 1959)
Organization: Coordinated display by 2–4 or more males.
Display perch: Slightly sloping branch near ground.
Display: Males perching side by side in a row, forming a vibrating mass; lowest bird jumps up, hovers, and lands at upper end of row, then next bird, and so on (accounts are discrepant).

Ilicura militaris (Sick, 1959)
Organization: 2–3 males in neighboring trees; chasing, but no group display.
Display: Mechanical wing-noises; flights to and fro between perches several feet apart.

Corapipo gutturalis (Davis, 1949*a*)
Groups of 6–12 birds, 10–50 ft up in trees. Chasing, with whirring flight; crouching, with bill raised and white throat displayed. Precopulatory displays on fallen log: male crouching and crawling toward female, with wings spread horizontally.

Corapipo leucorrhoa (Aldrich and Bole, 1937)
Solo display by male, no other birds nearby: slow flight with rapidly vibrating, humming wings, up to 50 ft from one perch to another; explosive *puff* sounds made at intervals.

Manacus manacus (Snow, 1962)
Organization: Groups of up to 70 males, each occupying a court a few feet or yards apart.
Display perch: Cleared court on ground, with one or more upright saplings.
Display: Calls; several mechanical wing-noises; jumping to and fro between saplings; jump to ground and back up onto sapling; "slide down the pole"; "fanning" with wings.

Manacus vitellinus (Chapman, 1935)
Organization and display as in *M. manacus*, with minor difference as noted in Snow (1962*a*).

Neopelma chrysocephalum (Davis, 1949*b*; Snow, unpublished)
Organization: Males spaced out within hearing distance.
Display perch: Various perches 10–60 ft above ground; no special perch.
Display: Advertising call; upward jump with crest raised and spread, accompanied by twanging call.

Neopelma pallescens (Sick, 1959)
Organization: Males spaced out about 100 ft apart.
Display: No special perch; upward jump with crest spread, accompanied by wing-noise and call on landing.

Heterocerus linteatus (Sick, 1959)
Display perch 10–13 ft above ground. Advertising call, with white throat-patch spread laterally to cover sides of head. Chasing between males.

Courtship and Mating Behavior and the Phylogeny of the Grebes

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Grebes are an ancient group and are widely distributed throughout the world. Nineteen species are currently recognized (Table 1). The current systematic arrangements of the grebes have been based almost entirely on characters visible in study skins, with what I believe to be undue emphasis on differences in the ornamental plumes of the head. The elaboration and differentiation of these plumes are greatest in the four species *Podiceps cristatus, P. auritus, P. nigricollis,* and *P. grisegena,* which are sympatric over large areas, a situation under which strong selective pressures can be expected to favor the elaboration of such species-specific differences. In order to achieve a better understanding of the phylogeny of the grebes, I have initiated a series of studies on the comparative behavior and anatomy of members of the group. This paper is in essence a progress report on the behavioral aspects of the problem.

Peters (1931) divided the family into five genera (*Poliocephalus, Colymbus* [now *Podiceps*], *Centropelma, Aechmophorus,* and *Podilymbus*). Since then, two changes at the generic level have been suggested: In 1939 Wetmore

TABLE 1.—THE DISTRIBUTION OF THE SPECIES OF GREBES

Species	South America	North America	Eurasia	Africa	Madagascar	East Indies	Australia	New Zealand
Tachybaptus ruficollis			X	X	X	X		
T. novaehollandiae						X	X	
T. pelzelni					X			
T. rufolavatus					X			
Podilymbus podiceps	X	X						
P. gigas		X						
Rollandia rolland	X							
R. micropterum	X							
"Podiceps" major	X							
Podiceps poliocephalus							X	
P. rufopectus								X
P. dominicus	X	X						
P. grisegena		X	X					
P. cristatus			X	X			X	X
P. auritus		X	X					
P. nigricollis	X	X	X	X				
P. occipitalis	X							
P. taczanowskii	X							
Aechmophorus occidentalis		X						

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(p. 180) proposed that *Poliocephalus* be merged with *Podiceps,* and in 1954 Wetmore and Parkes transferred the species *major* from *Aechmophorus* to *Podiceps.* It now seems advisable to divide the family into two groups, perhaps best called tribes. Members of the tribe Podilymbini may be characterized by the combination of a well-developed flexor perforatus digiti II muscle in the shank with a separate canal (Fig. 1) through the hypotarsus for its tendon of insertion and the similarity of their copulatory behavior, described below. In the following species, the extra canal in the hypotarsus is present: *podiceps, gigas, ruficollis* (and presumably its close relatives *novaehollandiae, pelzelni,* and *rufolavatus*), *rolland chilensis,* and *micropterum.* The copulatory behavior of *podiceps* and *ruficollis* is similar; that of the remaining species in this group is unreported. The available evidence indicates that neither *dominicus* nor *poliocephalus* and *rufopectus* belong with the *ruficollis* group, hence the generic name *Tachybaptus* Reichenbach must be revived for *ruficollis, novaehollandiae, pelzelni,* and *rufolavatus.* (The genus *Sylbeocyclus* Macgillivray, 1842, suggested for these birds by Simmons [1962:112] is preoccupied by *Sylbeocyclus* Bonaparte, "1831" [1832?], type "*Pod. carolinensis*" [= *Podilymbus podiceps*], a synonym of *Podilymbus* Lesson. This matter of synonymy was cleared up by Sclater [1874:98–99], who, however, dated the genus from 1834, instead of 1832.) I agree with Simmons (1962:111) that the species *rolland* (including *chilensis*) and *micropterum* are closely related. Pending further studies, it seems best to consider them a separate genus, *Rollandia* Bonaparte; their behavior, as far as known, and the presence of the canal for M. flexor perforatus digiti II in the hypotarsus exclude them from *Podiceps.*

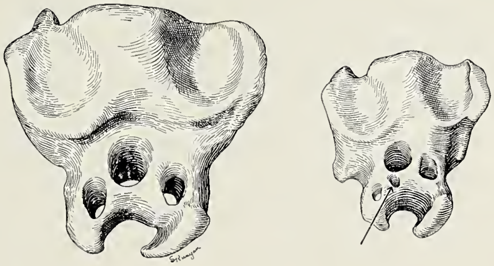

Fig. 1. Posterior view of the left tarsometatarsus of *Podiceps grisegena* (left) and *Podilymbus podiceps.* The arrow points to the canal for the tendon of insertion of M. flexor perforatus digiti II.

Members of the tribe Podicipedini are characterized by the absence of the extra canal in the hypotarsus and by their copulatory behavior. Six closely related species, *grisegena, cristatus, auritus, nigricollis, occipitalis,* and *taczanowskii,* form the nucleus of the genus *Podiceps,* to which I tentatively add the little-studied species *dominicus, poliocephalus,* and *rufopectus,* all of which agree with *Podiceps* in the hypotarsal character. *Aechmophorus* is best considered a valid genus with one species, *occidentalis*. The species *major* is difficult to place generically. As Wetmore pointed out (1954), it does not belong in *Aechmophorus*. Simmons' suggestion (1962:112, 115) that it is close to *Podiceps grisegena* is based on the superficial similarity of head patterns. I have reported elsewhere (1963) that the behavior of *major* differs strongly from that of the "nucleus" species of *Podiceps* and am unwilling to make even a tentative generic placement at this time.

The behavior of one species, the Great Crested Grebe (*Podiceps cristatus*), has been described in detail by Huxley (1914) and Simmons (1955), and shorter papers have appeared on the behavior of other species (e.g. McAllister, 1958, on *P. nigricollis*; Hartley, 1933 and 1937, on *Tachybaptus ruficollis*; Buddle, 1939, on *P. rufopectus*; and Wobus, 1960, on *P. grisegena*); but little has been done on the comparative aspects, aside from McAllister's comparison of *nigricollis* with *cristatus*. For several years I have been collecting field data on the behavior of the five common North American species: the Western, Red-necked, Horned, Eared, and Pied-billed grebes (*Aechmophorus occidentalis*, *Podiceps grisegena*, *P. auritus*, *P. nigricollis*, and *Podilymbus podiceps*, respectively). In 1961, Frank B. Gill and I spent 5 months in South America studying the five endemic species, "*Podiceps*" *major*, *P. occipitalis*, *P. taczanowskii*, *Rollandia rolland chilensis*, and *R. micropterum*. Parallel anatomical studies on these birds have begun. The work of Huxley and Simmons on *P. cristatus* forms an excellent basis for comparison with the American species, and a few gaps have been filled by odd bits of information in the literature. More detailed reports on individual species and groups of species are being prepared for publication elsewhere.

The sexual behavior of grebes is divisible into two phases: courtship and platform behavior. The former consists of a series of displays and ceremonies which Huxley (1914:509) has referred to as "self-exhausting," that is, not leading directly to further sexual activity. The latter is centered about copulation, which occurs on the nest or a similar platform. The courtship activities are complex and appear to function in forming, maintaining, and strengthening the pair bond. With one possible exception, each species has a unique combination of courtship displays and ceremonies, which, like the marked specific differences in the pattern of the head and bill, are of adaptive value in insuring that a bird will mate with an individual of the same species. Some of the courtship ceremonies are similar in overall pattern among several species. This similarity may be considered indicative of close relationship, particularly in the case of very complex ceremonies. In contrast, the platform behavior varies little between species, or even genera. As pairs have been formed prior to the start of this behavior, the interspecific differences which are found are not of adaptive value in preventing the formation of mixed pairs. The one striking and apparently constant difference in copulatory behavior separates the two tribes and probably had its origin early in the evolutionary history of the group.

COURTSHIP DISPLAYS

In *Podiceps* and allied genera (tribe Podicipedini), the displays and ceremonies that compose the courtship activities range from simple to extremely complex. Some of the simple displays, such as Head-shaking and Habit-preening, differ little from one species to another. In these, however, the specific patterns of the head and neck are conspicuous. Advertising, performed in similar postures by at least nine species (*cristatus, grisegena, auritus, nigricollis, occipitalis, taczanowskii, rolland, major*, and *occidentalis*), is accompanied by a species-specific call. In species that nest in colonies, there may be individual differences in this call. Such differences are particularly marked in the case of *Aechmophorus occidentalis*, in which the number of syllables, the stressing of syllables, and even the quality of the call are subject to variations. The almost constant repetition of these notes undoubtedly permits the birds to recognize their neighbors and may well be a factor in reducing aggressive behavior within the colony. It may be particularly important during the birds' nocturnal activities.

Most, if not all, grebes have displays in which the bird rises nearly vertically in the water, its feet paddling rapidly all the while. When two birds do this face to face, it is referred to as a "Penguin-dance"; when the birds move forward side by side in this posture, it may be called "Rushing" or "Barging" (Storer, MS.), depending upon the speed with which they move. The birds may carry aquatic vegetation in their bills during these activities. A Penguin-dance with weeds is known for *Podiceps cristatus, P. grisegena*, and *Ae. occidentalis*, whereas a Weed-rush is characteristic of *P. auritus*. Rushing without weeds has been described in *P. dominicus* (Zimmerman, 1957) and as a variant of the Penguin-dance of *P. nigricollis* by McAllister (1958:295). In a highly modified form, it appears as the "Race" of *Ae. occidentalis*. What I have termed "Barging and Diving" (Storer, MS.) is characteristic of *P. occipitalis* and its relative *P. taczanowskii*. In this, two or more birds alternately Barge side by side and dive in unison.

Display flights low over the water, often with the head held low, occur in several species. Such a flight is part of the "Display Ceremony" (Huxley, 1914:513) in pairs of *P. cristatus*, and somewhat similar ceremonies are performed by pairs of *P. major* and *P. occipitalis*. Group display flights are a feature of the behavior of *R. rolland chilensis*. I have not witnessed display flights by any of the North American species; if such occur, they must be rare.

The species of the Podicipedini for which there are adequate behavior data all have at least one elaborate complex of displays which comprise a courtship ceremony. The best known of these is the "Discovery Ceremony," which was named and first described by Huxley in his pioneer work on *P. cristatus* (1914). This ceremony has also been reported for *P. nigricollis* by McAllister, who thought it "an incomplete form of the penguin dance"

(1958:295). In *nigricollis*, however, as in the other species in which I have observed it (*P. auritus*, *P. grisegena*, *P. occipitalis*, and *P. taczanowskii*), this ceremony is highly ritualized and far more complex than the Penguin-dance. In all six species for which it is known, it is very similar in pattern, from the Cat Display through the underwater approach, Ghostly-penguin, and climactic Head-shaking or Penguin-dance, to the Ceremonial Turning-away. As far as I could determine, the ceremony is similar in the two closely related species, *P. occipitalis* and *P. taczanowskii.* However, the four northern species differ markedly in the details of the ceremony. For instance, the Cat Display may be performed with the wings spread (*cristatus* and *nigricollis*) or closed (*auritus* and *grisegena*), the underwater approach may be a "Ripple-dive" (*cristatus*) or punctuated by emergences in a "Bouncy Posture" similar to a posture assumed during bathing (the other three species), and the climax of the ceremony may be performed with the body horizontal (*cristatus*) or in a Penguin-dance (the other three) with Head-shaking (*cristatus*), Habit-preening (*auritus*), or neither. This ceremony appears to be an important one in forming and strengthening the bond between members of a pair, and the specific differences in the display and the marked differences in the pattern of the head must be important in preventing the formation of mixed pairs. In the past, selective pressures have undoubtedly favored accentuation of these behavioral and morphological differences where the four species (*cristatus*, *auritus*, *nigricollis*, and *grisegena*) are widely sympatric in Eurasia and the last three in North America. On the other hand, the essential similarity in the form of this ceremony in the six species in which it is known to occur is good evidence that these six species are closely related. This group of species has its headquarters in the Northern Hemisphere, and it is probable that the South American forms (*andinus*, *occipitalis*, and *taczanowskii*) resulted from two invasions from the north of the line to which *nigricollis* belongs.

P. major has a Nodding and Turning Ceremony (Storer, 1963), which may correspond with the Discovery Ceremony. Its points of resemblance are its initiation by one bird's Advertising and its ending in a Ceremonial Turning-away. After Advertising by one bird, the members of a pair approach, facing each other with crests raised, and nod several times. Then they turn and swim side by side for a foot or two, turn face to face, swim side by side in the opposite direction, etc., repeating the turning as many as twenty times before turning away ends the ceremony.

The Rushing Ceremony of *Aechmophorus occidentalis* (described as the "Race" by Nero, in Palmer, 1962:100–101; and personal observations) is completely different from the Discovery and the Nodding and Turning ceremonies. Starting with mutual Threat-pointing, Dip-shaking, and a characteristic call, it proceeds through the very rapid Rushing and a nearly synchronous dive to the final slow Barging accompanied by slow Head-shaking and the peculiar "Tea-kettle Whistle." The last part of this ceremony is similar to the Barging and Diving of *P. occipitalis* and *P. taczanowskii* in general pattern (although the dive and the Barging are not repeated in *occidentalis*) and in the fact that more than two may display together and the roles of all birds are similar. Although ordinarily a pair performs the Rushing Ceremony, not infrequently two males and rarely two females have been observed to do so. When more than two birds race, the extra bird or birds are males. There is no evidence to date that Advertising initiates this ceremony.

R. rolland chilensis has a unique Bumping Ceremony. Members of a pair face each other in a stiff posture resembling that used in Advertising, then one dives and comes up under the other, breast to breast, often with such force that it knocks the second bird clear of the water. The stiff posture and the diving and coming up under the mate are repeated several times, the birds alternating roles or repeating the same one.

The courtship behavior of the Podilymbini is little known in spite of the considerable amount of time that Hartley (1933, 1937), McAllister, Storer, and others have spent observing at least two species (*Podilymbus podiceps* and *Tachybaptus ruficollis*). No complex ceremony comparable to the Discovery Ceremony has been described for any species of this group, and it is likely that none exists. Calling between members of a pair while separated and a greeting duet (at least in *Podilymbus*) while swimming side by side after separation are commonly observed. It is likely that these calls may in part replace the more elaborate ceremonies of the Podicipedini in forming and strengthening the pair bond. I have witnessed several actions by *P. podiceps*, which may be displays, and there are several descriptions of such activities by *T. ruficollis* (e.g. Hamling, 1953; Hartley, 1933 and 1937; Huxley, 1919; and Wilson, 1959).

PLATFORM BEHAVIOR

Platform behavior is quite similar in all grebes so far studied. Two soliciting displays appear to be universal. These are Rearing and Inviting (see photographs by Hosking in Hosking and Newberry, 1946). Rearing at times is accompanied by a slight raising and vigorous shaking of the closed wings. Both soliciting displays are performed by birds of both sexes, and reverse mounting probably occurs in all species, especially early in the season. Slight differences in the posture of the neck appear to be the only interspecific differences in these displays. Copulation occurs on a platform following Inviting by the "passive" bird. In the Podilymbini so far as known (*P. podiceps* and *T. ruficollis*), the "passive" bird strokes the breast of the "active" bird with the back of the head and nape during copulation; in the eight species of Podicipedini so far studied, the "passive" bird remains in the Inviting posture throughout the act. This appears to be the major character of phylogenetic significance in platform behavior. Postcopulatory displays usually include water treading in the Escape-bathing Posture by the "active" bird and Head-shaking by both birds, but there appears to be considerable individual variation within at least some species, hence differences in these displays are probably unimportant as indicators of relationships.

SUMMARY AND CONCLUSIONS

Summarizing the available behavioral evidence, we can reach the following conclusions regarding the relationships of the species of grebes:

1) The apparent replacement of complex courtship ceremonies by vocalizations and the stroking of the breast of the "active" bird during copulation set the Podilymbini (*Podilymbus* and *Tachybaptus*) apart from the Podicipedini.

2) The species *rolland* and *micropterum* resemble the Podilymbini in possessing a canal for the tendon of M. flexor perforatus digiti II in the hypotarsus. The Bumping Ceremony and group-display flights of *rolland* and a suspected underwater display of *micropterum* involving the strikingly colored feet (chrome-yellow above and black below) and possibly derived from the Bumping Ceremony further set these species apart from *Podiceps*. Whether they belong to the Podilymbini or to the Podicipedini or to a third tribe remains to be shown.

3) The species *major* is unique among the species studied in its Nodding and Turning Ceremony. In its copulatory behavior and Ghostly-penguin display, it resembles the Podicipedini. Its generic placement is at present uncertain.

4) *Aechmophorus occidentalis* differs from the other species of the Podicipedini in its striking Rushing Ceremony, in using courtship feeding, and in certain arching postures of the neck. The similarity of its Penguin-dance with weeds to those of *Podiceps cristatus* and *P. grisegena* points to a relationship with birds of that genus.

5) The six species *cristatus*, *auritus*, *grisegena*, *nigricollis*, *occipitalis*, and *taczanowskii* resemble each other closely in possessing a Discovery Ceremony. They form the nucleus of the genus *Podiceps* (type *cristatus*).

6) The behavior of *dominicus*, *poliocephalus*, and *rufopectus* is not sufficiently well known to suggest where their relationships lie.

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Virology in the Biology of Birds

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The human disease best known to result from an avian parasite possessing some characteristics of a virus is called ornithosis, or psittacosis when resulting from association with psittacine birds. The usual mode of natural transmission is by inhalation of an aerosol containing the infectious agent. This is also the mechanism of infection for another avian parasite, the true virus of Newcastle disease which has been isolated from naturally infected wild birds (Gillespie et al., 1950; Shah and Johnson, 1959). Considering the wide range of viral zoonoses—"infections of animals that are secondarily contagious to man" (Meyer, 1955)—contact is the simplest mechanism for transmission of viruses to man and other animals. There are a number of other virus infections of birds, those of domestic fowl being of particular concern to veterinary science, but since they do not frequently, if ever, produce disease in man, they are of no further importance here.

The most complicated and variable mechanisms of virus transmission involve some arthropod. The complexity of these mechanisms is conveyed by the term arthropod-borne virus, which has been condensed to "arbovirus" for linguistic convenience. An arbovirus has been defined as one "which in nature, can infect haemophagous arthropods by their ingestion of infected vertebrate blood. It multiplies in their tissues and is transmitted by bite to susceptible vertebrates" (World Health Organization, 1961). A great variety of arthropod-borne viruses involve many wild avian species as natural and sometimes essential vertebrate hosts in numerous ecological situations occurring in most major zoogeographical areas.

ARBOVIRUS ISOLATIONS FROM BIRDS

Having established the parameters of the most diverse but biologically related viral parasites of birds, it is pertinent to focus attention on the arboviruses with which wild birds are commonly infected in nature. Because domestic fowl were observed to be closely associated ecologically with equine and human hosts in early investigations of outbreaks of western (WEE) and eastern (EEE) equine virus encephalitis (Ten Broeck, 1938; Ten Broeck et al., 1935), experimental (Giltner and Shahan, 1933, 1935) and serological (Ten Broeck, 1938) evidence and finally actual virus isolations (Tyzzer et al., 1938; Fothergill and Dingle, 1938; Van Roekel and Clarke, 1939) established that WEE and EEE viruses were natural parasites of domestic birds.

Logical projection of such a role to include the potential infection of other avian components of ecological situations involved in encephalitis epidemics

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led to the first isolation of virus from a wild bird, WEE virus from a Prairie Chicken (Cox et al., 1941). Like many fundamental scientific hypotheses, progressively substantiated by accumulation of objective evidence, expanding investigations of an increasing variety of arboviruses added to the number of different arboviruses isolated from or serologically implicated in natural infection of wild birds. A list of arboviruses, classified according to the group concept of Casals (1957) and already isolated from naturally infected avian hosts is given in Table 1. This list is necessarily incomplete because many isolates now being characterized and identified in various laboratories, or not yet reported, are not included. In contrast, it should be emphasized that not all arboviruses are infectious to avian hosts. Indeed, the class Aves appears to be totally refractory to even experimentally induced infection with such arboviruses as yellow fever of Group B (Strode, 1951) and at least some members of the Bunyamwera Group (Casals and Whitman, 1960).

TABLE 1.—ARBOVIRUSES ISOLATED FROM BIRDS

Group	Complex	Virus	Abbreviation	Vector	Known Geographical Range
A		Eastern equine encephalitis	EEE	Mosquito	Eastern Canada and U.S., Mexico, Panama, Trinidad, Colombia, Brazil, Argentina, Philippines
A	Sindbis	Western equine encephalitis	WEE	Mosquito	Canada, U.S., Mexico, Trinidad, British Guiana, Argentina
A	Sindbis	Sindbis	SIND	Mosquito	Egypt, Sudan, South Africa, India
B	JBE–WN	Japanese B encephalitis	JBE	Mosquito	Japan, China, Taiwan, Thailand, Malaya, Burma, India, Indonesia, New Guinea, Guam, Philippines
B	JBE–WN	St. Louis encephalitis	SLE	Mosquito	U.S., Caribbean Islands, Central America, northern South America
B	JBE–WN	Ilhéus	IL	Mosquito	Trinidad, Central America, northern South America
B	JBE–WN	West Nile	WN	Mosquito	Africa, Near East, South Asia
B	RSS	Russian spring summer encephalitis	RSSE	Tick	European, Siberian, and Asiatic U.S.S.R.
B	RSS	Central European encephalitis	CEE	Tick	Central and eastern Europe from the Baltic to the Balkans

ARBOVIRUS INFECTION IN BIRDS

Limitation of time precludes comprehensive presentation of the substantial amount of carefully derived evidence that supports the presently accepted biological principles underlying arbovirus infection in avian hosts. Some of the most detailed and extensive work entailing special attention to EEE and

WEE viruses, accomplished by Kissling, Chamberlain, Stamm, and associates of the USPHS Communicable Disease Center, is documented in another paper in this symposium (Stamm, 1963). The accumulated knowledge that serves as a basis for the principles presented below results from analysis of investigations on the ecology of different members of the mosquito-borne Japanese B–West Nile (JBE–WN) virus complex of arbovirus Group B. In addition to the four listed in Table 1, these human disease-producing viruses include Murray Valley encephalitis (MVE), which is presently known from Australia and New Guinea. All viruses of this complex, except MVE, have been isolated from naturally infected avian species in the wild. Such a variety of investigations by a number of different scientists working in circumglobally dispersed localities suggests how basic and geographically extensive are these biological mechanisms of arbovirus maintenance and dissemination in avian reservoir hosts.

The isolation of a virus, usually from blood sterilely extracted from the bird, but sometimes from spleen, brain, or other tissue obtained post mortem, represents but a single point in a long time sequence of pathogenesis of the virus in such a vertebrate host. According to Taylor's (1953) analogy of virology to criminology, the isolation of a virus is comparable to capture of the criminal in the act of committing the crime. But just as criminologists seldom catch criminals in the act, the virologist only occasionally is fortunate enough to isolate a virus from a bird collected in a suspect area.

Just as the criminologist recreates a crime through accumulation of material and circumstantial evidence, the virologist recreates the pathogenesis of arbovirus activity through detailed study of the whole course of experimental infection of birds under controlled conditions in the laboratory. This consists of the introduction of the virus by means simulating the mechanism of natural infection by bite of a blood-sucking arthropod, systematic serial collection of blood for animal inoculation to measure time and extent of virus multiplication and circulation during the stage of viremia, and subsequent bleedings for measurement of specific antibodies developed by the avian host to the infecting virus; in Taylor's analogy, the antibodies are comparable to detection of fingerprints in analysis of a crime.

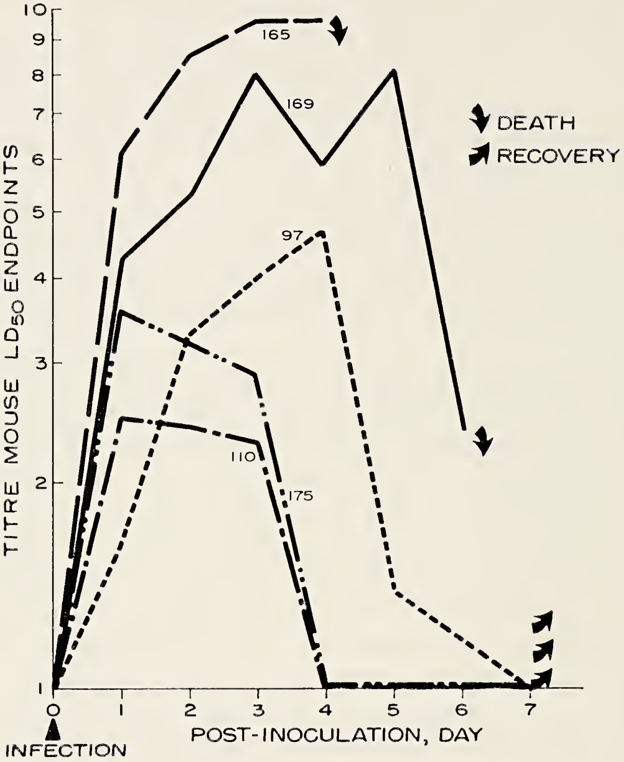
Antibody studies were, in fact, the means by which birds were implicated in the epizootology of St. Louis encephalitis (SLE) virus by American investigators associated with K. F. Meyer at the Hooper Foundation Laboratories of the University of California (Howitt, 1942; Howitt and van Herick, 1941). This implication was given further substance by experimental infection (Reeves et al., 1942; Hammon et al., 1946, 1951) and isolation of SLE virus from a naturally infected Yellow-shafted Flicker (*Colaptes auratus*) (Razenhofer et al., 1957). In 1942, Smithburn (1942) reported the close antigenic relationship of West Nile virus isolated in East Africa in 1937 (Smithburn et al., 1940) to SLE, and also to Japanese B encephalitis (JBE) virus, thereby establishing the framework for the JBE–WN complex.

It was the published information on SLE virus in avian hosts and the antigenic relationship between SLE and West Nile viruses that stimulated investigation of wild birds as potential circulating-virus reservoir hosts in our study of the ecology of West Nile virus in Egypt (Taylor et al., 1956). These studies led to the isolation of WN virus from the naturally infected Hooded Crow (*Corvus corone sardonius*) and Rock Pigeon (*Columba livia*) (Work et al., 1953) and to experimental studies that demonstrated the variable susceptibility and viremia of a number of wild avian species to West Nile virus (Work et al., 1955).

The classic demonstration of the role that birds may play in an appropriate environment can be simulated in the laboratory. An infected mosquito is attracted to feed on particular and susceptible avian species, thereby infecting the bird and producing a viremia of sufficient titre and duration to infect other mosquitoes attracted subsequently to feed during the period of infectious viremia. This is accomplished by feeding laboratory-reared mosquitoes on a viremic bird, holding the mosquitoes under proper climatic conditions during a 10- to 14-day extrinsic incubation period, during which the virus multiplies in the mosquito, moves to biting mouthparts, and is then ready to be introduced into the vertebrate host tissues at the next mosquito feeding. This was done many times with different birds of different species. Fig. 1 is a diagrammatic presentation of the course of such infections with West Nile (WN) virus in five different avian species. Rather than presenting mean points for the daily postinoculation viremia levels according to species, the relationship of these points each day is given for a single bird. The curves selected reflect the viremia typical of experience with that particular species.

It should be noted that some birds died, apparently as a result of the virus infection which, under experimental conditions, may have been excessive. While the finding of virus in the brain and spleen of the crow and sparrow may only reflect virus present in the blood supply to those organs, virus is frequently recovered from certain tissues and organs after viremia has ceased. In testing possible mechanisms of long-term survival of virus, i.e. overwintering, in tissues of birds, asymptomatic experimental WEE virus infections have been observed by Reeves and associates (1958) in the Brewer's Blackbird (*Euphagus cyanocephalus*), Brown-headed Cowbird (*Molothrus ater*), Tricolored Blackbird (*Agelaius tricolor*), House Finch (*Carpodacus mexicanus*), and House Sparrow (*Passer domesticus*), with recovery of virus from gall bladder, lung, liver, brain, and spleen after periods of up to 306 days after inoculation. This illustrates a phenomenon of great biological significance, even though its immunophysiology is not yet understood.

It is generally believed that most birds involved as successful circulating reservoirs of arboviruses necessarily survive following inapparent or subclinical infections. On the other hand, our first WN virus isolation from a pigeon came from a bird found paralyzed on the ground in its natural habitat. Quantitative data for any species infected with one or another virus have not been obtained under natural conditions because observation of transient illness in such mobile vertebrates has been impractical.



Bird No.	Species	VIRUS RECOVERY		NT Antibody Response
		Brain	Spleen	
169	House Sparrow (*Passer domesticus*)	+	+	
165	Hooded Crow (*Corvus corone sardonius*)	+	+	
97	Kestrel (*Falco tinnunculus*)			+
110	Buff-backed Heron (*Bubulcus ibis*)			+
175	Palm Dove (*Streptopelia senegalensis*)			—

Fig. 1. Representative viremias of mosquito-transmitted West Nile virus infection in different avian species represented by five individual birds.

ARBOVIRUS IMMUNE RESPONSE IN BIRDS

The infection, propagation, and circulation of arboviruses in vertebrates stimulate reaction by mechanisms of immunity, the most measurable being the production of antibodies. Three different types of antibody are usually produced which are characterized by their properties in laboratory tests rather than their performance in the host. These are neutralizing (NT), complement-fixing (CF), and hemagglutination-inhibiting (HI) antibodies.

Neutralizing antibodies are usually the first to appear and endure possibly for the entire life of the host. For most arboviruses, they are most specific and for this reason are the best retrospective evidence of specific virus infection. Complement-fixing antibodies are of shorter duration and therefore, when detectable in substantial titre, indicate recent exposure to a virus. They have a wider-spectrum reactivity with antigenically related viruses beyond the agent actually responsible for the infection. Unfortunately, avian sera often nonspecifically inhibit fixation of complement in the presence of specific antigen for which the serum contains antibodies (Karrer et al., 1950), invalidating this for reliable routine study of avian sera.

Recent development of the HI test for arboviruses (Clarke and Casals, 1958) has provided another means for study of the serological epizootology of arbovirus infection in wild birds. This is a complicated test to perform and interpret, particularly with bird sera, because of limited experience. There are nonspecific inhibitors of red-cell agglutination in avian sera that are not consistently removed by kaolin, which works well for mammalian sera. Even the more tedious acetone treatment cannot be relied upon to remove these inhibitors completely. Therefore, the growing use of the HI test in the study of arbovirus infection in birds is but a preliminary approach to serological study of arbovirus epizootology. The value of the HI test, however, is twofold. Within an antigenic group, HI antibody has broad reactivity which can give clues not available by any other test. Its titre is highly dilutable, allowing extended use of sera that are necessarily limited in quantity because the avian source is small in size.

Basic studies still rely on the neutralization test, which uses relatively large quantities of serum. Fig. 1 shows that the Kestrel and Buff-backed Heron had the expected NT antibody response but that this antibody failed to appear in the Palm Dove following viremia. This phenomenon has been observed with SLE virus infection of the Mourning Dove (*Zenaidura macroura*) (Reeves et al., 1954). Blood collected from shot birds occasionally contains nonspecific neutralizing substances. These are three important reasons why serological surveys of avian species by means of the neutralization test leave much to be desired, even though this technique has been used effectively in such studies as those we carried out on West Nile virus in Egyptian birds. There the seasonal appearance and geographical distribution of specific neutralizing antibodies to WN virus were supported and confirmed by the epidemiology of the infection in man (Taylor et al., 1956).

The most significant study of the HI test in comparison to the NT is that of Buescher, Scherer, Rosenburg, and McClure (1959) with JBE virus in ardeid birds and starlings.

RELATING ARBOVIRUS INFECTIONS OF BIRDS TO HUMAN DISEASE

Concepts of virology in relation to ornithology have been outlined here. It is beyond the scope of this presentation or this conference to delve into the ramifications of the role that arthropods play in finding the infected avian host, feeding upon it, propagating the virus, and transmitting the virus to man or other vertebrates by bite. One might observe that the entomological aspect of the problem is as complicated and equally intriguing as those that have been outlined.

The utility of a bird or species as an effective vertebrate host in the maintenance, propagation, and extrusion of an arbovirus such as West Nile is not only dependent upon its susceptibility, level and duration of viremia, and attractiveness to specific arthropod-vector species, but also its availability to the arthropod vector. The detailed studies by Scherer et al. (1959) of Japanese B encephalitis in the Tokyo Bay area show that the relatively immobilized colonial nestling ardeid species, particularly the Black-crowned Night Heron (*Nycticorax nycticorax*), served as a concentration of susceptibles which provided an immense viremic pool of virus at a critically important time in the epizootology of JBE virus in that ecological situation.

A similar avian ecology in the Nile Delta of Egypt provided such a viremic pool of Quaranfil virus for a soft tick (*Argas persicus*), which reproduced its life history under the bark of the nesting trees and obtained an annual blood meal by an infectious bite on susceptible nestling Buff-backed Herons (R. M. Taylor et al., unpubl. MS.). There is a high morbidity and mortality among these nestlings, apparently due directly to the virus infection. West Nile virus, however, appears to have been mainly transmitted among roosting juveniles after they left the nest, this conclusion being drawn from serological data which demonstrated antibody conversion later than the nesting season.

By applying these techniques and resulting concepts, the epizootology and epidemiology can be hypothesized, as we did for West Nile virus. A diagrammatic presentation of this hypothesis is given in Fig. 2. A similar concept has evolved for SLE, and the most intensive and detailed studies of this sort yet published are by Buescher, Scherer et al. (1959), who found that JBE virus in Japan performs in a similar pattern.

AVIAN HOSTS AS AN ESSENTIAL ELEMENT IN ARBOVIRUS ECOLOGY

From the original implication of wild birds in the epizootology and epidemiology of arboviruses a quarter century ago, we have come a long way in evaluating a number of arthropod-borne virus infections in various species of wild birds. There is little question that in certain situations wild birds play a basic role in the provision of virus to arthropod vectors which may then transmit the virus to man. Facing some of the questions and uncertainties that have been outlined here, biologists and virologists have begun to investigate the avian host as a key virus source, not only in local ecological situations, but increasingly as long-distance carriers and disseminators of virus, whether this be a matter of miles or intercontinental spread.

Intensive study of the antigenic characteristics of certain types of viruses, such as yellow fever and EEE, isolated in widely separated geographical localities, has pointed out antigenic differences that indicate how unlikely it is that the tested viruses were recently associated with a common source. But this limited information, based on tests with few strains of various passage levels from different virological systems, does not yet invalidate the general hypothesis. What is required for comparison by the virologist is a series of strains isolated from birds collected simultaneously over a longitudinally dispersed selection of collection points. This requires ornithologists as collaborators.

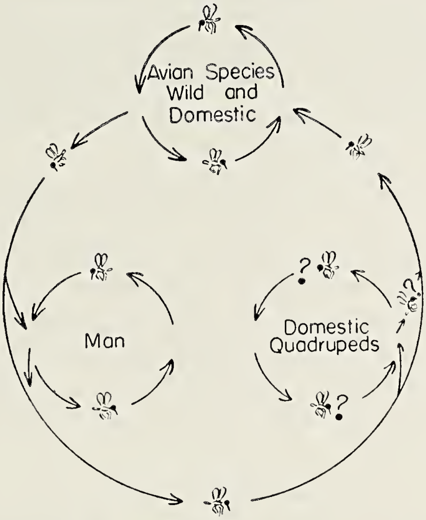


Fig. 2. Hypothetical cycles of West Nile virus (after Taylor et al., 1956).

Intensive investigation of arboviruses during the past decade has isolated a large number of new arthropod-borne viruses. Max Theiler, Director of the Rockefeller Foundation Virus Laboratories in New York, the definitive world center for antigenic studies of this group of viruses, has analyzed them according to their zoogeographic distribution and has pointed out that most arboviruses are restricted to one zoogeographical area (Theiler, pers. comm., 1961).

However, in reviewing the extensive field studies that have been carried out to isolate these viruses, which now number more than 160, it is peculiar that those mosquito-borne viruses that have been recovered from birds (Table 1) are just those that have been shown to be active in more than one zoogeographical area. This is why it has proved fitting that a global view of the scientific work being pursued on birds and arthropod-borne viruses, a subject already of concern to the World Health Organization (1959, 1961), should be included as a significant symposium in an international congress of ornithology.

SUMMARY

Many different avian species provide particular blood-sucking arthropods with a variety of viruses, which, when transmitted by bite to man, produce other diseases of serious consequence. Many different arboviruses have been isolated from wild birds in almost all zoogeographical areas. Serological evidence implies that other birds sustain infections with still other arboviruses. Only rarely has a bird been observed to suffer or succumb due to deleterious effects of a natural arbovirus infection. The avian host serves as a medium for propagation and blood circulation of arboviruses.

Viremia of substantial titre and adequate duration provides a pool of virus available for appropriately attracted hematophagous arthropod species. After a required extrinsic incubation period, the arthropod transmits virus to other susceptible avian species in the natural maintenance cycle, or to man with resulting infection that may produce disease and even death, but which in any case is usually a dead-end for the virus.

In the Japanese B–West Nile group, which has a marked affinity for birds, five different antigenic types are transmitted by bird-biting culicine mosquito species which also, on occasion, bite man and produce disease ranging from epidemic fever to fatal encephalitis. The viruses of the group have geographic distributions comparable to different species of an avian genus. Birds provide not only a reservoir of virus in a particular ecological situation where man may or may not be infected, but can on occasion be responsible for transporting viruses over distances and areas of relatively small or great magnitudes.

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Birds in Relation to Arthropod-borne Viruses in Trinidad[1]

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Numerous studies (cf. Kissling, 1958) in the United States have already served to direct attention to birds as vertebrate hosts of some of the arthropod-borne viruses (arboviruses), e.g. St. Louis virus (SLE) and Eastern equine encephalomyelitis (EEE) virus. Virological studies on Trinidad birds were started at the Trinidad Regional Virus Laboratory in 1956.

This laboratory, opened in 1953, is one of a series of field laboratories established by The Rockefeller Foundation to participate in a world-wide study of arbovirus diseases of man and animals (Downs et al., 1956). Trinidad was selected as a site in part because of its convenient location at the hub of air and sea travel lanes to the West Indies and North and South America, and in part because the island has an equatorial climate with rain forest, savannah lands, and coastal marshes, and thus offers a variety of ecological zones. A good road network makes these regions easily accessible. A provisional ecological zoning of Trinidad is presented in Fig. 1. This zoning is based mainly on physical, geographical, and climatological features. Fig. 2 presents the rainfall data. The drop in rainfall as one progresses from east to west is noteworthy. Located close to the coast of South America, the fauna and flora of Trinidad are largely derived from adjacent South America. While there are a few endemic plant species, there are no endemic bird species, although some subspeciation is evident.

Investigations carried out in Trinidad from early 1953 to the present have shown that many arboviruses exist on the island, the current total being 25.

Junge and Mees (1958) list the total number of bird species from Trinidad as 348. Of these, 56 or 16 percent are migrants from North America, 5 or 1.5 percent are migrants from South America, and 287 or 82.5 percent are resident or presumed resident species. North American migration records are reasonably complete with gross gaps in knowledge of arrival and departure dates. Data on South American migrants are not so complete, but there can be no doubt of free movement of many waterfowl, for example, between the Orinoco Delta marshes of Venezuela and the Caroni Swamp of Trinidad. The Fork-tailed Flycatcher (*Muscivora tyrannus*) is an interesting South American migrant. Large numbers annually appear in February and stay through July. This bird breeds in the Orinoco llanos country. Large flocks localize around the fringes of the Caroni Swamp, and birds frequently

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[1] The studies and observations upon which this paper is based were conducted by the Trinidad Regional Virus Laboratory with the support and under the auspices of the Government of Trinidad and Tobago, the Colonial Development and Welfare Scheme, and The Rockefeller Foundation. Scientific collaboration of Charles R. Anderson, T. H. G. Aitken, David W. Snow, and Leslie Spence is gratefully acknowledged.

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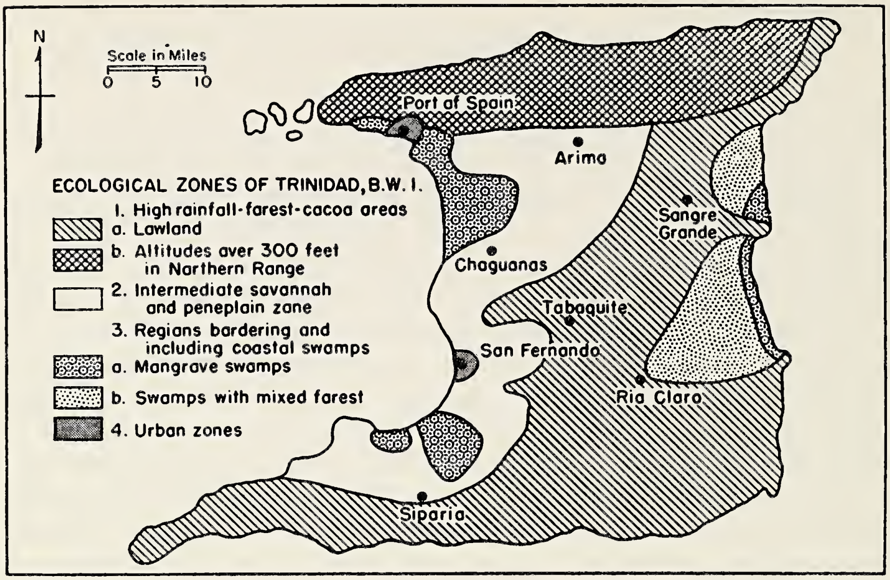

Fig. 1.

move inland to almost any part of the island singly or in small flocks. Although Junge and Mees list 56 migrants from North America, actually in the period 1951–60 only 5 of these have been picked up as banded birds: Common Tern (*Sterna hirundo*), Roseate Tern (*S. dougallii*), Blue-winged Teal (*Anas discors*), Herring Gull (*Larus argentatus*), and Peregrine Falcon

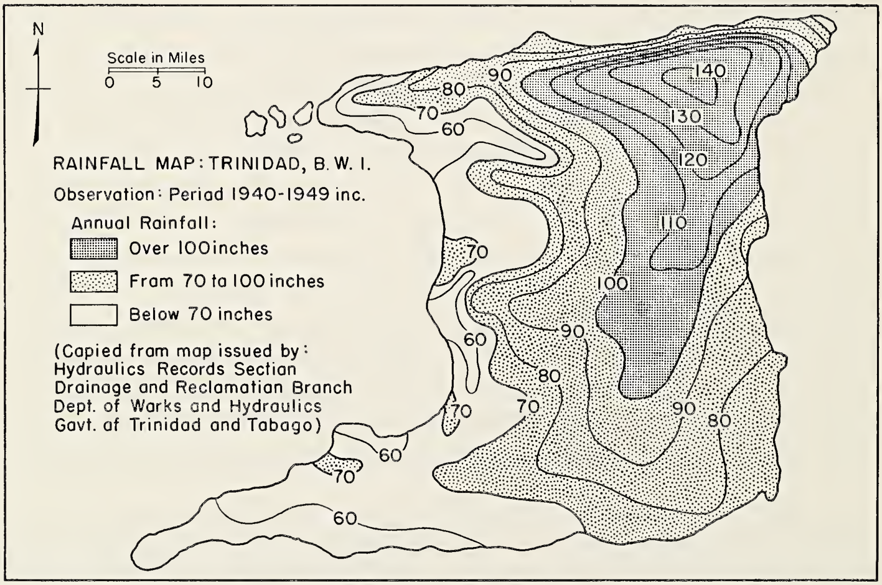

Fig. 2.

(*Falco peregrinus*) (Worth and Downs, 1962). The Common Tern is a frequent migrant and has often been picked up banded. The same holds for the Blue-winged Teal. Many sandpipers and plovers pass through Trinidad annually. Among the Passeriformes, the Barn Swallow (*Hirundo rustica*) is a regular passage migrant, as is also the Dickcissel (*Spiza americana*). The Yellow Warbler (*Dendroica petechia*), the Northern Waterthrush (*Seiurus noveboracensis*), and the American Redstart (*Setophaga ruticilla*) are common winter residents. Nesting residents include some 287 species of birds, some common, some decidedly rare. Nesting birds may be found throughout the year, but the peak of breeding occurs during the course of the rainy season, namely from May through September or October. Some species, such as the House Wren (*Troglodytes aëdon*), can be found breeding in almost any month of the year. The majority of the species have much more restricted nesting periods, still somewhat broader than the nesting periods in more temperate climates.

In commencing studies on viruses in relation to birds, work has been largely concentrated in the eastern part of the island in the region of Vega de Oropouche and Sangre Grande. This is a region with high rainfall, approaching 100 inches per year, and with a dry season of only a month or two when rainfall drops below 2 inches per month. It nearly meets the definition of tropical rain forest as defined by the classification of Köppen (1936). Earlier work in this same area had already demonstrated the presence of a number of arboviruses, as attested by recoveries from mosquitoes, monkeys, and man; these agents include yellow fever (Downs, 1957), Mayaro (Aitken et al., 1960), Manzanilla (Anderson et al., 1960), Oropouche (Anderson et al., 1961), Kairi (Anderson et al., 1960), St. Louis (Anderson et al., 1957), Ilhéus (Anderson et al., 1956), Eastern equine encephalitis (Downs et al., 1959), Bimiti (Spence et al., 1962*a*), Melao (Spence et al., 1962*b*), and Venezuelan equine encephalomyelitis viruses (Downs et al., 1962).

Working Methods.—Correct identification of material collected is of basic importance to bird-virus studies. Every effort was made to control collection by the preparation of bird skins. Skins were routinely made where there were doubtful identifications and of rare species as they were encountered. This material was dispatched at intervals to the ornithologists in The American Museum of Natural History and somewhat later was worked over extensively by David W. Snow, who served as a consultant to this program for several years while he was in Trinidad. Collected birds were examined for ectoparasites and often also for blood parasites and endoparasites.

Studies first began in 1955 with serum specimens from birds obtained by shooting. Specimens from such birds were often contaminated and often disappointingly small in quantity, and after several hundred specimens had been thus obtained, emphasis was shifted toward obtaining specimens from nestling birds. This program got started in mid-1956 and was continued for 2½ years. Two field employees were at work full time finding bird nests. On routine weekly field trips, nestlings were bled from the jugular vein with syringe and needle and then returned to the nest unharmed. At the time of bleeding, the nestlings were examined for ectoparasites, particularly *Philornis* maggots. Nests were routinely examined for nidicolous fauna.

In July 1958 the mist-netting of adult birds was started as a routine procedure. Captured birds were bled and liberated except in those instances when virus isolation from brain and internal organs was contemplated, in which case the entire specimen was saved. Under such circumstances the birds were exsanguinated, then placed in an ice bag, brought to the laboratory, and heart, liver, spleen, and kidneys removed, pooled, and used for the virus-isolation attempt. The serum was saved for serological studies. Blood was obtained by bleeding from the jugular vein or from the heart via the sternal notch. Bovalbumin diluent, 0.75 percent, with added antibiotics (penicillin and streptomycin) was used routinely to dilute the blood specimens. Specimens of 0.2 ml or less were diluted to 1 ml; larger specimens were not diluted. Specimens were refrigerated immediately after taking, centrifuged in the laboratory, and the supernatant serum inoculated intracerebrally into baby mice. A portion was stored for re-isolation attempt. Hemagglutination–inhibition (H–I) tests were performed on serum specimens following acetone extraction.

Results.—In the period 1955–60, virus-isolation attempts were made on 1,029 immature birds and 1,676 adult birds (Table 1). The virus-isolation procedure used, namely baby mice inoculated intracerebrally, permits of

TABLE 1.—VIRUS-ISOLATION ATTEMPTS ON MOST EXTENSIVELY EXAMINED SPECIES OF WILD BIRDS, 1953–60

Species Examined	VIRUS-ISOLATION ATTEMPTS	
	Immature	Adult
Columbigallina talpacoti	38	35
Glaucis hirsuta	—	59
Pipra erythrocephala	—	60
Manacus manacus	1	154
Troglodytes musculus	37	13
Turdus nudigenis	152	46
Thraupis virens	81	27
Thraupis palmarum	80	20
Ramphocelus carbo	113	132
Coereba flaveola	27	275
Cacicus cela	60	—
Sporophila minuta	3	54
Volatina splendens	17	45
Subtotals	609	920
134 other species	420	756
Totals	1,029	1,676

the isolation of any of the 25 arboviruses now recognized in Trinidad. Only two agents, namely SLE and Ilhéus viruses, have been isolated from the birds. We thus tested 147 species of birds, and in 51 species more than 10 individuals were studied. Table 1 lists the numbers of birds examined among the more commonly encountered species.

TABLE 2.—VIRUS RECOVERIES FROM TRINIDAD BIRDS

Species	Age	Date	VIRUS STRAIN	
			St. Louis	Ilhéus
Leptotila verreauxi	imm.	21 Aug. 1956	13375	
Crotophaga ani	imm.	4 May 1958		19395-A
Ramphocelus carbo	imm.	29 July 1958	20984	
Turdus fumigatus	ad.	21 Aug. 1958	21361	
Manacus manacus	ad.	28 Aug. 1958	21495	
Tachyphonus rufus	ad.	5 Sept. 1958		21640
Sporophila minuta	ad.	5 Sept. 1958		21645
Pipra erythrocephala	ad.	30 Aug. 1960	33757	

Table 2 presents the virus isolations that were made. The recovery rate of viruses was not high. An episode occurring in 1958 indicates that not only is the over-all recovery rate from random work even lower than illustrated, but correspondingly, under certain defined conditions when work is not randomly oriented, rates may be considerably higher. SLE virus was isolated from a nestling *Ramphocelus carbo* on 29 July 1958 from a nest located in a low tree by the roadside, almost in a farmyard at Vega de Oropouche. The countryside around Vega de Oropouche is low lying. The swampy-margined Oropouche River is only a few hundred yards away. Extensive citrus and cacao plantations are found in the region, and there are scattered clumps of forest. Since this SLE isolation was picked up within a few days of bleeding the bird, an immediate program was started to study the area intensively. This program centered around the collection of nestling birds, the mist-netting of adult birds, an intensification of the mosquito-collecting work which was already going on in the region, and investigation of chicken flocks and the human population in the area. It shortly became evident that we were in the midst of a small SLE virus epidemic. Further isolations of the virus were made from an adult *Turdus fumigatus* collected on 21 August, and from an adult *Manacus manacus* collected on 28 August from the same immediate area. Also, isolations were made from three mosquito species, one being a pool of *Culex taeniopus* collected between the dates of 9 and 29 September, another a pool of *C. coronator* collected between the dates of 26 August and 4 September, and the third, a pool of *C. spissipes* collected between the dates of 10 and 19 September. No isolations were made from chickens bled in the region or from the entire population of school children in the Vega de Oropouche school. All of these children were bled and serum inoculated into mice.

However, quite unexpectedly on 15 September, a small boy from Sangre Grande, some 10 miles away, seen in the health clinic with a headache, yielded another strain of SLE virus. We immediately moved a portion of operating activities over to the region of this boy's house, but made no further isolations from birds in this area, nor from mosquitoes collected both outside and inside the house. In the same intensive investigation of a localized SLE virus outbreak, we also picked up two isolations of Ilhéus virus from birds, one from a *Tachyphonus rufus* adult and the other from an adult *Sporophila minuta* collected in Vega de Oropouche on the same date, 5 September. An isolation of Ilhéus virus was also made from a pool of the mosquito *Culex caudelli* collected in Vega de Oropouche between the dates 25 August and 16 September 1958. Evidently episodes including two Group B arboviruses and involving birds and mosquitoes of the region were going on at the same time.

The other isolations of viruses from birds, namely SLE from a *Leptotila* dove in 1956 (Downs et al., 1957) and a manakin (*Pipra*) in 1960 and an additional isolation of Ilhéus from *Crotophaga ani* in 1958, all represent quite isolated occurrences not tied in as far as we know with local epidemic conditions. However, intensive observations were not being carried out at the time of these isolations, and immediate intensive investigation was not started. Had we done so, it is quite possible that we might have encountered situations similar to the one described for 1958.

Immunological Studies on Bird Sera.—It was early thought that serological studies carried out on the serum specimens obtained from nestling birds might yield information of value. The hope was that maternal antibodies transmitted to the egg from immune mothers might be detectable in the serum of the baby birds and might give a clue as to immunity rates in the species (Kissling et al., 1954). However, in the hemagglutination–inhibition (H–I) tests these nestling birds were uniformly negative and this approach was dropped. Many H–I tests using viruses of the Group B series, namely Ilhéus and SLE, were carried out on sera from adult birds. It was soon noted that low-grade positive reactors often could not be confirmed in appropriate neutralization (N) tests, and further work was carried out using the N test alone. Most of the testing work has been done with Ilhéus virus and on sera of birds collected by shooting. Impressed by the results of workers in Japan comparing serum from shot birds with serum from birds bled from the vein, we are not prepared to interpret our Ilhéus N-test results rigidly. However, in 294 adult bird sera examined from 76 species, 31 positives were encountered. Only a limited amount of serological testing has as yet been done on bird sera from Trinidad using SLE virus hemagglutinin. Correlation of H–I positive reactors with N-test positive reactors has been poor.

The position of the virus of EEE as regards birds is a most interesting one. No virus isolations have been made from Trinidad birds. However, in H–I testings done on 651 adult-bird sera from 80 bird species, 33 positives have been encountered among 16 species. Four of 21 *Pipra erythrocephala*, 5 of 69 *Manacus manacus*, and 7 out of 14 *Turdus nudigenis* were positive. The results of this H–I testing are viewed with some confidence since there were no instances, when adequate serum volumes permitted testing, where the H–I test was positive and the N test negative. In 31 N-test positive sera where H–I tests were also run, the H–I test was positive in 19 instances and negative in 12. It appears that H–I positives indicate EEE immunity, but that an H–I screen would miss some 40 percent of the EEE immunes that might be detected by N testing. Since bird sera are often available only in small quantity, study using more than one test is often precluded. Our present procedure is to screen for EEE-positive birds by use of the N test only. EEE-positive birds have been detected at Cumuto, Vega de Oropouche, and Fort Read, all in north-central or northeast Trinidad.

Parasitology.—It was considered desirable to study the blood parasites of birds in Trinidad in order to have an index from another angle of how frequently the birds might be exposed to vector insect species. The rate of infection in birds with various species of avian hemosporidia was surprisingly low, not exceeding 2 or 3 percent, with no infections detected in several hundred nestling birds. Infections were scattered through a wide range of bird species. It was not considered profitable to pursue these studies further, after several thousand bird smears had been examined.

Ectoparasitic collections were made routinely from birds collected, and included collections of Mallophaga, trombiculids, ticks, and the very interesting anthomyid fly *Philornis*. A number of different species of *Philornis* have been encountered in Trinidad. In some of these the larvae live as maggots subcutaneously in nestling birds. In other species the maggots may be outside, either in the nesting material or plastered to the feathers of the bird. They obtain their nourishment by rasping the skin of the bird and taking up the serum exuding. Other species are in the nesting detritus in certain hole-nesting species. The possibility of these flies being involved in a virus-transmission cycle encouraged us to inoculate SLE virus into some of the *Philornis* maggots. Virus survived and multiplied and could be demonstrated in adult flies several weeks later (Aitken et al., 1958). However, further studies have not been encouraging. In one instance, a clutch of nestlings infested with young *Philornis* larvae was inoculated with SLE virus and the nestlings actually circulated virus during a period when the larvae were living subcutaneously. The flies that came off from these larvae did not have any virus demonstrable in them.

Host-preference Studies.—Another angle of the bird-vector-virus relationship that merits serious consideration is the study of the biting insects that may preferentially attack birds. Such studies are in progress but are far from complete. One avenue of approach is to determine those species of mosquitoes, for example, that can be caught coming to birds used as bait and to compare such catches with those obtained using other animals, reptiles, or humans as bait. Another approach is through collecting, in the natural habitat, mosquitoes with blood meals and then analyzing these blood meals to determine the hosts from which the blood came. Both of these avenues are being explored. One product of such investigations has been the recovery of EEE virus on six occasions in the years 1959 and 1960 from mosquitoes of the genus *Culex*. Unfortunately, in five instances these culicid collections had been pooled to include specimens captured in chicken-baited traps as well as specimens captured biting man. However, those caught in chicken-baited traps outnumbered those caught biting man by 10 or 20 to 1. In the sixth instance, virus from a collection of *Culex taeniopus*, all of the mosquitoes came from chicken-baited traps. These are the only isolations of EEE virus that have been made in Trinidad. Since these isolations were so clearly associated with mosquitoes attracted to chickens, it was thought that the chicken might serve as a useful sentinel animal to signal EEE activity. However, examination of 625 chicken sera collected from all parts of Trinidad revealed only one immune bird.

Discussion.—The factual information obtained in the studies here reported cannot well be disputed. The viruses of SLE and Ilhéus have, indeed, been recovered from wild birds in Trinidad. Furthermore, Galindo and de Rodaniche (1961) have reported recovering Ilhéus virus from *Florida caerulea* and *Rhamphastos sulphurata*, both isolations being made from birds captured in a lowland swampy forested region near Bocas del Toro, Panama, in May 1960. That a large number of arboviruses were not recovered in wild birds in Trinidad merits comment. The technique used for examining birds for virus presence was as sensitive as any currently available, and yet the number of virus recoveries and the rate of virus recovery are so low that it appears that this type of an approach is a most expensive one. It can be utilized to good advantage in the presence of a recognized outbreak, as was demonstrated with the SLE outbreak that we encountered in 1958 in Vega de Oropouche.

The inferential data obtained from serological studies on bird sera present a challenge to those who wish to try to interpret the results of H–I testing and N testing on bird sera. In the case of EEE, it appears that the relationship between H–I and N tests is good enough to enable one to use either of these techniques, and preferably both, in looking over the bird population for evidence of virus activity. Since the N test appears to reveal more immune birds than the H–I test, this is the recommended procedure if only one can be done. There are many unknowns still remaining in this field concerned with specificity of reaction and duration of immunity. With the Group B viruses the serological study is even more difficult than it is with Group A agents. H–I testing on large numbers of bird sera in Trinidad using Group B agents demonstrates a considerable amount of Group B immunity present in the bird population. Just which viruses—SLE and Ilhéus and possibly other Group B agents—may evoke this immunity is still a matter for conjecture. Also, with Group A and Group B agents we have no idea how long immunity, once induced, may persist.

The use of sentinel chicken flocks for studying the seasonal epidemiology of EEE, although a useful technique in the United States, does not hold promise in Trinidad.

The studies of the past few years in Trinidad have been diffuse, scattered over a large geographical area, and involving many bird species. Birds are very abundant and widespread creatures. Studies involving birds can be literally overwhelmed by the vast amounts of material available. It would seem desirable in planning future studies to select a certain problem area with a specific virus problem, to narrow the number of bird species to be studied down to the limits of a few, and to correlate studies with research on vectors, including host-preference studies, in an attempt to get closer to an understanding of the actual mechanisms in operation—in other words to concentrate such studies upon carefully specified objectives. Improvements in current serological techniques, which would permit a confident interpretation of results, are greatly needed.

SUMMARY

Observations on birds in relation to arthropod-borne viruses in Trinidad began in 1953 and have been continued through 1960. SLE virus has been recovered five times from birds in the interval of 1956–60, each isolation being from a different species of resident bird. Ilhéus virus was recovered three times in 1958, each being from a different species of resident bird.

Immunological studies indicate an approximate 10 percent rate of immune reactions to EEE in N tests run on serum of birds from eastern Trinidad, and an approximate 8 percent rate of immune reactions to Ilhéus virus.

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Susceptibility of Bird Populations to Eastern, Western, and St. Louis Encephalitis Viruses

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Birds were first suspected of being carriers of encephalitis virus in 1938 (1). Since then, ample evidence has been assembled to indicate that birds are the usual source of virus for mosquitoes that infect man and domestic animals with eastern (EE), western (WE), and St. Louis (SLE) encephalitis (2, 3).

Susceptibility of a bird species to infection with an arthropod-borne virus is established by isolation of the virus from a naturally infected individual or by experimental inoculation and demonstration of infection in the laboratory. With references to supporting data, Table 1 lists 86 species of birds known to be susceptible to EE, WE, or SLE viruses. Species known to be susceptible to one or more of these viruses are members of 26 of the 75 families and 10 of the 20 orders of North American birds (67). No species of bird has been shown to be refractory to infection with any of these viruses. Therefore, it is likely that many more or all other species are also susceptible.

In species tested to date, EE virus concentration in the blood of small passerines reaches much higher levels than in larger species, such as herons and ibis (6). Larger birds may therefore be less important as sources of virus for mosquito infection. However, when areas of a square mile or more are considered, individuals of larger species usually make up less than 5 percent of the total individuals present. Mist nets are especially useful in studies of arbovirus infections in populations of smaller birds. Birds can be captured alive, banded, and blood samples obtained from the jugular vein.

Tests for antibody in bird-blood samples furnish retrospective estimates of the extent of virus activity in bird populations. Table 2 shows the proportions of birds, collected in a 100-acre area 14 miles northeast of Mobile, Alabama, between November 1959 and February 1960, that were positive in serum-neutralization tests against EE or WE virus. A positive result in this test indicates that a bird was infected with the virus at some time in the past but does not tell where or when the infection occurred. Individual birds may lose their positive reaction to this test; therefore, a negative result does not establish that the individual was never infected. For this reason, the estimates in Table 2 must be considered incomplete and a minimal expression of previous virus activity in the population.

In the four permanent-resident species collected in largest numbers (Blue Jay, Tufted Titmouse, Carolina Wren, and Cardinal), percentages positive to EE or WE do not vary greatly. Comparatively few woodpeckers are posi-

(Text continued on page 598)

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Table 1.—Species of Birds Found to Be Naturally or Experimentally Susceptible to Encephalitis Viruses

Virus		EE		WE		SLE	
Type of Infection		Nat.	Exptl.	Nat.	Exptl.	Nat.	Exptl.
CLASSIFICATION	VERNACULAR NAME	WHERE REPORTED IN THE LITERATURE					
Ciconiiformes							
ARDEIDAE							
Butorides virescens	Green Heron	—	—	—	—	4	—
Casmerodius albus	Common Egret	—	5, 6	—	—	—	—
Leucophoyx thula	Snowy Egret	—	6	—	—	—	—
Nyctanassa violacea	Yellow-crowned Night Heron	7	4	—	—	—	4
CICONIIDAE							
Ciconia ciconia	White Stork	—	—	—	8, 9	—	—
THRESKIORNITHIDAE							
Eudocimus albus	White Ibis	—	6	—	—	—	—
Anseriformes							
ANATIDAE							
Anser anser	Graylag Goose	—	—	—	8	—	—
Anas platyrhynchos	Mallard	—	—	—	8, 10	—	—
Anas sp.	White Pekin Duck (Domestic)	11	12, 13	—	10	—	14, 15
Falconiformes							
ACCIPITRIDAE							
Vultur fulvus	Tawny Vulture	—	—	—	8, 16	—	—
Buteo jamaicensis	Red-tailed Hawk	—	17	—	—	—	—
Buteo lagopus	Rough-legged Hawk	—	17, 18	—	—	—	—
Circus aeruginosus	Marsh Harrier	—	—	—	8	—	—
FALCONIDAE							
Milvago chimango	Chimango Caracara	—	—	—	19	—	—
Galliformes							
TETRAONIDAE							
Tympanuchus cupido	Greater Prairie Chicken	—	—	20	—	—	—
PHASIANIDAE							
Colinus virginianus	Bobwhite	—	21	—	—	—	—
Lophortyx californicus	California Quail	—	—	—	10	—	—
Phasianus colchicus	Ring-necked Pheasant	18, 21, 22, 23, 24, 25, 26	18, 22, 23, 27	—	—	—	—

TABLE 1.—(CONTINUED)

CLASSIFICATION	VERNACULAR NAME	WHERE REPORTED IN THE LITERATURE					
Alectoris graeca	Chukar	28	—	—	—	—	—
Gallus gallus	Chicken (Domestic)	—	13, 21, 23, 29, 30, 31, 32, 35	—	10, 31, 33, 35	—	14, 15, 34
NUMIDIDAE							
Numida galeata	Guinea Fowl	—	35	—	35	—	—
MELEAGRIDAE							
Meleagris gallopavo	Turkey	36	1, 36	—	1, 10	—	4
CHARADRIIFORMES							
CHARADRIIDAE							
Totanus flavipes	Lesser Yellowlegs	37	—	38	—	—	—
COLUMBIFORMES							
COLUMBIDAE							
Columba livia	Rock Dove	23, 37, 39, 40	41, 42	38	10, 29, 43	44	45, 46
Zenaidura macroura	Mourning Dove	—	17, 41	47	47	3, 47	47
Streptopelia sp.		—	—	—	—	—	15
Leptotila verreauxi	Rusty Dove	—	—	—	—	48	49
CUCULIFORMES							
CUCULIDAE							
Crotophaga ani	Smooth-billed Ani	—	—	—	—	49	—
STRIGIFORMES							
STRIGIDAE							
Otus asio	Screech Owl	—	4	—	4	—	—
Bubo virginianus	Great Horned Owl	—	17, 18	—	—	—	—
Speotyto cunicularia	Burrowing Owl	—	50	—	50	—	—
PICIFORMES							
PICIDAE							
Colaptes auratus	Yellow-shafted Flicker	—	—	—	—	51	—
PASSERIFORMES							
PIPRIDAE							
Pipra erythrocephala	Flame-headed Manakin	—	—	—	—	—	49
Manacus manacus	Black-and-white Manakin	—	—	—	—	—	49
TYRANNIDAE							
Tyrannus tyrannus	Eastern Kingbird	7	—	—	—	—	—

TABLE 1.—(CONTINUED)

	Virus	EE		WE		SLE	
	Type of Infection	Nat.	Exptl.	Nat.	Exptl.	Nat.	Exptl.
CLASSIFICATION	VERNACULAR NAME	WHERE REPORTED IN THE LITERATURE					
Sayornis phoebe	Eastern Phoebe	—	—	7	—	—	—
Empidonax virescens	Acadian Flycatcher	4	—	4	—	—	—
HIRUNDINIDAE							
Hirundo rustica	Barn Swallow	—	—	3, 47	—	—	—
Petrochelidon pyrrhonota	Cliff Swallow	—	—	38	—	—	—
CORVIDAE							
Cyanocitta cristata	Blue Jay	—	4	52	53	—	4
Pica pica	Black-billed Magpie	—	—	38, 54	—	—	—
Corvus brachyrhynchos	Common Crow	—	17, 18	7, 38	—	—	—
PARIDAE							
Parus carolinensis	Carolina Chickadee	7	—	55	—	—	—
Parus bicolor	Tufted Titmouse	56	4	4	—	—	—
TROGLODYTIDAE							
Thryothorus ludovicianus	Carolina Wren	7, 56	—	—	—	—	—
MIMIDAE							
Mimus polyglottos	Mockingbird	7	—	—	—	—	—
Dumetella carolinensis	Catbird	7, 37, 55	—	4	—	—	—
Toxostoma rufum	Brown Thrasher	4	4	—	—	—	—
Toxostoma lecontei	Le Conte's Thrasher	—	—	—	10	—	—
TURDIDAE							
Turdus merula	Blackbird	—	—	—	8	—	—
Turdus fumigatus	Pale-vented Robin	—	—	—	—	49	—
Hylocichla mustelina	Wood Thrush	4	—	4	—	—	—
Hylocichla guttata	Hermit Thrush	55	4	4	—	—	—
Hylocichla ustulata	Swainson's Thrush	4	—	—	—	—	—
Hylocichla minima	Gray-cheeked Thrush	4	—	—	—	—	—
Hylocichla fuscescens	Veery	4	—	4	—	—	—
Sialia sialis	Eastern Bluebird	56	—	—	—	—	—
SYLVIIDAE							
Regulus calendula	Ruby-crowned Kinglet	4	—	—	—	—	—
LANIIDAE							
Lanius ludovicianus	Loggerhead Shrike	—	—	55	—	—	—

Table 1.—(Continued)

CLASSIFICATION	VERNACULAR NAME	WHERE REPORTED IN THE LITERATURE					
VIREONIDAE							
Vireo griseus	White-eyed Vireo	7	—	—	—	—	—
Vireo flavifrons	Yellow-throated Vireo	7	—	7	—	—	—
Vireo olivaceus	Red-eyed Vireo	4	—	7	—	—	—
PARULIDAE							
Mniotilta varia	Black-and-white Warbler	—	—	4	—	—	—
Dendroica coronata	Myrtle Warbler	4	—	—	—	—	—
Seiurus aurocapillus	Ovenbird	4	—	—	—	—	—
Seiurus noveboracensis	Northern Waterthrush	7	—	—	—	—	—
Oporornis formosus	Kentucky Warbler	4	—	—	—	—	—
PLOCEIDAE							
Passer domesticus	House Sparrow	7, 37, 57, 58, 59, 60	6, 22, 41, 61, 62	3, 7, 38, 47, 63	10, 14, 53, 62, 64	—	14, 46, 47
Serinus canarius	Canary (Domestic)	—	—	—	66	—	—
ICTERIDAE							
Cacicus cela	Yellow-rumped Cacique	—	—	—	—	—	49
Sturnella magna	Eastern Meadowlark	56	4	—	—	—	—
X. xanthocephalus	Yellow-headed Blackbird	—	—	38	—	—	—
Agelaius phoeniceus	Red-winged Blackbird	—	6, 41	38, 54	4	—	46
Agelaius tricolor	Tricolored Blackbird	—	—	—	14, 64	—	—
Euphagus cyanocephalus	Brewer's Blackbird	—	—	47	64	—	—
Quiscalus quiscula	Common Grackle	52, 65	6, 7, 18, 41	7	—	—	4
Molothrus ater	Brown-headed Cowbird	—	41	—	64	—	46, 47
THRAUPIDAE							
Ramphocelus carbo	Silver-beaked Tanager	—	—	—	—	49	49
FRINGILLIDAE							
Richmondena cardinalis	Cardinal	7, 55	6	55	53	—	4
Carpodacus purpureus	Purple Finch	—	—	—	53	—	—
Carpodacus mexicanus	House Finch	—	—	3, 47	14, 64	—	14, 47
Pipilo erythrophthalmus	Rufous-sided Towhee	56	4	4	53	—	—
Junco oreganus	Oregon Junco	—	—	—	10	—	—
Zonotrichia leucophrys	White-crowned Sparrow	—	—	47	10, 14	—	10, 47
Zonotrichia albicollis	White-throated Sparrow	4	4	4	53	—	4
Melospiza melodia	Song Sparrow	7	4	—	4	—	—

TABLE 2.—EE AND WE SERUM-NEUTRALIZING ANTIBODY IN AN ALABAMA BIRD POPULATION

"Migratory" Group and Species	No. Birds Captured	EST. NO. PRESENT A*	EST. NO. PRESENT B*	SERUM-NEUTRALIZATION TEST RESULTS No. Tested	Positive EE		Positive WE		Positive EE or WE	
					No.	%	No.	%	No.	%
WINTER RESIDENT**										
Pigeon Hawk (*Falco columbarius*)	7		9	6	3		5		6	
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	1		1	0						
Whip-poor-will (*Caprimulgus vociferus*)	2		2	2	0		0		0	
Yellow-shafted Flicker (*Colaptes auratus*)	10		12	10	1	10	2	20	3	30
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	4		5	4	0		0		0	
Eastern Phoebe (*Sayornis phoebe*)	3		4	3	1		2		2	
Brown Creeper (*Certhia familiaris*)	9		11	6	1		1		2	
Winter Wren (*Troglodytes troglodytes*)	1		1	0						
Catbird (*Dumetella carolinensis*)	2		2	2	1		1		1	
Brown Thrasher (*Toxostoma rufum*)	28		34	28	26	93	17	61	26	93
Hermit Thrush (*Hylocichla guttata*)	30	21	37	30	16	53	12	40	22	73
Golden-crowned Kinglet (*Regulus satrapa*)	5		6	2	1		1		1	
Ruby-crowned Kinglet (*Regulus calendula*)	41		50	17	10	59	3	18	10	59
Solitary Vireo (*Vireo solitarius*)	2		2	2	0		1		1	
Orange-crowned Warbler (*Vermivora celata*)	4		5	2	0		0		0	
Myrtle Warbler (*Dendroica coronata*)	14		17	14	0		1		1	
Hooded Warbler (*Wilsonia citrina*)	1		1	1	0		0		0	
American Goldfinch (*Spinus tristis*)	3		4	3	1		0		1	
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	74		90	70	26	37	20	29	37	53
White-throated Sparrow (*Zonotrichia albicollis*)	181	228	222	171	29	17	21	12	43	25

* Numbers in columns *A* and *B* were calculated as explained in the text of this paper.

** *Winter Resident* includes those species present in the study area only during fall and winter months.

TABLE 2.—(CONTINUED)

"Migratory" Group and Species	No. Birds Captured	EST. NO. PRESENT		SERUM-NEUTRALIZATION TEST RESULTS						
		A*	B*	No. Tested	Positive EE		Positive WE		Positive EE or WE	
					No.	%	No.	%	No.	%
PERMANENT RESIDENT										
Red-shouldered Hawk (*Buteo lineatus*)	1		1	0						
Broad-winged Hawk (*Buteo platypterus*)	1		1	0						
Screech Owl (*Otus asio*)	4		5	4	4		1		4	
Pileated Woodpecker (*Dryocopus pileatus*)	2		2	1	0		0		0	
Red-bellied Woodpecker (*Centurus carolinus*)	14		17	14	0	0	1	7	1	7
Hairy Woodpecker (*Dendrocopos villosus*)	2		2	2	0		0		0	
Downy Woodpecker (*Dendrocopos pubescens*)	8		10	6	1		0		1	
Blue Jay (*Cyanocitta cristata*)	25		28	25	21	84	17	68	22	88
Carolina Chickadee (*Parus carolinensis*)	7		9	3	0		1		1	
Tufted Titmouse (*Parus bicolor*)	74	76	90	63	39	62	28	44	47	75
Carolina Wren (*Thryothorus ludovicianus*)	26		32	25	18	72	9	36	20	80
Cardinal (*Richmondena cardinalis*)	31		38	28	24	86	15	54	24	86
UNSTABLE***										
Robin (*Turdus migratorius*)	52			51	4	8	5	10	9	18
Red-winged Blackbird (*Agelaius phoeniceus*)	35			35	3	9	2	6	4	11
Rusty Blackbird (*Euphagus carolinus*)	1			1	0		0		0	
Total Winter Resident	422	669	516	373	116	31	87	23	156	42
Total Permanent Resident	195	265	235	171	107	63	72	42	120	70
Total Unstable	88			87	7	8	7	8	13	15

*** The migratory group *Unstable* includes those species present in the study area only during winter months that are present only occasionally in large flocks and do not roost there.

tive, and the same observation regarding this well-distributed family has been made elsewhere (55).

Adults of those species grouped as "winter residents" in Table 2 are not present in the study area from May through August. They breed farther north in the United States and Canada and begin arriving in southern Alabama in September. The greatest influx occurs in November and December. Some species, such as the Brown Thrasher and Rufous-sided Towhee, do breed within a mile of the netting location. However, during fall and winter months, local-breeding individuals cannot be distinguished from those that breed farther north. The marked differences in percentages positive between the Brown Thrasher, Hermit Thrush, Rufous-sided Towhee, and White-throated Sparrow are probably due to successively later arrival of these species during a period of diminishing virus activity. It is also possible that these differences are due to variation in exposure to vectors. However, as it is not known precisely where these species spend the night, this possibility cannot yet be evaluated.

The three species grouped as "unstable" are present only during winter months and occur in large flocks. They forage over areas of many miles and roost in marshes or on high ridges outside of the study area. The relatively low percentage of positives in this group is probably due to less exposure to vectors at night.

Birds listed in Table 2 were collected by a standardized netting procedure that permits estimation of the number of birds present on the basis of recapture of marked individuals (68). Numbers in the column headed "Estimated Number Present *A*" were calculated from recapture data. Numbers in the column headed "Estimated Number Present *B*" were calculated by figuring the percentage composition by species of 617 (permanent- and winter-resident) individuals actually captured and applying these percentages to the total estimate of 751 birds based on recapture data. (For example, the 31 Cardinals captured make up 5 percent of the 617 birds captured. If it is assumed that they also make up 5 percent of the recapture estimate of 751 birds, one arrives at an estimate of 38 Cardinals present.) These data illustrate the difficulty of obtaining sufficient numbers of birds of all species present to permit meaningful comparisons. Although more than half of the total population of a 100-acre area were tested, 24 of the 35 species present are represented by less than 20 individuals.

An expression of the known susceptibility of a bird population can be obtained by applying the information in Table 1 to the birds listed in Table 2. Of the 617 permanent- and winter-resident individuals captured, 87 percent are of species known to be susceptible to infection with EE virus.

A measure of the intensity or rate of virus transmission may be based on the proportion of bird-blood samples, collected during a given period, that contain virus. Table 3 presents data on virus isolations from samples collected in New Jersey and Alabama. During the course of infection of birds with EE or WE virus, the virus is present in the blood in detectable quantities for only 3–5 days. The four instances cited when between 7 and 14 percent of a bird population were circulating virus demonstrate that extremely rapid spread of virus can occur.

TABLE 3.—PROPORTION OF BIRD-BLOOD SPECIMENS CONTAINING EASTERN OR WESTERN ENCEPHALITIS VIRUS

State and Year	NEW JERSEY 1956		ALABAMA 1959–60
County	Atlantic	Middlesex	Baldwin
November	—	—	2/172
December–January	—	—	2/503
February	—	—	0/276
May–July	—	—	0/1,079
July	0/109	—	—
August	6/42	—	—
September	7/101	3/46	—
September–October	—	—	53/680
November	0/54	—	—
November–December	—	—	5/164

In summary, the data presented demonstrate wide susceptibility, extensive involvement, and high rates of transmission of EE and WE viruses in wild bird populations.

Epidemics of arthropod-borne disease occur most frequently in late summer and fall. During this period, bird numbers are at an annual high, and the maximum amount of bird movement is in progress. Field studies have repeatedly shown highest rates of EE and WE virus infection in birds at this time of the year. Concurrent studies on virus-infection rates in mosquitoes in the same places have shown highest rates of infection in those species that prefer to feed on birds.

These diseases occur in places characterized by "disturbed," "mixed" habitats, with higher proportions of "edge" than more natural areas not altered by human activity. These diversified, man-made habitats generally support much higher bird populations than undisturbed ones.

Field and laboratory studies and ecological and epidemiological observations strongly implicate birds as reservoirs of viruses that produce disease in man and domestic animals. Information on the life cycles and mode of long-distance transport of these viruses is very incomplete. The ultimate objective of the sort of studies cited is the development of methods of prediction, prevention, and control of epidemics. Progress toward these objectives has been reported in California (69). However, much remains to be done in adapting such techniques to other areas and in evaluating their effectiveness and safety.

Increased participation by ornithologists is critically needed to solve the public-health problems involved and to assure that attempts at control of these diseases do not violate principles of conservation.

SUMMARY

Eighty-six species of birds have been demonstrated to be susceptible to eastern, western, or St. Louis encephalitis virus on the basis of virus isolation from naturally infected birds or experimental infection in the laboratory. Virus isolation and antibody studies indicate extensive involvement and rapid transmission of eastern and western encephalitis viruses in wild-bird populations. Epidemics of disease produced by these viruses occur during late summer and fall when bird populations are at an annual high and when they are most mobile. Epidemics occur in man-disturbed habitats where bird concentrations are highest. Birds are therefore strongly implicated as reservoirs of viruses that produce disease in man and domestic animals. A solution to the public-health problem must be in harmony with principles of conservation and can be achieved only by greater collaboration between ornithologists and virologists.

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Birds and the Epidemiology of Japanese Encephalitis

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The epidemiology of Japanese encephalitis (JE) has been under study for many years, and bird involvement with the virus has been known for at least 25 years. It is the objective of this discussion to present some of the facts, concepts, and problems of the avian position in the epidemiology of this widespread virus group.

In 1937 Japanese workers isolated two virus strains from 25 pools of 126 Tree Sparrows (*Passer montanus*), and they also found some antibody response in sparrows and wild gallinaceous species, but so little that they concluded that birds could not be important in the proliferation and dispersal of the virus (Mitamura et al., 1938). Later studies, in 1950–51, during which tests were made of 154 species of most of the families represented in Japan, revealed that at least 65 species had been exposed to the disease and had developed neutralizing antibodies to it (Hammon et al., 1958). (Tree Sparrows and gallinaceous birds were among the more resistant and less often infected species, which verified Kitaoka's earlier findings.) Further work (unpublished) threw doubt on the validity of the techniques used in the 1950–51 study, so that the rate of infection among wild birds is still not known except for that of the herons and egrets under intensive study from 1953 to 1958 (Buescher et al., 1959). Much of the work in the past has been done with blood from shot birds, in which are found antibody-like substances as well as true antibodies. This has resulted in data suggesting higher rates of infection than may normally occur. However, it has been demonstrated that wild birds in Japan are infected by virus transmitted by the mosquito *Culex tritaeniorhynchus*, that the virus proliferates and becomes available in the peripheral blood to mosquitoes, and that neutralizing antibodies are developed by the infected individuals. Furthermore, these antibodies can pass from the hen to her eggs and later to the chicks, which are then protected from the disease during the early part of their lives. Some of the avian species tested were more susceptible to the disease than others, and in most species their susceptibility decreased with age.

The accompanying charts demonstrate something of the involved epidemiology of this disease and how birds may fit into the picture.

In Fig. 1 are shown some of the relationships between time of year, proliferation of virus, and some of the known hosts. Encephalitis is a disease of late summer in Japan where the vector mosquito begins breeding in rice fields as soon as adults leave their hibernaculae; after several generations, mosquitoes reach peak numbers in July and August. It is believed that by means

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of inapparent infections in several host cycles a pool of infected mosquitoes is built up which can precipitate epidemic conditions among humans.

In Japan, man is probably the most abundant vertebrate (possibly excepting rats), and a large percentage of the people in most areas have been exposed to the disease and have antibodies. Other vertebrates heavily infected by the virus include pigs and horses, up to 100 percent of which have been found to carry antibodies. Birds have shown antibody responses in percentages varying from 0 to 70, and second to man these are among the most abundant vertebrates. Man has the fewest new susceptible individuals available to mosquitoes each year. Domestic stock offers many new individ-

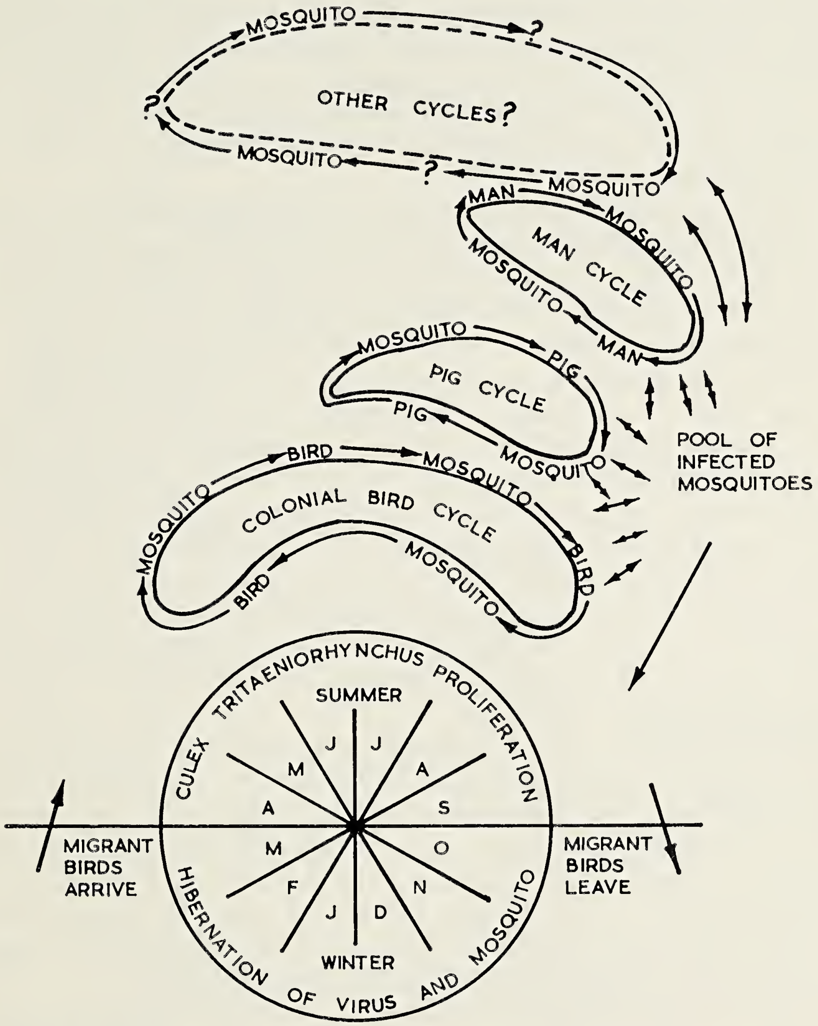

Fig. 1. Some of the cycles of Japanese encephalitis infection in Japan.

uals (i.e. pigs) and the number of juvenile birds available to mosquitoes makes up 60 percent of the population each year. The accumulative effect of all of these hosts upon the infectivity of the mosquito population is still poorly understood.

The role of noncolonial birds in this cycle has not been determined. Efforts to demonstrate viremia among nestling Blue Magpies (*Cyanopica cyanus*) were unsuccessful, yet the adults showed a high percentage with neutralizing antibodies. The colonial-nesting egrets and herons were both easy to work with and had a high rate of infection. They have been shown to be definitely involved with the disease, and colonies possibly act as centers of virus dissemination.

All of these factors, man, birds, pigs, etc., are superimposed, and all may become infected by and infectious to mosquitoes until, by late summer, the virus reaches a peak of infectivity and dissemination. Following this peak, most of the susceptible juvenile hosts develop antibodies, the weather cools, mosquitoes go into hibernation, and the virus disappears from the scene.

Within the egret colony, a great many factors become involved (Fig. 2). In the colonies that we had under observation, there were five species of birds nesting together. Each had its own susceptibility to the disease (Little Egrets, *Egretta garzetta*, were much less susceptible to a natural infection than the Black-crowned Night Heron, *Nycticorax nycticorax*); each had its own palatability to *C. tritaeniorhynchus* (the night heron was much the tastiest as far as the mosquito was concerned); and each had its own rate of immunity. Immune mothers passed their immunity to nestlings, which retained it for as long as 16 days. Early in the season this period of immunity was long enough to avoid infection at the nest since fewer infected mosquitoes were present.

There were also such factors as the duration of nestling life (much longer for Great Egrets, *Egretta alba*, than for Cattle Egrets, *Bubulcus ibis*), the number of broods, and number of nonbreeding adults which were involved in the development of the virus. Other relationships between the organisms included the flight range of mosquitoes, flight range of adult birds, and juvenile dispersion. Much thought and research related to migrating birds, and their role in virus dispersion is at present occupying biologists on a worldwide basis, but little more than theories have been developed.

In Fig. 3 are presented some of the known facts and suggested avian relationships. Within the temperate zone we know that some colonial-nesting species develop viremia and are capable of seeding large numbers of mosquitoes and that such colonies are nuclei of infection. We know less about the position of noncolonial birds. We also know that pigs, in Japan at least, are the favorite host of *C. tritaeniorhynchus* and that every open pig pen is a source of numerous infected mosquitoes. The virus can and probably does travel from man to man via mosquito, although he is the least palatable of the hosts that we have tested.

We do not know where the virus overwinters nor how it gets its start in the spring months. The virus has rarely been found in the mosquitoes and their hosts other than in August and September. When the nesting season closes, many migratory birds which may become infected at that time could start south during the incubation period of a week or more and even arrive at or near their terminal destinations in the tropics at the time that they become viremic.

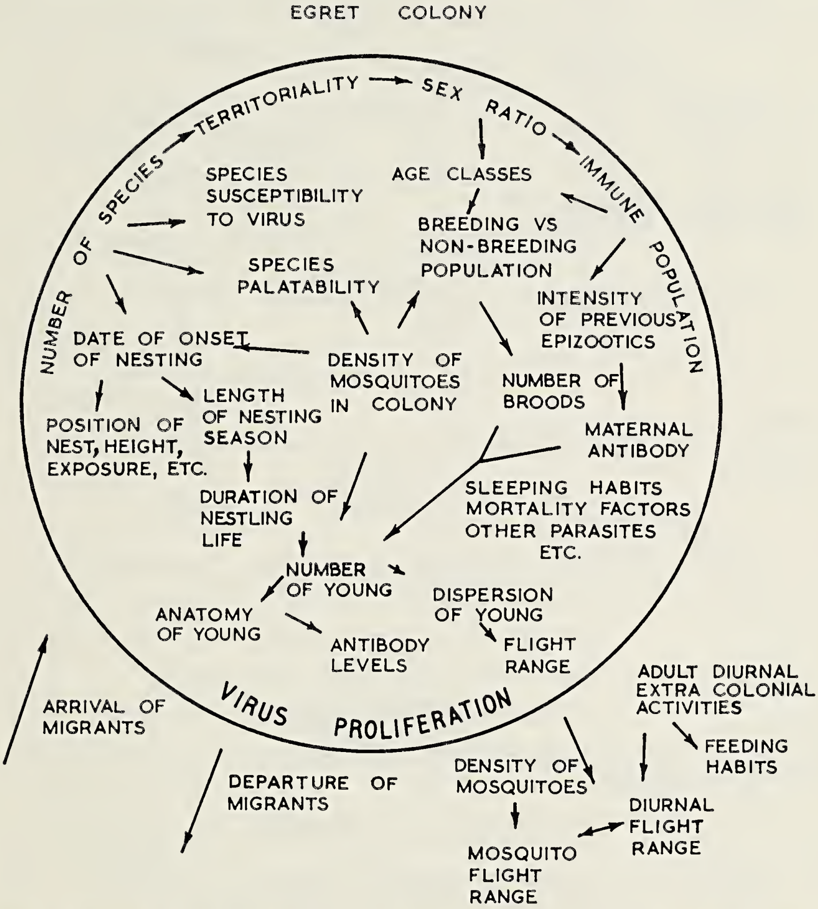

Fig. 2. Some of the ecological factors affecting the relationship between birds–mosquito–virus in an egret colony in Japan.

In tropical Asia, and I must limit my discussion to Malaysia, the epidemiology of JE is much less understood. No such concentrated study has been made here as is being made in Japan. We know that the virus is present and probably active all year round and that the vector mosquitoes include *C. gelidus*, *C. tritaeniorhynchus*, and possibly others which also breed the year round. It is possible in almost any month to collect these mosquitoes and isolate the virus. This would suggest that there is a readily available source of susceptible vertebrates to keep the cycle rolling. A high percentage of the coastal rural human population have antibodies, and no other vertebrates have been systematically studied. A few birds have been tested for neutralizing antibodies, but only an occasional positive one has been found.

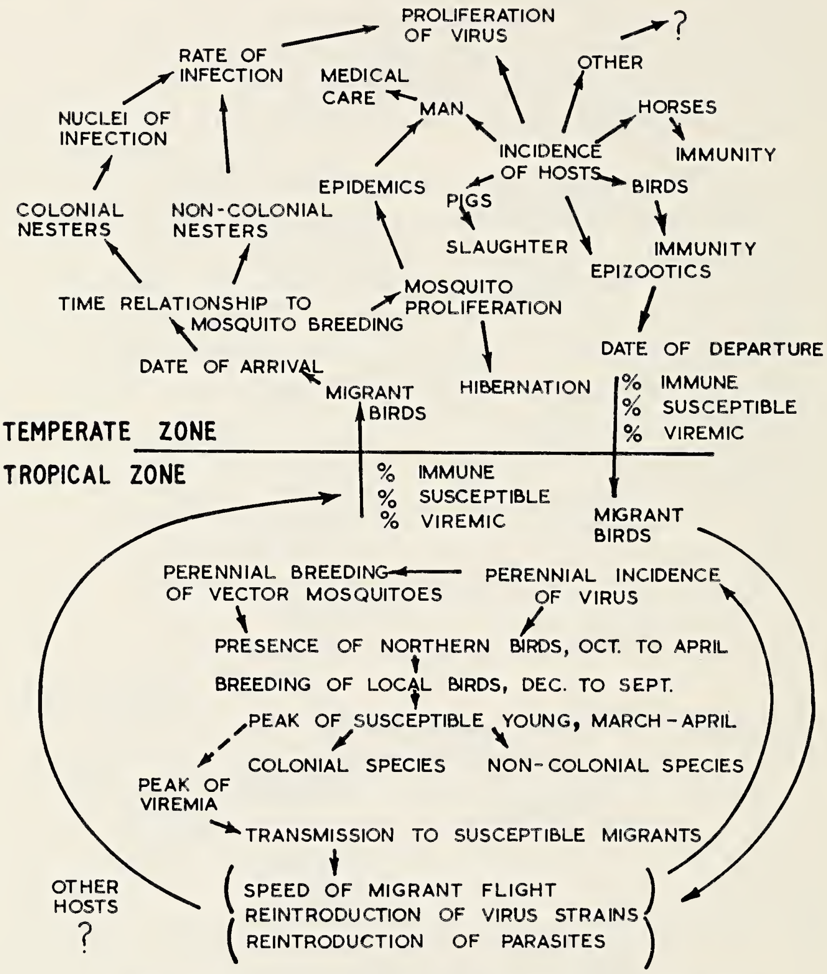

Fig. 3. Zoogeographical epidemiology of Japanese encephalitis.

No matter what the serological position of the migrant bird—immune, susceptible, or viremic—it arrives in a habitat (lowland, forest, parkland, or swamp) in which the virus and vector are already present. Within Malaya the peak of the year's rains comes in November–December, and at this time the vector populations are also maximum; therefore the migrant enters a habitat of increasing vector pressure.

At the same time, the breeding of local bird species starts. It increases rapidly in February and March, and maximum-susceptible young are available to the mosquitoes just at the time that the migrants are starting north.

A summary of what we know of coexistent phenological events involving the disease in man, adult mosquito populations, and birds at the latitudes of Tokyo, Okinawa, and Kuala Lumpur is shown in Fig. 4. As I have indicated throughout this discussion, the interrelationships are manifold and the actual cause-and-effect relationships between other vertebrates, mosquitoes, and man still remain unknown.

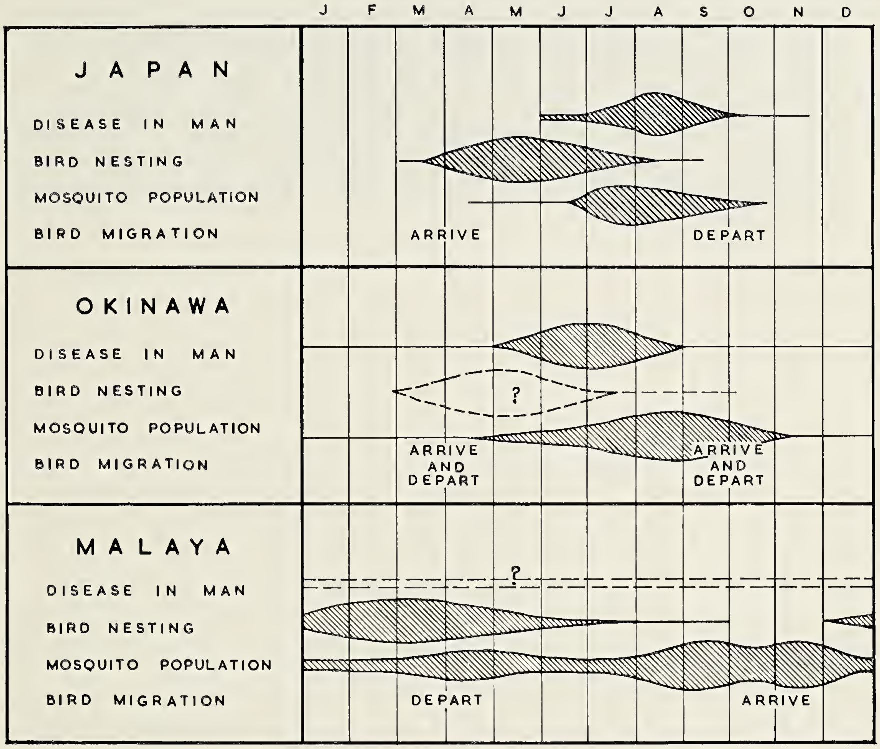

Fig. 4. The avian–mosquito–Japanese encephalitis in man correlation in eastern Asia.

SUMMARY

The extremely complicated epidemiology of Japanese encephalitis is demonstrated in four charts. It is best known in Japan where the disease among humans is a late-summer phenomenon. The vector mosquito *Culex tritaeniorhynchus* breeds in rice fields and occasionally in containers and is capable of carrying the virus from man to man, bird to bird, domestic mammal to domestic mammal, and to any combination of these. There appear to be natural cycles of infection involving these hosts. The rate of infectivity among the mosquitoes and the extent of infection among wild birds is demonstrated by the multiple factors in an egret colony involving age of birds, anti-

body levels, nesting, flight, and migratory habits as well as flight habits and density patterns of the mosquitoes. The epidemiology of the disease becomes more complex when its global distribution is considered. The seasons of nesting of birds, breeding of vector mosquitoes, and proliferation of the virus vary from the equator northward, and these data suggest that migratory birds could be involved in the dispersal of the virus or its introduction into areas from which it has disappeared.

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