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Illustration of Bank Swallow by Louis Agassiz Fuertes

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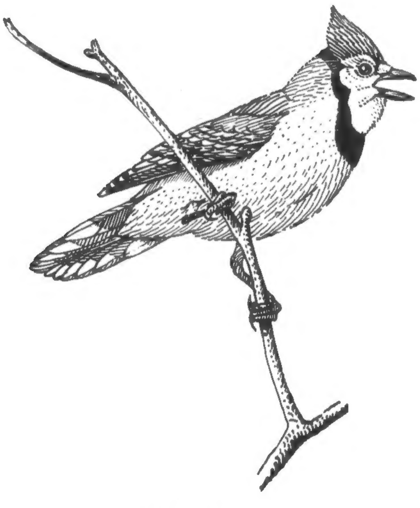

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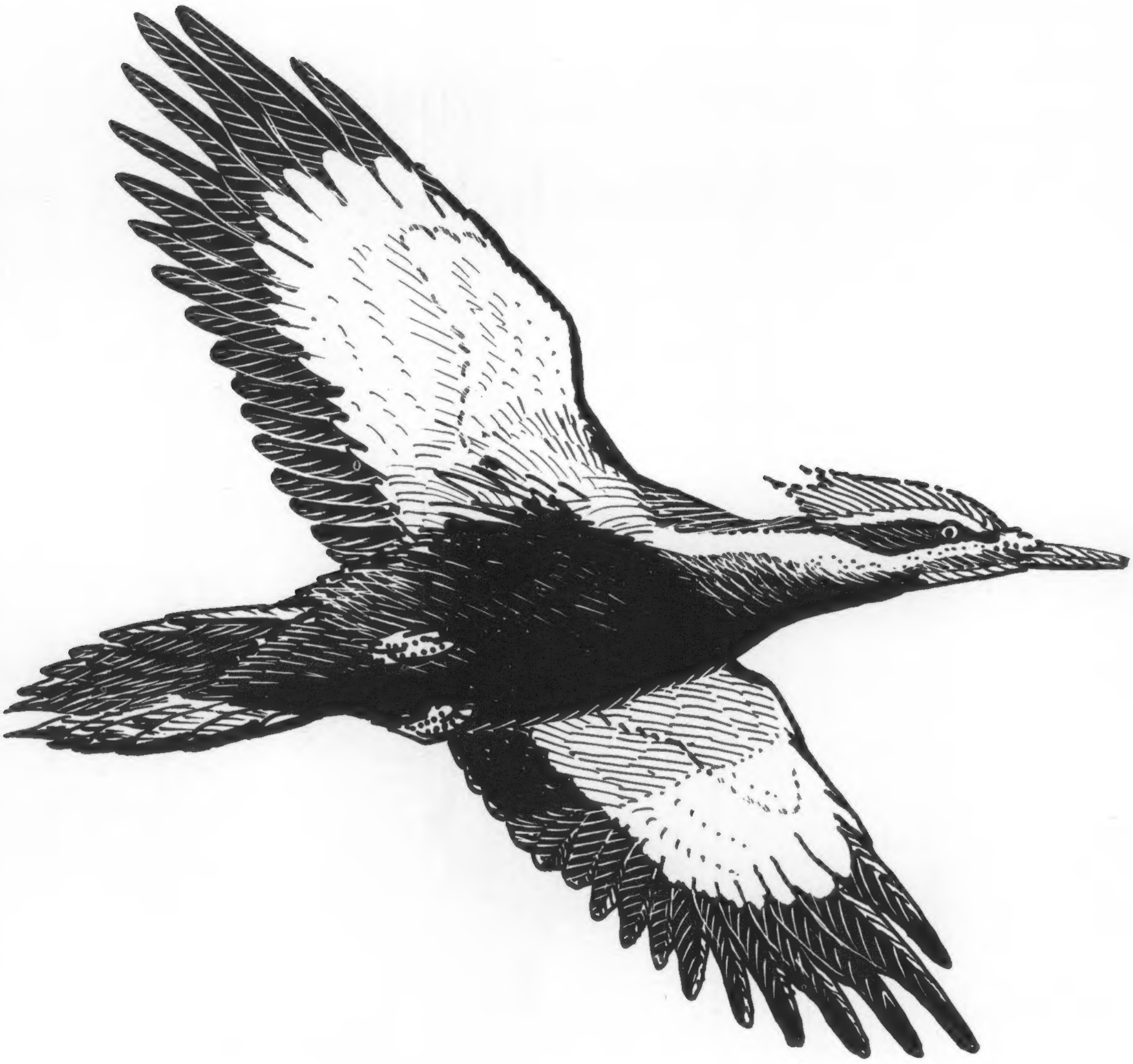

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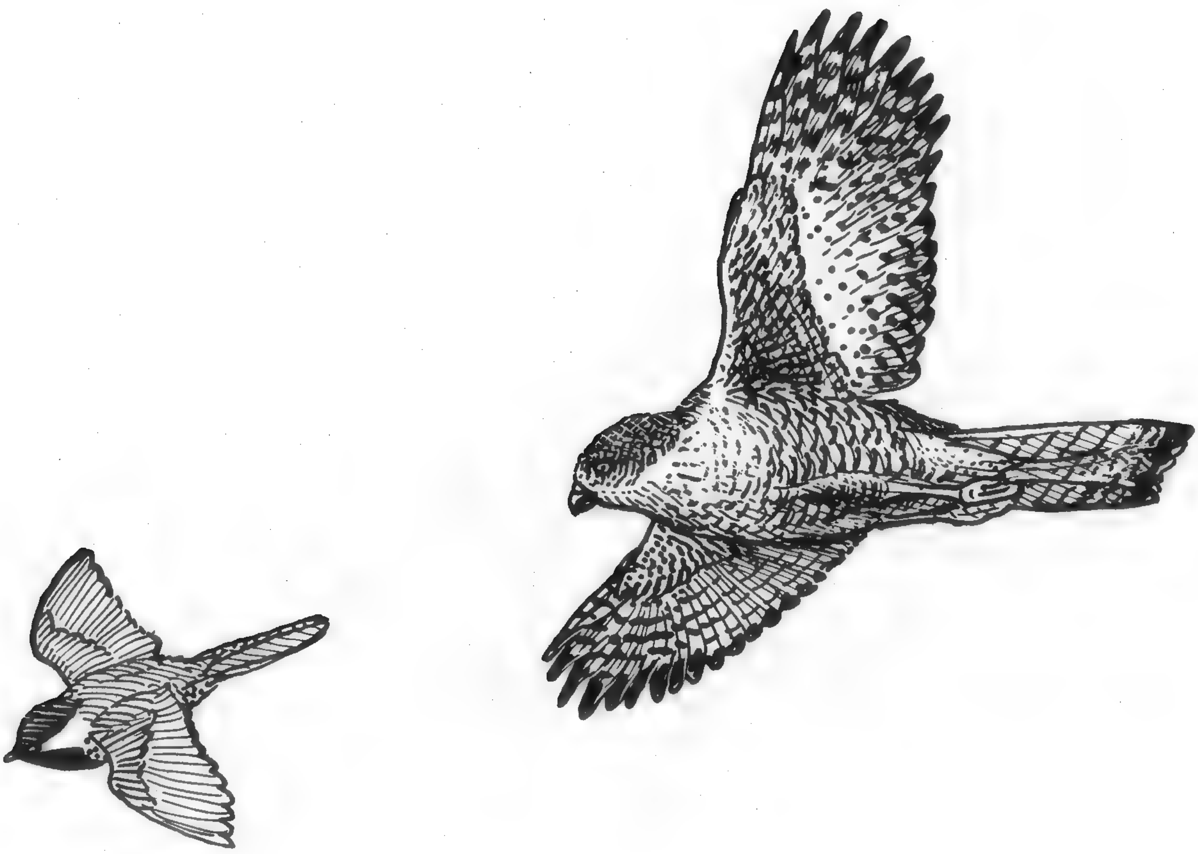

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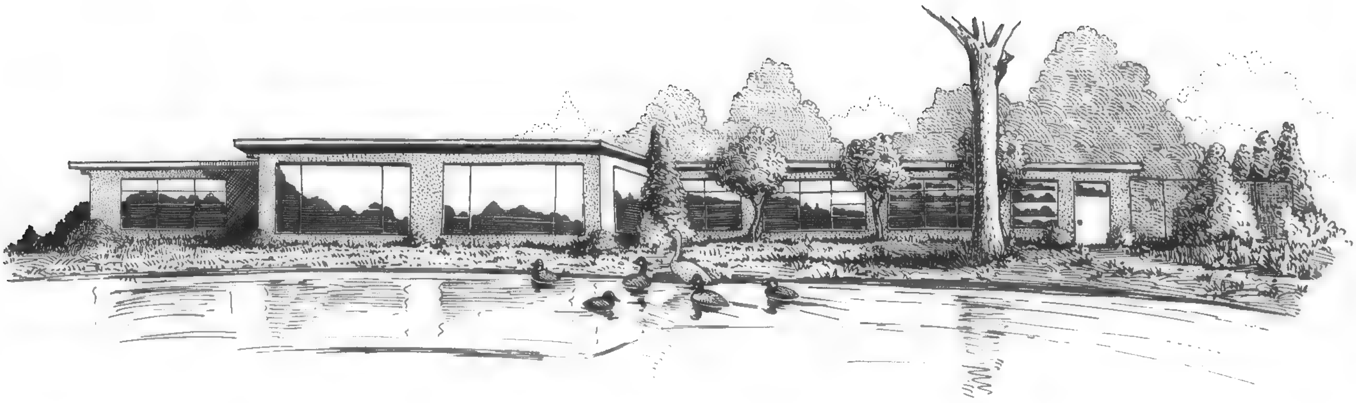
An Amercian Woodcock on its nest in Sapsucker Woods during a postseasonal snowstorm. Photographed on 27 April 1932 by Olin Sewall Pettingill, Jr.



CORNELL'S LABORATORY OF ORNITHOLOGY

ARTHUR A. ALLEN

The Laboratory of Ornithology at Cornell University has enjoyed a long, productive life. Its beginning actually dates back nearly fifty years to 1915 when the author was appointed Assistant Professor of Ornithology in the Department of Entomology. The Chairman at that time, Dr. James G. Needham, suggested the name "Laboratory of Ornithology" to justify space for an ornithologist in a department devoted to the study of insects. The name was accepted and retained, although the Laboratory as such was without official status in the administrative complex of the University. After some years the Laboratory was transferred to the Department of Zoology and, in 1948, to the newly formed Department of Conservation where it continued its active program of teaching, research, and public education. Finally, in 1955, the Laboratory became a separate department of the University, with research and cultural development as its objectives. Thus, like the familiar Robin which has been shifted three times by taxonomists from one genus to another, it has retained its identity through the years and has remained the same old well-known species.

The Teaching Program

Prior to 1915 the author taught in the Department of Zoology, devoting his major time to ornithology. Shortly after receiving his Ph.D. in 1911 he was admitted to the faculty of the Graduate School so that he could direct the advanced work of several students, including Ludlow Griscom, who were knocking at Cornell's door with ornithology in mind. At that time there was no other university in the country — and possibly the world — where one could take a doctorate in the study of birds.

In the years to follow, until the author's retirement in 1953, over a hundred students were granted advanced degrees in ornithology by Cornell. To show the scope of their research projects, a list of their theses by title is given on pages 167-170 of this *Annual.*

The great majority of our graduate students applied their ornithological training to their professions. Today, fifty-six are teaching ornithology in universities, ten are curators in museums, eight are in Federal service, and two are in state conservation departments. Twelve others are conducting ornithological research on an independent basis and nine are deceased.

Over the years the number of students introduced to ornithology through the undergraduate courses in the regular academic year and in summer school totals nearly 10,000. Some of these students have taken advanced degrees in ornithology at other universities as the opportunity has become available.

We like to think that our teaching program has played a significant role in the rapid development of ornithology in other universities, and as a field of investigation and a source of personal enjoyment. If the current roster of the American Ornithologists' Union is a measure by which to judge the important part played by Cornell ornithologists in ornithology today, we are happy to report that 13 of the 82 Fellows are Cornellians and 28 have been chosen by their colleagues as Elective Members. We do not know how many Cornellians are regular Members of the AOU, nor do we know exactly how many Cornellians are participating in the other national and local organizations devoted to ornithology. We only surmise from the letters we have received that many hundreds of our alumni have found immeasurable pleasure from their exposure to ornithology while in the University.

Like most teachers, the author has enjoyed a wide and very pleasant association with his students and feels especially grateful to those who have served as his assistants. He has watched their progress with great pride and his greatest joy is derived from their return visits to the Laboratory and the letters telling of their activities.

The Laboratory and Wildlife Conservation

In 1917 the American Game Protective Association was instrumental in setting up in the College of Agriculture a program of wildlife conservation and game breeding. A Committee on Conservation, consisting of Professor Needham, Professor James A. Rice, and the author, represented the faculty in this program and the Laboratory of Ornithology was placed in charge of the program, which included both teaching and research. When, after several years, appropriations for its financial support failed to materialize, the Laboratory of Ornithology took over the general course in Conservation of Wildlife and the advanced course in Game Management. The only research to be continued was the author's problem on grouse cycles. This included breeding Ruffed Grouse in captivity — the first time that it had ever been accomplished. Financial support for his work came from the Heckscher Fund of Cornell University and later a grant from the New York State Conservation Department.

The course in the Conservation of Wildlife was set up as a cooperative undertaking with lecturers from several departments of the University concerned with the various phases of conservation. With the formation of the Department of Conservation in 1948 this course was given to Professor

The "Grad Lab" group in 1942. Standing from the left, William Montagna, Lloyd C. Hurlbert, John F. Wanamaker, Henry M. Stevenson, Dwain W. Warner, Southgate Y. Hoyt, Ernest P. Edwards and Stephen W. Eaton (in front of Edwards). Seated, Robert B. Lea, Oliver H. Hewitt, and Allan R. Phillips.

The author with some of his hand-reared Ruffed Grouse. One of the achievements of the Laboratory's research program from 1917 to 1930 was the successful breeding of Grouse in captivity. Photograph by Elsa G. Allen.

Gustav A. Swanson, and the course in Game Management was eventually placed under the direction of Professor Oliver H. Hewitt who joined the Department in 1949, after having assisted the author from 1941 to 1944.

The Laboratory and Sound Recording

In 1929 Dr. Peter Paul Kellogg, now assistant Director of the Laboratory and Professor of Ornithology and Biological Acoustics, was appointed Instructor in Ornithology, and that same year, Mr. Albert R. Brand came to the Laboratory as a special student. These two men started the sound-recording project which resulted in the Library of Natural Sounds and the production of phonograph records of birds and other natural sounds. This unique story is told by Dr. Kellogg in the next article of this *Annual.*

The Laboratory Acquires Official Status and a New Home

In the early years the Laboratory of Ornithology was housed in McGraw Hall in the small tower room where the Department of Entomology had its birth under Professor John Henry Comstock. In 1935 it moved to Fernow Hall to share this relatively new building with the Department of Forestry. Here it remained until it was organized as a separate department and moved to its new quarters.

The occasion for the reorganization of the Laboratory was the gift to Cornell University from Mr. Lyman K. Stuart, Cornell '21, and his aunt, Mrs. Kenneth E. Stuart, of a 150-acre woodland near the campus called Sapsucker Woods. This tract was augmented by a gift of 20 acres at its north edge from Mr. and Mrs. Walter C. Heasley and by a gift of five acres, including an old homestead, from Mr. Arthur Lane. The entire property was designated the

Above, Dr. George M. Sutton's class in "Speciation" (1941-42). From his right are Allan R. Phillips, Robert M. Mengel, and Robert B. Lea. From his left, John F. Wanamaker, Peter Crowe, William M. Longhurst, and William Montagna.

Below, twenty years ago—a summer-school class in ornithology.

Sapsucker Woods Sanctuary. Finally, through Mr. Stuart, the Arcadia Foundation of Rochester, New York, financed the construction of an attractive building on the shore of a new 10-acre pond, which had been formed at the north edge of the Sanctuary with help from the New York State Conservation Department.

The Laboratory building was dedicated on 18 May 1957. Attending this event were some 300 persons, including many distinguished scientists from different parts of the country.

The Laboratory Building

Of ranch-type construction the Laboratory building is fire proof with cement-block walls, cement floor, slab roof, and sound-proof ceilings, all attractively painted. It is 120 feet long and 50 feet wide with a large observatory whose plate-glass picture windows on the west overlook the pond. At the south end of the building is an aviary and office space, while at the north end are four rooms for graduate students and research associates. Special rooms include one for indoor photography containing a built-in tank with heavy plate-glass front for studying and filming underwater activities of birds; an air-conditioned room for processing, editing, and storing film; a sound room built on specifications from the Bell Laboratories for giving the best acoustical performance with no echoes or standing waves. The sound room is intended for indoor rerecording and housing the Library of Natural Sounds. (At the present time Dr. Kellogg's acoustical laboratory and the Library of Natural Sounds are temporarily in Fernow Hall on the main campus.) The staff offices overlook the pond — that of the author is especially designed for photographing activities of the birds that appear outside the large window.

The wide, main hallway serves as an art gallery. Its southern portion is given over to original paintings by Louis Agassiz Fuertes, the northern to original paintings by Roy A. Mason, Richard E. Bishop, George Miksch Sutton, Robert Verity Clem, W. C. Dilger, and other bird artists who are members of the Laboratory. Photographs taken in Sapsucker Woods or on various Laboratory expeditions are displayed on walls in the foyer and the observatory.

Support and Objectives of the Laboratory

To help support the newly organized Laboratory, Dr. Kellogg and the author presented to Cornell University their personal interests in the Library of Natural Sounds, which had built up through the years, and transferred to the University all the income from royalties received on the phonograph records they had produced and would produce from the recordings. Through this understanding with the University and the transfer of properties mentioned, the Laboratory became a largely self-supporting department with the following objectives as approved by President Deane W. Malott and the Board of Trustees in a memorandum dated 12 June 1955.

a) To maintain the Laboratory of Ornithology at Cornell University and to encourage support for its work from Cornell alumni and others interested in the study of birds and biological acoustics.

b) To encourage the study of ornithology at Cornell in any of its aspects, but with special emphasis on scientific and cultural studies of living birds irrespective of any economic implications.

c) To provide for the establishment of Fellowships or Scholarships in Cornell University, to promote research, and to help deserving students in ornithology.

d) To maintain the Cornell Library of Natural Sounds in a suitable repository and to support its objectives.

e) To encourage studies based on the recordings or involving the use of recordings, and studies involving the hearing mechanism and voice production of animals, especially birds.

f) To encourage studies in the life histories and behavior of birds, bird photography, and other methods of bird portrayal.

g) To maintain good public relations among the alumni and others interested in birds through public lectures, radio, television, field trips, demonstrations, and work shops, and by the provision of a bird observatory and meeting room at Sapsucker Woods.

h) To encourage continued publications from the Laboratory of Ornithology by subsidizing such publications when necessary.

i) To provide for the purchase of necessary equipment including the development of new or improved means of recording or photographing.

j) To finance expeditions, the primary object of which is the study of birds through recording and photography.

k) To encourage bird and other natural-sound-recording studies by others than the staff of the Laboratory through grants-in-aid or loan of equipment.

l) To carry out such other projects in connection with the Laboratory of Ornithology and Sapsucker Woods, which from time to time may be deemed desirable by the advisory Council, so as to promote a better understanding of nature in its broadest sense, including all natural phenomena.

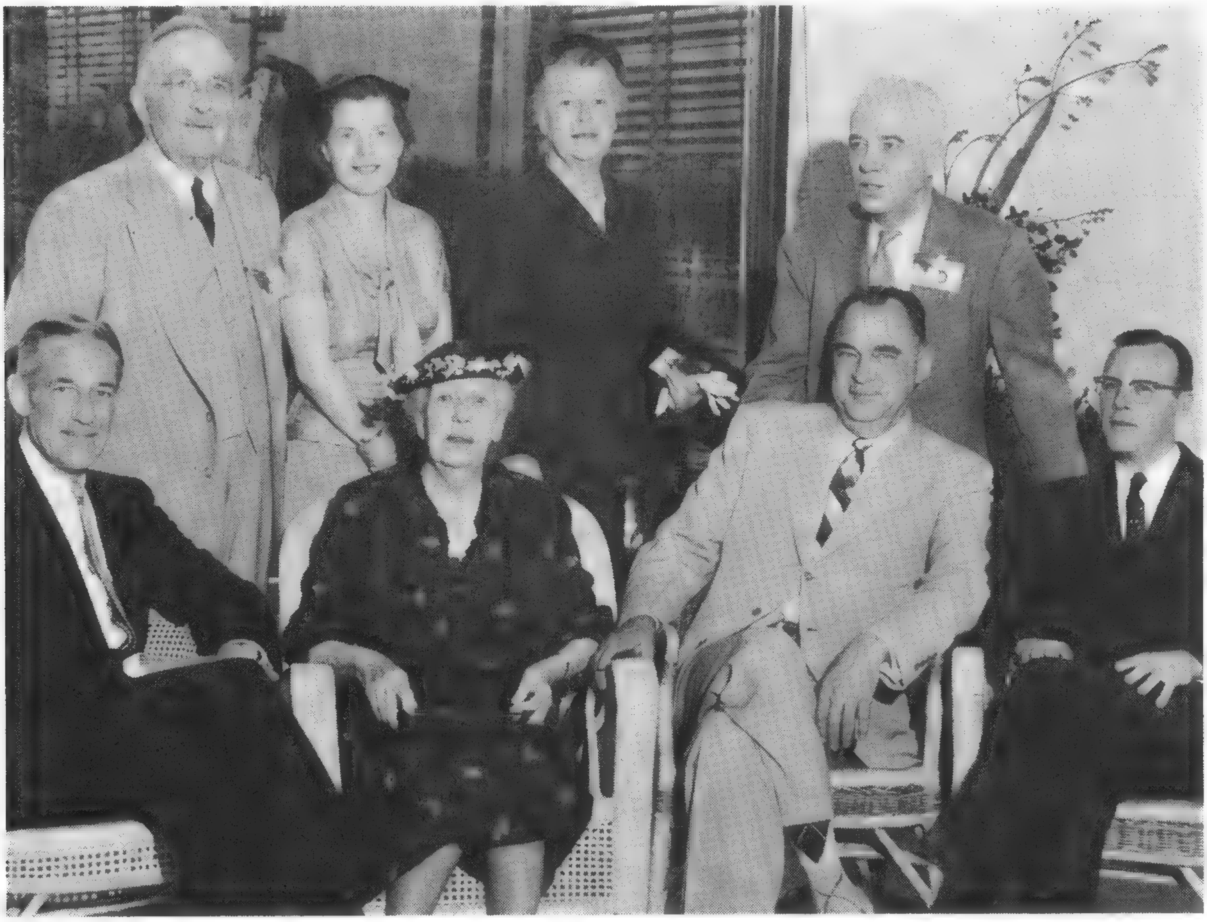
Through the Years with the Staff

During the Laboratory's fifty years, the author has enjoyed the benefits of a small but devoted staff who have shared with him the multitude of responsibilities that go with a program of education, research, and public relations. In the early days the Laboratory assistant was a graduate student who gave one half of his time to teaching and the care of the collection and the other half to his research. Later the Laboratory supported a curator or instructor as well as an assistant and, finally, another professor. The author recalls with much pleasure his association with Claude W. Leister, Miles D. Pirnie, Herbert Friedmann, George Miksch Sutton, Southgate Hoyt, Lee Kutz, Dwain W. Warner, Austin L. Rand, Kenneth C. Parkes, Oliver H. Hewitt, William C. Dilger, and, of course, Peter Paul Kellogg.

In 1922 Louis Agassiz Fuertes, the famed bird artist and a beloved Cornellian from whom the author derived great inspiration, was appointed Lecturer in Ornithology. During the last few years of his life until his untimely death in 1927 he gave a series of fascinating lectures, largely on bird coloration, that were well attended by students and faculty alike. It was Fuertes who christened Sapsucker Woods when, on a Sunday morning in 1909, he and the author and two other students discovered there a nesting Yellow-bellied Sapsucker, the first breeding record for Ithaca.

Dr. Kellogg came to the Laboratory in 1925 as a special student and received his Ph.D. from Cornell in 1938. In addition to teaching, sound recording, and the production of records that have made bird songs a part of everyone's daily life, he has, on Saturday mornings for the past twenty-five years, presented local radio talks on birds. His wife, Beryl Jorgensen Kellogg, is a trained librarian. It is she who undertook the enormous task of organizing the factual data of the sound-recording project and has since prepared a meticulous and indispensable catalogue of the thousands of recordings in the Library of Natural Sounds.

The author's wife, Elsa Guerdrum Allen, assisted in the summer courses for many years. She received her Ph.D. from Cornell in 1929 and has continued



Above, principals at the dedication of the new Laboratory, 18 May 1957: Seated from the left, Deane W. Malott, President of Cornell University, Mrs. Charles H. Stuart, Lyman K. Stuart, and Wilmot Craig (representing the Arcadia Foundation). Standing, the author, Mrs. Stuart, Mrs. Malott, and Peter Paul Kellogg. Photograph by M. Dameron, Photo Science.

Below, four generations of Stuarts, from the left: Mrs. Charles H. Stuart, Lyman K. Stuart, Mrs. James Stuart Beale, and Sarah Coventry Beale (a great granddaughter). Photograph by David G. Allen.

Above, Sapsucker Woods from the east — a gift to Cornell University from Lyman K. Stuart and Mrs. Kenneth E. Stuart. Cayuga Lake in the background, the Cornell campus to the left, and the airport to the right. Sapsucker Woods Road divides Sapsucker Woods Sanctuary into east and west sections of about equal size.

Below, the Laboratory building from the west showing the 10-acre pond at the north edge of Sapsucker Woods. Photographs by David G. Allen.

Above, foundation of the Laboratory building and the pond as they appeared 29 May 1956.

Below, the Laboratory building 2 August 1956. The roof is being laid with flexicore slabs. Photographs by David G. Allen.

Above, watching waterfowl through an observatory window.

Below, viewing the photographic exhibits on the east wall of the observatory. The prints are from various Laboratory expeditions. Photographs by David G. Allen.

Above, alumni, crowding the observatory during Reunion Week, hear about the Laboratory of Ornithology and its recent achievements.

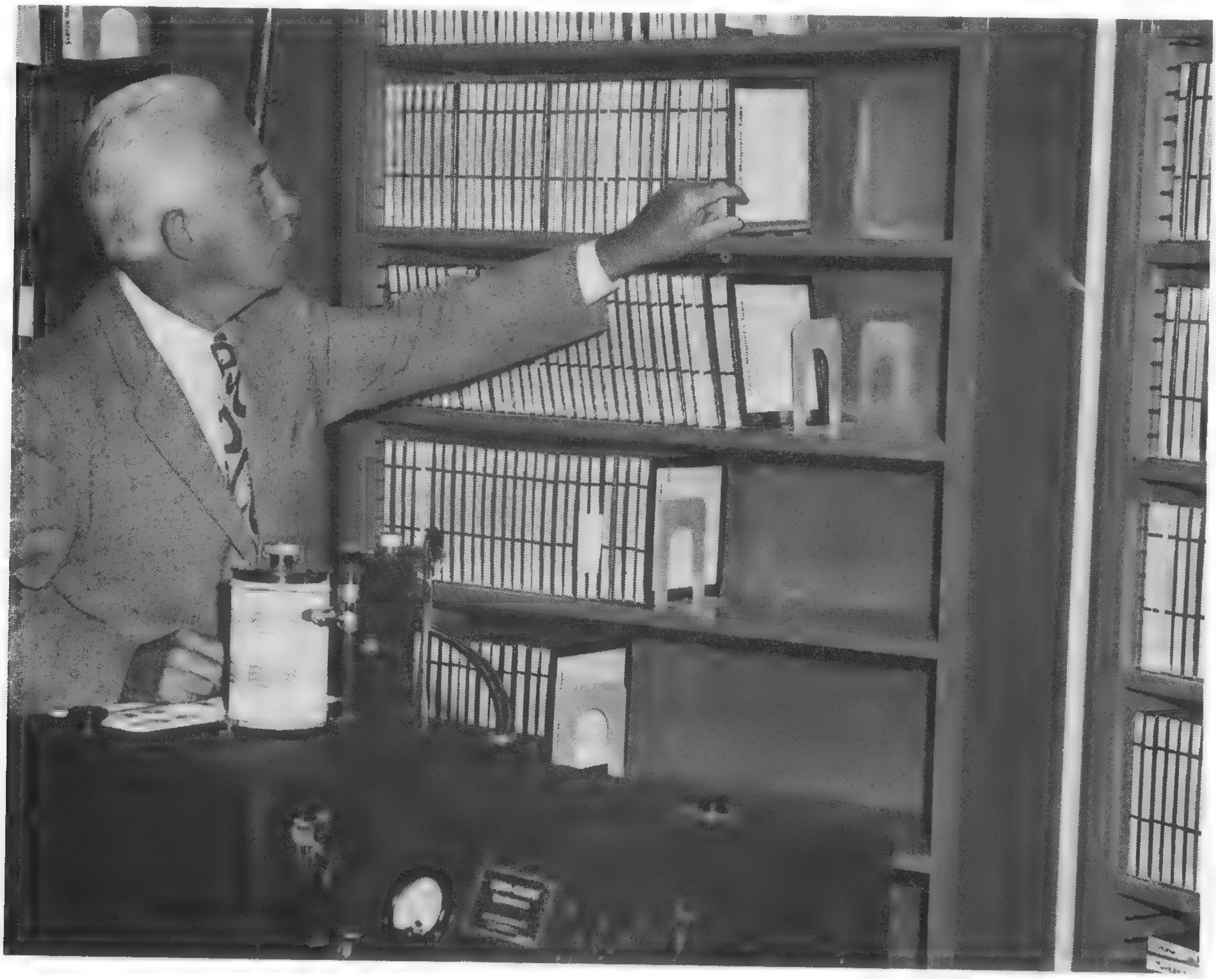
Below, Cornell Freshmen being introduced to the Laboratory's program and objectives. Photographs by David G. Allen.

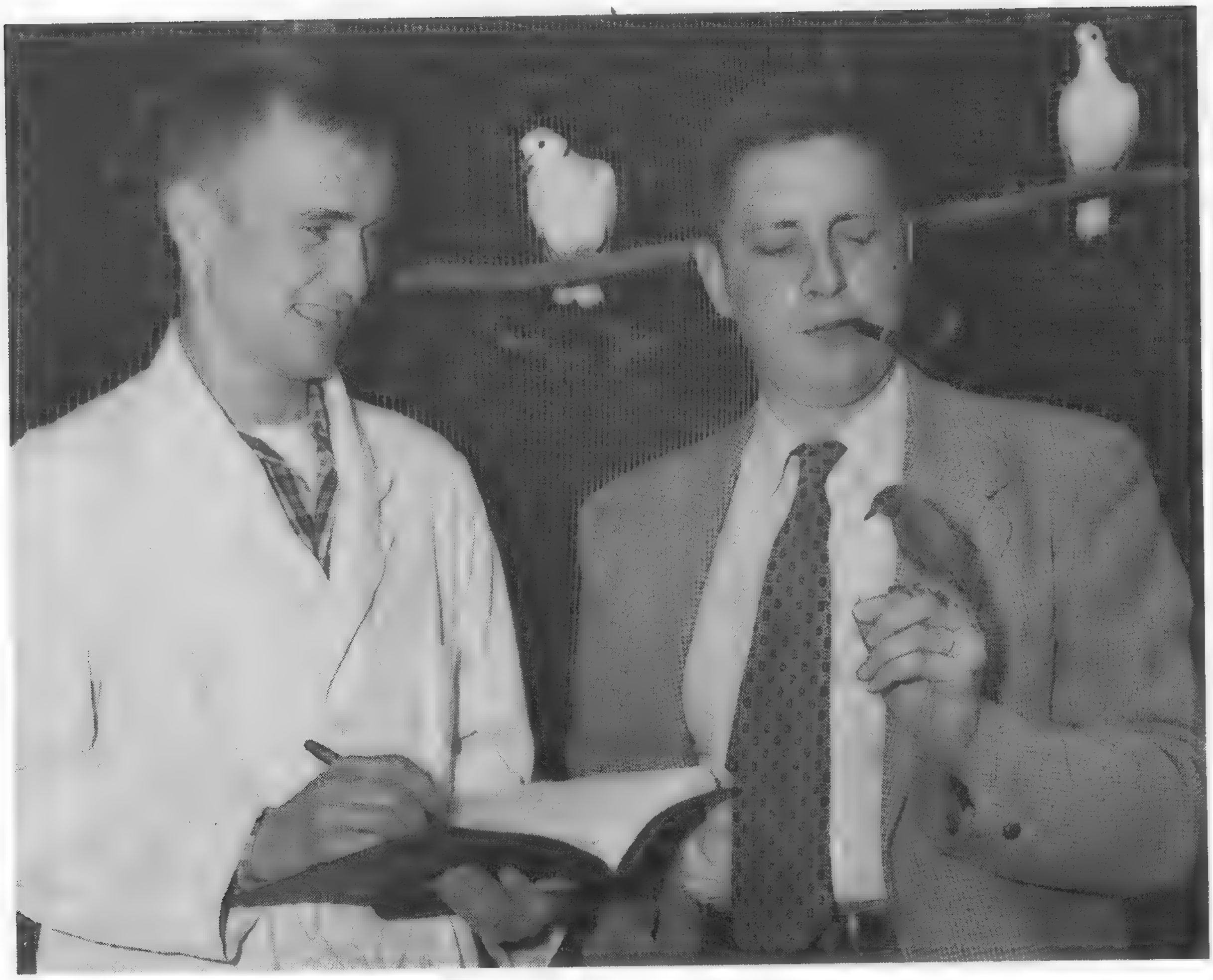
Above, a tank for studying and photographing birds under water. With suggestions from Executive Secretary Sally Hoyt, David Allen adjusts a balsa-wood goldfish for later work with an Osprey. Photograph by the author.

Below, released in the tank, a female Hooded Merganser pursues a minnow, propelling itself by feet only. Photograph by David G. Allen.

Above, the Director of the Laboratory, O. S. Pettingill, Jr., at his office desk. Photograph by George L. Wetzel.

Below, Assistant Director Peter Paul Kellogg in the Library of Natural Sounds. An audiospectrograph is in the foreground. Photograph by M. Dameron, Photo Science.





Above, Assistant Director William C. Dilger (holding an Eastern Bluebird) and Research Associate Robert W. Ficken in the Aviary. Photograph by Richard B. Fischer.

Below, the author at his office window ready to photograph incoming waterfowl. Photograph by David G. Allen.

Above, Lyman Stuart (left) and the author feed the waterfowl in the customary place in front of the author's office window.

Below, a flock of Wood Ducks arrive for food. Photographs by David G. Allen.

Above, from the window: Six Mallards and a Black Duck caught by the camera as they come in to feed.

Below, a "Lightnin Mixer," the gift of Fred Gordon, keeps a hole in the ice before the observatory windows. The hole, amply supplied with food for decoy ducks and geese, attracts many wild ducks all winter. Photographs by David G. Allen.

Above, Evening Grosbeaks on the "Early American Feeder" in front of the south observatory window. Made of old fence rails and pine stumps, stocked with sunflower seeds and finely cracked corn, the feeder attracts many varieties of land birds. Even the waterfowl clamber on it for food.

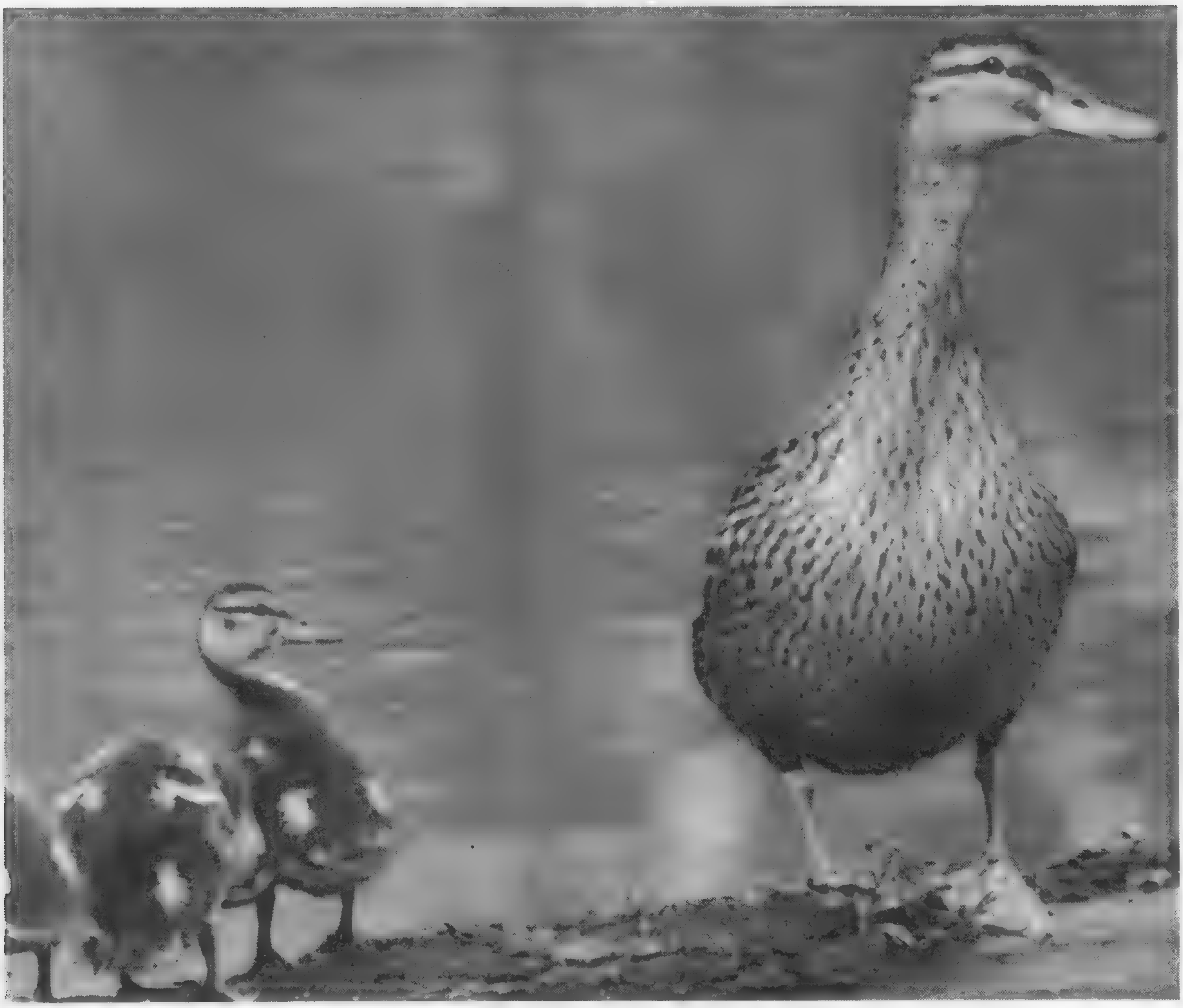
Below, a covey of Bobwhites. Introduced by the New York State Conservation Department in 1961, they frequent the Early American Feeder. Two coveys came regularly during the winter of 1961-62. Photographs by David G. Allen.

Above, a Common Loon raises its frontal crest as it swims by the observatory window. The pond is well stocked with goldfish and golden shiners for all fish-eating birds. Photograph by the author.

Below, a Horned Grebe in winter plumage spreads its lobed toes. Like the Common Loon, it finds the pond's supply of fish quite adequate. Photograph by David G. Allen.

A partially submerged log beneath the author's office window serves a number of purposes. *Above,* a fishing station for a Green Heron, which is displaying to intimidate an invading muskrat.

Below, a feeding station for a muskrat and a pair of captive Trumpeter Swans. Photographs by the author.



The same partially submerged log. *Above,* a resting area for a Mallard family and, *below,* for a Canada Goose family. Photographs by the author.

Southgate Hoyt with a Pileated Woodpecker in Sapsucker Woods. Photographed by the author in 1942. Much of Dr. Hoyt's Ph.D. thesis on this species was based on studies made in the sanctuary.

her special interest in the history of ornithology, visiting libraries and museums in Europe and America, publishing articles and books about early ornithologists, and working as a post-doctoral fellow at Cambridge, England. She serves as librarian at the Laboratory.

Dr. George Miksch Sutton, now Research Professor at the University of Oklahoma, received his Ph.D. from Cornell in 1932 and continued as Curator of Birds until 1945. Between expeditions to Mexico, Hudson Bay, and Labrador he reorganized and built up the Fuertes Ornithological Collection, which had been presented to the University by Alpha Delta Phi Fraternity shortly after Fuertes' death. A monument to both Fuertes and Sutton, the collection has been augmented by succeeding graduate students and assistants until it now numbers over 30,000 specimens. It is housed in Fernow Hall and administered by Dr. Charles G. Sibley in the Department of Conservation.

Dr. Olin Sewall Pettingill, Jr., who received his Ph.D. from Cornell in 1933, has, after an interesting and varied career, returned to Cornell as Director of the Laboratory. This is particularly appropriate because Dr. Pettingill spent much time, during his student days, in and about Sapsucker Woods, studying the American Woodcock, the subject of his thesis and later a book.

Dr. Sally Foresman Hoyt, the widow of Dr. J. Southgate Y. Hoyt, received her Ph.D. from Cornell in 1948. Since her husband's death in 1951, Dr. Hoyt has finished some of his research on the Pileated Woodpecker, written papers of her own, and carried on an extensive bird-banding project. She is a Regional Editor, as well as Notes Editor, for *The Kingbird,* the organ of the Federation of New York State Bird Clubs. Most important of all, she is the Executive Secretary of the Laboratory, a hostess in the observatory, and, occasionally, a substitute for Dr. Kellogg on his weekly radio program.

The author on 18 June 1909 climbs to a Yellow-bellied Sapsucker nest — the first ever found in the Cayuga Lake Basin. Louis Fuertes (left) thereupon named the area Sapsucker Woods. James S. Gutsell (center) and Francis Harper (the photographer) participated in the christening.

Dr. William C. Dilger, Assistant Director of the Laboratory, received his Ph.D. from Cornell in 1955. As a graduate student he displayed unusual skill in the art of bird portraiture, served as Curator of Birds, and assisted in advanced courses in ornithology. Since 1955 he has held a research position in bird behavior, financed by the R. T. French Company. Much of the space at both ends of the Laboratory building is devoted to the behavioral investigations by Dr. Dilger and by graduate students, research associates, and visiting scientists. In addition to directing the research on behavior, Dr. Dilger gives a course in Comparative Vertebrate Ethology in the Department of Conservation.

After considerable experience on many Laboratory expeditions as a photographer and assistant in sound recording, and three years of training as conservation-education assistant in the New York State Department of Conservation at Albany, David G. Allen, the author's son, has returned to the Laboratory to manage the Sapsucker Woods Sanctuary, supervise the non-academic activities in the Laboratory building, and serve as the Laboratory's photographer.

Mr. Arthur Lane still lives in his home where many students in past years used to watch his tame Black-capped Chickadees, and acts as caretaker of the lawns, trails, and feeding stations at the Sanctuary.

The Sapsucker Woods Sanctuary

The Sapsucker Woods Sanctuary is enclosed by a chain-link fence having four unlocked gates. These lead into four miles of trails which were laid out the first year to keep the traffic where it will do the least harm. Over two of the wettest areas catwalks have been constructed. Two attractive shelters, the gift of the Federated Garden Clubs of New York State, have been built in spots along the main trails where they will do the most good during showers. There are three small ponds along the trails and four others in an open area north of the Laboratory, making the sanctuary more attractive to water birds and the trails more productive for bird watchers.

The fenced area is a real sanctuary where all wild creatures and plants are protected. There is no predator control except that stray cats and dogs are ushered out and an occasional Sharp-shinned or Cooper's Hawk, that consistently frightens the aviary birds, is removed. Over 200 species of birds have been seen in the sanctuary and 84 have been found nesting.

It is not surprising that when Mr. Stuart volunteered to do something for the Laboratory of Ornithology, we all thought of acquiring Sapsucker Woods, already the setting of a number of our research projects. Here, besides Dr. Pettingill's work, Dr. Southgate Hoyt made many notable observations on a pair of Pileated Woodpeckers; Mr. Brand and Mr. M. Peter Keane did much of their early bird-song recording; the author produced a sound-color film of the Ruffed Grouse, the first of its kind; and Oliver Owen did the field work for his thesis, "The Bird Community of an Elm-Maple-Ash Swamp in Central New York." With other woodlands near the campus fast disappearing, Sapsucker Woods became increasingly important to ornithologists.

How the Laboratory Operates

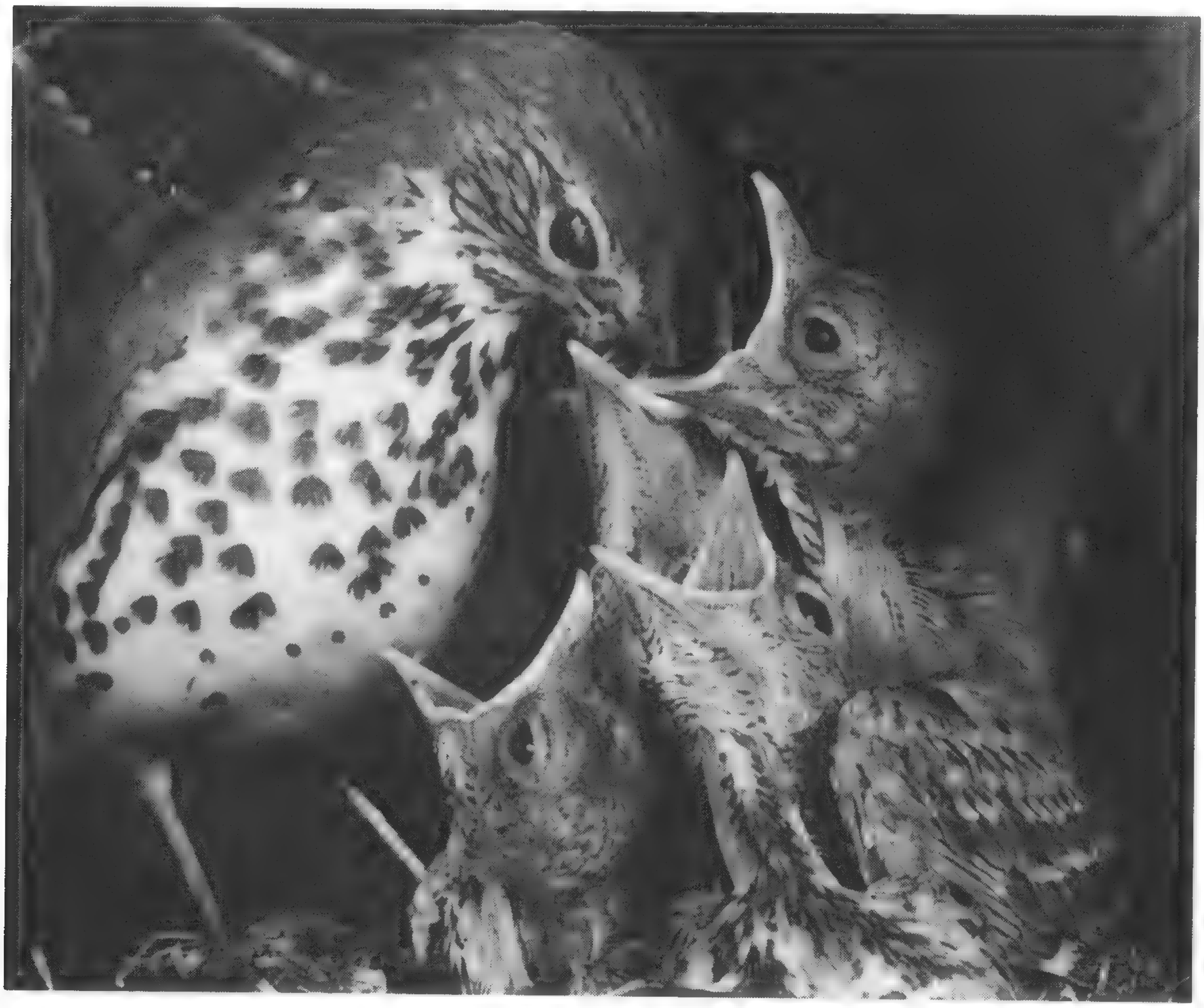
The Laboratory, a separate department of the University, is administered by a Council responsible to the President of the University. Appointed by the University's Board of Trustees, the Council itself consists of 15 members that include professional ornithologists and businessmen as well as faculty and alumni of Cornell. From these Council members the Laboratory has received tremendous support and encouragement. In fact it is hard to imagine how we

In Sapsucker Woods. Three miles of chain-link fence and an occasional sign *(above)* remind visitors that Sapsucker Woods is a sanctuary. A glacial boulder with a memorial plaque *(below)* at the entrance to the sanctuary. Photographs by David G. Allen.

In Sapsucker Woods. *Above,* Dr. Sally Hoyt leads her bird class via a catwalk over one of the swampy places. *Below,* the President of the Federated Garden Clubs of New York State, Mrs. Dunham C. Jones (wearing a white hat), presents one of the two shelters given to the sanctuary in 1957 by her organization. Photographs by David G. Allen.

Sound recording and photographing the drumming of a Ruffed Grouse in Sapsucker Woods. *Above,* Charles Brand fastens a microphone near the drumming log. A blind for photography is in the background. After the drumming *(below)* had been sound-recorded and filmed by cinema photography, the sound and pictures were synchronized, providing the first realistic reproduction of the performance for the theater screen. Photographs by the author.

Two summer residents in Sapsucker Woods. *Above*, a Red-shouldered Hawk feeds a mouse to its downy young. The nest is in a beech tree 30 feet from the ground. *Below*, a Wood Thrush fills a gaping mouth. Photographs by David G. Allen.



Above, nest and eggs of the Harris' Sparrow. The first known eggs of the species were found on 16 June 1931 near Churchill, Manitoba, by George M. Sutton, at that time a Cornell graduate student on an expedition for the Carnegie Museum in Pittsburgh, Pennsylvania. On the same expedition was another Cornell graduate student, O. S. Pettingill, Jr.

Below, a Bristle-thighed Curlew standing over its nest on the tundra north of the Yukon. The most notable result of the Laboratory's 1948 Alaskan expedition for the National Geographic Society was the discovery, on 15 June, of the nest and eggs of the Bristle-thighed Curlew — the last North American bird to keep its nest a secret from science. Photographed by the author.

could have developed our current program to its present extent without their loyal backing.

In order to encourage the study of living birds through the staff and facilities of the Laboratory, we frequently invite persons who have a deep interest in birds and the work of the Laboratory to become members. If they accept, they are appointed to membership by the President of the University. Our members at the present time total about 730.

In addition to members, we have ten research associates who are ornithologists either centering their investigations in the Laboratory or representing the Laboratory while conducting their investigations elsewhere.

Public Relations

Not the least important and profitable activity of the Laboratory has been its efforts to interest the general public in living birds. Some of our efforts have been made through bulletins and films, through lectures illustrated with color slides and films, and through recordings of bird songs and the production of phonograph records. More recently, through loan collections of phonograph records of bird songs with matching color slides and through sets of slides with matching scripts on such subjects as bird migration, bird coloration, and the home life of birds, the Laboratory has tried to be useful to schools and bird clubs. One of our latest efforts is a new sound-film on the Bald Eagle, made by one of our Council members, Mr. Bayard W. Read.

At the Laboratory building the general public is always welcome to share with the staff our art gallery, library, exhibits, and the pleasant view over the pond from the observatory windows. Binoculars and telescopes are available so that people at the observatory windows can enjoy a novel kind of bird watching in which the birds come to the observers instead of the observers going after them. In addition, the songs and calls of the birds outside are brought inside through microphones under the eaves and are broadcast from speakers on the walls, giving the effect of no glass in the windows. On windy days or whenever the outside sounds are few, our phonograph records are played through these same speakers. Our slogan is, "Don't wait until spring for the birds to sing, play Cornell records now!" The response to our daily open house has been gratifying. According to the signatures in our guest book since 1957, an average of 7,000 people visit us each year. Represented are all the states and 70 foreign countries.

Although we are not sufficiently staffed to offer guided bird trips through Sapsucker Woods, Dr. Hoyt does lead one trip a week for a special class. Every Saturday morning during May, the Laboratory assumes responsibility for organizing and leading bird walks, started by the Cayuga Bird Club in 1913 and continued ever since. From 50 to 100 adults and children assemble at 6:00 AM at the Cayuga Street Bridge over Fall Creek. They are divided into groups of 10 or 15 and each is assigned a competent leader. The groups then separate to follow trails through the Fuertes Bird Sanctuary at the head of Cayuga Lake and meet at 8:00 at the duck pond. There they make up a combined list of all birds seen. These walks added to Dr. Kellogg's Saturday morning radio programs have done much to stimulate local interest in birds.

Each Monday evening, except during the summer, an open seminar meeting is held in the observatory of the Laboratory for a roll call of birds seen during the week and a report, often illustrated, on a recent expedition or a new piece of research. The observatory, which seats only 100 comfortably, is often filled to capacity and occasionally cannot accommodate all who would like to attend.

First nest of the Coppery-tailed Trogon found in the United States. Photographed by the author 1 June 1939 in Madera Canyon near Tucson, Arizona, on a Laboratory expedition with Charles Brand and David G. Allen.

Expeditions and Field Work

The staff, graduate students, and research associates of the Laboratory have traveled rather widely in their ornithological studies, covering much of North America, venturing into many parts of Central and South America, Africa, Australia, and New Zealand, and visiting many museums in this country and abroad. Films, sound recordings, books, and numerous technical papers have resulted from these expeditions. A phonograph record of Mexican bird songs recorded by Mr. L. Irby Davis and one of African bird songs by Mr. Myles E. W. North have been published by the Laboratory. To the Laboratory's modest but steadily growing film library have recently been added African films by Mr. Donald S. McChesney, Mr. Bayard W. Read, and Dr. Lawrence I. Grinnell; and New Zealand and Australian films by Dr. Grinnell.

In past years, expeditions by staff and associates of the Laboratory resulted in many "firsts." In 1931, for example, on an expedition for the Carnegie Museum to Churchill on Hudson Bay, Dr. Sutton was the first to find and later describe the eggs of the Harris' Sparrow. In 1939, on an expedition to the Pacific Coast, the author, David Allen, and Charles Brand found in Madera Canyon near Tucson, Arizona, the first nesting of the Coppery-tailed Trogon in the United States. In 1948, on an expedition for the National Geographic Society north of the Yukon in Alaska, the author and David Allen, together with Henry Kyllingstad and Warren Peterson, discovered the first nest, eggs, and downy young of the Bristle-thighed Curlew. For this they received the Burr Award of the National Geographic Society.

Other firsts by Laboratory personnel have included the use by Drs. Wilbur K. Butts and Marguerite Heydweiller Baumgartner of colored bands and dyed feathers for marking individual wild birds under study, and the first sound recordings of the nearly extinct Whooping Crane and Ivory-billed Woodpecker.

On expeditions or in other work our Laboratory people have never followed the well-charted course, and it is doubtful that they ever will. New methods, new facts, and new concepts lie along the obscure byways. Here we shall expect our people to discover many more firsts in the years to come.

LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK

BIRD-SOUND STUDIES AT CORNELL

PETER PAUL KELLOGG

The history of sound studies at Cornell is a story of teamwork, cooperation, and much hard work. But above all it is a story of teamwork, in which faculty, undergraduate and graduate students, engineers, physicists, industrialists, and serious amateurs have been drawn together in a common effort.

In looking back at the emphasis placed on field studies at Cornell by such men as Burt G. Wilder, Simon Henry Gage, David Starr Jordon, John Henry and Anna Botsford Comstock, Albert Hazen Wright, E. Laurence Palmer, and Arthur A. Allen, it is easy to understand why biological acoustics, once developed, should have been quickly recognized here as applicable to the study of living birds and other animals.

Louis Agassiz Fuertes' keen interest in bird sounds is a legend at Cornell and this interest, coupled with his uncanny ability to imitate them, won him wide renown. His "Impressions of the Voices of Tropical Birds," published serially in *Bird-Lore,* beginning with the November-December number in 1913, is a classic of its kind. Fuertes' popularity enabled him to interest many people in the calls and songs of birds and it was natural that identification of birds by their sounds was emphasized in ornithology classes at Cornell.

First Experience in Recording Songs of Wild Birds

In 1928 William W. Vogt wrote to Arthur A. Allen asking if he thought a project of recording wild bird sounds would be feasible. Dr. Allen replied that it would be if there were a practical technique.

In May of 1929 the Fox-Case Movietone Corporation appealed to Dr. Allen for help in recording a singing wild bird. Birds, they said, would not stay still. On Saturday, 18 May 1929, the Movietone truck with two men appeared, by prior arrangement with Dr. Allen, at Ithaca's Stewart Park at 5:00 AM — an almost unheard of hour to the operators. Dr. Allen had invited me to be with him. In the next hour the songs of three birds, Song Sparrow, Rose-breasted Grosbeak, and House Wren, had been recorded on film synchronized with motion pictures. Later that morning I developed test strips of the recordings and pictures in the darkroom at McGraw Hall. We were convinced that we had achieved at least some success, but for final proof we had to wait three weeks until the film could be presented as a "short," entitled "Sounds of Spring," at the Strand Theatre in Ithaca. This was our first cooperation with industry and, while it was thrilling and opened up new vistas, it was not entirely satisfying, partly because of poor quality but more importantly because of the enormous cost of the equipment required — about $30,000! Recording bird-sounds ourselves was far beyond our wildest dreams.

Practical Recording Equipment Still Unavailable

Later in 1929, with the crash of the stock market, a period of lean years began. We wanted the cooperation of industry again, this time to make it possible for us to get sound recordings for study and teaching, but we were turned down at every door. Money was scarce; moreover, no one seemed convinced that collecting bird songs had any practical value. George B. Saunders, a graduate student who was studying meadowlarks, and I investigated the possibilities of recording sounds on aluminum discs. Visiting our Physics Department to study equipment being used there, we were appalled by the complexity of the electrical apparatus and even more disappointed by poor quality of the recorded sound. We concluded that the time was still not ripe for us to record bird songs.

Mr. Brand Comes to Cornell

Albert R. Brand entered our picture through the good offices of Dr. Frank M. Chapman at the American Museum of Natural History in New York City. Brand had retired from the New York Stock Exchange, where he was a successful broker, in early 1928 at the age of thirty-nine. He had tried studying economics at Columbia University but disliked it. Having an amateur interest in birds, he offered his services to the American Museum. Dr. Chapman, though happy to have him as a volunteer worker, suggested that he would be much more useful to the Museum if he would first attend Cornell and take some course work in ornithology under Dr. Allen. Brand thereupon registered as a special student in the fall semester of 1929. All of us, staff and students, liked Brand instantly, and we were soon sharing many of our thoughts and plans with him. During his first year we talked at length about the wonderful possibilities for recording and studying bird songs. Brand showed keen interest and continued to listen. In an unpublished report on his work in ornithology, he gives June 1930 as the time when he began to consider seriously his own participation in recording sound.

Deciding to record, then actually securing equipment and getting started were very different problems. After many discouragements, we placed an order for equipment in November 1930. Three months later the first version of the recorder was delivered but it failed to work. Most of the following spring was devoted to efforts in recording bird songs. M. Peter Keane, an undergraduate student, spent all of his spare time that year with Brand and was of great assistance to him. In June a new recorder was purchased and by the end of 1931, Brand notes, 41 species of birds had been recorded. Many of the recordings were barely recognizable above the extraneous noise but, even so, it was already the largest collection of bird songs in the world. That year in Detroit, at the meeting of the American Ornithologists' Union in October, a paper on the work was presented and the Secretary's report later said: "The outstanding contribution was doubtless Brand's 'Preliminary Report of a New Method for Recording Bird Songs' illustrated by reproductions of the songs of some thirty species . . ."

Thus, by the end of the first 18 months, we had had some success and were encouraged to go on. We now understood the principal problems in recording and the shortcomings of the equipment. We understood, too, that if we were to achieve any kind of perfection, we would have to develop our own specialized equipment and techniques for field work.

The author shows Albert R. Brand (right) a new battery-operated preamplifier which enabled weak microphone signals to be increased so that they could be transmitted over an open wire line to the sound truck (in background) several miles away. Photograph taken in 1937 by Arthur A. Allen.

Development of Suitable Equipment

Through the winter months of 1931-1932 Professor True McLean of our Electrical Engineering School and Mr. Arthur Stallman, a local consultant in electrical engineering, designed and constructed new electronic equipment and Mr. Arthur Jenkins rebuilt and modified the mechanical details of the recorder.

When Peter Keane returned from the Christmas recess, he brought with him a copy of *Radio News* for January 1932. On the cover was a parabolic reflector being used in a box of a theater to catch the voice of an actor on stage. Both of us saw its direct application to bird-sound recordings but the engineers discouraged us because of its poor low-frequency response. Professor Hugh Reed of the Zoology Department encouraged us to try it anyhow. Professor Harley Howe of the Physics Department located old World War I molds of reflectors and we worked for weeks in the basement of McGraw Hall, mixing, casting, and finally correcting and finishing our parabola. The experiment was an immediate success. The fact that few birds produce low frequencies prevented the expected faults from affecting the sound. This development of the parabola for picking up and concentrating bird songs on the microphone was probably our greatest piece of good fortune. Recording would have been possible without a reflector but the results with it were so superior as to make the instrument a universal tool in this field.

First Phonograph Records of Wild Bird Songs

In the spring of 1932, Brand, with Peter Keane, published privately the first phonograph record of wild bird songs made at Cornell. This was a 12-inch, 78 rpm disc, two sides, containing the songs of 21 species of birds and one amphibian, and titled "Bird Songs Recorded from Nature."

In the period of a little more than one-and-a-half years we had replaced practically every piece of recording equipment — a good indication of the high rate of obsolescence in the field. However, we now felt that we were ready to proceed and really accomplish something in the way of building up a collection with which to work.

Again, at the next AOU meeting (October 1932 in Quebec), we presented another paper. This time the Secretary reported: "The outstanding contribution, as at the last meeting, was Brand's 'Sounds as an Aid to Bird Study,' illustrated with moving pictures and slides and reproduction of bird notes on the phonograph. Great progress over the results of last year was shown in the clearness of the notes and in blotting out discordant sounds which distract the attention of the listener." At this meeting we also presented a paper on "The Drumming of the Ruffed Grouse" which showed how readily film recordings could be used for study and how they could be coupled with motion pictures. Dr. Allen had made the motion pictures, while Keane and I had recorded the sound in Sapsucker Woods; we had all worked at putting it together.

Although we were achieving some success, our results were always uncertain since our films had to be developed in New York City, causing a time lag of as much as a week, or longer if we were in the field. To overcome this handicap, a study of photographic sensitometry was begun with Professor L. A. Burckmyer, Jr., and a special darkroom was set up to process our own films.

In our film-recording system were made many more improvements, the most conspicuous of which was a complete redesign engineered by Mr. J. A. Maurer. This resulted in a relatively small, light, 16 mm film recorder especially suited for bird studies and weighing less than 100 pounds. However, the delay in processing was still a great handicap and plagued us. The start of World War II stopped all operations.

Albert Brand died in 1940 after an illness of nearly seven years. From the time he had decided to record bird songs in 1930, he had taken an active part in all of our work. It would be equally correct to say that we had taken part in his, since he had paid all the bills and all publications had come out under his name. It was teamwork in every sense. Decisions were usually made in conference and everyone did what he was best qualified to do. As Brand's illness became more confining, he turned to analytical studies of the recorded bird songs and everyone helped him. A small, new aviary was built on the roof of Fernow Hall where we measured the ability of birds to hear. New techniques were developed for microscopically examining and evaluating the recorded wave forms. Besides publishing many technical papers, we produced films with sound, selling some of them as professional motion pictures.

First Book-Records of Bird Sounds Published

In 1934 Brand published his first book, "Songs of Wild Birds" (Thomas Nelson and Sons, New York), with two double-faced discs containing recordings of 35 species; and in 1936 he brought out a sequel, "More Songs of Wild Birds" (same publisher), and three records containing 43 more species. He arranged for our cooperation with the American Foundation for the Blind and the "talking books" on bird songs which are still published.

The Cornell University-American Museum of Natural History Expedition prepares to leave Ithaca in February 1935 for a six-month quest of vanishing birds in southern and western United States. The author is on the tower of the photographic truck. Left to right in front of the sound truck are James T. Tanner, Arthur A. Allen, and George M. Sutton. Photograph by Fenner.

Brand was an unusual personality. I do not recall ever seeing him cross with anyone or about anything — although he certainly had good cause many times! When a project failed, he wrote it off immediately and almost completely forgot about it. When things were right, his enthusiasm knew no bounds and a bit of success would be so highlighted as to overshadow any failure. The years he was with us were busy and fruitful. We remember him as a great inspiration.

Early Recording Expeditions

In 1935 Brand had arranged with Cornell and the American Museum to sponsor a six-month field trip to record the voices of vanishing species of birds. Dr. Allen, James T. Tanner and I were the full-time members of the expedition; Brand and Dr. George Miksch Sutton joined us at times. Our most notable success was with the Ivory-billed Woodpecker in central Louisiana, but we were successful with many other species too, such as the Lesser Prairie Chicken and Trumpeter Swan. In 1939, taking our newest equipment, Brand sponsored another trip to the west coast with Dr. Allen, his son David, and Brand's son Charles.

The Laboratory's First Album of Bird-Sound Recordings

After Brand's death, and before the war stopped all work, an album of six 10-inch, 78 rpm discs, titled "American Bird Songs," was produced in the Laboratory with the assistance of Professors True McLean and Elmer Phillips and Charles Brand. It was published and distributed by the Comstock Publishing Company (later to become the Cornell University Press) and was an immediate, though small, success. The royalties received were the primary financial support of the Laboratory of Ornithology's recording projects for many years.

Sound Recording During the War

Soon after the war started I was invited to join the Western Electric Company where I organized and directed a radar school in which engineers could be hurriedly indoctrinated into the technical mysteries of this latest development in electronics.

In 1943, when the armed forces became concerned about military operations in the tropics, Rutgers University accepted a contract with the United States Army to investigate the acoustical problems of jungles. Dr. Allen, David Allen, and I joined this project under the direction of Dr. Carl Eyring and in 1944-1945 worked in Panama. Because of film censorship and also because of the deterioration of film under tropical conditions and the excessive time lag between recording and possible playback, we decided to change to instantaneous disc recording, using professional equipment which by that time had developed to a point where it compared favorably with the best film-recording methods. In Panama we took full advantage of our wonderful opportunity to study birds and record their sounds. When we prepared our report, which the Office of Scientific Research and Development published confidentially, we included an album of two, 12-inch, 78 rpm discs of bird, amphibian, mammal, and other sounds of the tropical environment.

By 1947 we had recorded so many amphibian sounds that we decided to make them available. Although no publisher wanted them, we persisted and "Voices of the Night" resulted, an album of four, 10-inch, 78 rpm discs containing the vocalizations of 26 frogs and toads of eastern North America. Its success surprised us all.

Recording by Magnetic Tape

Disc recording continued to serve us until the end of 1949 when we changed to magnetic tape recording. We began our experiments with tape recorders in 1947, but not until 1949 could we find portable or semi-portable equipment which compared favorably with disc equipment.

One of the results of my sabbatic leave during 1949-1950 was the design concept of a truly portable tape recorder. I presented it to Mr. N. M. Haynes of the Amplifier Corporation of America, who readily took it, combined it with ideas of his own, and, in 1951, commercially produced the first Magnemite Tape Recorder, a unit weighing under 20 pounds. This recorder became the workhorse of our projects and was generally adopted by almost everyone interested in natural-history recording. For the first time many new habitats, which could not be reached except on foot, by horseback, or by boat, were accessible to sound recording, making possible such sound studies as those in Florida Bay (1952), coastal Labrador (1953), and Hudson Bay (1954). Thousands of these little units were sold all over the world — an indication of the tremendous interest in recording natural sounds. New developments, especially in Europe, have to a large extent replaced the Magnemite, but many are still in service and doing good work.

The Laboratory of Ornithology now has eight portable recording channels, several of them in the field all of the time. Their combined weight is but a small fraction, perhaps a tenth, of the weight of one original field recorder. Today the dependability and operational simplicity of recorders have increased to a point where anyone seriously interested can, with a little experience, learn to make scientifically and aesthetically satisfactory recordings of sounds in nature.

The Library of Natural Sounds

As sounds have been collected, either through the efforts of the Laboratory staff or by others, they have been added to the Library and catalogued on cards. The collection now exceeds 1,500 species, and 17,000 selections or "cuts." Over half of the cuts are on tape and we plan to copy all of the earlier selections from film and disc so that the Library will be more uniform and more readily available. There is a great need for a printed catalogue and we hope to have one, at least for the tape collection, available in 1962.

In one way the Library is unique, since users are never asked to return recordings. The finest facilities enable us to duplicate our original recordings with such fidelity that it is almost impossible to tell the copy from the master. The copies are made on tape supplied by the prospective user and thus record-keeping and accounting are greatly reduced.

This historical account touches only the highlights of our adventures in studying bird sounds to date. The manner in which the biological-acoustics program is handled in the Laboratory, the accomplishments of our projects, the contributions of cooperators, both professional and amateur, and especially the opportunities for amateurs and professionals to make outstanding and highly useful scientific contributions in a relatively new field, is the most thrilling part of the story and will be briefly summarized.

Cooperation in the Biological-Acoustics Program

For the most part, cooperation in our biological-acoustics program is quite informal. Often it goes on effectively for years without anything more formal than an exchange of correspondence.

A fundamental concept of the Laboratory is that it should offer leadership, inspiration, encouragement, material help (when possible), and recognition to anyone wishing to study living birds. In the field of sound, the Laboratory often performs a valuable service to cooperators by storing copies of useful recordings — thus giving additional protection against loss. The recordings are edited, filed, and catalogued to the credit of the originators.

Another service is to make the collection available to scholars anywhere in the world for scientific study. The Laboratory cooperates with the British Broadcasting Corporation in the exchange of material for scientific and educational purposes between their two libraries.

Occasionally grants are made to Cornell University for specific projects in the field of biological acoustics. Under these grants, the work may be carried out by a member of the staff, a graduate student working under a staff member, or by the donor of the grant. (In some instances, a special investigator is brought into the Laboratory temporarily to conduct the project.) A person wishing a grant first makes a proposal to the Laboratory, often after extensive consultation. If this is approved by the Council, a formal agreement is drawn up setting forth the objectives of the project along with the rights, privileges, and responsibilities of both parties.

Many of our members, who are interested in carrying on research, prefer to do the work under the nominal direction of the Laboratory. This has many advantages, among which are the recognition of working with a well-established institution and the satisfaction of cooperating with a group interested in ornithological research.

Current Projects in Biological Acoustics

Several of our more important projects in biological acoustics now being undertaken are briefly summarized below.

Above, about to leave the Laboratory for another expedition to Mexico, Research Associate L. Irby Davis stands beside his multipurpose truck remodeled for use in the field. Photograph taken in 1958 by David G. Allen.

Below, Mr. Myles E. W. North, Research Associate of the Laboratory of Ornithology, beside his Jeep station wagon specially fitted for his use in studying the voices of African birds. Photograph taken in 1956 north of Nairobi, Kenya, by Donald S. McChesney.

Above, Mr. Paul Schwartz, Research Associate of the Laboratory of Ornithology, recording bird voices in Venezuela with a Magnemite. The reflector was supplied by Dr. William W. H. Gunn of Toronto, Canada.

Below, Mr. William V. Ward using a Magnemite to record the vocalizations of Sooty Terns nesting on Rabbit Island, Oahu, Hawaii, in 1961.

The Mexican Project

Mr. L. Irby Davis of Harlingen, Texas, has cooperated with the Laboratory for over 20 years and has been a Research Associate for over five years. Since 1950 he has been recording bird sounds in Mexico and Central America and has deposited over 1,000 cuts of 350 species in the Library of Natural Sounds. Mr. Davis' particular interest is in finding acoustical evidence of taxonomic relationships in birds. In addition to scientific papers, Mr. Davis has published a 12-inch, 33⅓ rpm disc, "Mexican Bird Songs," in cooperation with the Laboratory.

The African Project

In September 1950 Dr. James P. Chapin of the American Museum proposed closer cooperation between Mr. Myles E. W. North, then a District Commissioner in Kenya, and the Laboratory. In December 1951, at the suggestion of Dr. Chapin, the late Walther Buchen of Chicago made a grant to Cornell to set up a Special Investigatorship for the purpose of studying the voices of African birds, with the understanding that Mr. North would be the investigator. This grant, with additions each year, made it possible for the Laboratory to undertake a study project in Kenya with the best equipment available. Mr. North was appointed a Research Associate of the Laboratory. In 1956 the Cornell-McChesney Expedition to East Africa had the close assistance of Mr. North, with the result that the Laboratory now has recordings of over 300 African species. In cooperation with the Laboratory, Mr. North has published a 12-inch, 33⅓ rpm disc, "Voices of African Birds."

The Venezuelan Project

Mr. Paul Schwartz of Caracas began working with the Laboratory in 1953 and was appointed a Research Associate in 1957 in recognition of his contribution of valuable recordings to the Library of Natural Sounds (more than 250 species) , his research studies on Northern Waterthrushes and other birds in Venezuela, his scientific publications, and his bird photography. Mr. Schwartz has organized and is Director of the Instituto Neotropical, the primary purpose of which is to encourage the study of living birds in Venezuela. In 1961 I accompanied Mr. Schwartz on an expedition to the Orinoco basin in eastern Venezuela.

The Waterfowl Project

Colonel Donald S. and Marian P. McChesney were appointed Research Associates in 1956, but their cooperation with the Laboratory began a year earlier with an expedition to Florida. In addition to sponsoring the Laboratory's four-month expedition to Kenya, East Africa, in 1956, the McChesneys have, since 1958, been engaged in a study of the voices of geese and ducks. To obtain recordings and other data, they have conducted expeditions to Quebec and Louisiana and sponsored special studies on geese in the District of Keewatin, Canada. From these excursions, the McChesneys have deposited more than 100 recordings with the Library of Natural Sounds and presented to the Laboratory three 1,600-foot sound films.

The Caribbean Project

Dr. George B. Reynard, a geneticist by profession, has been cooperating with the Laboratory since 1956. He has recorded vocalizations of some 200 North American bird species, chiefly along the eastern seaboard from New Jersey to Florida. Many of his recordings are now in the Library of Natural Sounds. In 1959 Dr. Reynard proposed to study vocalizations of the birds of several islands in the Caribbean, and was consequently given an appointment as Research Associate to facilitate this work. The project has been supported by a contribution from the Campbell's Soup Company, Dr. Reynard himself, and the Laboratory. An unexpected result of Dr. Reynard's undertaking is the rediscovery of the Puerto Rican Whip-poor-will. The exciting story of finding the species, long thought to be extinct, is told by him in this *Annual.*

The Hawaiian Project

Mr. and Mrs. William V. Ward of Honolulu have been cooperating with the Laboratory since 1950. The Laboratory has assisted Mr. Ward and the Bishop Museum of Honolulu in producing the first disc of Hawaiian bird voices ever published. All the voices were from recordings made by the Wards. Many of the recordings have since been deposited by Mr. Ward in the Library of Natural Sounds. Mr. Ward recently made available his extensive collection for use in the album, "Field Guide to Western Bird Songs," produced by the Laboratory and currently being published by Houghton Mifflin Company.

The Brazilian Project

In 1960 Mr. Rodman Ward made a proposal to the Laboratory which has resulted in the start of a study of vocalizations of Brazilian birds by himself and Mrs. Ward. Already the Wards have contributed a dozen recordings of Brazilian species (our first) to the Library and supplied a small collection of recordings which they made in Bermuda.

The Bio-Acoustics Bulletin

The *Bio-Acoustics Bulletin* was originated by Dr. William R. Fish, a chemical engineer in California. In 1956 and 1957 Dr. Fish issued six numbers of the publication, acting as author, editor, printer, and publisher. Two years later he agreed to resume editorship of the *Bulletin,* if the Laboratory would assume responsibility for finances, printing, publication, and distribution. This the Laboratory agreed to do. An editorial board consisting of Dr. William W. H. Gunn of the Federation of Ontario Naturalists, Toronto, Dr. Peter Marler of the University of California at Berkeley, and Dr. P. P. Kellogg was appointed to assist the editor. The purpose of the *Bulletin* is to "provide a means for the exchange of information that may be helpful and newsworthy to those who are interested in good recording techniques and results and in the advancement of bio-acoustics research."

The Study of Function, Variation, and Development of Bird Sound

In June 1960 Dr. Robert C. Stein, who received his Ph.D. in ornithology from Cornell, commenced work at the Laboratory with the support of a National Science Foundation Grant and the able assistance of a graduate student, Robert B. Angstadt. His project has consisted of an intensive study of the vocalizations of several closely-related species over their entire range and a more general study of vocalizations of several groups of birds. Some of his work is summarized in his article, "A Comparative Study of Songs Recorded from Five Closely Related Warblers," appearing in this *Annual.*

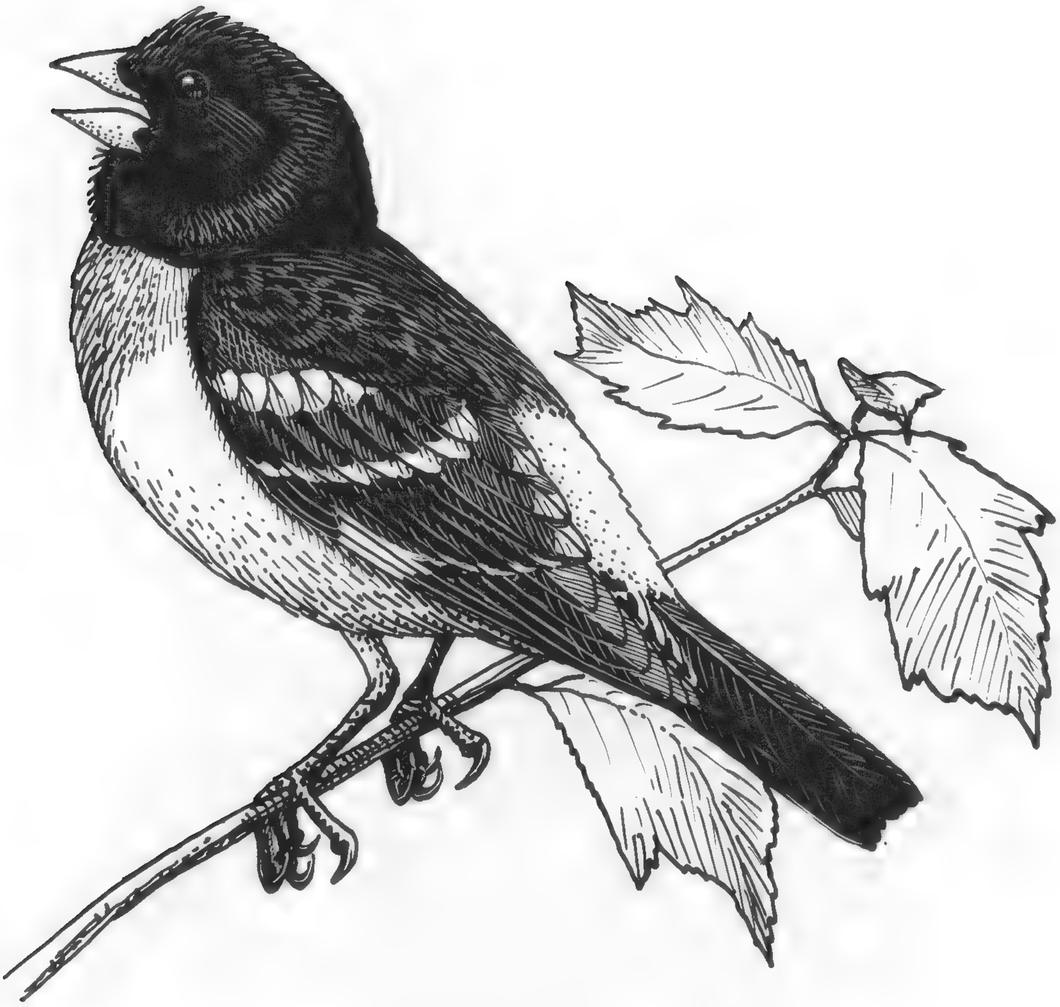
The Aesthetics of Bird Song

Dr. Charles Hartshorne, Professor of Philosophy at Emory University and the author of a number of papers on bird music, has used the Library of Natural Sounds for comparing and evaluating musical qualities of bird songs. With a keen ear for avian sounds, Dr. Hartshorne has devised a scheme for the actual comparison of elements which he considers important in a bird's vocal performance. In pursuit of his interests, he has traveled to every continent. To our Library he recently contributed the vocalizations of half a dozen species recorded by him in Central America.

The projects I have briefly described do not mention all the cooperation and assistance which the Laboratory has recently enjoyed. We have had, for example, the skilled help of Dr. William W. H. Gunn in editing the "Field Guide to Western Bird Songs," and further help from the following: Randolph S. Little, a student assistant, whose knowledge of electronics has proved invaluable in our field work; Charles Sutherland, an undergraduate, who has led two expeditions totalling 14 weeks to Florida and the west coast for the purpose of recording vocalizations needed in the Library of Natural Sounds (while in Florida, he added a new species of tern, the Black Noddy, *Anoüs minutus atlanticus,* to the check-list of birds found in the United States); Lewis F. Pearsall, who has designed and built special cases for field equipment; and Arthur W. Jenkins, who designed and built special equipment for recording sounds.

For all the assistance that has made our sound work at Cornell a story of teamwork we are most grateful. My sincere hope is that, in this cooperative endeavor, the Laboratory has lived up to its objective of offering leadership, inspiration, and encouragement to all who would study living birds.

LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK



ORNITHOLOGY AT CORNELL TODAY

GUSTAV A. SWANSON

Professors Arthur A. Allen and Peter Paul Kellogg have already described in this *Annual* the development of the major programs of the Laboratory of Ornithology, and its present scope of activities. It remains for me to mention the ornithological work elsewhere in the University, and particularly the study opportunities for students at Cornell.

When the Laboratory of Ornithology was formally organized in 1955 as a separate department, it was not in one of the teaching colleges of the University, but placed directly under the President and a specially appointed Council, for the purpose of supplementing the ornithological work of the University in research and general public education. All of the formal teaching of courses and the direction of graduate study in the ornithological fields, as well as a considerable amount of the research, is still conducted in the College of Agriculture, in the Department of Conservation, as it has been for many years. When Laboratory staff members teach or direct graduate students in the University, it is by virtue of their faculty appointments also in the Department of Conservation. The historical adoption of ornithology by the State College of Agriculture at Cornell began with Professor Allen's first appointment in 1915, and reflects the willingness of the State of New York to support the University program in ornithology, thus recognizing the close relationship of birds to man.

At present, and for a number of years, there have been three formal courses in ornithology taught at Cornell by Professor Charles G. Sibley. The first is General Ornithology (Conservation 9), an introductory course, including both field and laboratory work, taught each spring semester.

The other two are advanced courses for graduate students and upperclassmen, offered during the fall term, one each year, alternating: Systematic Ornithology (Conservation 126), covering the birds of the world, and The Biology of Birds (Conservation 127), a modern consideration of all aspects of avian biology.

In addition there are several other courses in the Department of Conservation and elsewhere in the University which are concerned to a large extent with birds. In the Department of Conservation are courses in Biological Acoustics given by Professor Kellogg, Comparative Vertebrate Ethology by Professor William C. Dilger, and several courses in Conservation of Wildlife, Wildlife Management, Economic Zoology, and the Literature of Vertebrate Zoology. In other departments there are several courses dealing in part with birds which I shall not list individually, but those in Physiology of Avian Reproduction (Poultry Husbandry Department), in Comparative Vertebrate Anatomy (Zoology Department), and in Genetics (Departments of Plant Breeding and of Poultry Husbandry) are taken by most of our students.

What type of training is expected of a university student preparing himself for professional work in the field of ornithology? Employment which relates to ornithology is primarily in college or university teaching and research, in state or Federal Government positions involving management or research, and in a few private agencies including museums and conservation organizations. At Cornell University the student who signifies an interest in ornithology is expected as an undergraduate to take a broad course of study which includes the humanities and social sciences as well as the physical and biological sciences, but the major is in vertebrate zoology. The Department of Conservation supplies a "List of Suggested Courses" to those who inquire. With this broad trainng as a background, the superior students continue with postgraduate work toward the M.S. and Ph.D. degrees, the latter usually being required for university and museum positions, and for many of the government positions.

Cornell University is an unusually appropriate place to study ornithology and the related biological sciences because of a remarkably favorable ecological setting, as well as the long tradition here of ornithological study and training. As a result, there is each year an active group of both undergraduate and graduate students engaged in studies relating to birds, and they gather frequently for field trips, in classes, and at informal meetings, thus providing much mutual intellectual stimulation.

Some of the research projects involving birds currently in progress or recently completed in the Department of Conservation are appropriately mentioned in conclusion, and it should be stressed that each of these projects has provided opportunity for the participation of graduate students who were working toward advanced degrees.

Professor Sibley's research in recent years, generously supported by grants from the National Science Foundation and the National Institute of Health, has centered largely upon basic studies of the phylogenetic relationships of birds as revealed in the genetically determined composition of their egg-white and blood-serum proteins. These studies, which are continuing, have already made very important contributions to our knowledge of bird phylogeny. In addition, Professor Sibley's graduate students have worked on several other types of problems, usually relating to systematics and speciation.

Professor Oliver H. Hewitt, because of personal familiarity with waterfowl and the Far North, has directed a number of graduate studies involving geese or ducks in Canada. Another, supported by the Federal Government, has been on the biology and behavior of Red-winged Blackbirds, economically important for their crop depredations. Several graduate students of Professor Hewitt's and my own have worked on problems involving the management of game birds.

With many studies of these varied types continuing at the same time, a student of ornithology at Cornell has an abundant opportunity to participate in research himself, and to benefit from the associations of research-oriented faculty and students.

DEPARTMENT OF CONSERVATION, CORNELL UNIVERSITY, ITHACA, NEW YORK

THE REDISCOVERY OF THE PUERTO RICAN WHIP-POOR-WILL

George B. Reynard

In southwestern Puerto Rico the vegetation on the many hills varies from limited grass and thorny shrubs to somewhat restricted growth of trees and cacti. Rainfall of less than 30 inches per year, falling principally in summer and fall, and limestone hills with a very thin clay soil add to the restricted growth and limit animal life. Even the amphibian chorus, so common in most parts of the island, is missing on many of the hills. Here, in one of the more heavily wooded sections, classed as a tropical dry forest, an area was set aside in 1919 as a reserve, with limited public access.

In connection with my interest in sound recording, I was taken to this area by Mr. Ricardo Cotté of the Fish and Wildlife Section, Department of Agriculture, Commonwealth of Puerto Rico, to attempt to hear and identify an unknown night call. We arrived in the forested area about 10:30 PM, 8 March 1961.

At 11:00 PM we heard the first calls, a series of whistled notes resembling in quality the sounds of a caprimulgid. They were distinctly different from the calls of the mainland Chuck-will's-widow (*Caprimulgus carolinensis*) and Whip-poor-will (*C. vociferus*). I tape-recorded them immediately and made additional recordings at 5:30 the following morning. All attempts to locate the source of the calls at night or to flush a bird by day were unsuccessful on this first visit.

Local Information

A series of inquiries began at once, at first locally, then farther afield. Using the playback speaker of a battery-operated Nagra IIIB tape recorder, we reproduced the calls for some of the oldest people living in the area. All were familiar with the calls, having heard them every night of the year. In general they attributed them to an unknown amphibian or to the Pájaro Bobo (cuckoo). Both the Lizard Cuckoo (*Saurothera vieilloti*) and the Mangrove Cuckoo (*Coccyzus minor*) are found in the area. The suggestion of the Puerto Rican Screech Owl (*Otus nudipes*) was discarded because I was familiar with its calls and knew they were entirely different from the unknown calls.

Don Luis Soto, over 86 years of age, had worked in the forest for at least forty years and had heard the calls here every night for as long as he could remember — at least from 1900. He thought they were made by a bird like a capacho (nighthawk) which is found in Puerto Rico only in the spring and summer.

Mr. Diego Martinez, who now lives in the forest, had also heard the calls nightly for years. We also learned from local residents that the workers in the Civilian Conservation Corps, which had a camp in the forest from 1935 to 1943, were so annoyed by the night singers that they asked to have them chased away if possible.

The possibility that the call was made by an amphibian was ruled out by Dr. Juan A. Rivero, Director of the Institute of Marine Biology at Mayagüez, who had recorded calls of the amphibians of the island and found nothing similar to it.

We played the recordings for Dr. James B. McCandless of Mayagüez, author of a booklet on Puerto Rican birds (1958). The sounds recalled to him a letter he had written in 1958 to Mr. James Bond:

> Near my home at 1000 feet just east of Mayagüez, I fairly frequently hear a nocturnal flight song which I have been unable to identify. It is a short "eyerp," more musical than the Ani's rolplaning call. The call is repeated two or three times with slight variations. Is there any description of the call of the Puerto Rican Whip-poor-will other than Wetmore's notes? Could this be the call of the Bare-legged Owl?

Mr. Bond was unfamiliar with any call of this description.

Available Information on Whip-poor-wills in Puerto Rico

The possibility that the unknown call might be a Puerto Rican Whip-poor-will's seemed highly unlikely. The only specimen ever taken from the island was a female, collected in 1888 and reported by Cory (1889). Bond (1961) and McCandless (1958), in publications covering the birds of the island, listed this bird as "presumed extirpated" and "extinct." Wetmore (1916) published a sight record of one bird seen in 1911, and in a later report (1922) stated (p. 323): "The country people in Porto Rico told me on several occasions of a bird that in former times called loudly and continuously at night, that no one was ever able to see." He also stated (p. 324): "The species may still exist in small numbers, as a small goatsucker flushed in a tract of forest near Río Piedras in December 1911 may have been the present bird. None was heard singing during a period of ten months spent in field work on the island so that, if still existent, the Porto Rican Whippoorwill must be very rare."

The 1888 female, taken by Clark P. Streator and deposited in the Chicago Natural History Museum (then the Field Museum), was entered by Cory (1889) as a migrant Whip-poor-will. Wetmore (1919), studying the bones of a whip-poor-will from cave deposits in Puerto Rico and examining the 1888 bird, described it as a new species, *Setochalcis noctitherus* Wetmore. It was later united by Peters (1940) with the mainland species as *Caprimulgus vociferus noctitherus* (Wetmore).

Information Sought from Other Sources

Tape recordings of the unknown call were played for or sent to ornithologists, who had worked in Puerto Rico, including Dr. Virgilio Biaggi, Jr., University of Puerto Rico at Mayagüez, Mr. James Bond, Academy of Natural Sciences, Philadelphia, and Dr. Alexander Wetmore, Smithsonian Institution, Washington, D.C. The call remained unidentified.

With the thought of comparing this call with those of the Caprimulgidae, the recording was sent to Dr. P. P. Kellogg of the Laboratory of Ornithology, but it was not duplicated among the caprimulgids in the Library of Natural Sounds nor did Dr. Kellogg or his associates recognize it. The call was also unfamiliar to Mr. L. Irby Davis of Harlingen, Texas, an expert on the sounds of birds in Mexico and Central American countries. Mr. Herbert L. Stoddard and Mr. and Mrs. E. V. Komarek of Thomasville, Georgia, and Mr. Paul Schwartz of Venezuela, all familiar with a wide range of bird songs, had never heard the Puerto Rican song in question. The same was true of several members of the Delaware Valley Ornithological Club in Philadelphia and of members attending a meeting of the Linnaean Society of New York.

Attempt to See and Capture "the Bird"

With the failure to identify the tape recording, subsequent overnight stops were made in April and July 1961, and, in November, approximately a week was spent in an effort to discover the source of the song. On 19 April and 8 and 9 July, mist-netting, with tape-recorded calls played on the opposite side of the nets from the direction of near-by singing, failed to entice the singer into the nets. Repeated attempts to find something in daylight by scanning the ground and tree branches were in vain, even though at the cessation of singing at daylight the calls seemed to be as close as 75 feet.

On 9 July at 7:00 PM one bird was finally seen flying overhead while its call was being played from the tape recorder. Although there was not sufficient light for identification, this was the first real proof to me that the sound was from a bird.

Mr. Stephen T. Harty of the Philadelphia Academy of Natural Sciences and a member of the Eastern Bird-Banding Association accompanied me in November when efforts were continued with mist nets. We had from four to 10 nets up for six nights. The highest net reached to about 15 feet. Knowing by now the possible identity of these birds and hearing them singing loud and long, we approached the net area with great anticipation each morning only to be disappointed. The nets caught several known species but none that were unfamiliar.

New Sightings

At 7:00 PM on 24 November, Mr. Harty caught a singing bird in the beam of his flashlight and was able to approach within 20 feet. The bird stopped singing and gave short *quert* notes. It was resting on a network of twigs at the top of a small tree. The vivid eye reflected in the light and, from below, the white-ended tail feathers were clearly seen. It was to all appearances a whip-poor-will!

At 2:30 AM on 30 November, I saw the bird resting lengthwise on a limb. It was silent, having been located by a flashlight from the large, bright, yellowish-orange eye reflections. As it turned its head from side to side, one and then two reflections were seen alternately. The bird flew off on silent wings.

On this same day, several trees, believed to be singing perches, were shown to Mr. Cotté. With this information, added to his knowledge of perches from his previous visits, he made plans to revisit the area with a hunter that same evening. We removed our nets and decamped, preparatory to leaving the island the following day.

"Capturado"

Mr. Cotté and an expert marksman, Mr. William Blasini of Yauco, Puerto Rico, returned at dusk to the area of the singing birds. In response to whistled imitations of the call, a bird flew overhead and was secured with one shot. It was taken immediately to Dr. Biaggi in Mayagüez together with the following notation: "Capturado por Ricardo Cotté y William Blasini en el Bosque de Guánica Nov. 30, 1961, a las 6:30 P.M." Dr. Biaggi and his family, Dr. Mc-

Candless, Mr. Harty, and I were present and examined the "mystery bird." It was a male caprimulgid. That same evening it was photographed in black and white by Mr. Harty.

On the following morning, 1 December, both black and white and color photographs were taken; Dr. Biaggi prepared the skin and I took it to the States, delivering it on 3 December to Dr. Wetmore in Washington. The body and contents were kept for future study.

Nomenclature and Commentary

by Dr. Alexander Wetmore

The ancient bones from prehistoric cave deposits near Morovís in north central Puerto Rico that led me to the description of the Puerto Rican Whip-poor-will, Wetmore (1919), are so different from those of the mainland species that I have never been satisfied that it was proper to allocate the bird that I named *noctitherus* as a geographic race of *Caprimulgus vociferus.*

The single museum skin (No. 42,099) in the Chicago Natural History Museum that finally served as type, had been long identified by Cory (1889) as a supposed migrant from North America, and the external differences in color, markings, and size found in it are those normally accepted as of subspecific value. I believe it was these facts that influenced Peters (1940) to unite the Puerto Rican bird with typical *vociferus* in his review of the Caprimulgidae in the fourth volume of his check-list, since he had not had the advantage of study of the osteological material.

It was, therefore, with the keenest interest that I listened to the first brief recording by Dr. Reynard of the curious calls that indicated the presence of an unidentified nocturnal species in the Guánica region. News of the capture of an example of the bird came to me by radio-telephone on 1 December 1961, the morning after it was taken, and two days later Dr. Reynard and Stephen T. Harty, who had been his companion in Puerto Rico, brought me the specimen. This had been prepared with care by Dr. Virgilio Biaggi, Jr., but only partially, since the body was fat and the skin, as is always the case with birds of this group, was flimsy. Fortunately it was possible to place it immediately in the skilled hands of Mrs. Roxie Laybourne who made it into an excellent museum specimen.

The type specimen for the original description was a female taken by Clark P. Streator on 29 October 1888 labelled only as from the island, but I learned from Mr. Streator subsequent to my published accounts that he had collected it near Bayamón.

The second specimen, now U. S. National Museum No. 476,241, a male, when compared with the continental whip-poor-will, shows the same main differences in small size and darker color that are found in the female. The color difference is shown to some degree in Figure 3, with the male *C. noctitherus* between two male specimens of *C. vociferus.* Color difference in the male is in definitely darker color, though this is masked somewhat by the blended pattern of the markings found in all birds of this genus. The back in *noctitherus,* compared to typical *vociferus,* is decidedly black, the brown shades in the pattern on the crown much darker, being russet, and those elsewhere on the ear coverts and across the hindneck ochraceous-tawny instead of paler buff. The dorsal view, Figure 1, gives an indication of the dark coloration as well as showing the vertical, light wing patches and the tail markings.

The throat and upper breast, and the edge of the wing, are marked with russet, and the black pattern on the under surface is bolder and in stronger contrast (Figure 2).

The tail was damaged in shooting so that the four outermost rectrices are missing on the left side, as is the second from the outside on the right (Figure 2). The amount of white marking at the tip on the first and third rectrix which remain is decidedly less than in *vociferous.* The character is one that is variable in birds of this group, but in no male in the extensive series of *vociferus* in the National Museum is it as reduced as it is in the bird from Puerto Rico (Figure 3).

Table 1 gives measurements of the new specimen compared with those of the female, secured in 1888, and with measurements for males of the continental form *Caprimulgus vociferus vociferus* given by Ridgway (1914). The wing measurements for *noctitherus,* 135.8 and 135 mm for the male and female specimens, respectively, are well outside the range of 149 to 168.5 mm for males of *vociferus.* The tail length of the island species male is within the limits of *vociferus* but at the lower limit of the range. Exposed culmen and tarsus measurements are similar for the two species.

In my account of the cave bones published in 1922 I noted that the humerus in *noctitherus,* compared to that of *vociferus,* was shorter, with the various processes weaker, and the shaft slightly more curved. The metacarpal also was smaller. These are differences of greater value than those that separate subspecies, and have always seemed sufficient in my own mind to warrant specific status, which now appears fully established through the really extraordinary difference in voice.

In the present study of this interesting problem I have examined again my personal field notes from Puerto Rico, and find that on the afternoon of 23 December 1911, in a remnant of forest across a hilltop above the experiment station at Río Piedras, I flushed a whip-poor-will from a low stump only a few feet away. While I reported this as questionable in subsequent accounts (1916, 1919) of birds of the island, I feel certain now that it was *noctitherus,* since that bird is still known to be living, and no migrant whip-poor-wills have been known in the Greater Antilles east of Cuba.

TABLE 1

Comparative Measurements of *Caprimulgus vociferus*
(Ridgway, 1914; range for males) and *C. noctitherus*

	C. vociferus	*C. noctitherus*	
	Males	1961 male	1888 female
Wing	149-168.5	135.8	135
Tail	113.5-128	116.1	112
Exposed culmen	10.5-14	11.7	11
Tarsus	15.5-18	16.7	16.3

Song

General description. A series of nearly identical, short, abruptly but only slightly ascending, richly whistled calls. Each call lasts only about one-fifth of a second. Careful listening reveals an almost "two-note" effect, which is shown in the arch-shaped spectrogram (Figure 4). Although a word is rarely adequate for a call it might be best described as *whler.*

Singing is sometimes begun with a few introductory, comparatively faint "quert" notes, similar in pitch to the call, but without the whistled quality. This practice is in common with the mainland Whip-poor-will. The same note apparently is used also as a disturbance note and was heard from birds at rest as well as in flight. Once in July during a quiet period — about 10:00 PM— the recorded call was played for ten seconds and a bird flew overhead giving three of its quert notes in flight.

A third vocalization, heard by both Mr. Harty and myself, was a "gaw" or "growl" note similar to that of *vociferus* but of shorter duration.

From a distance it seemed at first that some songs were heard from birds in flight, but we now consider this erroneous, the effect having been achieved by frequent changes of singing perches. On no occasion were birds flushed from roads at night, nor were their eyes reflected in the lights of the cars as is sometimes the case with *vociferus* and the Chuck-will's-widow on the mainland.

Period of Singing. All singing was nocturnal; the most abundant, crepuscular. In November, for example, singing commenced about 6:05 PM, reaching a peak with six or more birds singing within earshot in about 15 minutes, continued for an hour, diminishing to sporadic calls about 7:30. Morning twilight singing began about 5:15, continuing heavy until about 6:00. Scattered calls were heard as late as 6:30 as daylight increased.

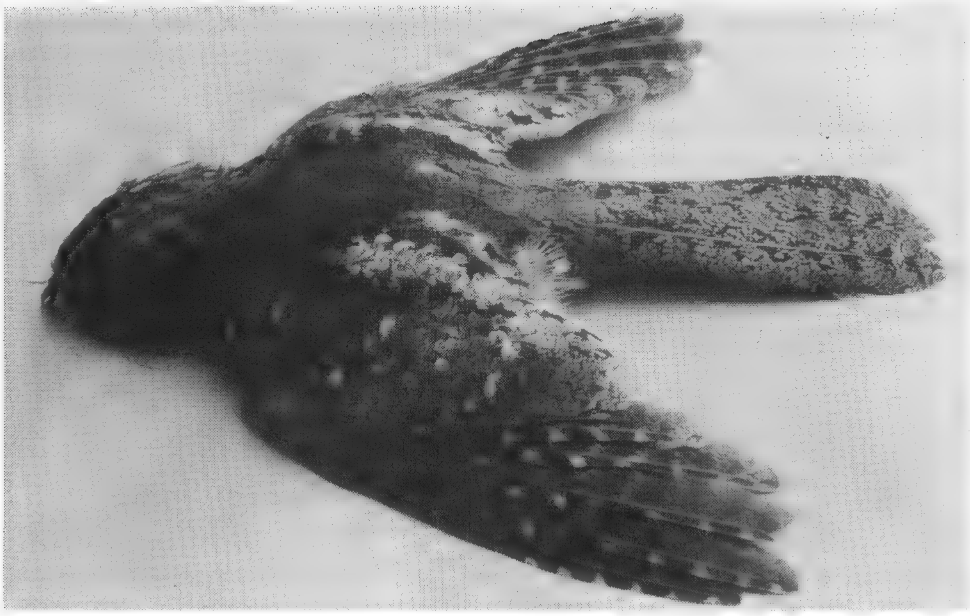


Figure 1. The male Puerto Rican Whip-poor-will *(Caprimulgus noctitherus)* collected on 30 November 1961. Photographed by Stephen T. Harty about four hours after it was shot.

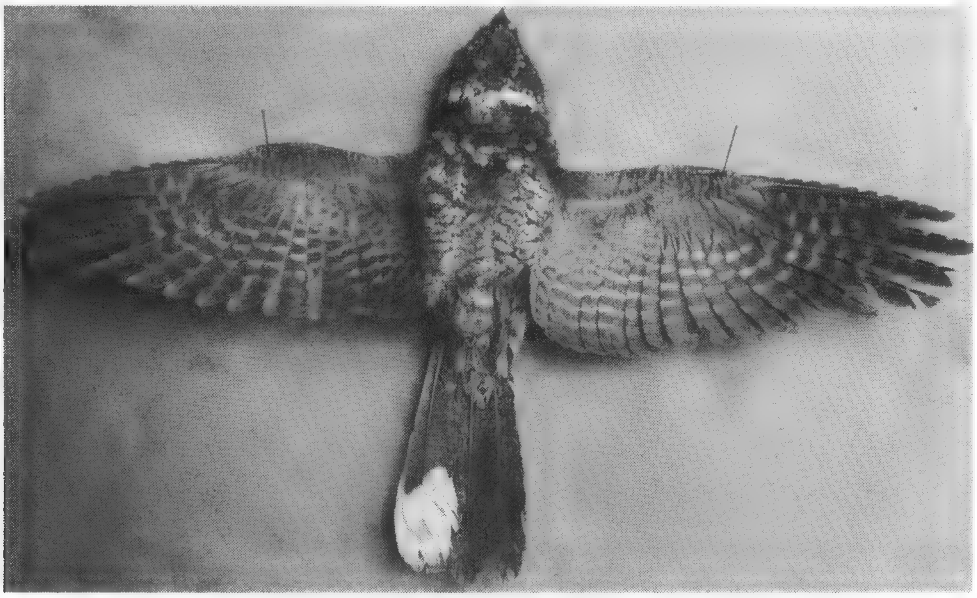


Figure 2. Ventral view of the same bird, showing wing pattern. The tail was damaged by shooting. Photographed by Stephen T. Harty.

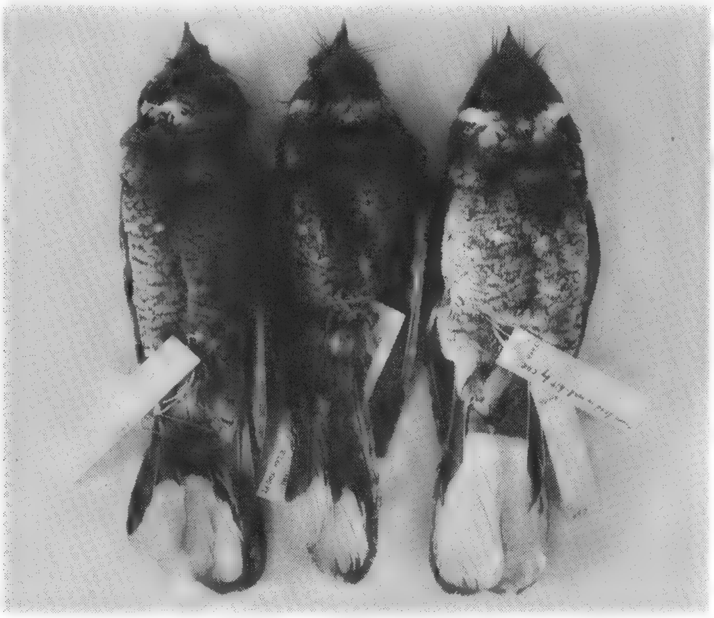


Figure 3. The 1961 Puerto Rican specimen between two male specimens of the mainland Whip-poor-will *(C. vociferus)* taken in eastern United States. Note the reduced white in the lateral rectrices of the Puerto Rican specimen.

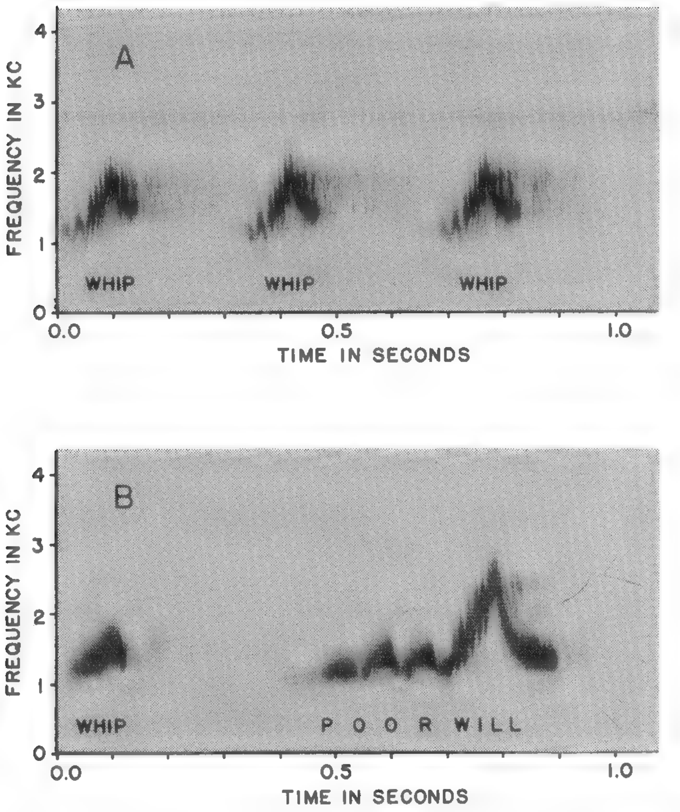


Figure 4. Spectrograms of songs of the Puerto Rican Whip-poor-will (A) and mainland species (B), selected from recordings to show the great differences in vocalizations.

Throughout the main period of darkness the amount of singing was apparently regulated by the amount of moonlight and cloud cover — the brighter the night, the more frequent the singing. During comparatively dark nights singing was erratic with periods of an hour or more of silence. On one occasion, when continuous observations were made from 7:00 PM until 3:00 AM, the amount of singing before midnight was restricted. At 12:15, as moonlight reached the area, the singing recommenced and continued with greater frequency until dawn.

Singing was somewhat "contagious." When a long period of silence was broken by one bird, others near by joined in. Several times singing was initiated by the playing of the recorded song.

Pitch. Songs of *noctitherus* in my tape-recording collection are essentially of same pitch as recordings of *vociferus*. Although the vertical frequency scale is not shown in the spectrogram (Figure 4), measurements of the originals from the songs illustrated show the range frequency for *noctitherus* to be from 1200 to 2200 cycles. The "whip" of *vociferus* ranges from about 1500 to 2000 and the "poor-will" from 1200 to 2800 cycles. To the ear, the predominant pitch of the song of *noctitherus* was near the third A above middle C.

Quality. General quality of songs of *noctitherus* and *vociferus* was alike. It was the character of the quality, supported by the generally repetitive nature of the calls and their nocturnal delivery, which originally convinced me that the unknown call was from one of the Caprimulgidae. Ornithologists who heard the tape-recorded song, without knowing its source, generally agreed that it could belong to one of this group.

Cadence of delivery. Irregularity was one of the most characteristic features of the song of *noctitherus*. This is in marked contrast with the almost metronome-like regularity of the song of *vociferus*. The calls of the former are given in short series varying in number of calls per series. There are, for example, first 3, then 2, then 10, then 3, then 6, then 3, then 4 calls per series, or similarly unpredictable numbers in the next performance.

A segment of a tape-recorded song of *noctitherus,* illustrating the frequent breaks in singing, is shown in Figure 4. The calls were delivered with approximately 0.3 second between the first notes of three successive calls, and then the next call came 0.5 second after the first note of the previous call. As the song is heard, it resembles a "breath-catching" interruption.

The difference in number of calls per minute, related in part to the length of the calls themselves, is indicated by the time-interval marks in Figure 4. The rate of delivery for *noctitherus* was about 3 calls per second, or, without pauses, 180 per minute, in contrast with *vociferus* which utters slightly less than one "whip-poor-will" per second, or about 53 per minute. The speed of the song delivery of *noctitherus* varied somewhat from individual to individual and periods of faster or slower delivery were noted, as is the case with *vociferus.* In some instances, the speed of the song of the Puerto Rican bird accelerated as dawn approached.

Discussion

It is of interest to consider the possible reasons why this bird has not been detected over the years and why it has been able to survive as a permanent resident in a very restricted area. The reason must be in part attributed to chance, that for more than a hundred years no ornithologist spent time at night, or more particularly at dusk or dawn, in an area of singing; or, if he were there, did not recognize the call as different from that of a known species.

Considerable ornithological work was done in Puerto Rico before Wetmore, Danforth, and Bond. Danforth (1936: 4) referred to investigations and publications as early as 1810, with periodic additions by a dozen or more people up to his time. Gundlach (1878), in a major work, summarized the published lists of species to date and added his own contributions. In commenting on the Chuck-will's-widow, then *Antrostomus carolinensis,* he reported (1878: 202) that on rare occasions he had heard its song. Since this species is believed to be silent (Bond, 1961) in its winter quarters, it is suggested that Gundlach actually may have heard the Puerto Rican Whip-poor-will. This is the only published reference we have found concerning the possibility of the song having been heard by an ornithologist.

Danforth (1936), although never having seen or heard the Whip-poor-will in Puerto Rico, reported it as a resident because of the 1888 female specimen (Cory, 1889) and the work of Wetmore (1919, 1922). He assumed its call was *gau-bai-ro* like that of the Cuban bird, the Greater Antillean Nightjar, *Caprimulgus cubanensis,* which he had heard in that island, and he assigned the common name "Guabairo Pequeño."

In view of the fact that the present bird does not sing *gua-bai-ro* or *whip-poor-will,* and has been known erroneously as Pájaro Bobo, it really has no appropriate "common name." However, since it was originally described as a whip-poor-will (Cory, 1889; Wetmore, 1919) and is of close appearance to the mainland bird, the name Puerto Rican Whip-poor-will is continued here.

An explanation is needed for the fact that the night song, so well known to local residents in the immediate area of this population, was unknown or uninvestigated by ornithologists. Whether the ornithologists ever questioned the local residents about the bird life in this forest is unknown. Probably the general belief that the Pájaro Bobo called here at night was so taken for granted that no one ever bothered about further investigation.

Dr. Biaggi has made a recent, thorough study (unpublished) of the known birds of the island and Dr. McCandless has made many field trips in southwestern Puerto Rico, but neither happened to find this singing population.

Many bird students have made daytime visits to seashore areas within two miles of the hilltop haunts of this bird. Mr. Frank H. Wadsworth, Director of the Institute of Tropical Forestry in Puerto Rico, informs me, in personal correspondence, that he had heard the night calls and, knowing of the presence of the Chuck-will's-widow in Puerto Rico, assumed the calls were made by this bird.

Even more intriguing is the question of why the bird survived at all. It is only conjecture at this point, but two reasons may be considered: First, the character of the habitat, so uninviting with its tangled, thorny undergrowth and small trees, its limited rain, and its few roads, added to the fact that it was in a forest preserve, definitely resulted in a minimum of human disturbance. Second, the thin cover of only dry leaves and practically no refuse may have limited such possible predators as mongoose and rats.

With the exception of verbal information from island residents (Wetmore, 1922) and the one female specimen, there has been nothing known to science about the life history of this species. The present study contributes something to the knowledge of its song. Yet to be learned are the time and place of nesting, size and color of eggs, courtship, and daytime haunts. The all-important information on distribution and number of survivors is under way by investigators, making use of the tape-recording, playback techniques which first tracked down *Caprimulgus noctitherus,* the source of the mysterious night calls of the Guánica forest.

Summary

On 8 March 1961, an unknown nocturnal call from an unseen source was heard and tape-recorded in southwestern Puerto Rico. Local residents, interviewed after hearing the recording, indicated that the call had been heard nightly, at least since 1900, and expressed the belief that it came from the Lizard Cuckoo or the Mangrove Cuckoo. Unsuccessful attempts were made to identify the call by sending copies of the recording to ornithologists.

The song had the quality of a caprimulgid's, but was not the song of the Chuck-will's-widow which winters on the island. One caprimulgid, a female taken in 1888, one sight record in 1911, and the bones of specimens (1919) were the only evidences of this bird's presence, and most publications listed it as probably extinct. The one specimen had first been called a migrant Whip-poor-will, *Antrostomus vociferus,* by Cory, then designated a full species, *Setochalcis noctitherus,* by Wetmore, and later listed as *Caprimulgus vociferus noctitherus* by Peters.

Unsuccessful attempts were made to see the bird clearly and to catch it in mist nets by using its song playback to attract it. On 30 November 1961, a bird was finally collected. It was a male caprimulgid. Photographs were taken; it was then brought to Washington; and, in a section of this paper contributed by Dr. Wetmore, the bird is described and returned to specific status as *Caprimulgus noctitherus* (Wetmore), the Puerto Rican Whip-poor-will.

The song is described for the first time and compared with the entirely different song of *C. vociferus* by means of spectrograms. Possible reasons are presented as to why the bird, although a permanent resident, has escaped detection and why it survived at all.

The distribution and size of the remnant population are not known, and, with the exception of the song, all phases of its life history remain to be determined.

Acknowledgments

The success of this venture is due to a great many people. Acknowledgment is made of the assignment of sound-recording equipment from the Laboratory of Ornithology, and of help from two of its members, Dr. P. P. Kellogg for advice and training in its use, and Dr. Robert C. Stein for the preparation of the two important spectograms (Figure 4). The assistance of Mr. Stephen T. Harty in the critical November trip is greatly appreciated together with two photographs from his series (Figures 1 and 2). Dr. James B. McCandless arranged for field trips, directed me to Mr. Cotté, and shared his knowledge of the birds as well as permission to quote from his correspondence. Dr. Virgilio Biaggi, Jr., resident ornithologist, although rightfully skeptical of the species' presence, shared in the enthusiasm of our success and made the initial skin preparation.

Special thanks are due the Fish and Wildlife Section of the Department of Agriculture in Puerto Rico through their agent, Mr. Ricardo Cotté of Yauco, who initiated my quest and supplied valuable aid in the field and in the collection of the specimen; and the expert marksman, Mr. William Blasini, for his important contribution in actually securing the bird.

Finally, I am particularly grateful to Dr. Alexander Wetmore for contributing an important section of this paper, with the description and identification of the specimen, returning it to full species status.

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A COMPARATIVE STUDY OF SONGS RECORDED FROM FIVE CLOSELY RELATED WARBLERS

ROBERT C. STEIN

The identification of North American warblers (Parulidae) by their songs is difficult for many persons interested in birds. Some obvious reasons are that warblers exist in great variety (about 54 species regularly breed north of Mexico), are nearly all small, and are often so concealed by foliage that they cannot be watched and heard at the same time. But another more important reason is that the average person is unable to hear and describe song patterns as efficiently as he can see and describe color patterns.

The study of warbler songs and those of other birds has long been dependent on such descriptive methods as phonetics (representing sounds by human speech), symbols, diagrams, and musical scales. In all cases these methods have relied on the human ear, which is subject to individual, and consequently variable, interpretation. Recently because of marked advances in sound recorders and spectrographs, it has been possible to collect song specimens and put them down on paper in the form of spectrograms. Thus we can *see* song patterns, just as we can see color patterns.

Song spectrograms provide a useful tool in identification. With experience and practice it is possible for a person to relate the various marks to sound and to memorize sound patterns. When he next hears the songs, he can recognize them more readily because he can visualize them.

Being mechanically produced, and hence not subject to the vagaries of human hearing, spectrograms provide more reliable data than subjective analysis. We have found that songs on paper show characteristics of species just as do color patterns, form, and structure. We have, therefore, another dependable basis on which to compare species and determine relationships.

Basis of the Study

During the spring of 1960, while on an expedition to study and record the sounds of flycatchers and warblers in southwestern United States, I had the opportunity to record for the first time the songs of the Golden-cheeked and Hermit Warblers *(Dendroica chrysoparia* and *D. occidentalis).* These two species are so closely related as to be considered members of a so-called superspecies, which also includes the Black-throated Green and Townsend's Warblers *(D. virens* and *D. townsendi).* These four species are generally allopatric, i.e., their breeding ranges do not overlap (see Figure 1). Also closely related

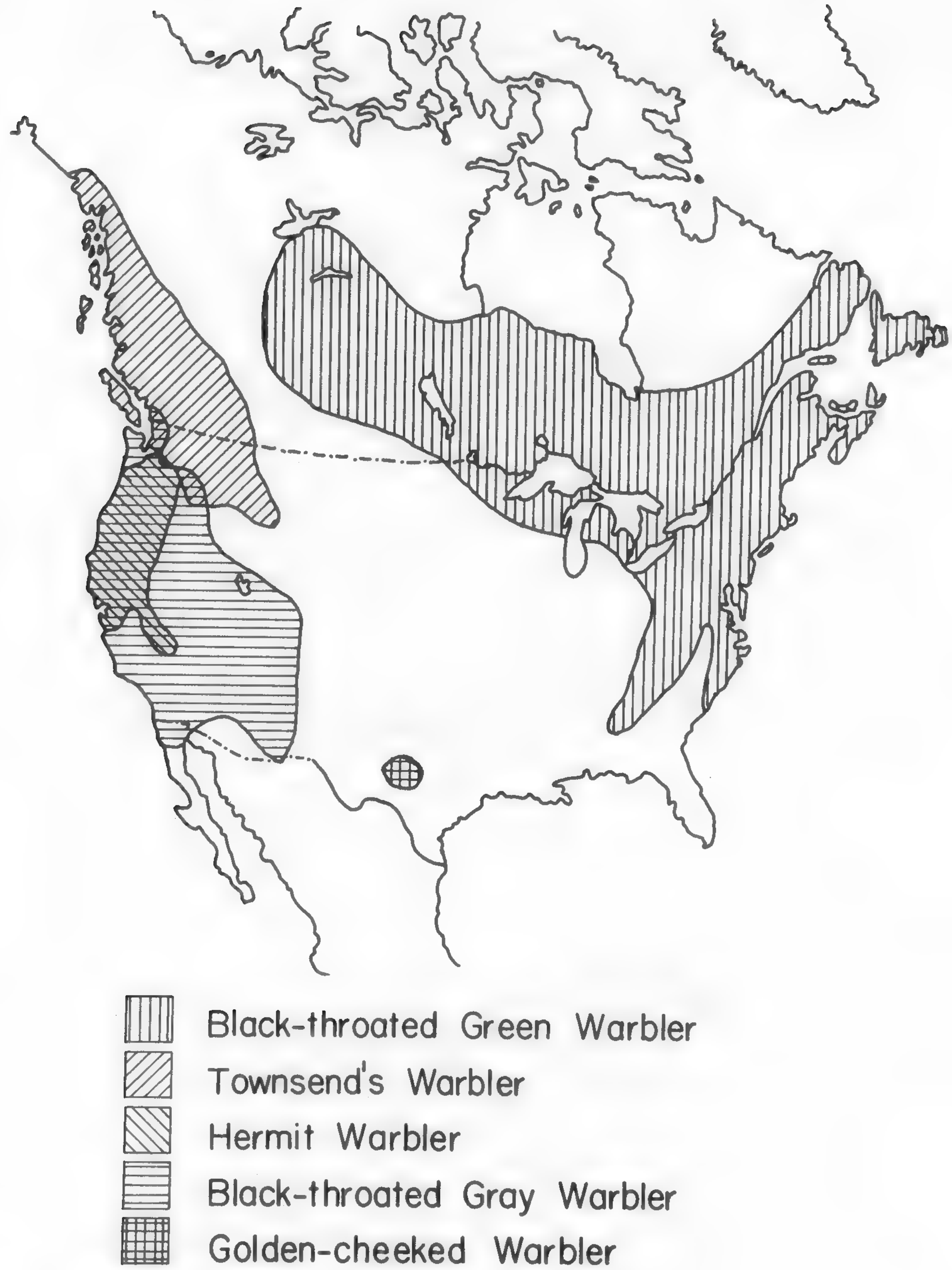

Figure 1. Breeding ranges of five species of *Dendroica*.

is the Black-throated Gray Warbler *(D. nigrescens)*, whose range widely, but not entirely, overlaps the ranges of the Hermit and Townsend's Warblers and is, therefore, sympatric with these two species.

On my return from this expedition I analyzed recordings of these five species. (Tape cuts from the recordings analyzed are listed at the end of this article.) By studying the spectrograms made from them, I was able to discern certain song characteristics shared by these species and found clues to some factors which may have influenced the form of the song patterns of these birds.

Before comparing the song patterns, I must present certain data relating to each of the five species. Information is given first on the Black-throated Green Warbler because more is known about it.

Black-throated Green Warbler

This species breeds in the coniferous forests of eastern United States and Canada as far west as Minnesota and Alberta (Figure 1) and usually nests near

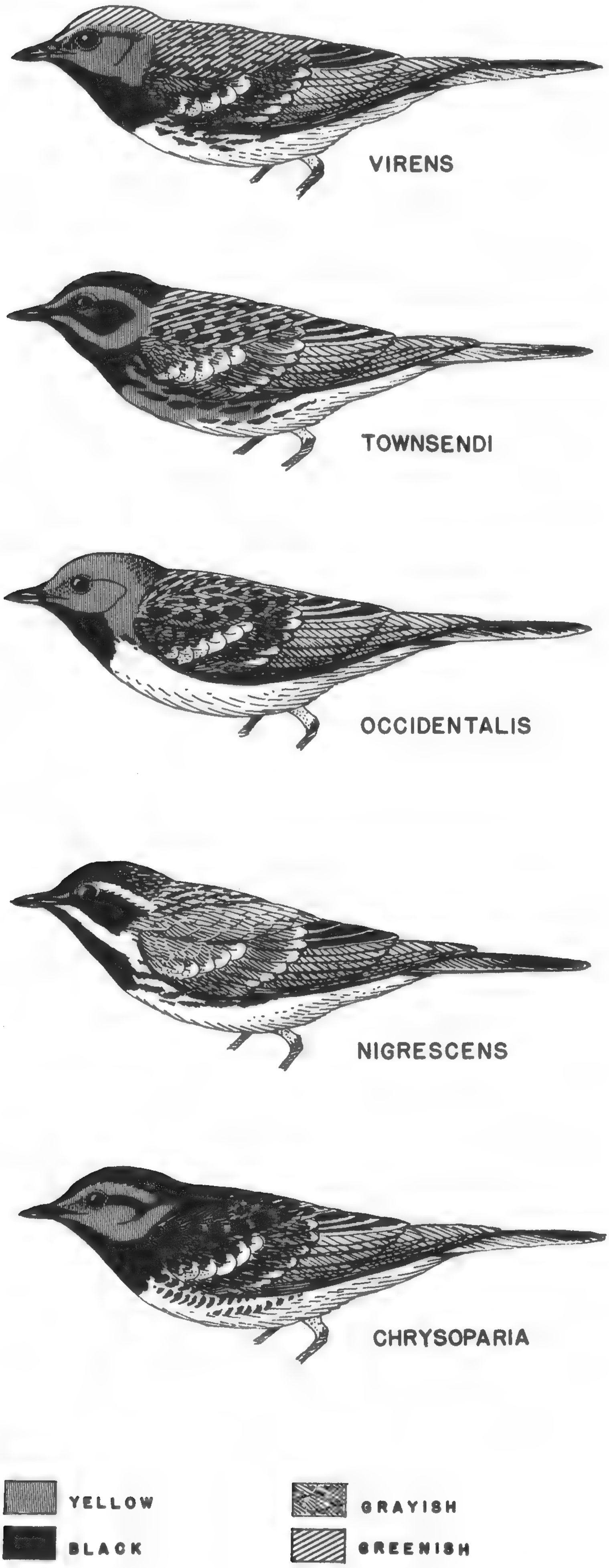

Figure 2. Patterns of plumage color in five species of *Dendroica*. From top to bottom: Black-throated Green Warbler, Townsend's Warbler, Hermit Warbler, Black-throated Gray Warbler, and Golden-cheeked Warbler.

the tops of conifers. At the extreme western edge of its range the Black-throated Green nears the range of Townsend's Warbler (see map in Salt and Wilk, 1958), but there is apparently little or no contact between the two species. The male Black-throated Green has a greenish back, black throat, and an almost clear yellow-green cheek (Figure 2). Some specimens show traces of a darker patch in the middle of the yellow-green area. The black of the throat extends as a few streaks down the sides of the white breast.

The songs, I find, are quite stereotyped and fall into two categories which Nice and Nice (1932) called Types A and B. Type A, interpreted by the Nices as *trees, trees murm'ring trees,* is shown by spectrogram in Figure 3A. This type usually has five syllables. The first two and last are sibilant and on about the same frequency. The third and fourth syllables are clearer — more like whistles — and on a noticeably lower frequency. Saunders (1951) illustrated three examples of this type, and indicated that the frequency of each of the different parts may vary in relation to one another, except that the third and fourth always seem to be on the same frequency. He stated that the last part was often missing and suggested that this may be characteristic of eastern birds. This is not supported by the recordings I have studied. Several recordings have *chip* notes between the songs of this type.

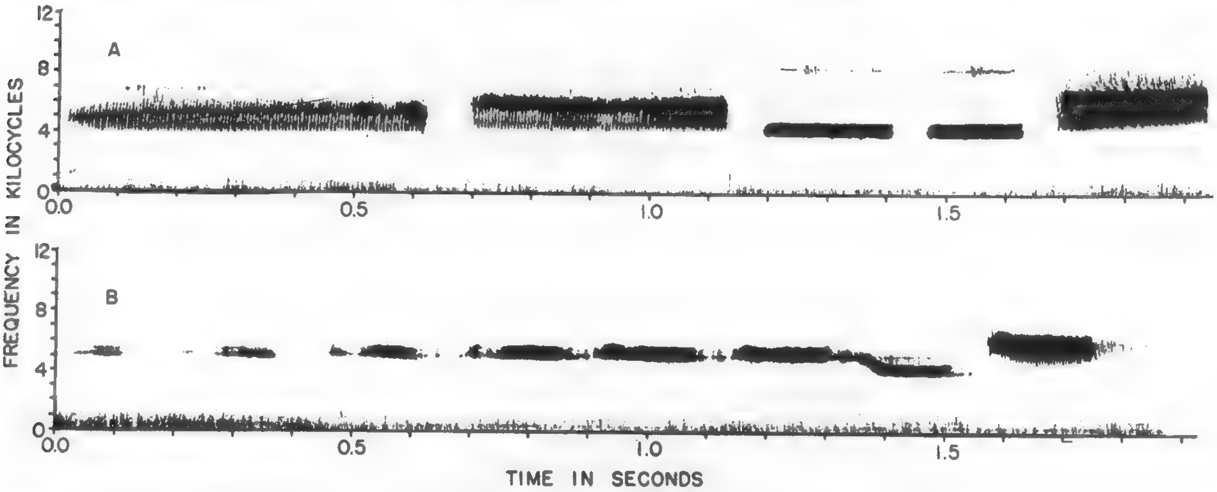

Figure 3. Spectrograms of songs of the Black-throated Green Warbler.

Type B, which the Nices interpreted as *see see see see wee see,* has the third and fourth syllables of Type A. The penultimate syllable is lower in frequency. A spectrogram of this type is shown in Figure 3B.

Little seems to be known about the relationship between the two types or their functions. Both types are evidently given at any period in the breeding season. Both seem to serve not only in pair formation, but also in pair maintenance. Kendeigh (1945) noted that individual males used almost one or the other type exclusively, though he mentioned exceptions. Pitelka (1940) observed that the sounds may be "an apparent warning" to the brooding female as the male approaches the nest with food. He found that Type B was twice as frequent as Type A. Saunders (1951) and Chapman (1907) considered the two types to be equally common, but Chapman remarked that Type B was given more frequently in mid-summer. There is a parallel with the two types of songs of the Kirtland's Warbler *(Dendroica kirtlandii),* described by Mayfield (1960).

Townsend's Warbler

This species, considered by Coues (1892) to be the western representative of the Black-throated Green Warbler, breeds in the coniferous forests from

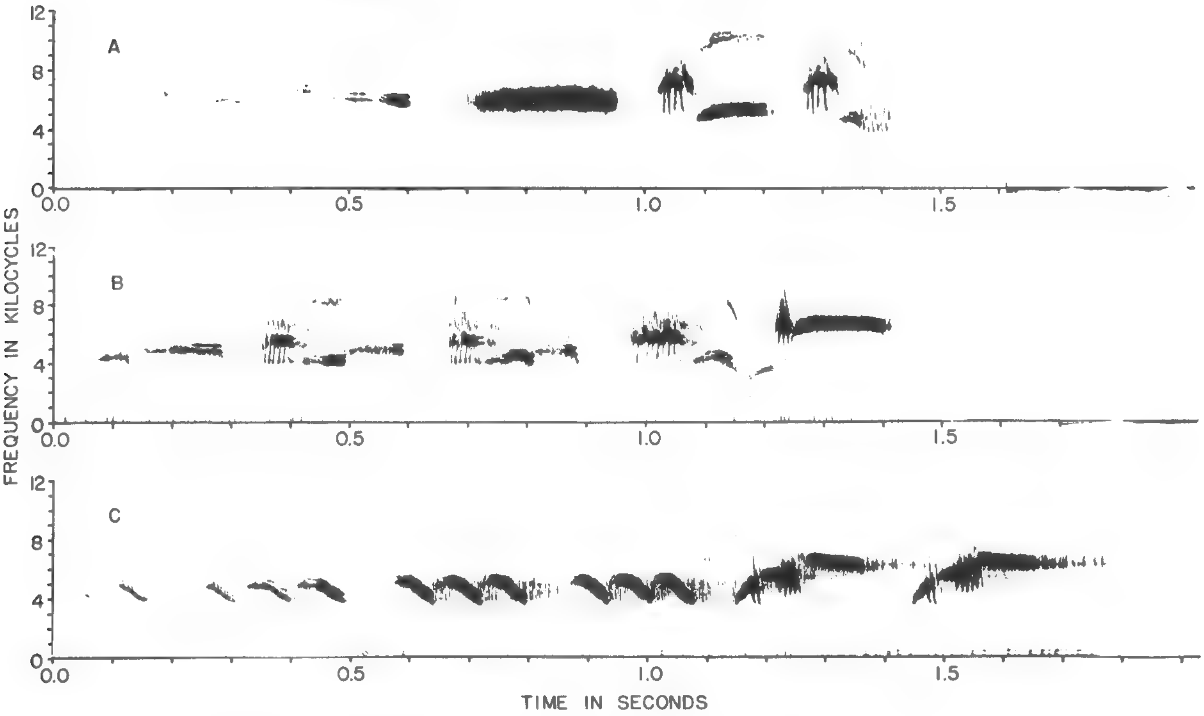

Figure 4. Spectrograms of songs of the Townsend's Warbler.

southern Alaska to Oregon and east to Idaho and Wyoming (Figure 1). Its activities are centered in the tops of conifers, where it usually nests (Jewett et al., 1953). The Townsend's Warbler is in a sense a darker, yellower version of the Black-throated Green, with a yellow breast, black crown, and pronounced dark patch in the middle of the yellow cheek (Figure 2). In Washington and Oregon, where the range of the Townsend's Warbler overlaps that of the Hermit, several hybrids between these two species have been reported by Jewett (1944).

The song pattern of this species (Figure 4) has much more variation than in the Black-throated Green, and more closely resembles the Hermit and Black-throated Gray Warblers' (see Hoffmann, 1927). The song is divisible into two parts, each with several syllables. Those of the first part are often like those of a Black-throated Green in length and quality (Figure 3A). This similarity was noted by Merrill (1898), who interpreted the song as *deé deé deé — dĕ dĕ,* and added that he heard a different song later in the season. Dawson (1923) commented on the variable quality and cadence, and the occasional similarity to the song of the Black-throated Green. Figure 4B shows the opposite extreme. Here the sound is broken into more units, which may be joined into small groups. The units have quality similar to the Black-throated Green's. The syllables of the second part of the Townsend's song are more varied and of a composite nature (i.e., they have components with different qualities). The syllables are often repeated. A few recordings have chips interspersed between the songs.

Hermit Warbler

Like the Black-throated Green and Townsend's Warblers, the Hermit is a coniferous-forest species, nesting in the upper stratum. But its breeding area is notably restricted to the high mountains from British Columbia into California (Figure 1). The fact that it normally occurs in Washington and Oregon at higher elevations than the Townsend's accounts for its hybridizing with that species only occasionally (see above, under Townsend's Warbler). The male Hermit is gray-backed with a black throat and an all-yellow head (Figure 2), which is invaded by a varying number of black feathers from the mid-dorsal line of the back.

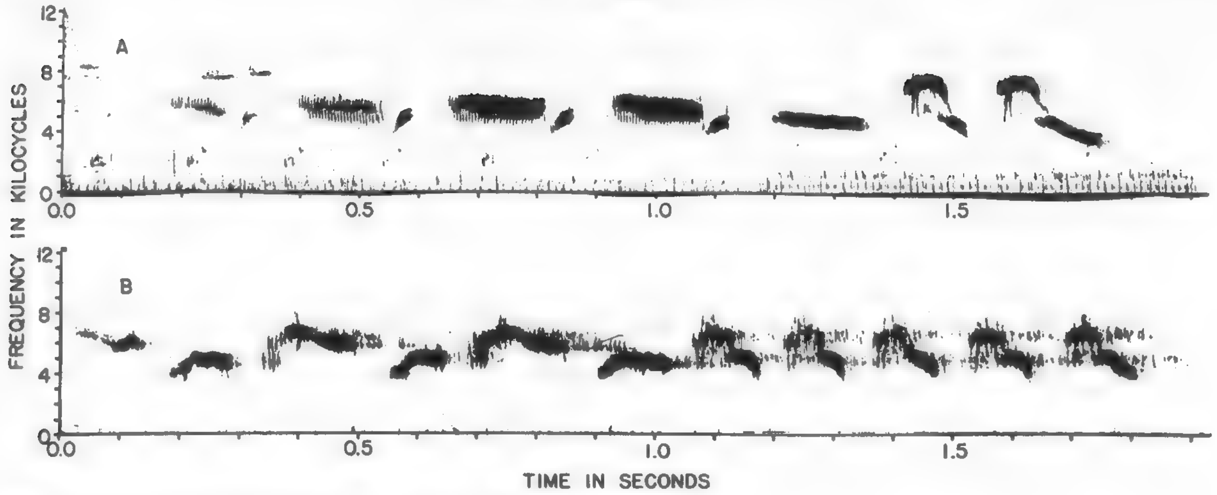

Figure 5. Spectrograms of songs of the Hermit Warbler.

The song has been given by Barlow (1899) as *tsit, tsit, tsit, tsit, chee chee chee* and appears to be two-parted. Three recordings from Yosemite National Park show two patterns. The first (Figure 5A) starts with several sibilant syllables followed by a clear whistle-like syllable and down-slurs. The second type (Figure 5B) has several clear, warbled syllables, and ends with several down-slurs. The fourth recording, made by W. R. Fish, is the only one with *chips* between the songs.

While "a series of warbles or buzzes followed by several down-slurs" might describe the song of the Hermit Warbler, the Townsend's and Black-throated Gray Warblers occasionally have songs which fit this description too. Moreover, Dawson (1923) describes the song of a migrant Hermit Warbler as *zeegle, zeegle, zeegle, zeet,* which suggests an up-slur at the end. Jewett (1944) mentioned the difficulty he had in recognizing differences between the songs of Townsend's and Hermit Warblers in places where he collected hybrids. He quoted A. H. Miller as having similar difficulty in another area of hybridization.

Golden-cheeked Warbler

This species breeds mainly in the "cedar brakes" of the Edwards Plateau in Texas (Figure 1), placing its nest in the upper parts of junipers which have a maximum height of about 20 feet. It is totally allopatric to the four other species. Black-backed, with a black throat and streaked belly (Figure 2), the male Golden-cheeked looks like both a dark-backed and dark-headed Black-throated Green Warbler or a Hermit Warbler.

Phonetic interpretations of the song usually refer back to H. P. Attwater (in Chapman, 1907) who described it as *tweah, tweah, twee-sy,* sometimes with

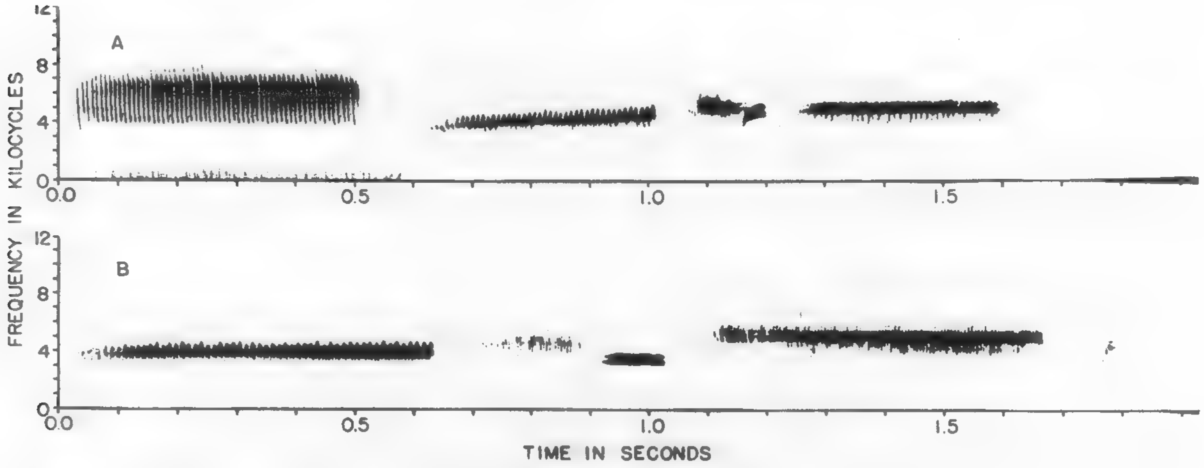

Figure 6. Spectrograms of songs of the Golden-cheeked Warbler.

an extra note or two, or as *twee-ah, eseah, eachy*. We obtained five recordings of different individuals near Austin, and another at Boerne, Texas, in late April. The song patterns from Austin are practically identical, while the one from Boerne is different. Spectrograms in Figure 6 indicate sounds quite similar to those in Type A of the Black-throated Green — i.e., they are made up of about four parts which are sibilant and vary in relative frequency. Three specific comparisons can be made: 1. The third syllable of Figure 6A is very similar to the first four syllables from the Hermit Warbler (Figure 5B). 2. The third syllable of Figure 6B is a clear whistle, and bears the same relationship to the sibilant parts of the song as do the third and fourth syllables of Type A of the Black-throated Green. 3. The species regularly intersperses *chip* notes between songs.

Black-throated Gray Warbler

The Black-throated Gray Warbler's breeding range extends from British Columbia south to Baja California, eastward to Colorado and New Mexico (Figure 1), and thus has a broad sympatry with that of Townsend's and Hermit Warblers. Its habitat in the northwest is mainly shrubby openings in coniferous forests, but elsewhere it varies from shrubby openings in mixed woods to dry slopes covered with oaks, junipers, and pinyon pine, and even chapparal (Chapman, 1907). Nest sites vary in height, though as a rule they are in shrubs or in low trees (e.g., see Jewett et al., 1953). The Black-throated Gray male may be described as a Townsend's Warbler without yellow, except on the lores (Figure 2). Dawson (1923) made particular note of this. The presence or absence of yellow in some warblers has been explained by a simple genetic mechanism (see Parkes, 1951), and the shift from "warbler green" to

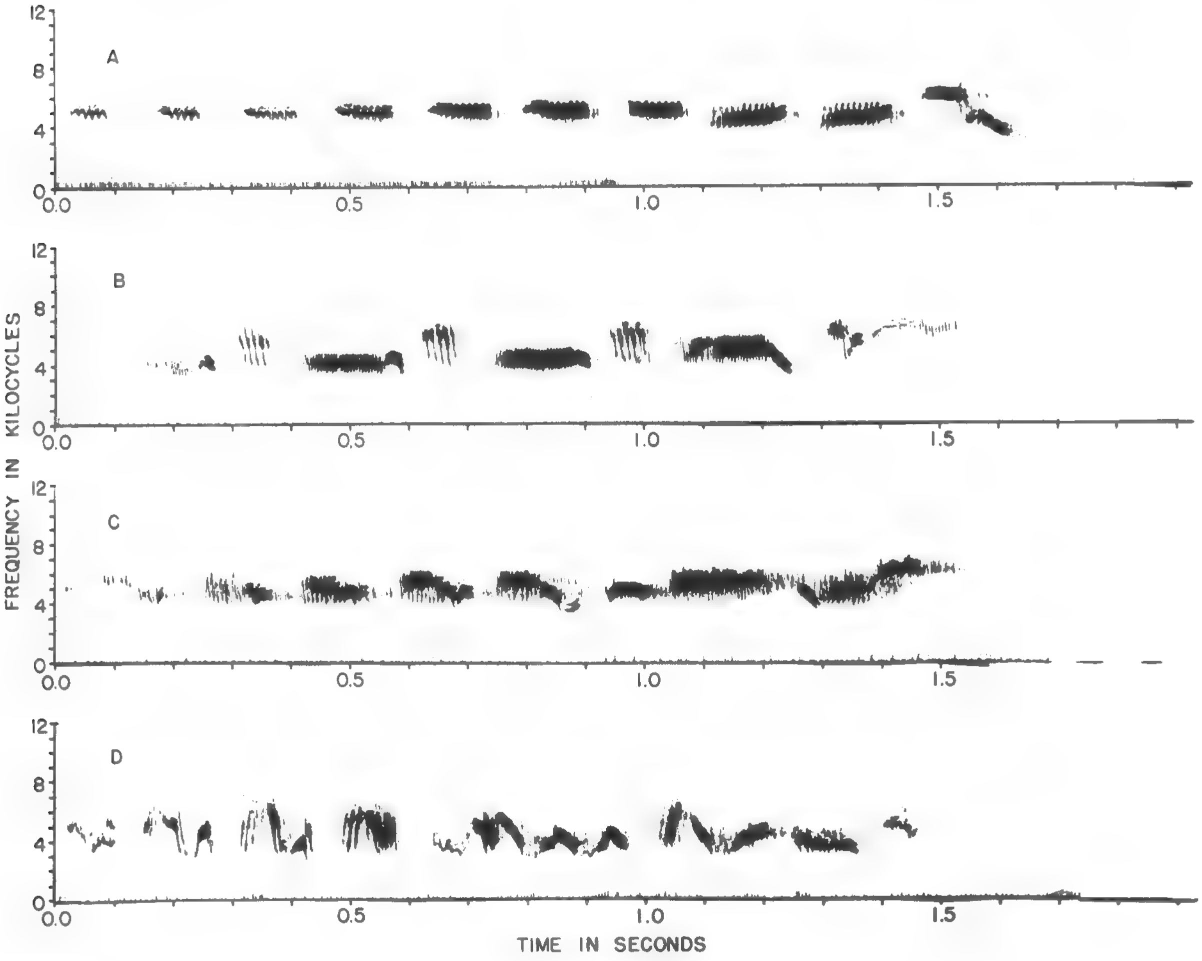

Figure 7. Spectrograms of songs of the Black-throated Gray Warbler.

"warbler blue" could be accomplished by this mechanism. I know of no specimens or reported evidence of hybrids between the Black-throated Gray and Hermit, or between the Black-throated Gray and Townsend's.

The song of the Black-throated Gray (Figure 7) shows two types, though they are not sharply defined. The first type (see Figure 7A) has an initial series of sibilant syllables followed by a down-slur. These syllables may be simple or complex. The second type (see Figure 7B) has a warbled first part which may blend into the last part. The song, therefore, is not definitely two-parted as in the Hermit and Townsend's Warblers, but the last syllable is distinctive. Hoffmann (1927) gives phonetic interpretations as *zee ee, zee ee, zee ee, zee, zip* or *wees-a, wees-a, wees-a, wee zee,* among others. Some parts of the spectrograms of songs were similar to those of the Hermit Warbler (compare Figures 7A and 7C to 5A); some to Townsend's Warbler (see Figures 7B and 4B; 7C and 4C).

Comparison of Song Patterns

Several characteristics in song pattern are shared by the species: an increase in amplitude toward the end of the song; similar frequency range; two general patterns, one of which is sibilant, the other clear (except possibly the Golden-cheeked); a two-part pattern within the song (except possibly the Black-throated Gray and Black-throated Green); and the use of *chip* notes between songs.

The songs of the two "eastern" species are more stereotyped and seem to have the *chips* interspersed to the greatest extent. This sharp stereotypy for easy, quick means of recognition by individuals within a species may be advantageous in areas where many warbler species breed (as in the Black-throated Green), or where there is a sparse or scattered population not occupying all suitable habitats (as in the Golden-cheeked). Since recordings from the Golden-cheeked were made in only two locations, the stereotypy may not be as pronounced as supposed.

The songs of western species are more variable. This may be explained by the fact that there are fewer species, with habitats more often sharply separated. Thus there is less chance for species confusing one another.

In general, the Black-throated Gray is the most distinctive in color of the five species. It is the blackest and has the least yellow. It does not center its activity high in a coniferous forest. Its song is about the most variable and the least stylized. Though the other four species vary in color pattern, all have much yellow, at least in the head region. In color and song pattern, the Black-throated Gray appears to be closest to the Townsend's, though not as close as the Black-throated Green.

The Hermit and Townsend's have very similar songs, but since their breeding ranges are primarily allopatric, interspecific confusion is minimized. The similarity of their songs probably contributes to hybridization where the ranges of the two species meet. Judging from my field experience and study of recordings, there is no way of definitely distinguishing these species from the Black-throated Gray by voice in *every* case.

The song of the Black-throated Green is most similar to the sibilant song of the Townsend's, but I had little or no difficulty distinguishing it. The songs of the Golden-cheeked and Hermit have some strikingly similar syllables. The Hermit can be interpreted as a less black version of the Golden-cheeked.

A comparative summary of the principal features of plumage color, habitat, and song in each of the five warbler species is given in Table 1.

TABLE 1

Comparative Summary of Plumage Color, Habitat, and Song in Five Warbler Species

	Plumage Color	Song	Habitat
Black-throated Green Warbler	Head black and yellow Yellow-green cheek Back green	Stereotyped Two types Buzzes and clear notes Chips frequent between songs	Coniferous forest
Townsend's Warbler	Head black and yellow Dark face markings Back green	Variable Two-parted Buzzes and/or warbles Chips occasional	Coniferous forest
Hermit Warbler	Head yellow with black on nape Back gray	Variable Two-parted Buzzes and/or warbles, usually ending with down-slur Chips occasional	Coniferous forest
Golden-cheeked Warbler	Head black and yellow Dark stripe through eye Back black and gray	Stereotyped (?) Buzzes and clear notes Chips frequent	Cedar brakes
Black-throated Gray Warbler	Head black and white Dark face markings Back gray	Variable Two-parted (indistinct) Buzzes and/or warbles Chips occasional	Mainly chapparral and shrubby areas

Conclusion

The song patterns of the five species, then, can be said to show a relationship parallel to that suggested by plumage. The Black-throated Gray Warbler is more closely related to the Townsend's Warbler than to the other three. The Townsend's is the western counterpart of the Black-throated Green, the Hermit the far western counterpart of the Golden-cheeked. The data also suggest that allopatric species can have very similar songs.

Acknowledgments

I wish to express my appreciation to the National Science Foundation for its support, Dr. W. R. Fish and the Cornell Library of Natural Sounds for the use of their recordings, Mr. R. B. Angstadt for his field assistance and preparation of the map and spectrograms, and Dr. William C. Dilger for his drawings of the five warblers.

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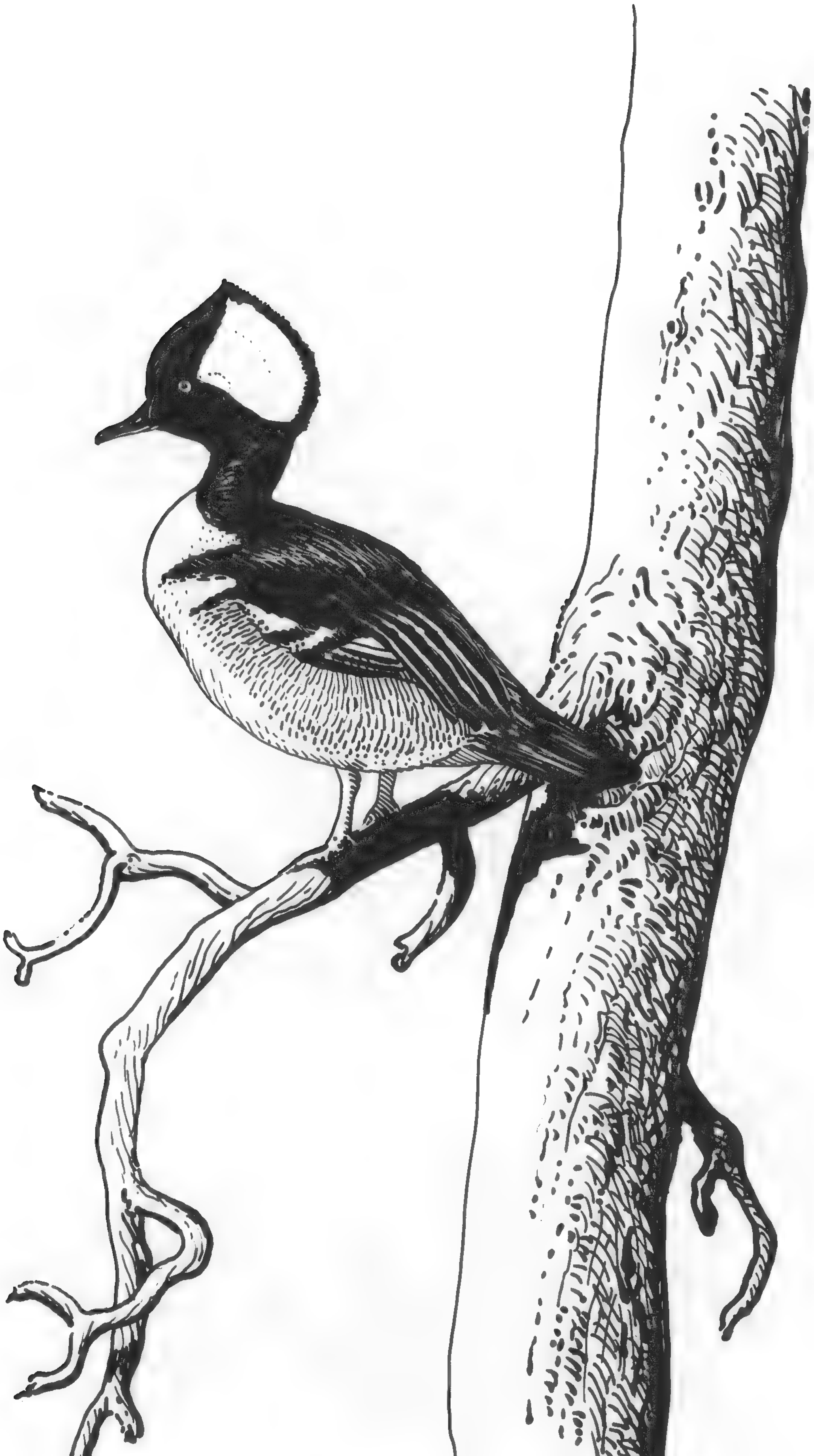
Tape Cuts Analyzed in the Study

	Originator	Cut No.	Date Recorded	Location
Black-throated Green Warbler	CU	1	16 May 1952	Ithaca, N. Y.
		2	28 May 1959	Little Simon Pond, N. Y.
		3	28 May 1959	Little Simon Pond, N. Y.
		4	18 June 1957	Rensselaerville, N. Y.
		5	18 June 1957	Rensselaerville, N. Y.
		6	27 May 1959	Little Simon Pond, N. Y.
		8	18 April 1961	Birmingham, Ala.
		9	18 April 1961	Birmingham, Ala.
	B&G	1	June	Maine
		2	June	Maine
		3	July	Maine
	JES	1	5 June 1953	Swallow Falls St. Pk., Md.
		2	19 July 1953	Pocono Lake, Pa.
Townsend's Warbler	CU	1	19 June 1958	Langdon Lake, Oreg.
		2	2 May 1959	Nanaimo, B. C.
		3	13 July 1961	Mt. Rainier, Wash.
		4	13 July 1961	Mt. Rainier, Wash.
	WRF		13 May 1961	Balderston Sta., Calif.
Hermit Warbler	CU	1	27 May 1961	Yosemite N. P., Calif.
		2	19 June 1958	Yosemite N. P., Calif.
		3	2 July 1961	Yosemite N. P., Calif.
	WRF		13 May 1961	Balderston Sta., Calif.
Golden-cheeked Warbler	CU	1	25 April 1961	Austin, Texas
		2	27 May 1961	Austin, Texas
		3	25 April 1961	Austin, Texas
		4	25 April 1961	Austin, Texas
		5	25 April 1961	Austin, Texas
		6	26 April 1961	Boerne, Texas
Black-throated Gray Warbler	CU	1	23 April 1959	Chico, Calif.
		2	30 April 1959	Seattle, Wash.
		3	1 May 1959	Vancouver, B. C.
		4	7 May 1961	Silver City, N. Mex.
		5	7 May 1961	Silver City, N. Mex.
		6	24 June 1961	Big Sur, Calif.
		7	23 June 1961	Lucia, Calif.
		8	23 June 1961	Lucia, Calif.
		9	23 June 1961	Lucia, Calif.
		10	23 June 1961	Lucia, Calif.
	WRF	1	13 April 1955	Hastings Res., Calif.
		2	15 April 1956	Hastings Res., Calif.
		3	13 April 1956	Hastings Res., Calif.

CU = Cornell Library of Natural Sounds
WRF = W. R. Fish
B&G = Borror and Gunn (1958)
JES = J. E. Stillwell



IS BIRD-ART ART?

GEORGE MIKSCH SUTTON

Thirty years ago I wrote a chapter titled "Fifty Years of Progress in American Bird-Art" for a publication celebrating the semicentennial anniversary of the American Ornithologists' Union. I cannot remember who asked me to write this, but I do recall wondering, as I looked at drawing after drawing, hunted for books that no library seemed to have, and consulted encyclopedias for dates, whether there was any way of measuring progress in art. Obviously there was such a thing as drawing more and more pictures, as drawing every bird known to inhabit a given part of the world, as illustrating every plumage or plumage-stage a given bird species was known to wear. Any quantitative accomplishment of this sort might, I conceded, be called progress of sorts. But was it really progress? And were the thrilling, incredibly life-like drawings of Louis Agassiz Fuertes truly better in any explicable way than those of Audubon, of Wilson, of Gould, or — for that matter — of those early unknowns who so loved the buffaloes and rhinos and reindeer they killed and ate that they made paintings of the creatures on the walls of caves?

Much has happened since I wrote that at times discursive, at times pontifical piece about "progress" in American bird-art. I have watched the steady climb to maturity, to usefulness, to fame of three young men described there by me as "yet so young that they have not had time to show the full extent of their abilities" — men whose names are Terence M. Shortt, Roger Tory Peterson and H. Albert Hochbaum. I have donned a uniform and grumbled, along with hundreds of thousands of other uniformed Americans, about the military. I have written some books, illustrated others, made a series of life-sized drawings of Mexican birds, edited a journal, taught classes, led field-trips, toured the country lecturing. All this I set down not because it is important *per se,* but because my position as a commentator should be validated before I attempt to hammer home a point or two. I have not been lazy. I have tried to keep myself informed concerning trends in art, music, and literature. In France, in 1938, I made a point of studying certain paintings in the Louvre, of going back to these paintings time after time rather than seeing the rest of Paris. During World War II, while based in New York, I visited the Museum of Modern Art and other galleries that showed contemporary work. Especially did I enjoy the Picasso show. Since coming to the University of Oklahoma I have gone out of my way to look at, to study, to try to understand abstractionist painting. At this university any show that is not abstractionist is retrospective, any painting that is not abstract is no art at all. . .

An Unexpected Experience

The unexpected is often memorable, sometimes pleasurable. An unexpected, and pleasurable, "art" experience I had at this university is worth recounting. At one of our abstractionists shows — the first one-man show of a young painter named John Freed — I found myself truly interested in a certain picture. Why I was interested I could not, and cannot, say. It was a swirl of whites — gray-whites, blue-whites, green-whites. Perhaps it reminded me of a winter storm I had experienced in the arctic. I told John, whom I had never met before, that I liked this particular painting. I also told him that I could not explain why I liked it. John looked at me, at first incredulous, then credulous, and began blushing — as if embarrassed, as if confused, as if deeply, privately pleased. John knew something about me. One of the professors had told him of me, of my interest in birds. As he went on blushing, by this time almost violently, he said, "Do you know, Dr. Sutton, that painting is the only painting in my show that's of a bird!"

In telling this completely true story I am not poking fun at anyone. I need hardly say that there was no bird-figure of any sort in John's picture. Had there been such a figure the painting would have failed as an abstraction. Nor had the picture been hung upside down. John and I became friends. I made local history of a sort when I, of the Department of Zoology, and a non-abstractionist painter if there ever was one, was asked by our Graduate College to be on John's committee. Through John I have come to believe in the complete sincerity, the true dedication, of some abstractionists. (As for abstractionists in general, the ones who, for want of words, claw the air above their heads and consign to limbo those who cannot understand every syllable; the ones who throw paint at canvas by the bucketful; the ones who, disappointed with results obtained through smearing with their own fingers, rubbing with their own noses, and sitting on canvas with paint-daubed behinds, in final desperation coax and cajole chimpanzees into producing art for them . . . as for these, and as for that which they appear to be striving toward, give me time, oh give me time, for a deep breath of North Country air!) I cannot discuss John's ability as a draughtsman. I have no idea whether he had an "academic period" comparable to that of the young Picasso who not only could, but did, paint roses as pretty and as real looking as photographs in a seed catalog.

The point I am hoping to make is that John Freed is a sincere person, who longs to express himself in abstract painting. Why he feels this way is beyond me at the moment. Is it because he feels, deep inside him, that anything even approaching realism is mere imitation? Is it because what is real has disappointed him bitterly, let him down? Does he say to himself, as he looks at a realistic painting, "Cleverly drawn indeed — but no idea there, no originality, no thought, no reporting of experience"?

John is not as narrow as some of his professors, not one of whom has ever admitted that my bird drawings are art. John really likes my stuff. While selecting some of my big Mexican water-colors for a show in Oklahoma City he said, "Gosh, why don't we just hang them all, they're so beautiful!" You see, there is room in his world for drawings that are not abstract. He cannot have been completely embittered. His tolerance is disarming — and thought-provoking. If John can see something in my paintings, why should I not see something in his?

Attitude Toward Works of Fuertes and Audubon

Careful readers are thinking: "You *did* see something in one of his pictures. Or, whether you saw anything or not, you *felt* something!" Confronted with such a comment, what can I say? I did, and do, like that John Freed painting — the delicate colors, the swirl, perhaps (God knows!) the bird. But what is wrong with my birds that look like birds, that are instantly, unequivocally, recognizable as birds? Must their very authenticity damn them to oblivion? Why are bird paintings, generally speaking, unacceptable for gallery showings? Why was Louis Agassiz Fuertes' work not included in that monumental volume, "Fine Bird Books," published in London and New York in 1953 by Collins and Van Nostrand? Why is John James Audubon the only American painter of birds most contemporary artists are willing to admit they've ever heard of?

This last question is partly rhetorical, but perhaps I should try to answer it in my own way — for the record. Everything about Audubon seems to fascinate people. The name itself has charm, is useful. All an average person needs to do, if he wishes to prove that he knows a good deal about birds, is to mention Audubon. All life insurance companies need to do in proving how deeply interested they are in maintaining the cultural standards of the people whose money they want, is to reproduce some Audubons on a calendar. This sounds as if I don't like Audubon. Fact is, I admire him greatly. I think his Carolina Parakeets is one of the most beautiful, one of the most completely satisfying bird paintings ever made. But I cannot sit idly by hearing people mumble the word *Audubon* while getting away with a thousand forms of murder.

Bird Paintings Create Illusions

Queries that have crossed my mind over and over since that long-ago-day when a Fine Arts Department director informed me that my paintings were material for display ("a very nice display, too") in a natural-history museum, but not in an art gallery, are these: Is bird-art really art at all? What do we bird-artists do to our drawings that keeps them from being art? Can it be that we who long so desperately to capture some of the beauty we have seen, and that we want others to enjoy, are not artists at all? Are we something else — hack-workers, artisans, charlatans perhaps? Do we become mere makers of charts, mere cartographers, because we insist that our birds be identifiable? I have heard my friend Roger Peterson say, more than once, that he longed to get away from making diagrams, the sort he has been obliged to turn out season after season, year after year, for his numerous field guides. I can imagine Roger Peterson having a whale of a time doing a lively, even boisterous painting of a Bobolink, but I cannot imagine, not for the life of me, a Peterson Bobolink that did not look like a Bobolink.

I long ago came to a full realization of the not wholly obvious fact that there is no such thing as saying everything in one bird drawing. Beautiful as the other side of the bird may be, only the near side can be shown. This is a truism, of course, and I use it only to emphasize the well-nigh universal tendency among bird-artists to make the most of all the beauty their subject matter possesses. This over-use, or attempt to over-use, may be poor art. My well considered guess is that no bird-artist ever tackled a Wood Duck drawing without wishing there were some way of forcing the light to play, the rainbows to shift, on the dark parts of the painting as he puts them down. This shifting, this moving of light, cannot be duplicated. All that can be captured is a suggestion — of the coming at one point, of the going at another, even as the successful painter of a running horse, in showing the farthest-forward leg in one position, the next leg in the position of a horse that has moved forward a bit, and so on, creates the illusion of a horse that is actually moving. The creator of such an illusion sees to it that no other part of the painting destroys his illusion; that which immediately surrounds the horse may be blurred or out-of-focus in such a way as to give the eye of the viewer no chance to check the relationship of that which the artist intends shall be moving to that which the artist intends shall stay still.

No, a bird-artist cannot, and therefore must not try to, tell everything in a given drawing. He cannot show every feather as he knows it to be. If every tiny marking is to be the point of the representation, then why not work out a technique of gluing feathers to paper? Representations made in this way would not need to be as hideous as the aniline-hued feather-birds that are made for the tourist trade in Mexico. A method could be worked out. Could be . . .

But Bird Paintings May Also Be Good Representations

Now suppose we have in front of us a good Roger Peterson or Don Eckelberry or Lee Jaques painting of a Blue Jay. Not a diagram with little black lines pointing to the crest, black collar and white wing-bars, but a painting, a painting intended, let us say, to capture the mischievousness or rowdiness of jays. Is there anything basically wrong, basically dishonest, in showing jays of normal shape and color? Is such representation plagiarism? Does a bird-artist prove himself a mere imitator if his Blue Jays are instantly recognizable as Blue Jays? Must a bird-artist declare his "freedom" by putting *black* wing-bars and *black* tail-corners on his jays, his imaginativeness by making their bills and feet twice as large as they should be?

I recall deciding, once upon a time, that it would be good fun to paint a lot of snow-white birds in a cornfield and call the picture "Crows." I had the plan all worked out; I knew people would say, "But crows are black!" To which I would reply, "Black crows! How miserably obvious! It's not a blackness that I see in crows. It's something else. It's a sort of whiteness. Yes, a sort of blinding, smiting whiteness!" By this time an ethereal look would have spread across my face and a genuinely worried look across the face of everybody else. I gave up that plan. Time was too precious. Besides, I felt that declaring my "freedom" by painting crows white was, in its own perverse way, just as obvious as leaving them black, so back I switched to painting crows as black as the blackest ever seen by the Pilgrim Fathers.

May I discuss further the colors of crows? When I say that I have seen normal (i.e., non-albinic) crows that looked white, only the very careful observer will sense that the prankish mood of the above paragraph has changed. A crow can, with wings spread horizontally in such a way as to form a mirror, become the exact opposite of black. A bright sun is required, or a very white sky. The whiteness of crow exists for only an instant. But the glossiness, the phenomenon of sunlight caught on a feather-plane and shot on to viewer is there. No one who has made a point of watching crows in all sorts of weather will deny this.

Am I arguing that a flock of white crows in a cornfield might, after all, make an acceptable painting? Certainly not. No two crows, or three crows, or ten crows, are ever going to spread their wings in such a way as to become mirrors at the same instant, the obvious reason being that the mirror a crow becomes is a matter of relationship; since no two crows can occupy exactly the same space at the same time no two of them will ever be likely to become mirrors at the same time for a given observer. No, what the observer sees is a scattering of black crows, a flash of white here, a flash of white there, and the mind is likely to be slow in accepting the eye's sound decision that while the flash was happening the blackness of crow disappeared.

The More Illusion in a Bird Drawing the More Successful It Is

Good bird drawing, like good drawing of any sort, is a creating of illusion. The more adroitly, the more easily, the illusion is created the more successful the drawing. I recall how amazed I was when Louis Fuertes showed me the trick of working out in detail the dark parts of a bird's folded wing, then of bringing the wing to life by covering all of it, except for the parts that needed to stay untouched, with a pale swift wash. The Japanese are wonderfully successful in creating illusions with a few strokes of the brush. A Japanese drawing that hangs in my living room was done so simply, so directly, that I sometimes inspect it closely just to convince myself that such things can be done. The drawing is of a Tree Sparrow *(Passer montanus)* perched on a sprig of mountain ash. The leaves required one stroke each. The sparrow required a dozen strokes or so, markings and all. What a far cry from the "feathery" drawings I made forty years ago! The "featheriness" I achieved in those days was a sort of porcupine effect produced by a multitude of little brush-strokes along the outer edge of the bird. Hardly any bird actually has contour surfaces of that sort. I was sacrificing my bird on the altar of featheriness.

Bird Artists Paint What They See and Feel

Most of the young bird-artists in America today are not making sacrifices to false gods of any sort. They are observing for themselves, painting what they see and feel. Most of them will admit, I believe, that they are following the lead of Louis Agassiz Fuertes. Don Eckelberry has delighted his admirers far and wide by his direct-from-life studies. A puff-bird of his, reproduced recently in *The Auk,* was an extremely good piece of work. Not long ago I was privileged to look over proofs of some of the color-plates for Alfred M. Bailey's forthcoming book on Colorado birds; a plate of owls done by Donald Malick, a young man who spent time with me at the Edwin S. George Reserve some years ago, was so beautifully done that I could hardly believe my senses. *"What a charge Louis Fuertes would get out of this picture!"* I kept thinking, over and over. The work of Orville Rice, a young Kansan, I have watched with great interest; it has become steadily better. Some of the work of Robert Verity Clem ranks, in my opinion, with some of the best bird-art that has ever been done. Robert M. Mengel has, I understand, been working at illustrations for the forthcoming "Handbook of North American Birds." I have not seen any of these pictures, but a Christmas card he sent me had on it a covey of quail ready to follow the most adventurous of them in scampering to the safety of another thicket — a delightful and authentic bit of line drawing.

Bird-Art Is Valid Art

Does it matter to these fine young men whether their work is shown in the art galleries of the land? Assuredly it does. They have to make a living. They long to be known, to be recognized for what they are. They long to point, with a sure finger, to that which they know to be wonderfully, unfailingly beautiful. Their art is not quite the bird-art of Morris Graves, whose squiggling pictures of shorebirds demand attention, say what you will of the technique; it is not quite the bird-art of Andrew Wyeth, whose drawing of a Turkey Vulture with wings spread wide is a thrilling study; nor is it the bird-art of Picasso, whose "Bird on Branch" may, for all I know, be caricature or even a thumbing of the Picasso nose. What the young bird-artists I have mentioned are doing is valid. It is a record of man's tussle with self. The beautiful creature, like the mountain, is there — the bird to be painted, the mountain climbed. The bird's beauty must be acknowledged, understood, captured. *I am the one to capture it,* says the bird-artist: *I shall do the best I can.*

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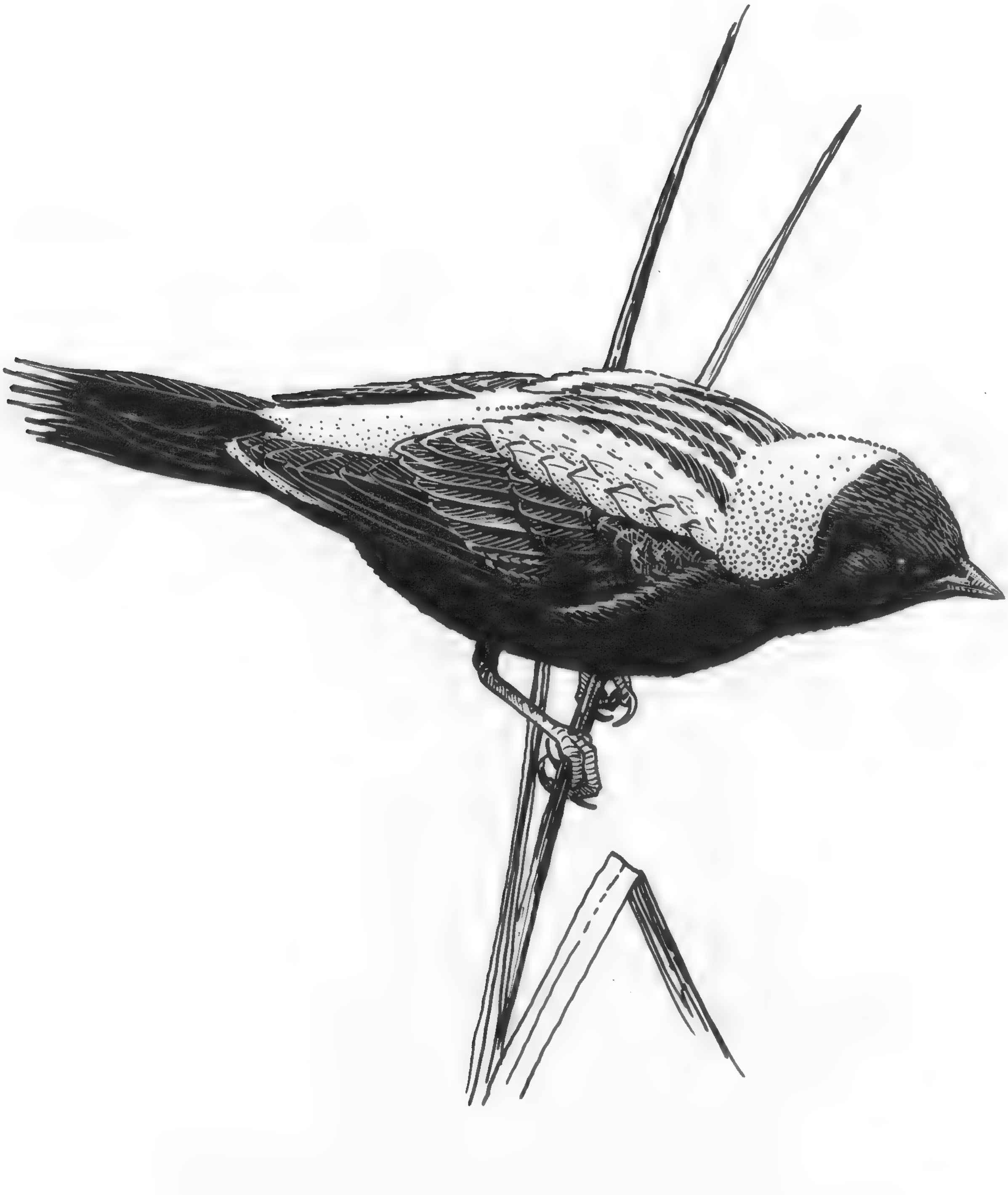

BEHAVIORAL RESEARCH AT THE CORNELL LABORATORY OF ORNITHOLOGY

NIKO TINBERGEN

The study of animal behavior is at the moment in an extremely interesting phase. This phase has two striking characteristics. One is the growing tendency to return to renewed, increasingly accurate observation of the behavior of many different species as they show it in their natural surroundings —a kind of "back-to-nature" tendency; the other is the extension of "feelers" into various "no-man's-lands" which are to be explored — broad boundary zones between the behavioral sciences and other fields of biology in its widest sense.

Both these trends — the return to the natural phenomena and the growth of inter-disciplinary contact — are due, in part, to inherent, specific developments in the behavioral sciences themselves and, in part, to changes in the outlook of scientists generally.

The return to observation was (as has been pointed out by several authors) to a certain extent a reaction to certain developments in psychology (by which I mean the various modern forms of behaviorism) ; it was also the result of a return of interest among zoologists in the functions of the live animal.

Animal psychology had, for a long time, been exploring ways towards an understanding of behavior, probing now in this direction, now in that. One of the developments which stimulated the growth of ethology was a tendency in behaviorism to concentrate, with the aid of experimental methods, on problems considered to be "general" — problems which could be studied in almost any animal (and which therefore *were* studied in the most convenient animal: "M (us) N (orvegicus) A (lbinus) "). Admittedly, these problems were derived from observations of animal and human behavior. But the initial period of observation and reconnaissance (of which period the *Journal of Animal Behaviour* bears witness) was rather short, and was soon followed by the development of a science which was almost exclusively built on the ways in which one kind of mammal responded to mazes, discrimination tests, and other standardized experiments.

There is no point in elaborating this original contrast between psychology and ethology. It is just a matter of fact that an increasing number of workers became convinced that the original inductive basis of the behavioral sciences was too narrow — that the switch from observation to experimentation had been made too early. I am convinced that this criticism was fully justified. The pioneers of what was later to be called ethology were all people who were interested in "unconventional" animal species, or in unconventional phenomena. In America, Whitman (working on pigeon behavior) and Schneirla (perhaps best known through his work on ants and through his contribution to the classic Maier-Schneirla book) rather went their own way; in Europe, Heinroth, Huxley, Portielje, and Lorenz (all zoologists with a wide knowledge of the natural ways of animals) found that conventional psychology could not give them much help in their attempts at an understanding of the manifold behavior patterns of their animals. Ethology definitely owes much of its inspiration to this reaction against the excesses and limitations of an "ism." In so reacting, ethologists perhaps made their science swing too far to the other extreme, away from laboratory experimentation. Another source of modern ethology was the experimental work on sensory functions, initiated by the beautiful studies of von Frisch and his numerous followers.

At first, "ethology" stood for naturalistic description, for simple experimentation in the field, and, in its more general utterances, for a rather cheeky, rather rash kind of theorizing which, with a splendid disregard of the positive achievements of behaviorism, concentrated aggressively on exposing its shortcomings. No wonder the work of the ethologists was in turn criticized by psychologists. However, as O. Koehler said years ago, this criticism was the first stage of a process in which increased contact was to lead to cooperation. Very soon the situation changed: ethologists were sobered, psychologists began to "sit up," realizing that there was something in ethology. Contact became less exclusively an occasion for arguing how wrong the other fellow was, and both parties became more receptive. At present, a fusion of ideas is very gradually being accomplished in which psychologists and ethologists are working towards what one could call a "biological science of behavior."

One of the most urgent tasks was, and still is, that of filling the gap which the psychologists rather left open in their haste to step into the twentieth century: descriptive work (which alone could show us the phenomena which we want to understand). It is only gradually becoming clear what a tremendous task even this preliminary work is; and naturally, as analysis proceeds, the demands put upon accuracy of description grow.

Of course, modern behavior studies do more than merely describe: Analytical probes are being made in many directions. With increasing clarity a general pattern of research begins to emerge, a pattern very familiar to biologists. One can classify the problems roughly into four categories: those of causation; of function or survival value; of ontogeny or individual development; and of evolution. This development, while leading to increased specialization, has at the same time stimulated inter-disciplinary contact, since studies of causation naturally lead to attempts to link up with sensory and nerve physiology; studies of evolution cannot be fruitful without contact with taxonomy, ecology, and genetics; behavior ontogenists learn from the work of experimental embryologists.

As I said, both these trends — the return to the natural phenomena in all their diversity, and the tendency to counteract the effects of specialization by inter-disciplinary research — are not confined to the sciences of animal behavior but are noticeable throughout the natural sciences. A glance at a journal such as *The Scientific American* (which is just the kind of magazine that is bound to reflect such tendencies) is sufficient to show these trends in physics, chemistry, geology, biology, psychology, anthropology, and sociology. Thus the character of modern ethology has not merely been determined by its special history as a reaction against psychology, but also by the history of science in general. It is a natural consequence of this development that the justification for the use of the separate terms "psychology" and "ethology" is in the process of disappearing, and I believe it is no exaggeration to say that we are witnessing the birth of a general science of animal (and human) behavior.

The behavioral research program of the Laboratory of Ornithology at Cornell has, under the energetic and inspiring leadership of Dr. William C. Dilger, attracted a large number of enthusiastic research students who have been working on a great variety of problems. Typical of the way this center works is the fact that, in the list of research workers (which includes eighteen names), we find three new members whose research projects are described as "No question as yet." These people do not as a rule come with a set problem and aim in mind, but just with a general interest in animal behavior. They are given the time to look around, to see what others are doing, to hear discussions in which unsolved problems are considered, and to make up their minds about the kind of problem they would like to study, and which they could profitably tackle. Some of them receive their inspiration from watching birds outdoors (for which Sapsucker Woods provides the opportunity); others seize the opportunity offered by Dr. Dilger's colony of *Agapornis.* Some are concentrating on a specific problem in one species; others compare species and try to understand their evolutionary relationships and histories, for which they have to do an enormous amount of descriptive work, and to develop "ecological intuition." Some have technical inclinations, spend months in the workshop, and emerge with new apparatus; others spend countless hours just watching the birds, and use nothing but field glasses and notebooks (and that wonderful computer, the human brain).

This first issue of the *Annual* bears ample witness of the growth and maturation of our science, and also of the stimulating atmosphere of the Cornell Laboratory. Even the small sample of studies it offers illustrates the wide range of the group's activities. As one would expect from any ethological center, there is a great deal of descriptive work in all five research reports. However, each of them transcends mere description and deals with a particular problem. Mrs. Brockway reports on the effect of visual and auditory stimuli from colony members on the reproductive activities of single birds of Budgerigars, and adds valuable and much-needed material to the problem of social activation of reproduction. The Fickens have tackled a formidable task of trying to understand the evolutionary radiation of wood warblers. They suggest various connections between the general ecology and the character of displays (such as those between ground-feeding and tail-wagging) and they argue that the fact that distraction displays occur in 34 species, including many arboreal ones (while it is absent in sympatric species belonging to other taxonomic groups), suggests that the wood warblers are descendants of ground forms. This is a type of study of which we need many more if we want to understand evolutionary radiation of behavior. Klopman gallantly refuses to be beaten by the baffling complexities of the behavior of geese, animals so fascinating that Lorenz, after 40 years of concentrated study, is still discovering new aspects of their behavior almost every day. Hartshorne reports on part of his prolonged Eastern Bluebird studies, for which he developed not only a system of window-sill nest boxes, but also his now famous Hartshorne Sound Isolation Chamber (which, as I discovered last summer, has already migrated to California). Payne's work on the acoustical localization of prey by the Barn Owl penetrates into the mysteries of the most highly developed ear to be found among birds, and perhaps in the animal kingdom (though Donald Griffin might disagree with me here). Payne's experiments with "probe-tube microphones," revealing the directional capacities of the ear, and his experiments in which owls were trained to strike at a concealed loudspeaker, open up many possibilities for the analysis of acoustical orientation.

Thus, this first *Annual* is an impressive sample of the many activities in which Cornell ethologists are engaged, and the high standard of the contributions fully justifies this new series. Ethologists all over the world will welcome its publication and will be looking forward to subsequent volumes.

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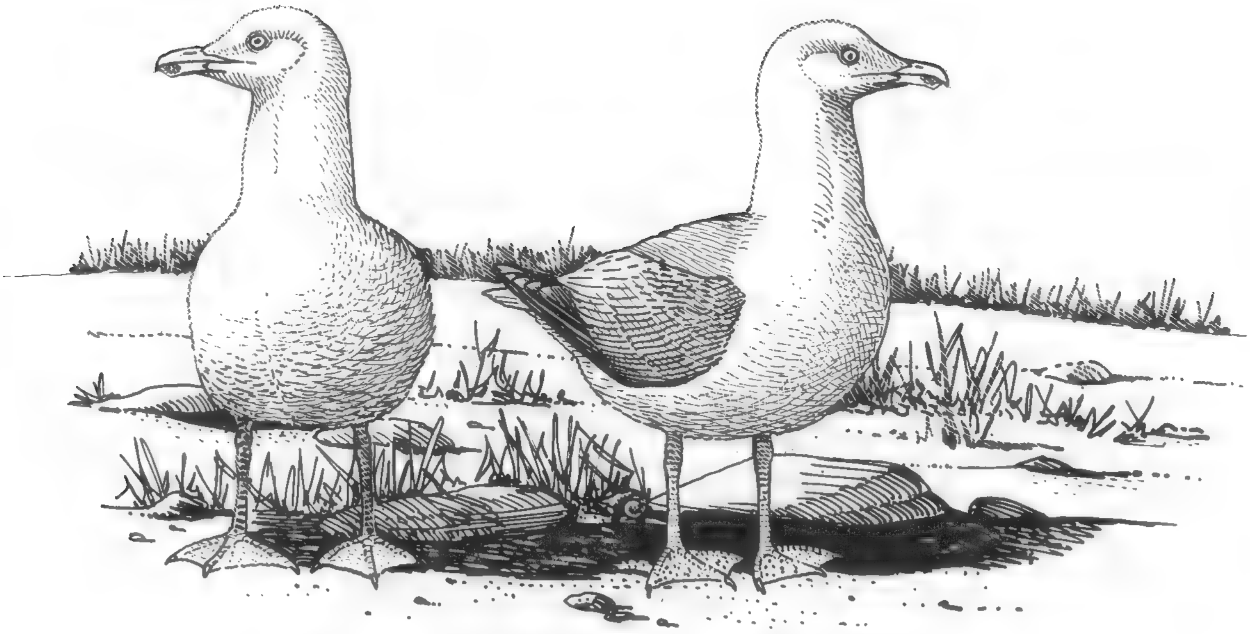

METHODS AND OBJECTIVES OF ETHOLOGY

William C. Dilger

Ethology is a relatively new science. Hence it is not surprising that its methods and objectives, and even its connection with other approaches to the study of behavior, are often not entirely clear. My purpose here is to help remedy this situation by discussing the objectives and some of the methods of ethology.

The Meaning of Ethology

Modern ethology dates from the appearance of the now classic "Der Kumpan in der Umwelt des Vögels" [The Companion in the Bird's World] by Konrad Lorenz in 1935. Prior to this date, in the earlier part of the century, ethology sometimes meant simply the study of animal behavior. Shortly after 1935 it came to signify the comparative study and analysis of the instinctive or stereotyped movement of animals — a more restricted (and sterile) sense than that used today. Ethology has now come to mean the study of function, biological significance, causation, and evolution of species-typical behavior. This is close to a more precise restatement of the earliest meaning (Thorpe, 1961). Tinbergen (1951) and Thorpe (1956) have recently provided summaries of our knowledge and thinking.

Although modern ethology is only about thirty years old, the work of such men as Wallace Craig and C. O. Whitman in the United States, Oskar Heinroth in Germany, and J. S. Huxley and H. E. Howard in England provided initial impetus. The development of ethology was largely a reaction against earlier approaches to animal behavior in which either the animal's subjective feelings were regarded as causes of behavior (many European animal psychologists), or only learned behavior and attendant theories were deemed of prime concern (many American comparative psychologists). Psychologists commonly work with just a few domesticated animals, often kept in environments providing very few natural requirements, thus making normal behavior impossible. In the beginning, modern ethology often erred in the opposite direction by placing disproportionate emphasis on the "innate" elements of animal behavior. This, quite naturally, prompted sobering comment by experimental psychologists (e.g., Lehrman, 1953 and 1956). Fortunately, in the past ten years or so, there has been a gradual increase in highly profitable cooperation among psychologists, ethologists, and physiologists.

An ethologist can be identified neither by the kinds of animals with which he works nor by their variety, although the tendency is to deal mainly with undomesticated species ranging from protozoans to man. The ethologist at the present time investigates both innate and learned behavior and the interrelationship of the two. As a matter of fact, it now seems apparent that the distinction between innate and learned behavior may not be based on biological reality. All behavior is the result of experience. Experience resulting in selective pressures causes changes in genotypes and consequent "programed" behavior. Programed behavior may be modified by additional individual experience acquired at any time from the fertilized egg to death (Dilger, 1962).

Ethologists are aware that animal behavior is a part of zoology. To achieve a full understanding of animal behavior, ethologists, like all zoologists, ask questions about function, biological significance, causation, and evolution. (This takes us back to the modern meaning of ethology already stated.) Thus, by their questions, ethologists chiefly distinguish themselves from other animal behaviorists.

The methods used by ethologists are so numerous that a complete discussion of them here is impossible. However, certain general concepts of methodology must be emphasized because they are basic to ethological investigations.

Describing Behaviors

The first step in any ethological study is to make a carefully detailed description of *all* the behavior exhibited by the animal being investigated. Descriptions of behavior pose problems not encountered in descriptions of structure. For one thing, behavior is ephemeral— it takes place and is gone, to be replaced by another behavior. Many behaviors last but a fraction of a second while some (e.g., sleeping) may last hours. Behaviors not only have the normal intraspecific variation found in structures but also have short-term and long-term intraindividual variation. This, of course, means that sample sizes must often be larger than those necessary for describing structures. As in structural studies, adequate sample sizes must be based primarily on the amount of variability encountered. For example, if we want to know whether a particular species walks or not, our sample size can validly be quite small. On the other hand, if we want to know how much variability there is in bill-wiping, a large sample may be necessary.

Adequate description of behavior is also difficult because even the seemingly simplest behaviors are at times very complex. Every behavior has speed, duration, and amplitude. Each of these may vary independently of the others. In addition, more than one part of the animal is normally integrated into a single act. A given behavior may incorporate two or more acts and these may vary in the manner in which they are integrated. An act is a set of observable activities regularly seen in combination and not analyzable into separately occurring components (Russell et al., 1954).

In the Peach-faced Lovebird *(Agapornis roseicollis),* which carries nest material amidst its feathers, we have an example of the number of acts making up the behavior in tucking these strips of nest material among the feathers of the lower back and rump (Figure 1). The first act is to *point* the strip either to the right or to the left. Next, the head is turned back over one shoulder, bringing the bill with the strip into the feathers of the lower back *(tuck),* which are *raised* at the same time. The strip is then *thrust* hard into the feathers with a *trembling* motion of the head, *released,* and the head brought forward *(head-forward)* while the feathers are *compressed.* Involved in this behavior are at least eight separate acts performed in a characteristic manner and arranged in a definite sequence, enabling the animal to conduct the behavior of tucking one strip of nesting material.

Identifying Behaviors

Identifying the acts is sometimes difficult. We thought for a long time that the Lovebird's trembling and thrusting of the strip comprised a single act. These two motions are very brief and normally occur simultaneously. Experiments have shown, however, that there are really two separate acts with a particularly strong link between them and that we can, by manipulating the early experience of females, get birds which will tremble but not thrust.

Motion pictures, particularly those which are precisely timed, and tape recordings are excellent methods of sampling visible and audible behaviors. These are supplemented with notes made from direct observation, sometimes dictated to a tape recorder — a refinement which allows the investigator to observe his animals continuously without having to look away to write.

After sufficient information has been obtained, the different units of behavior can be recognized and described and a measure of their variability determined. Each separate behavior must be named for future reference and discussion.

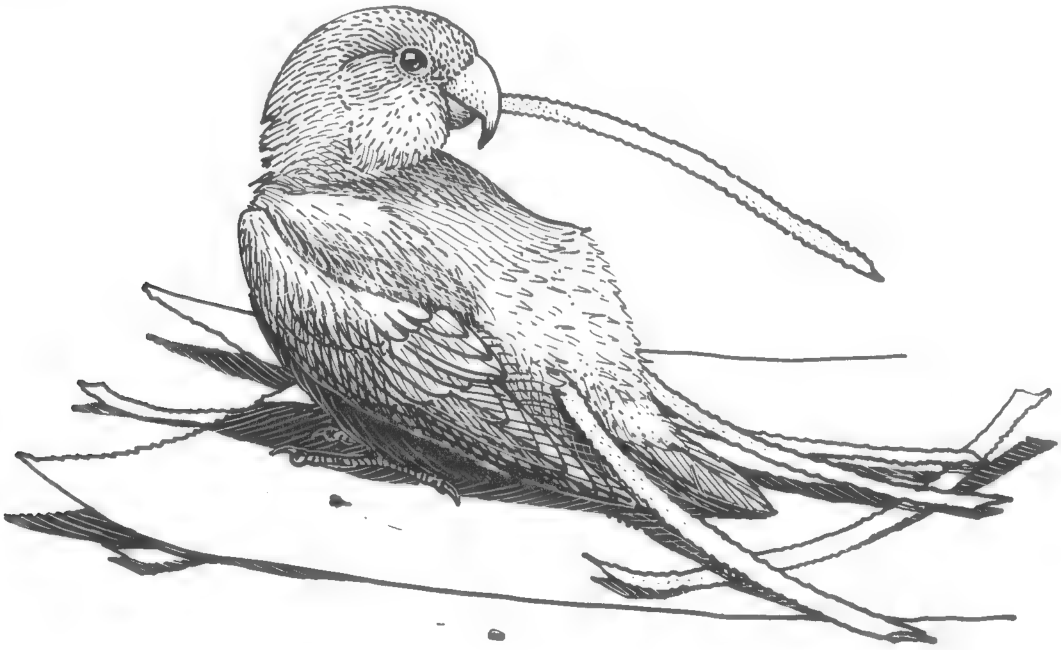

Figure 1. Peach-faced Lovebird tucking nesting material in its feathers.

Naming Behaviors

The best names for behaviors are those which are purely descriptive such as Head-forward, tremble, Squeak-twitter, or shake. (Names of displays are customarily capitalized to distinguish them from names of other behaviors which are not capitalized.) Ideally, such names are actually "shorthand" descriptions of a conspicuous element of an otherwise complex behavior. Sometimes function and causation are implied in the names— e.g., Head-forward Threat or Aggressive Upright. This practice, though often useful, must be employed very cautiously because wrong interpretations, easy to make in the naming stage of an investigation, are difficult to correct later, and, worse still, may unconsciously bias thinking through the whole investigation.

Behavioral Interpretation of Vocalization

Because of the rapidly growing number of people engaged in recording and studying bird "songs" and other sounds, I am prompted to comment on their interpretations. Vocalizations are behavior — audible behavior — and must be sampled, described, and named just as other behaviors. The word "song," for instance, has no place in the scientific analysis of audible behavior. It is a very general term applied to a heterogeneous assemblage of complex, often pleasing, vocalizations which, like other behaviors, have a variety of functions, causations, biological significances, and evolutionary histories. The uselessness of such a term can be better appreciated perhaps if one tries to imagine deriving a term for all the complex and beautiful visible behaviors combined!

All vocalizations and many other audible behaviors are displays by definition. A display is a behavior which has evolved specifically as a signal (Moynihan, 1955). Furthermore, these audible elements are often acts integrated with visible acts making up the whole display. An understanding of these behaviors can be achieved only through studying *all* of the behavior involved. One must keep in mind that an animal is more than the sum of its structures and behaviors; it is an integrated, very complex functional system. This means that, in order to understand any part, one must understand the whole.

Interested amateurs can make substantial contributions to our knowledge by recording animal behavior with a tape recorder or camera and supplying data which trained scientists can then analyze. However, such persons must take careful supplementary notes, not only putting down the usual information as to identification of species and place and date of recording, but also determining as accurately as possible the stage in the animal's life cycle and the situation in which the behavior occurred. Knowing the stage of the life cycle is important in making an estimate of the dominant physiological state of the animal at the time. Knowing the situation immediately before, during, and after the behavior is equally important in judging its function and biological significance.

I cannot encourage too strongly recording the *full variety* of sounds made by different birds. The tendency has been to record the more conspicuous and pleasing vocalizations. Most species have a very rich repertoire of vocal displays, some being so faint that they may be heard by the human ear only at very short distances. For instance, the various parrots of the genus *Agapornis* have several distinct vocalizations audible only if one's ear is within a few inches of them.

Studying Captive Animals

Ideally animals should be studied both in captivity and in the wild for best results. Each situation yields information impossible to obtain from one alone. I am, of course, well aware of the two main criticisms of studying animals in captivity — it is unkind to the animals and their behavior is so abnormal that it cannot be depended on as typical of the species.

The first criticism — that it is unkind — is not based on fact. If the investigator, as he should, determines what a particular species' requirements are and meets them, the animals cannot possibly suffer from confinement. The word "captivity" implies that the animal is captive only when it is aware of its inability to escape confinement. All animals, including man, are captives in the sense that they cannot travel beyond certain spatial limits for one reason or another. If animals are provided with everything they need, they are perfectly content. When we finish studying native birds, we ordinarily release them. Not infrequently some of these spend days, even weeks, attempting to return to their former quarters which represent safety, food, water, and other conditions necessary for their welfare. This is far more upsetting than watching birds living contentedly in the laboratory.

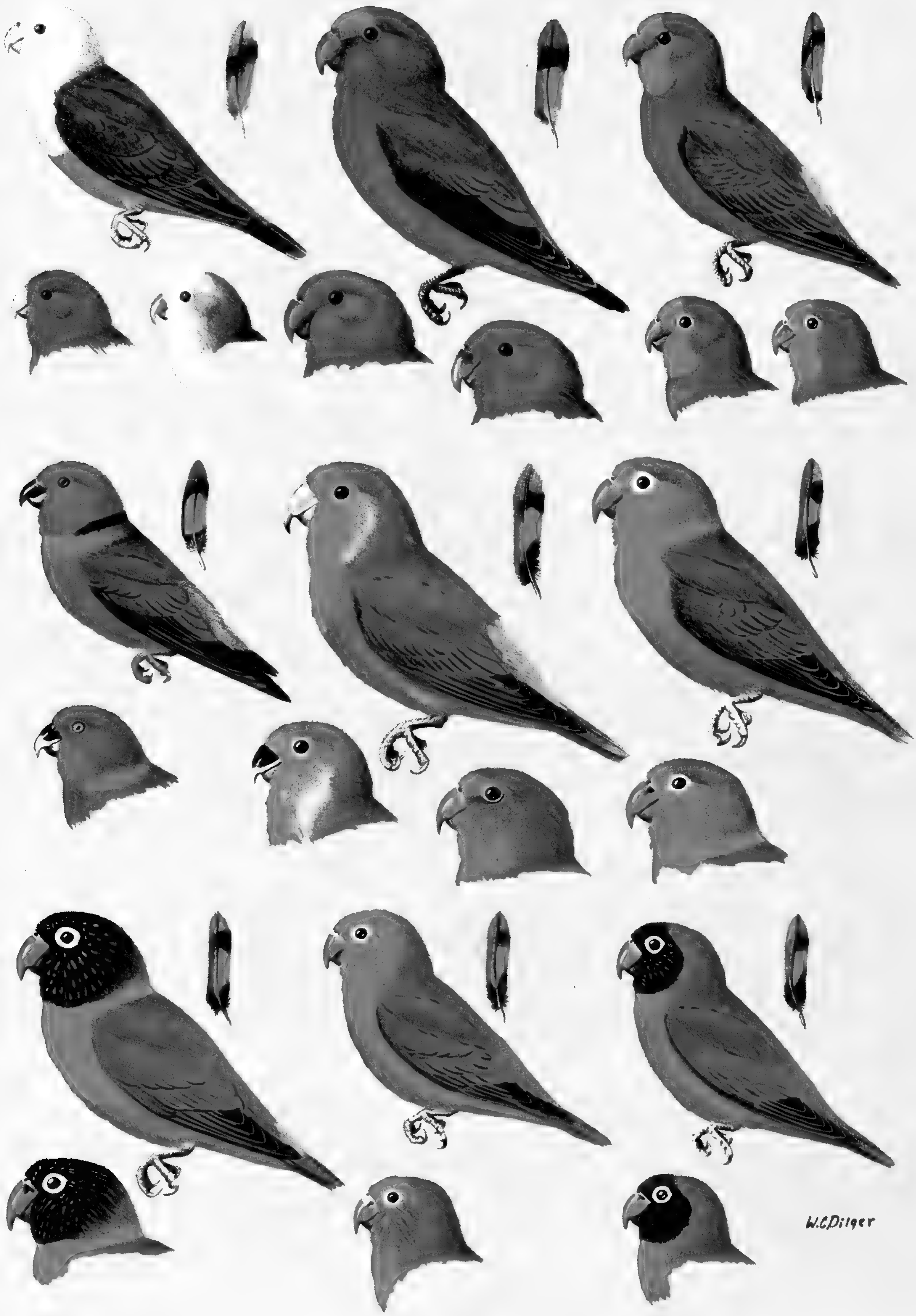

Plate I

Parrots of the genus *Agapornis*

First row, left to right: Adult male *cana*, adult male *taranta*, adult male *pullaria*. Second row: Heads of adult female *cana*, juvenile male *cana*, adult female *taranta*, juvenile *taranta*, adult female *pullaria*, and juvenile *pullaria*. Third row: Adult *swinderniana*, adult *roseicollis*, adult *personata fischeri*. Fourth row: Heads of juvenile *swinderniana*, juvenile *roseicollis*, adult hybrid between *roseicollis* and *p. fischeri*, and juvenile *p. fischeri*. Fifth row: Adult *p. personata*, adult *p. lilianae*, adult *p. nigrigenis*. Sixth row: Heads of juveniles of *p. personata*, *p. lilianae*, and *p. nigrigensis*. The feathers are outer right rectrices showing evolutionary trends in color, pattern, size, and shape (see Dilger, 1960).

The second criticism — that behavior of captive birds is likely to be abnormal — can be met as follows. First, it is true that behavior of captive birds *may* be abnormal. However, it is up to the investigator to provide conditions minimizing this possibility and to be aware of specific situations leading to atypical behavior even if nothing can be done about them. Second, the *form* of behavior does not ordinarily change in captivity. If the animal will perform the behavior, it will do it normally for that particular species, but *frequencies* of particular behaviors may be increased or decreased. For instance, a lone bird will not show much agonistic (attack-escape) behavior, and, conversely, birds abnormally crowded may show increased or decreased frequencies of such behavior. If a male has a flight display, he must either have enough room to perform it or he will not perform it at all. By and large, form of behavior can be depended upon to be normal. Frequency may vary but even this may be normal if the investigator can duplicate the essential conditions found in the wild.

Our studies of *Agapornis* have been conducted almost entirely on birds in confinement. We have from time to time checked their behaviors against behaviors of birds with complete freedom and found them dependable. Information on them in the wild, sparse though it is, has also helped. We have detected no significant differences in the same species behaving in small breeding cages, in large aviaries, or completely free. These findings are in agreement with the findings of other ethologists working with a large variety of animals.

I should emphasize, however, that the richer the natural environment is for a species, the more difficult it is to duplicate artificially. Much behavioral work done by psychologists, particularly on primates, has been at least partly invalidated because the investigators did not appreciate how seriously inadequate surroundings can affect species-typical behavior. Mildly inadequate surroundings may simply mean that the animal does not perform all of its normal behavior, although remaining healthy both mentally and physically. Seriously inadequate surroundings may cause the animal to become actually psychotic and even impair, directly or indirectly, its physical health. One of the advantages of working with birds is that it is usually comparatively simple to furnish them with all the items necessary for normal behavior. *Agapornis,* for example, require only one another, clean water, an adequate diet, nest material, a nest site, and a firm perch upon which to copulate. These are the only features necessary within normal ranges of light, humidity, and temperature.

Objectives of Ethological Research

After the behaviors have been sampled, described, and named, we still have not accomplished any research. Observation itself is not science and has no value except as a basis for interpretation and some degree of generalization (Simpson et al., 1960) . We must now proceed to determine function, biological significance, causation, and evolution.

Function

Function is simply what behavior does. Sometimes function, such as locomotion, is easy to determine. In this case, the behavior simply serves to transport the animal from one place to another by walking, hopping, flying, swimming, or crawling. But the function of other behaviors may be quite difficult to determine, and consequently require sophisticated identification procedures. This is often true of displays. A given male precopulatory display, for instance, may possibly serve one or a combination of several functions. It might be a long-term stimulus to a female's physiology, a short-term stimulus with the function of eventually releasing solicitation for copulation, or a stimulation to the performer himself in a variety of ways. Ordinarily, the function of a display is ascertained by recording its effect on the overt behavior of the recipient.

Biological Significance

Biological significance is how the behavior increases or decreases the probability of survival. For instance, flying simply functions in taking the bird from one place to another but it may vary the probability for survival in several ways. Its biological significance might be to bring the bird closer to food, water, a mate, and shelter, or to take the bird farther from a predator or some other deleterious feature of the environment.

One must be careful not to be teleological when explaining biological significance. Behavior is not ordinarily performed with conscious purpose. The male bird does not perform precopulatory behavior to cause the female to permit copulation any more than the heart beats to pump blood. A bird performs precopulatory behavior because he cannot help doing so when the internal and external conditions are just right. This may result in the female soliciting, just as a beating heart results in pumping the blood.

Causation

Causation is difficult to define because it may mean different things to different people. Commonly, causation refers to the physiological states underlying behavior and thus includes the concepts of "drive" and "motivation." It can also refer to the conditions of experience necessary for acquiring the possibility of performing a given behavior. Stimulation experienced by the organism from the moment it was a zygote (fertilized egg) influences the ultimate species-typical behavior patterns. Detecting the nature of these stimuli, when they occur and how long they last, is fundamental to the determination of causation.

Determining causation involves complex procedures which often must be prefaced by a thorough, descriptive study of the animal's entire behavior. Displays are normally based upon motivational conflicts occurring at the time the display is used. For instance, most reproductive displays incorporate movements, postures, and sounds derived from the motivations to attack, escape, and behave sexually (see Morris, 1956). It is obvious that one must have a thorough understanding of the elements associated with each of the conflicting motivations before the causation of the display can be understood.

One of the best ways to study the role of prior experience on the development of species-typical behavior is to use the so-called deprivation experiment. This requires that the animals be divided into two groups, one experimental and the other a control. The two groups are identical except that the investigator makes certain that the experimental group is deprived of an experience normally encountered and which the investigator believes, on the basis of a prior study, to be significant in the causation of the behavior pattern under study. Subsequent changes in the performance of the experimental group are compared to the "base line" of normal behavior established by the control group. Many such experiments are usually necessary. Each one, or group, of such experiments tests one variable while the others are held constant. This exceedingly valuable technique, like all techniques, may be completely invalidated if it is incorrectly employed. (See Lorenz, 1961, for the conditions which must be met in such work.)

Evolution

The ethologist, like any zoologist, is always interested in the processes of evolution. A behavior is like a structure — it has not always been in its present form. The evolution of behavior is, in principle, just like the evolution of structure with which it is intimately associated. Display evolution in particular has been the subject of much interest (e.g., Blest, 1961).

One of the most important reasons for studying the entire behavior of a species is to be able to recognize the ancestral, non-display behaviors contributing to the display being investigated. In general, displays have drawn upon the every-day maintenance activities, such as preening, scratching, biting, and so forth, for their evolutionary raw material. Other sources are "displacement activities," "redirected activities," and "intention movements."

(1) Displacement activities are seemingly irrelevant, "out-of-context" behaviors occurring when an animal is thwarted and are often performed in a curiously hurried, "nervous" manner (van Iersel and Bol, 1958, and Rowell, 1961). I must include a word of caution here. Displacement activities, because they are seemingly performed out of context, are vulnerable to misidentification. Many activities initially identified as displacement turn out to be something else as the knowledge of the animal's behavior increases.

(2) Redirected activities are behaviors directed at an object other than the one eliciting the response and occurring when the eliciting object is unavailable. An object may be unavailable because it moved away immediately after stimulating a response in another, or may have simultaneously stimulated an incompatible response (see Ficken and Dilger, 1960).

(3) Intention movements are essentially incomplete, "low-intensity" responses such as the sudden crouching (flight intention movement) of a bird when approached. Intention movements may either continue into the complete behavior or may subside as the situation warrants (see Daanje, 1950, and Andrew, 1956).

Moynihan (1955) discusses the types of behaviors which evolve into displays.

One great advantage in the study of behavioral evolution is that the precursory behavior and the derived form of the behavior incorporated into a display exist together, making a careful comparison possible. We know that various normally-occurring, precursory activities gradually become incorporated in a definite, stereotyped manner during the course of the evolution of display. The motivational state of the animal during the activity for which the signal is being evolved, the kinds of available precursory activities, and the precursory activities being "preadapted" as signal components determine which of these behaviors eventually becomes incorporated into a display.

In order to study the phylogenetic aspects of evolution one must conduct a comparative study of homologous behaviors, all existing at the same time, in a related group of animals. In this way it is possible to detect various stages of evolutionary attainment and reconstruct the course of evolution for each behavior.

The changes that precursory behaviors may undergo during the course of their evolution into displays involve the following: (1) Changes in thresholds of response, (2) changes in the dominant sensory modalities, (3) changes in the effects of various environmental stimuli, and (4) changes in coordination. Changes in coordination may involve amplitudes and speeds of movements, the development of rhythmic repetition, and the transfer of signal function from one set of effectors to another. In addition, changes in component coordination may occur, involving perhaps changes in component sequences and exaggeration.

Behavioral Evolution of Agapornis

Parrots of the genus *Agapornis* (Plate I) furnish one of the best examples of behavioral evolution, including the evolution of displays (Dilger, 1960). An example of display evolution in *Agapornis* is the history of head-scratching which has evolved to become a precopulatory display, Displacement-Scratching. A common displacement activity in the more "primitive" species of *Agapornis (cana* and *taranta)* is head-scratching. This is performed when, for instance, a male is thwarted in an attempt to mount the female. The amplitude, speed, and other characteristics of this scratching appears identical with scratching done during a bout of ordinary comfort behavior. However, this scratching must have had some stimulatory value to the female, or perhaps even to the male when done as displacement because it has become increasingly modified until, in the most "advanced" form *(personata),* it has become a highly stereotyped display in its own right and commonly occurs as a normal part of any precopulatory bout, even when no thwarting is apparent. Species demonstrating intermediate stages provide clues to the course that evolution has taken. The changes that have occurred, beyond a change in situation, include speeding up of the scratching movements, orientation of the scratching to the bill rather than to the head feathers, and the equal employment of either foot. Originally, scratching with the foot nearest the female was facilitated by that foot being the one already raised preparatory to mounting. Thus scratching always took place on the side toward her.

Examples of the evolution of non-display behavior in *Agapornis* are nest-material preparation and transport. Nest-material preparation is based on a behavior common to most, if not all, parrots—namely, chewing on almost anything. Transport was originally achieved by tucking the material into the feathers of the body, keeping it there, and carrying it, several pieces at a time, to the nest cavity. This behavior is based on an activity common to all birds — namely, preening. The most "primitive" species *(taranta* and *pullaria)* cut small bits of thin, pliable material such as paper, bark, or leaves and tuck these among feathers anywhere on the body. The cutting gradually changed from cutting small irregular bits *(taranta* and *pullaria)* to cutting short, curved strips *(cana)* to cutting long, straight strips *(roseicollis).* Once the long, straight stage of the cutting had been approached, the material would no longer stay tucked in the ventral surfaces as well; thus tucking gradually evolved in such a way that it became restricted to the lower back and rump *(roseicollis).* The most "advanced" species *(personata)* no longer tucks strips in the feathers but carries them one at a time in the bill. This species also carries twigs and similar objects — items which could never be carried among the feathers. The resultant nests reflect the nature of the material carried. The primitive species, with their small bits of nest material, can make only a soft pad upon which the eggs are laid. With its rather long strips, *roseicollis* is able to construct a rather well made cup, and *personata* makes an elaborate covered chamber with a tunnel leading into the cavity entrance.

The Most Difficult Step in Behavioral Research

The most difficult step in a behavioral investigation, as in any research, is asking the proper question, the answer to which should materially advance our understanding of biology. A question could be asked in such a way as to inhibit investigation. For example: Is a particular behavior innate or learned? This question assumes that there is a difference, which is by no means proven. Properly asked, the question should read: What must the animal experience, when, and for how long, in order for it to show this particular species-typical behavior? If one has several good questions, the problem then is to choose the one which, when answered, will help the most in solving the others. Once a question is selected and properly asked, finding the answer is relatively easy. The investigator simply has to decide what kind of information is necessary and how to get it, treat it, and present it. This merely requires time and intelligent effort by trained scientists. It is surprising how many investigators begin by just gathering items of information with no particular purpose in mind! This is like a carpenter sawing and nailing with no particular structure planned.

After analysis should come *synthesis*. Once a question is asked and answered for, say, the Purple Finch, this information should then be synthesized with answers of similar questions asked of other animals. In this way our general knowledge of particular topics is gradually increased and becomes more and more meaningful.

The Contribution of Ethology

Thus, the results of ethological investigations not only further our knowledge of the behavior of various kinds of animals, but each answered question helps us to understand all animal behavior, including that of man himself. This is why behavioral studies are so vitally important.

Human behavior is the most complex of all animal behavior. We are vertebrates just as are cichlid fishes, parrots, ducks, gulls, and chimpanzees. We share certain structural features, such as hearts, brains, and backbones, just as we share behaviors associated with fear, sex, and aggression. Understanding the functions, biological significances, causations, and evolutionary histories of homologous behaviors in "simpler" animals is fundamental to a thorough understanding of our own behavior in the same way that understanding simple circuits, switches, and so on is necessary before one can understand a highly complicated electronic computer. It is paradoxical that in this age characterized by technological capabilities of space exploration and threat of nuclear war, we have an understanding of our own behavior probably no higher than the general level of scientific achievement in the nineteenth century! This is undoubtedly an optimistic estimate and the situation is serious enough to endanger our own welfare. It does not seem likely that our future survival can be assured until we understand our behavior thoroughly enough to control it. Treaties, laws, and other agreements will be more effective when they can deal with the causes of undesirable behaviors rather than the symptoms.

We ethologists, concerned as we are in understanding the behavior of parrots, finches, and other animals, take satisfaction in the realization that with each question we successfully answer we contribute importantly to the better understanding of ourselves.

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THE EFFECTS OF NEST-ENTRANCE POSITIONS AND MALE VOCALIZATIONS ON REPRODUCTION IN BUDGERIGARS

BARBARA F. BROCKWAY

Budgerigars *(Melopsittacus undulatus)*, popular cage birds the world over, represent a monotypic parrot genus endemic to the dry open country of Australia where they are nomadic and colonial. They pair for life, although some degree of sexual promiscuity occurs, particularly among males; they build no nests, each pair merely selecting a natural cavity in which from four to seven white eggs are laid.

In the wild, Budgerigars are strongly social the year round and normally stay in large flocks. Single caged pairs, when isolated, do not ordinarily breed, but in the presence of other Budgerigars will ordinarily exhibit all forms of sexual behavior. However, if no nest sites are provided, the females neither lay nor do their ovaries develop fully.

Factors affecting the reproductive behavior and physiology of Budgerigars offer a wide field for investigation. In this article, it is shown that the position of the nest-box entrance in relation to the perches and male vocalizations affect certain aspects of reproduction.

Methods

Only domesticated varieties of Budgerigars were used. Thirty pairs and nine unpaired females were kept in cages (2 feet by 4 feet by 2 feet high; covered with ½-inch by 1-inch mesh screening) and provided with French's Parakeet Seed, French's Conditioning Food, cuttle bone, quartz gravel, and fresh water. To the side of each cage was attached a standard wooden nest box (6.25 inches by 6.25 inches by 9.25 inches high) with an entrance hole 1.5 inches in diameter.

My observations were made two or three times a week, for periods of one or two hours each, and totalled three to four hours per day. Observations were spoken into a tape recorder, thus enabling me to watch the birds uninterruptedly. I then transcribed the data into notebooks for subsequent analyses.

Female Nest-Box Activities

Females first indicate interest in nest boxes about two to three weeks before laying. While perching erectly, they repeatedly extend their heads and necks and look toward the nest-box entrances for varying periods, usually several seconds. This may be the extent of their interest for a day or two.

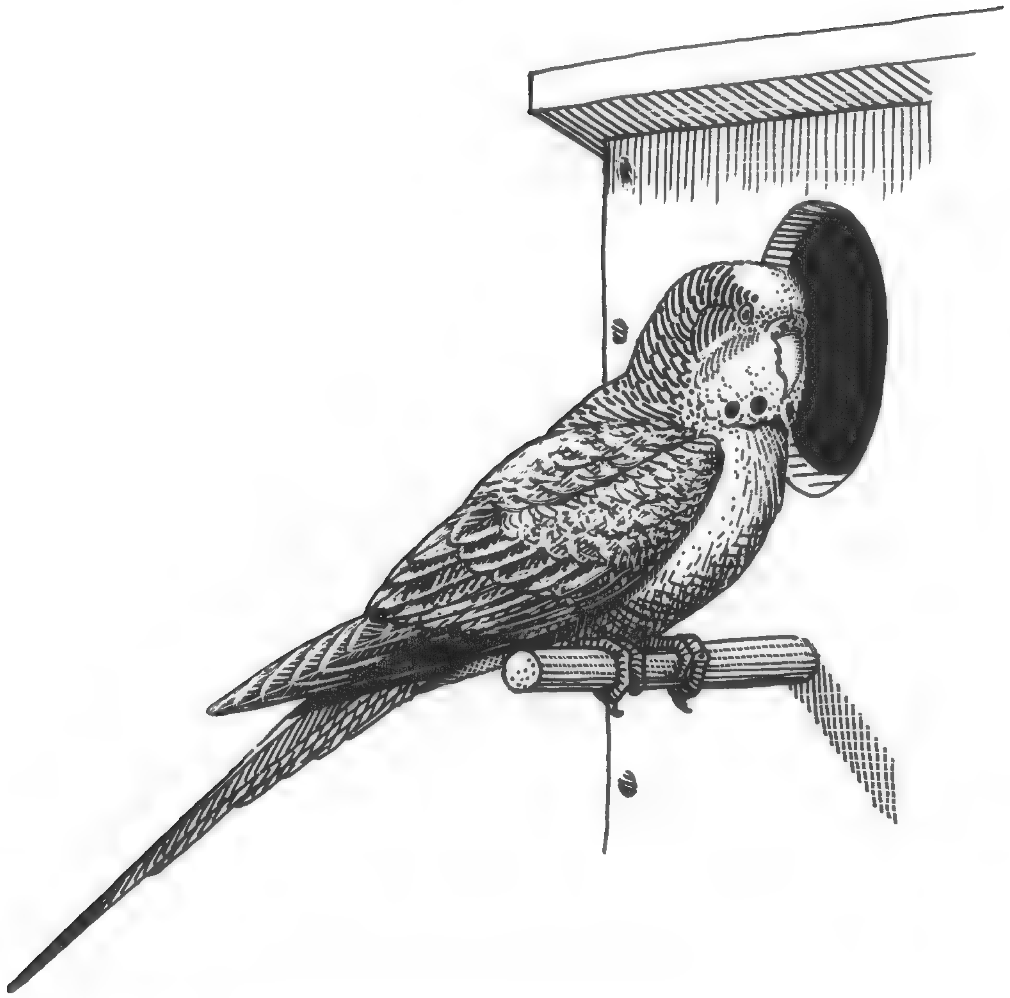

Figure 1. Nest-box examination by a female Budgerigar.

They then show further interest by walking or flying to the entrance and putting their heads inside the box. This behavior, in its first stages, involves prior cranings of the neck and simply looking at the nest box or entrance from a distance. Later, it involves going to the entrance without prior looking. While at the nest entrance, the females chew at the wood around the hole or remain at the entrance without putting their heads inside. The duration of both intra- and interindividual examinations, which I measured from the moment of initial insertion of a head within the hole to the moment the bird withdrew or went entirely inside the box, varied from 0.02 minute to 3.00 minutes. Females typically examine the nest box many times per hour and may do nothing beyond this for a day or two. This act of examining the nest box from closer quarters I have termed "examination." See Figure 1.

The next indication of increased interest is crawling part way into the nest box. After repeating this maneuver several times, the birds then terminate examination by going entirely into the nest box. This act of bringing the whole body within the nest box I call "occupation." Occupation was measured from the moment the female's body passed the rim of the nest hole until half her head passed the rim on her way out.

In the case of some females, presumably those with greater interest in the nest box, I observed the first examination and the first occupation on the same day. Usually such occupations were seen toward the end of an observation period. Regardless of the height of the nest entrance in relation to the nearest perch, the mean length of time from the first observed examination to the first observed occupation was 1.6 days (standard deviation 3 days) for 10 females that subsequently laid, and 6.5 (standard deviation 3) for females that did not.

Generally, examinations following the first observed occupation are shorter in duration than those seen prior to this initial occupation. Many examinations typically end in occupation. Each female spends only a few seconds inside the box during the first few occupations but during the next few days the duration of each occupation gradually lengthens to several minutes. Females also show an increasing tendency to go into the nest box directly, thus eliminating examinations. This tendency to occupy the nest box directly can be expressed mathematically in several ways, but I used the following formula:

$$T = \frac{P - N}{P} \times 100$$

T = Tendency to enter the nest box directly
N = Number of examinations that terminate in occupation per hour
P = Number of occupations per hour

The results presented in Table 1 are based on data from six females that subsequently laid. T, the tendency to enter the nest box directly, is expressed in percentages; E, the average time spent in examinations, in minutes. The tendency to enter the nest box directly for three females increased from 0 per cent to 75 or 100 per cent prior to egg-laying the days following the first observed occupation. (Zero per cent indicates that the female never entered the nest box without first examining it; 100 per cent means that she went directly into the nest box upon each visit.) The female of Pair 61 showed the slowest increase in the tendency to go directly into the nest box, whereas the female of Pair 55 showed the fastest. In all cases the tendency to go directly into the nest box was 75 to 100 per cent prior to laying.

The durations of a given female's occupations might vary from less than a minute to 60 minutes per hour during any single observation period, and was no doubt influenced greatly by the activities of the mate or other birds near by.

TABLE 1

Tendency For Direct Occupation of Nest Boxes

Days from first occupancy	*Pair 61*		*Pair 63*		*Pair 64*		*Pair 58*		*Pair 55*		*Pair 52*	
	E	*T*	*E*	*T*	*E*	*T*	*E*	*T*	*E*	*T*	*E*	*T*
0	2.89	0	0.07	33	0.20	0	0.04	0	0.02	50	0.02	50
1					0.02	90						
2			0.31	66					0.02	80		
3	0.26	0									0.02	73
4					0.0	100			0.0	100		
5	0.16	0	0.04	94			0.02	33				
7	0.22	40	0.15	90					0.0	100	0.02	83
8					0.0	100						
9			0.0	100								
10	0.16	66					0.02	75				
11			1st egg		0.0	100			0.0	100	0.09	50
12	0.10	66										
14	0.00	100							1st egg		0.02	75
15					0.0	100	1st egg				1st egg	
16	1st egg											
19					0.0	100						
20					1st egg							

E = Mean length of examination in minutes.
T = Tendency to enter box directly in percentage.

TABLE 2

Effects of Nest-Box Entrance Height on Nest-Box Activities and Egg-laying

Nest-box activities	*4 females, 90 days Nest entrance 2 inches below perch*				*10 females, 81 days Nest entrance 2 inches above perch*				*4 females, 35 days Nest entrance 6 inches above perch*			
	Performers		*Total*		*Performers*		*Total*		*Performers*		*Total*	
	$\bar{x}$	*Number of birds*	$\bar{x}$	*sd*	$\bar{x}$	*Number of birds*	$\bar{x}$	*sd*	$\bar{x}$	*Number of birds*	$\bar{x}$	*sd*
First examination	24.0	2	57.0	38.0	16.1	10	16.1	5.9	4.0	4	4.0	4.2
First occupancy	42.5	2	66.2	27.8	20.8	10	20.8	7.8	8.2	4	8.2	6.7
First 3/60	......*	0	90.0	0	28.1	10	28.1	12.1	12.5	4	12.5	7.9
First 30/60	......	0	90.0	0	45.1	8	47.8	23.0	16.0	3	20.7	26.7
First egg	......	0	90.0	0	58.2	6	61.5	25.4	24.0	2	29.5	7.1

*Nothing observed for the duration of experiment.

$\bar{x}$ = Mean number of days since beginning of experiment.

sd = Standard deviation.

Student's T-test

Nest-box activities	*2 inches below versus 2 inches above*		*2 inches above versus 6 inches above*	
	t	*P*	*t*	*P*
First examination	3.50	$<.005$	11.09	$<.005$
First occupancy	2.95	$<.01>.005$	9.0	$<.005$
First 3/60	10.0	$<.005$	2.36	$<.02>.01$
First 30/60	3.56	$<.005$	1.89	$<.05>.02$
First egg	2.19	$<.02>.01$	2.47	$<.02>.01$

t = Test value.

P = Probability value.

Degrees of freedom for all measurements = 12.

Consequently, the duration of individual occupations was an unreliable measure of interest in the nest box. The total time in the nest box per hour, on the other hand, increased fairly steadily from about a minute on the date first observed to 30 minutes or more in the week prior to laying, and was therefore a reliable measure of interest in the nest box.

For the purposes of this study, I arbitrarily divided the total time of nest-box occupation per hour into two categories: "3/60" in which the female spends 3 minutes or more per hour inside the nest box and "30/60" in which she spends at least 30 minutes per hour inside the nest box. I found that all females, which eventually laid, spent 30 minutes per hour or more inside the box for at least one week prior to egg-laying. Furthermore, they steadily increased their total time per hour inside and generally maintained these increases from the first observed occupations to egg-laying.

Females which subsequently did not lay showed erratic occupations and examinations. For example, sometimes they spent a total of 20 minutes per hour inside the box on one day, then only one minute the next day; sometimes they gradually increased their total time per hour inside the box, then either stopped entirely or spent much less than 30 minutes per hour inside.

Females spend about 50 minutes or more per hour in the nest box after laying the first egg. This correlates with the fact that incubation normally begins with the first egg and the tendency to enter the box directly (90 to 100 per cent in all cases observed) follows the onset of incubation.

Significance of Vertical Distance Between Nearest Perch and Nest Entrance

Three groups of pairs, able to see and hear other pairs within their group, were employed. Group A contained four pairs having the nest entrance 2 inches *below* all perches, Group B contained 10 pairs having the nest entrance 2 inches *above* all perches, and Group C contained four pairs having the nest entrance 6 inches *above* all perches.

The amount of precopulatory behavior as well as copulation was about equal in all groups. The ensuing nest-box activities and number of eggs laid are summarized in Table 2.

All measurements for any given "level" of nest-box activity as well as the date of the first egg laid were analyzed statistically by means of Student's T-test. A "P" (probability) level of 5 per cent or less was arbitrarily chosen as a value of significance prior to analysis. A 5 per cent level of probability means that the differences between the measurements might simply result from chance rather than from the experimental variables five times out of 100. Similarly, a P level of one per cent would mean that chance might be responsible for such differences between groups only one time out of 100. Any value of P, which is obtained by means of a statistical test *higher* than the arbitrarily chosen P level of significance, is then said to represent differences between groups due *not* to experimental factors but to chance. As can be seen from Table 2, all P values for differences between groups were *below* the level of 5 per cent. The data obtained the last day of the study were substituted as a value for analysis in those individuals not showing a given behavior for the duration of the study. This makes the figures much lower in all cases than would ordinarily be expected, but renders the analysis more objective. Even with such arbitrary treatment, all differences between groups are highly significant for each behavior compared.

TABLE 3

Effects of Male Vocalizations on Female Nest-Box Activities

	Identification of female	*Day of first examination*	*Day of first occupancy*	*Day of first 30/60*	*Day of first egg*
Group A	gwsb	9	14	14	—
No male	yell	14	14	—	—
vocal-	sybl	—	—	—	—
izations	wild	14	14	14	—
Group B	ysb3	1	3	3	9
Male	wild	1	3	3	9
vocal-	yhsb	2	3	4	11
izations	wld2	2	9	10	16
	opsb	2	9	12	18

Results are presented in both mean $(\bar{x})$ number of days since the beginning of the experiment for those individuals within a group that performed during the study as well as the mean $(\bar{x})$ number of days involving all females in each group. This latter mean contained, necessarily, some of the arbitrary values. Student's T-test was again used in analyzing these total means.

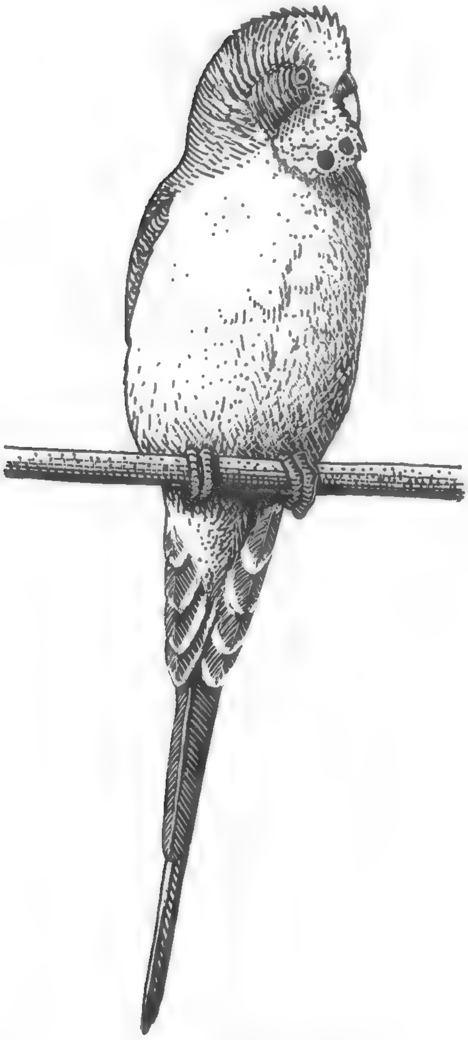

Figure 2. Male Budgerigar in the Loud Warble posture.

A comparison of all groups shows that nest-entrance heights 6 inches above the perches are the most stimulating, 2 inches the next most stimulating, and 2 inches below the least stimulating of all for both nest-box activities and egg-laying. Indeed, while it was shown that the presence of a nest box was apparently necessary for full ovarian development and laying, a nest entrance below perch level significantly inhibits such activity, even though approximately equal amounts of precopulatory activity and copulation took place in all three groups.

There are obviously perches and nest entrances at various distances apart in the wild. Free-living females in Australia have been reported (Klaus Immelmann, pers. com.) to nest in holes near or below ground level under buildings when higher sites were presumably already occupied or otherwise unavailable. It may be that wild females are stimulated to enter and occupy lower nest cavities by seeing other females with more desirable sites performing nest-cavity activities. All females in these experiments were able only to see others with the same distances between perch and nest entrance.

Several pairs in a large outdoor flight cage performed most, if not all, precopulatory and copulatory behavior on the perch nearest the nest box selected by the female. The perch was actively defended by the male of a pair engaged in precopulatory activities. Such reproductive behavior may be similarly carried out in the wild on a branch or other place near the nest site. The proximity to the nest site may be more critical than the vertical distance between hole and perch, although the vertical distance is clearly important.

Investigations on whether or not the relative entrance height of a nest from which an individual fledges may influence the subsequent preference by that individual during its own reproductive activity are obviously needed.

Effects of Male Vocalizations

Vaugien (1951) demonstrated that females placed in dark boxes and presumably able to hear each other did not undergo ovarian development nor did such females lay unless given the opportunity to hear other Budgerigars (including males). He recognized that the reduced light stimulated laying in such cases and suggested that this situation may be approached inside the nest box. I kept females in stock cages (without nest boxes) under 10 to 14 hours of light per day and also where they could hear male vocalizations. Laying was observed in only two cases out of 100. In both of these instances, each female had been under these conditions for some months prior to laying and only one egg each was laid. The idea that darkness stimulates ovarian development in the absence of nest boxes, provided male as well as female vocalizations are heard, is thus further supported.

Vocalizations from other Budgerigars kept under conditions of 14 hours of light per day was shown by Ficken et al. (1960) and Brockway (1961) to be highly important in stimulating egg-laying in females provided with nest boxes and mates. However, in those studies, the opportunity for hearing the vocalizations of other females was not separated from hearing those of other males.

I conducted the following study in order to investigate the influence of male vocalizations on examination, occupation, and egg-laying. Two groups of females, able to see and hear others within their group but unable to see any males, were provided with nest boxes having a vertical distance of 6 inches between perch and nest entrance. Group A contained four females with no opportunity to hear males. Group B contained five females with the opportunity to hear 13 males in an adjoining cage. These conditions were maintained for 30 days for both groups. All were observed for two hours at least once a week. Both groups received the same amount, roughly 14 hours, of light per day. Their ovaries were examined by laparotomy just prior to the study and weekly thereafter until eggs were laid.

Before presenting the results of this experiment, I should point out that the growth of an ovarian follicle of about 3.0 mm in diameter to an ovulatory size of about 9.0 mm, and laying it, takes about five days. This time is approximately the same as the observed minimum number of days females spend (30/60) inside the nest box prior to laying the first egg. In ovaries either examined by laparotomy or by autopsy, the largest follicles are generally 1.0 mm to 2.0 mm in diameter at the beginning of nest-box occupation while those examined when just beginning the 30/60 stage never showed a follicle larger than 2.0 to 3.0 mm in diameter.

I found that the largest ovarian follicles per individual in Groups A and B ranged between 1.0 and 2.0 mm in diameter at the beginning of the study. Observations of nest-box activity and laying are presented in Table 3.

All five females of Group B laid within 18 days of the start of the study, whereas none of Group A laid at all during the study. All levels of nest-box activity appeared earlier in Group B which was able to hear male vocalizations. On the other hand, in Group A, of the four females, only two performed all levels of nest-box activity. One female showed no interest at all in the box, and the remaining female did not reach the 30/60 stage, although she was fairly close to it, remaining in the nest box during the last 10 days of the study for periods averaging 24 minutes per hour.

The largest ovarian follicles of two females in Group A remained between 1.0 and 1.5 mm in diameter for the duration of the study. In the other two females, the largest follicular diameters were roughly 2.5 mm at the end of the second week and enlarged somewhat more during the rest of the study. The largest follicular diameter in one of these two females was 3.0 mm and in the other it was 4.0 mm at the termination of the experiment. These two females with the largest ovaries were the same two females that demonstrated the 30/60 stage of nest-box activity. Ovarian development in Group A was obviously much less than that in Group B where all females had attained follicular diameters of 9.0 mm within 18 days. These results indicate that while the opportunity to hear male vocalizations apparently stimulates earlier appearance of examination, occupation, and the 30/60 stage, it is not absolutely necessary for the appearance of these activities in situations where females may see and hear one another.

There is one major vocalization performed almost exclusively by males that I have termed the "Loud Warble." (See Figure 2.) Evidence indicates that this particular vocalization is responsible for stimulating the female activities I have just mentioned. It seems likely, too, that in this highly social species which breeds synchronously, the sight of one female performing nest-box activity may stimulate the other females. Ovarian development and egg-laying, however, do seem to be greatly influenced by the stimuli of male vocalizations. We can also understand why, under more "natural" conditions of lighting, females of this species will lay in the absence of the mate, supporting the work of Vaugien (1951). Thus it would seem that the precopulatory behavior performed by the male, while necessary for copulation, is not absolutely necessary for ovarian development and female nest-box activities, although it may still influence them. (Ovarian development and female nest-box activities may take place in the absence of male non-vocal sexual behavior provided the females receive the proper male vocal stimulation and are provided with suitable nest boxes or reduced lighting conditions.) Although hearing male vocalizations is necessary for *full* ovarian development (including egg-laying), I must point out that simply a suitable nest box, the opportunity for stimulation by male vocalizations, and even the presence of the mate do not induce egg-laying in many individuals.

Summary

A description of female nest-box behavior prior to laying is given for domesticated strains of Budgerigars *(Melopsittacus undulatus)*. Females spend at least 30 minutes per hour inside the nest box during, at least, the week preceding laying. The possible significance of this behavior with relation to lighting within the box and ovarian development is discussed. The vertical distance between the nest entrance and the perches plays an important role in stimulating female nest-box activities and egg-laying. Both appear to be inhibited in situations where the entrance is below perch level. Increased height of the entrance relative to the perches is associated with the earlier appearances of female nest-box activities and egg-laying.

Male vocalizations seem to stimulate earlier appearance of all levels of nest-box activity and full ovarian development and egg-laying.

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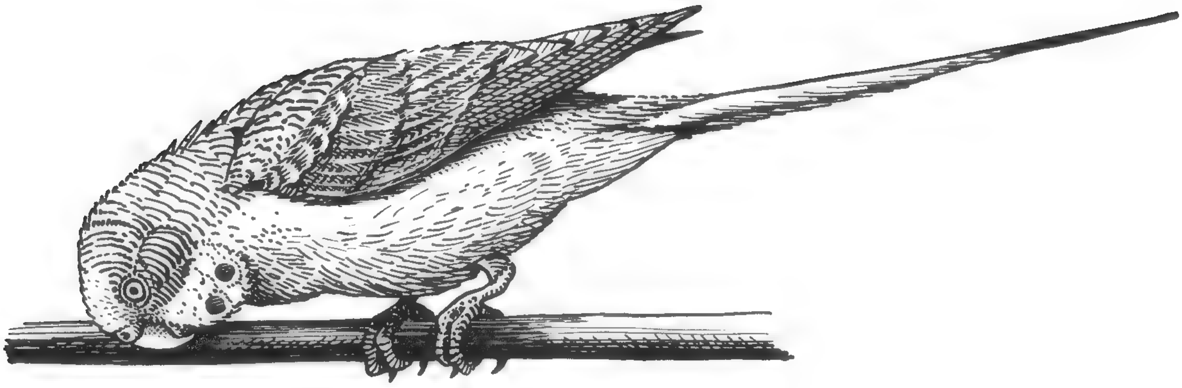

THE COMPARATIVE ETHOLOGY OF THE WOOD WARBLERS: *A Review*

Millicent S. Ficken and Robert W. Ficken

Wood warblers (Parulidae) are widespread in the New World and, judging by the large amount of literature devoted to them, few groups of birds have attracted as much popular attention. Early in this century, Frank M. Chapman (1907) authored an impressive book on the North American warblers, and fifty years later Ludlow Griscom and Alexander Sprunt, Jr. (1957) collaborated with others in a book dealing with the entire family. Between the appearances of these works, a volume devoted to warblers was published in the series of "Life Histories" by Bent (1953) and there has been a steady stream of articles and accounts about warblers in technical journals and regional treatises.

Although wood warblers are quite distinctive as a group, ornithologists do not agree on the exact number of species that comprise the Parulidae or on their relationships to other nine-primaried oscines. According to Griscom and Sprunt (1957) there are about 113 species assigned to 25 genera (11 monotypic). Beecher (1953) and Tordoff (1954b) include three genera of honeycreepers (Coerebinae), and, in addition, Beecher includes the emberizine finches (Emberizinae). Mayr and Amadon (1951) consider the wood warblers a subfamily of the Thraupidae (tanagers). More information is needed before an agreement is reached on the precise relationships of wood warblers to other closely allied oscines.

Adaptive radiation has resulted in different ranges (some overlapping, others separate; some widespread, others restricted), habitat diversity, varying degrees of plumage differences between the sexes, and cryptic versus conspicuous coloration, thus presenting fascinating but complicated evolutionary problems.

Despite the attention given to parulids, surprisingly little is known about their behavior, and in the few published descriptions little attempt has been made at an ethological analysis. It is our purpose here to review published information of ethological value on locomotion, feeding, tail movements, and agonistic and courtship displays, and attempt to interpret it with respect to function, adaptive significance, and possible taxonomic implications. To this information from the literature we have added our own data, obtained mainly from studies of the Golden-winged, Blue-winged, and Chestnut-sided Warblers and the American Redstart.

This review of available information will, we believe, provide certain clues to a better understanding of parulid relationships and, at the same time, point out gaps in our knowledge of warbler behavior and thereby encourage further investigations in the subject.

The scientific names of all species mentioned in this paper are listed at its conclusion.

Feeding

Warblers are primarily insectivorous, although a few are also vegetarian (e.g., the Myrtle Warbler). Extensive adaptive radiation has occurred in this group and since species living in the same area cannot have *exactly* the same feeding habits, different ways and places of feeding have evolved (Lack, 1949).

MacArthur (1958) has shown how five species of *Dendroica* — Cape May, Myrtle, Black-throated Green, Blackburnian, and Bay-breasted Warblers — that occupy the same spruce forest, minimize competition for food by relative differences in behavior and by using different feeding zones in trees. Of the five, the Cape May is the most restricted, feeding principally in the outer area of the upper portion of trees. There are also differences in the frequency of flight involved in feeding, the Black-throated Green flying the most frequently and the Cape May and Bay-breasted the least. This objective analysis bears out the subjective observation that the Black-throated Green appears "nervous" and that the Bay-breasted is slow and "deliberate." There are also differences in the principal direction of movement while feeding, the Myrtle and Black-throated Green moving in a "tangential" direction (i.e., around the tree), the Cape May vertically, and the Bay-breasted and Blackburnian radially (i.e., in and out along a branch). MacArthur also discussed the occurrence of various types of foraging behavior: hawking (pursuing moving prey in the air), hovering (seeking a nearly stationary prey amid the foliage), and long flights (those over 25 feet). The Cape May and Myrtle hawk and undertake long flights and the Black-throated Green hovers more frequently than the others.

Thus these warblers, by feeding in different ways and in different places, are exposed to different insects. The bills of these species (except the Cape May's, which is noticeably more slender) are very similar and the differences in food taken can be accounted for by differences in feeding behavior. The differences between species are usually not absolute — i.e., not gross differences involving the presence or absence of a feeding behavior — but relative, and there is some overlap between species.

MacArthur believes that in these species territory, in addition to functioning in pair formation and maintenance, reduces competition for food. Another variable which may minimize competition for food is that some of these birds nest at slightly different times.

Although the position of the nests of these five species reflects their preferred feeding zones, this is not true of many of the *Vermivora* which forage at medium to high elevations and nest on the ground.

It is possible that competition for food can further be reduced by slightly different feeding habits of the sexes, especially during periods when low insect populations might be a limiting factor. For example, we have the impression that, in May, males of the American Redstart typically feed higher and make more mid-air sallies than do females. This difference apparently disappears later in the season.

A broad look at the family reveals a similar pattern of relative and, more rarely, apparent absolute differences. Thus, climbing on tree trunks, to which the Black-and-white Warbler is adaptively committed, is only a relative

TABLE 1

Wood Warblers Showing Ground Locomotion by Walking

Species	*Walking*	*Also Hopping*	*Authority*
Swainson's Warbler	X	X	Brewster, 1885 Meanley, 1945
Worm-eating Warbler	X		Chapman, 1907
Pine Warbler	X		Ridgway, 1889
Palm Warbler	X	X	Pers. obs.
Ovenbird	X		Hann, 1937
Northern Waterthrush	X		Bent, 1953
Louisiana Waterthrush	X		Chapman, 1907
Kentucky Warbler	X		Chapman, 1907
Connecticut Warbler	X		Chapman, 1907
Buff-rumped Warbler	X	X*	Skutch, 1954

*Usually hopping

difference since it occurs to a lesser extent in some other species, particularly the Yellow-throated and Pine Warblers (Bent, 1953). Most arboreal species occasionally feed on the ground. Flycatching occurs in most species but is rare in many. Some behavior patterns may be typical of genera (e.g., bud- and flower-probing in *Vermivora,* flycatching in *Wilsonia, Setophaga,* and *Myioborus).* The American Redstart has an apparent absolute difference from such warblers as the Parula and many *Dendroica* and *Vermivora* in that it does not cling to the tip of a branch while hanging back downward. The detection of absolute differences requires prolonged studies of a species since some feeding patterns are apt to be rare, but not absent.

At least two important feeding methods, common in closely related passerines, are apparently absent in the parulids — i.e., scratching leaves, in emberizines (Nice, 1943) and holding food with the foot, in some vireos, icterids, and carduelines.

There are other facets of feeding behavior worthy of mention, although very little is known about them. In considering adaptability to changes in insect population levels, MacArthur (1958) found that the Cape May Warbler and, to a lesser degree, the Bay-breasted show changes in numbers according to food supply, and are abundant in years with spruce budworm peaks. This suggests that the amount of food available limits their numbers. The Bay-breasted lays significantly larger clutches of eggs in years of budworm outbreaks when food is most abundant. The populations of the other three species studied by MacArthur are more stable.

Another subject of interest is the manner in which prey are killed and softened before they are eaten. The American Redstart holds large caterpillars in the bill and bangs them on the perch with a whiplash action, and also holds moths by a wing and bangs them on the perch until the wings are broken off (M. S. Ficken, in press).

The selection of prey species and its development is a subject worthy of more study. Very young American Redstarts out of the nest are attracted to moving objects (M. S. Ficken, in press), and soon learn to reject certain insects, such as some bugs (Heteroptera), which are evidently distasteful. In our study of captive Redstarts and a Bay-breasted Warbler, we found that the Redstarts would readily catch flying insects whereas the Bay-breasted would not fly out after insects but ate them readily if they had first been stunned. This is substantiated by MacArthur's observations on the feeding habits of the Bay-breasted, which performs few flights while feeding.

An interesting sidelight is the relation of feeding habits to the time of migration. For example, six warblers (the Black-and-white, Myrtle, Pine, Palm, and Northern and Louisiana Waterthrushes) may arrive in the region of Ithaca, New York, before 15 April when most insects are still dormant. These warblers seek insect material by foraging on tree trunks (Black-and-white, Myrtle, and Pine), on the ground (Myrtle, Pine, Palm, and the two waterthrushes), and in or near water (the two waterthrushes). The Myrtle, Pine, and Palm also eat considerable vegetable matter.

Ground Locomotion

Most warblers forage above the ground but a few forage on the forest floor. Almost all primarily ground-foraging species walk (Table 1), as is true of other small ground-foraging passerines (Nice, 1943; Andrew, 1956). Arboreal species, even those (e.g., *Vermivora*) which nest on the ground, hop. (For a discussion of the adaptive significance of walking and hopping, see Dilger, 1956a).

Although almost all *Dendroica* are arboreal and hop, three forage on the ground to some extent (Bent, 1953) with the following locomotion: Pine Warbler, walking (Ridgway, 1889); Kirtland's Warbler, hopping (Mayfield, 1960); Palm Warbler, both walking and hopping (Ridgway, 1889). No doubt these species are only secondarily adapted terrestrial foragers.

A similar case exists in *Basileuterus* where two ground-foraging species have been observed: The Buff-rumped Warbler usually hops but may sometimes walk, although there may be individual or geographical variation (Skutch, 1954); the Rufous-capped hops (Sutton, 1951). Skutch states that "When it is recalled that most species of the large genus *Basileuterus* are arboreal rather than terrestrial in habit, it is not surprising that *fulvicauda* should be less adapted for terrestrial locomotion than members of the highly specialized warbler genus *Seiurus*."

In the genus *Oporornis* the primarily ground-foraging members, the Kentucky and Connecticut Warblers, walk, while the primarily shrub-foraging Mourning Warbler hops (Bent, 1953).

Swainson's Warbler, Worm-eating Warbler, and the waterthrushes walk. Hann (1937) notes that young Ovenbirds initially hop, then pass through a stage of walking and hopping, and finally walk all the time. Many other passerines, which walk as adults, first pass through a hopping stage (Nice, 1943), but the reverse process is unknown.

Tail Movements

Birds frequently show distinctive tail movements while foraging. Andrew (1956) has described these movements in various fringillids and convincingly suggests that they are given when a tendency to fly is in conflict with another tendency, such as remaining stationary. Many of these movements, having become further evolved from the movements of take-off or landing, now serve as social signals.

We have arbitrarily classified the tail movements of warblers into four categories — wagging, flicking, spreading, and fanning — and listed the tail

TABLE 2

Tail Movements of Wood Warblers

Species	*Type of Movement*				*Authority*
	Wagging	*Flicking*	*Spreading*	*Fanning*	
Swainson's Warbler		X			Brewster, 1885
Orange-crowned Warbler		X			Griscom, 1938
Nashville Warbler		X			Griscom, 1938
Magnolia Warbler			X		Bent, 1953
Cape May Warbler		X			Eaton, pers. com.
Myrtle Warbler		X D-U			Pers. obs.
Audubon's Warbler		X			Hoffmann, 1927
Bay-breasted Warbler		X D-U			Pers. obs.
Blackpoll Warbler		X			Roberts, 1936; Wing, 1933
Kirtland's Warbler	X D-U				Mayfield, 1960; Wing, 1933
Prairie Warbler		X L			Wing, 1933; Bent, 1953
Palm Warbler	X D-U				Wing, 1933; pers. obs.
Semper's Warbler		X			Danforth, 1935
Ovenbird		X U-D			Chapman, 1907; pers. obs.
Northern Waterthrush	X D-U				Pers. obs.
Louisiana Waterthrush	X D-U	X U-D (y)			Pers. obs.; Eaton, pers. com.
Kentucky Warbler		X			Bent, 1953
MacGillivray's Warbler		X L			Hoffmann, 1927
Fan-tailed Warbler				X	Griscom and Sprunt, 1957
Red-faced Warbler		X L			Chapman, 1907
Hooded Warbler				X	Bent, 1953
Wilson's Warbler		X L			Pers. obs.
American Redstart			X		Chapman, 1907; pers. obs.
Painted Redstart			X		Chapman, 1907
Slate-throated Redstart			X		Skutch, 1954
Rufous-capped Warbler		X			Sutton, 1951
Buff-rumped Warbler	X				Skutch, 1954

D-U = Down-up
L = Lateral displacement
U-D = Up-down
(y) = Young bird

movements of various species of warblers in Table 2. The tail movements included are only those which are shown while the birds forage. In other activities, especially in displays, warblers may show different tail movements (e.g., tail spreading occurs in distraction displays) .

Wagging is a continuous vertical movement while flicking is, by contrast, a somewhat discontinuous movement. Andrew classifies tail flicks as U-D (up-down) , a small upstroke followed by an equal downstroke; U-D-U (up-down-up) , a small upstroke, a larger downstroke, and a second upstroke that returns the tail to its original position; and D-U (down-up) , a downstroke followed by an equal upstroke. In addition, there may be a slight sideways movement (lateral displacement) of the tail during the flick (Table 2) . The U-D-U type of flick has not been reported in warblers.

Tail spreading is holding the tail in a spread position, while fanning is an opening and shutting movement. These movements (Table 2) are not as common in warblers as wagging and flicking.

Some warblers, including the Yellow, Chestnut-sided, Blue-winged, and Golden-winged, have not been observed performing tail movements while foraging, and exact descriptions of tail movements are needed for many others.

There is a correlation between tail movements and foraging. Wagging occurs only in ground-foraging warblers. In some other insectivorous passerines (e.g., pipits and wagtails in Motacillidae) wagging is also found in those species which gather food on the ground. As Andrew (1956) pointed out, wagging has probably arisen independently in different groups of warblers. It occurs in only some species of three different genera: *Seiurus* (Northern and Louisiana Waterthrushes, but not the Ovenbird) , *Basileuterus* (Buff-rumped Warbler), and *Dendroica* (only the Kirtland's and Palm Warblers, as far as we know) . Mayfield (1960) suggests that the Kirtland's Warbler's wagging is a "recognition" signal which is effective "through narrow, horizontal vistas." The Palm Warbler, the waterthrushes, and the Buff-rumped Warbler live in relatively open places where the wagging is probably very conspicuous and possibly functions as an intraspecific "recognition" signal. The Swainson's, Worm-eating, and Kentucky Warblers — ground-foraging species which do not wag — frequent relatively dense habitats where wagging might be a less effective signal.

Tail spreading is found only in species which do much of their feeding by flycatching (e.g., the American Redstart) . The strikingly patterned tails of these species make the spreading more conspicuous and may function in intraspecific recognition. The evolution of tail spreading in these birds was probably facilitated by its frequent employment in flight.

The only two species known to fan their tails exhibit conspicuously associated markings. One, the Hooded Warbler, does considerable flycatching (Bent, 1953). The other, the Fan-tailed Warbler, is a ground-forager consuming ants and traveling in rather dense habitat in conspecific groups; it would not be conspicuous except for the fanning of the tail which exposes the white tip (Griscom and Sprunt, 1957) .

It appears that the type of tail movement is often correlated with foraging behavior and does not necessarily indicate phylogenetic relationships. For example, there are three types of movements in *Dendroica,* and in *Wilsonia,* the Hooded and Wilson's Warblers differ markedly. However, as Andrew (1956) suggests, the form of tail flicking (D-U, U-D) is conservative and is useful as a taxonomic character at the subfamily and family level. This is borne out by the observation that most warblers have a D-U flick (Table 2) .

Head-scratching

There are two regular methods of head-scratching: Direct, by bringing the foot forward and under the wing, and indirect, by bringing the foot up and over the wing. Most passerines scratch indirectly, but direct head-scratching does occur, for instance, in the babblers (Timaliidae).

Nice and Schantz (1959a, 1959b) studied head-scratching in warblers by affixing gummed paper to various regions of the head and noting the responses of the birds. This technique of using an irritating stimulus to elicit head-scratching has been criticized by Simmons (1961) as "carried out abnormally in response to supernormal stimulation." From their study, Nice and Schantz report that nine species of *Dendroica* scratch indirectly (with some variation), as do the Yellowthroat and American Redstart. In *Wilsonia* it is variable, the Hooded scratching indirectly, the Canada directly, and individual Wilson's using both methods. Three species of *Vermivora* — the Tennessee, Orange-crowned, and Nashville — scratch directly. (We observed in the field two other species of *Vermivora*—-the Golden-winged and Blue-winged — scratching indirectly.) The Worm-eating Warbler, Ovenbird, and Yellow-breasted Chat scratch directly. We found that the Northern and Louisiana Waterthrushes change during development, scratching indirectly for a short period when young and later scratching only directly (Ficken and Ficken, 1958). At present head-scratching as a taxonomic character must be used with caution.

Agonistic Behavior

Behavior associated with both attack and escape is termed agonistic and involves both visible and audible displays. Agonistic displays occur during alarm, during violation of individual distance (i.e., when one bird approaches another too closely), and most commonly during territorial encounters, particularly at boundaries.

All warblers studied are territorial during the breeding season, although the degree of territoriality varies. For example, American Redstarts are very intolerant of male intruders and Chestnut-sided Warblers less so. According to Kendeigh (1945), Black-throated Blue Warblers have rather ill-defined territories and are more tolerant of intruders than most other warblers. Such differences in aggressiveness can lead indirectly to differences in displays without direct selection for display differences (Hinde, 1959). The principal difference in the visible agonistic displays of the Chestnut-sided Warbler and Redstart is in degree of exaggeration, those of the Redstart being more extreme. Since the Redstart is both more aggressive and fearful toward its opponents, more exaggerated displays are to be expected.

Visible Agonistic Behavior

Chases — When a male American Redstart enters another male Redstart's territory, the owner simply chases him out. On boundaries, chases take a different form and become meandering pursuits all over the boundary zone. Chestnut-sided Warblers differ from Redstarts in that their chases are less ritualized, being shorter in duration, faster, and more irregular in form with less meandering. In fact, one bird often simply supplants the other — i.e., lands in its place.

Circling — One of the most frequent boundary displays of the Redstart is Circling, which consists of a flight, often with stiffened wing-beats, toward the opponent and a return to the vicinity of the original perch, frequently ending with a glide (Figure 1). Long sequences of Circling in which the two birds display alternately are numerous. Chestnut-sided Warblers occasionally perform Circling toward the opponent, but there is no exaggerated wing movement and the opponent never performs Circling in response. Circling also occurs in the Black-throated Green and Magnolia Warblers, but it is not as exaggerated as in the American Redstart (Kendeigh, 1945). Shephen W. Eaton (pers. com.) reports Circling in the Louisiana Waterthrush and the Ovenbird.

Wings Out — This display (Plate I), in which the wings are held out from the body, occurs in the Redstart and Chestnut-sided Warbler after prolonged encounters.

Gliding — Male Redstarts often perform a Gliding flight for 15 to 20 feet upon leaving the encounter area. The Glides of the Chestnut-sided Warbler are much less common and of shorter duration. Gliding is frequent in both the Blackburnian Warbler and Louisiana Waterthrush (Eaton, pers. com.).

Fights — Fights sometimes occur among Redstarts after prolonged encounters but usually involve no contact; the birds either fly upward or downward together for a few feet, striking toward (but not hitting) each other with bill or feet. In many other parulid species there is contact, the birds sometimes locking together.

Male Soliciting — A male Golden-winged Warbler, defeated after prolonged boundary conflicts, may turn away from an opponent and perform a display resembling a female soliciting copulation. This incorporates quivering wings, raised tail and crown, and lowered breast (Plate I). An uncommon display in the Kirtland's Warbler is somewhat similar but lacks crown raising and adds other components such as gaping (Mayfield, 1960). Male Soliciting has not been reported in other *Dendroica.*

Other Visible Displays — The Redstart and Ovenbird have a Head Forward display, often accompanied by gaping, which occurs in many other birds.

Figure 1. Circling display of the American Redstart. A male (A) circles toward his opponent (B) and returns to the vicinity of his original perch.

Some displays by male warblers. Upper left, Chestnut-sided Warbler, showing Fluff. Upper right, Chestnut-sided Warbler, showing Wings Out (toward opponent). Center, American Redstart giving distraction display. Lower left, American Redstart giving courtship display. Lower right, Golden-winged Warbler, showing Soliciting posture (away from opponent).


W.C. Dilger

The Head Forward display appears during violations of individual distance but not in territorial encounters. The Myrtle Warbler has a display in which the body is horizontal and the tail is spread and held at right angles to the body (Eaton, pers. com.), and a similar display occurs in the Redstart. Yellowthroats wing- and tail-flick during boundary encounters (Stewart, 1953). Mourning Warblers, bob "violently," flip their wings outward rapidly, and fan their tails during territorial disputes (Cox, 1960). The Ovenbird has a threat display in which it tilts the tail upward, droops and slightly outspreads the wings, and "kneads" the feet by alternately raising and lowering them in place (Freeman, 1950). When alarmed, the Ovenbird raises its crown and flicks its wings and tail in a manner strikingly similar to the Fox Sparrow *(Passerella iliaca);* the Redstart, on the other hand, pivots with tail spread.

Crown Raising — Raising of the crown feathers during alarm has been reported in the following species with distinctly marked crowns: Swainson's Warbler (Brewster, 1885), Orange-crowned Warbler (Finley, 1904), Colima Warbler (Snyder, 1957), Myrtle Warbler (Smith, 1955), Chestnut-sided Warbler (Lawrence, 1948), Bay-breasted Warbler (pers. obs.), Ovenbird (Nice, 1931).

Audible Displays

From the extensive literature on "call notes" and "song" of warblers we have selected, condensed, and tentatively classified for convenience various descriptions which we deem useful in the comparative study of behavior. Although we have grouped call notes on the basis of similarity in sound, this does not imply that these calls are identical in different species. Actually, certain calls (e.g., chips) are often, like song, distinctive enough to be diagnostic of species. We have intentionally omitted a whole group of soft vocalizations that function as close-range "signals" because they are too difficult to describe. We have also omitted unusual calls that have been noted in only one or two species. Before a definitive study of warbler sounds can be undertaken, it is obvious that an audiospectrographic analysis of adequate samples under known conditions must be made.

Bill Snap — A snapping sound made by the mandibles closing shut. This has often been associated with attack and has been recorded in the Golden-winged Warbler (Bent, 1953), Parula Warbler (Graber and Graber, 1951), Yellow Warbler (Townsend, 1920), Chestnut-sided Warbler (pers. obs.), Bay-breasted Warbler (pers. obs.), Pine Warbler (Stewart, 1943), Kirtland's Warbler (Mayfield, 1960), and American Redstart (Hickey, 1940). It is rare in the Yellow-breasted Chat (Petrides, 1938).

Metallic Chip — A sharp-sounding chip, usually given in situations of alarm. This has been reported in at least 38 parulid species, representing all the North American genera, with some notable exceptions — Olive Warbler, Yellowthroat, and Yellow-breasted Chat.

Harsh Chip — A more rasping chip, often interpreted phonetically as *check, chuck, tchip, tchek,* and *thut.* This is common in parulids. At least four species give both Harsh and Metallic Chips: Prothonotary Warbler (Brewster, 1878), Ovenbird (Weeden and Falls, 1959), Hooded Warbler (Bent, 1953), American Redstart (pers. obs.). In the last two species, Harsh Chips express less alarm than Metallic Chips.

Zeep — A sibilant sound. We have often observed this in Redstarts before or during a flight. Others often Zeep in return. The *zeet* (= Zeep) of the Kirtland's Warbler, often given during flight, is also a location note, uttered when one individual seeks another which is not visible (Mayfield, 1960). In the Prairie Warbler it is also a location call, nearly inaudible to the human ear except at a range of a few feet (Val Nolan, Jr., pers. com.). The Zeep, more frequent after the nesting season, is common during fall migration in many warbler species (Tyler, 1916; Mayfield, 1960).

Titi — A vocalization sounding like *tititi*. This has been observed during territorial pursuits in the Kirtland's Warbler (Mayfield, 1960), Prairie Warbler (Saunders, 1951), and American Redstart; during flight in the Black-throated Blue Warbler (Griscom, 1938); and during alarm in the Bay-breasted Warbler. In the Redstart these calls resemble a series of modified, rapidly delivered *chips*. Weeden and Falls (1959) report that the Ovenbird, during agonistic encounters, also delivers a series of rapid notes that resemble its *chuck* calls.

Rattle — A loud, harsh, rattling *chur*. Prairie Warblers give this sound in fights between males and sometimes when singing (Nolan, pers. com.). Redstarts occasionally utter the call during the territorial encounters. There are other calls among parulids variously described as "wren-like" (e.g., in Yellowthroat, Chapman, 1907; Golden-winged Warbler, Griscom and Sprunt, 1957) or like a Purple Martin's (in the Kirtland's Warbler, Mayfield, 1960). In the last two species the Rattles occur during territorial encounters.

Snarl and Screech — A hissing snarl occurs in several species as a threat when individual distance is violated (e.g., by a female when the male approaches too closely). We have observed this in the Cerulean Warbler and Redstart. It has also been reported in the Parula Warbler when an intruder approaches the nest area (Graber and Graber, 1951), and in the Black-and-white Warbler when approached by a human being (Stanwood, 1910). Screeches are given by hand-held Redstarts (pers. obs.) and Kirtland's Warblers (Mayfield, 1960) and no doubt by many other warblers when alarmed or frightened by situations not previously experienced.

Song

Song refers to a heterogeneous assemblage of complex, often pleasing, vocalizations which may have a variety of functions, causations, biological significances, and evolutionary histories (Dilger, pp. 85-86). The warblers are an excellent group in which to investigate the ethology of song.

There is an almost perfect correlation between average height at which a species forages and the average pitch of its song (Table 3). Thus a species normally feeding near or on the ground sings at a lower pitch or lower frequency (fewer sound waves per second) than one feeding at a medium to maximum height. Since sounds at lower frequencies travel farther than those of the same volume at higher frequencies, penetrate barriers more easily, and are more widely broadcast, they might be considered adaptations to dense cover (e.g., shrubbery, forest undergrowth) or a noisy environment (borders of a rushing stream). Moreover, ground-foraging warblers are often cryptically colored, a fact which possibly increases the importance of their vocalizations in intraspecific "recognition" (see Dilger, 1956b).

In many *Dendroica* there are two songs differing primarily in the presence or absence of an accented ending, and each song may represent quite a different display. A familiar example is the Chestnut-sided Warbler, one of whose songs has the typical *beecher* or accented ending, the other, though similar, lacking it. There is evidently a seasonal shift, with the predominant type, the one without the accented ending, being given later in the season,

TABLE 3

Correlation Between Foraging Height and Song Pitch of Wood Warblers

Species	*Typical Foraging Height*[1]	*Average Song Pitch*[2]
Blackpoll Warbler	High	8900
Blackburnian Warbler	High	7300
Pine Warbler	High[3]	4150
Blue-winged Warbler	Medium	7675
Black-and-white Warbler	Medium	6900
Tennessee Warbler	Medium	6600
American Redstart	Medium	6200
Black-throated Green Warbler	Medium	6025
Yellow Warbler	Medium	5900
Chestnut-sided Warbler	Low	5125
Ovenbird	Low	4000
Louisiana Waterthrush	Low	4000
Hooded Warbler	Low	4000
Mourning Warbler	Low	3300
Northern Waterthrush	Low	2925
Yellow-breasted Chat	Low	2600

[1] From Griscom and Sprunt (1957)
[2] From Brand (1938)
[3] Feeds from ground to tree tops (Chapman, 1907; Bent, 1953)

usually after nesting has commenced. Other species showing this shift include the Yellow Warbler (Bent, 1953; pers. obs.), Magnolia Warbler (Kendeigh, 1945), Blackburnian Warbler (Kendeigh, 1945), and American Redstart.

In the Redstart and Chestnut-sided Warbler we found the unaccented songs more frequent at boundaries and after encounters than the accented, even early in the season. The unaccented songs (called "nesting" songs by Saunders) are often rather similar — strikingly so in the Chestnut-sided Warbler, Magnolia Warbler, Yellow Warbler, and American Redstart — even though the songs given during territory establishment and pair formation are distinctive.

The Palm Warbler shows a different trend in having an unaccented song early in the season; later songs have an accented ending (Wing, 1933). Information on songs of other *Dendroica* is fragmentary. The Black-throated Blue Warbler (Chapman, 1907), Cerulean Warbler (Chubb, 1919), and Bay-breasted Warbler (Chapman, 1907) have two songs, one unaccented, the other accented. Other species known to have two songs are the Cape May Warbler (Chapman, 1907), Myrtle Warbler (Chapman, 1907), Black-throated Green Warbler (Pitelka, 1940; Saunders, 1951), and Blackpoll Warbler (Jones, 1900). Songs of some of the other *Dendroica* given later in the season are described as being longer or more variable.

Some species of *Vermivora* have a different pattern, although with two songs which differ seasonally. In the Blue-winged and Golden-winged Warblers the later songs are longer and much more variable than the earlier. Later songs in Nashville and Tennessee Warblers differ from earlier songs in being more complex, falling irregularly in pitch, and having all notes equal in time (Saunders, 1951).

Saunders points out that the songs later in the season (i.e., the nesting songs) are often more similar in closely related species (e.g., the Blue-winged and Golden-winged Warblers) than are the earlier territorial songs, and that the nesting songs are probably primitive. The nesting songs of the Tennessee and Nashville Warblers are also very similar, probably indicating a close relationship of these two species (Saunders, 1951).

The Parula Warbler has two songs, one of which has an accented ending, but their correlation with the season, if any, is undetermined. The Black-and-white Warbler gives a monotonous, unaccented song during territory establishment and later, during nesting, changes to an accented song (Allen, 1919; Saunders, 1951). Species of *Seiurus, Oporornis, Geothlypis,* and *Wilsonia* (except the Hooded Warbler, Bent, 1953) apparently have only one perch song (i.e., the song given while the bird is stationary rather than in flight).

Muted or whispered songs occur in many parulids. These differ in context from other songs and are given by males in several circumstances — e.g., near each other at a boundary (Stewart, 1953; Mayfield, 1960), after prolonged chases (Bent, 1953), near the female or nest (Bond, 1937; Kendeigh, 1945), or on the wintering grounds (A. F. Skutch in Bent, 1953). In the Redstart, we found muted songs to be usually of the unaccented type. However, in the Chestnut-sided Warbler (pers. obs.) and Kirtland's Warbler (Mayfield, 1960) muted songs of both types are frequent.

A modified song may accompany copulation in Blackburnian Warblers (Lawrence, 1953) and Redstarts. Pursuit songs, reported in the Louisiana Waterthrush, are more hurried than the regular song (Eaton, 1958), and, in the Prairie Warbler, are shorter (Saunders, 1951).

Flight Song

Warblers with a flight song include the Prothonotary Warbler (Brewster, 1878), Worm-eating Warbler (Chapman, 1907), Ovenbird (Chapman, 1907), Northern Waterthrush (Eaton, 1958), Louisiana Waterthrush (Eaton, 1958), Kentucky Warbler (Chapman, 1907), Mourning Warbler (Bent, 1953), MacGillivray's Warbler (Chapman, 1907), Yellowthroat (Bent, 1953), Yellow-breasted Chat (Chapman, 1907), and Canada Warbler (Eaton, pers. com.).

With the exception of the Nashville, warblers with flight songs do not have two regular song types. As a rule, the flight song is accompanied by a peculiar flight pattern: A rising flight on slowly flapping or quivering wings (with tail bobbing in some species) and typically a direct and silent descent. The song itself, although usually a variable "warbling," often contains elements of the normal perch song. Since it is given more frequently at dusk and/or later in the season and presumably does not function in territory establishment and pair formation, its function in warblers remains undetermined.

Flight songs are absent in *Dendroica* except for an occasional song during a short flight by the Kirtland's Warbler (Mayfield, 1960). The American Redstart occasionally sings during flight (usually after encounters between males), but neither the form of the song nor the pattern of flight is modified. There is frequent song during flight in many *Vermivora* (Bent, 1953), but the song and flight patterns are modified only in the Nashville Warbler (Bowles and Bowles, 1906; Chapman, 1907).

Distraction Displays

Distraction displays ("injury feigning" actions), performed by one or both parents in the vicinity of the nest or fledglings, presumably function to divert the attention of predators. These displays are common in most warblers, occurring in at least 34 species. To the best of our knowledge they have never been reported in the Yellow-breasted Chat.

In most cases these displays involve spreading the tail, spreading and vibrating the wings, and sometimes moving on the ground peculiarly. In both the Prairie (Nolan, pers. com.) and Kirtland's Warblers (Mayfield, 1960), which normally hop, walking occurs during distraction displays — the Prairie Warbler even walks along a branch. Plate I illustrates a distraction display in the American Redstart. During the performance the wings are quivered. The distraction display of the Ovenbird seems to be unique among parulids in that it involves conspicuous ruffling of the back and rump (Hann, 1937). This is similar to the distraction display of the Reed Bunting, *Emberiza schoeniclus* (Andrew, 1961).

Armstrong (1954), in a discussion of the ecology of distraction displays among birds, generally finds them more prevalent in species nesting in situations vulnerable to diurnal predators. He comments on the widespread occurrence of these displays in North American warblers, notes that they are relatively rare in Old World arboreal passerines, and suggests that the difference may be due to the greater prevalence of snakes in North America. If this were true, one would expect distraction displays to occur in many other North

TABLE 4

Courtship Display Components in Male Wood Warblers

Species	*Fluffing Plumage*	*Crown Raising*	*Wing Movements*	*Tail Movements*	*Other Movements*	*Authority*
Prothonotary Warbler	X	X?	Spreading	Spreading		Brewster, 1878
Lucy's Warbler	X?	X	Spreading			Hoffmann, 1927
Magnolia Warbler			Spreading	Spreading		Kendeigh, 1945
Black-throated Blue Warbler			Spreading			Kendeigh, 1945
Myrtle Warbler	X	X	Spreading Raising Drooping			Townsend, 1920 Knight, 1908 Forbush, 1929
Blackburnian Warbler			Vibrating	Spreading		Lawrence, 1953
Chestnut-sided Warbler	X	X	Spreading Vibrating Extending	Spreading Vibrating Raising		Kendeigh, 1945 Pers. obs.
Ovenbird		X	Raising	Drooping	Drooping of head	Gibbs, 1885
Yellowthroat			Flicking	Flicking		Stewart, 1953
Yellow-breasted Chat	X[1]				Head up, sways from side to side	Townsend, 1920
American Redstart	X	X	Raising Waving Spreading	Spreading	Bowing	Pers. obs.

[1] Fluffing of neck only

American passerines subject to similar arboreal predation by snakes, which is evidently not the case. (For another possible explanation, see Discussion.)

Courtship Displays

Courtship embraces a complex of actions having the function of increasing the probability of eggs being fertilized. We will confine our discussion here to male courtship displays, since the female courtship displays, mainly soliciting postures, are so very conservative. (For descriptions of soliciting postures in warblers, see Mayfield, 1960, and Hofslund, 1959.)

Table 4 indicates some of the components of courtship displays in male parulids. These components do not necessarily occur together. Fluffing the plumage (including raising the crown) and moving the wings in various ways (raising, spreading, or vibrating) are common in *Dendroica,* and tend to accentuate the species-typical markings. Although courtship displays are subject to marked natural selection for specific distinctiveness (Marler, 1957), especially in a group such as *Dendroica* with so many sympatric species, this may be achieved through divergence in color pattern rather than by differences in the movements themselves (Hinde, 1959). Displays of the Prothonotary Warbler, Lucy's Warbler, and American Redstart are similar to those of *Dendroica,* while those of the Ovenbird, Yellowthroat, and Yellow-breasted Chat are different. More data will be needed before the displays can be satisfactorily compared.

We have found the courtship displays of the American Redstart to be very complex. One display, the Fluff, consists mainly of fluffing the body plumage, especially the rump feathers. This occurs early in the season and only rarely precedes copulation. A display of the Chestnut-sided Warbler is apparently identical (Plate I). Displays preceding copulation are usually highly variable and include such elements as tail spreading, bowing, and elevating and waving the wings (Plate I).

Courtship feeding occurs in a number of parulids (Lack, 1940; Nolan, 1958). In several species, too, there are modified flights performed near the female. These involve Gliding in the Blackburnian Warbler (Eaton, pers. com.), Cape May Warbler (Bond, 1937), and American Redstart; mothlike flights involving shallow, rapid wing-beats in the Kirtland's Warbler (Mayfield, 1960) and the Northern Waterthrush (Eaton, pers. com.). The Prairie Warbler performs near the female with slow wing beats (Nolan, pers. com.).

The reduction of male aggression is one of the important features of courtship and is an obvious prerequisite to increasing the probability of copulation. As Hamilton (1961) has pointed out, in most North American warblers the sexes differ in color, but in tropical species the sexes are usually colored alike. He believes that there has been selective pressure on northern forms for plumage differences between the sexes which may aid in reducing male aggression toward the female. (Males are aggressive toward birds in similar plumage.) In North American species, which breed in a region whose nesting season is much shorter than that of the tropics, aggression toward the female must be reduced rapidly so that nesting can commence.

Discussion

With the foregoing summary of warbler behavior in mind, certain items of taxonomic and evolutionary significance suggest themselves. It must be remembered, however, that the process of determining relationships requires more than simply drawing up a list of similarities and differences. Characters have unequal values and must be weighed accordingly.

Marler (1957) discusses some of the considerations necessary in using behavioral evidence to help determine relationships. He stresses the necessity of knowing the function of behavioral characters before using them in taxonomy, and also points out that releasers (i.e., color, patterns, and forms of structures as well as behavior), involved in reproductive isolation and selected for specific distinctiveness (e.g., song and courtship displays), are of limited use above the species level. Characters, which are selected for moderate specific distinctiveness and which include mobbing, pre-flight, and aggressive displays and sounds not involved in reproductive isolation, are useful for delineating genera and families.

In *Dendroica,* the song with accented ending, given primarily early in the season and generally more distinctive among different species than later songs with unaccented ending, has probably evolved as a species-recognition signal and probably serves as an isolating mechanism, at least in some species. For example, Yellow Warblers resident in the West Indies usually have songs that "resemble the more nondescript ones of North American forms" (Bond, in Griscom and Sprunt, 1957). In the West Indies there are fewer closely-related warbler species which are sympatric with the Yellow Warbler than on the mainland. Also, the Yellow Warbler, being rather confined to coastal mangroves (Bond, in Griscom and Sprunt, 1957), is more ecologically separated from other warblers. Hence there is not as much selection toward specific distinctiveness in song. This suggests that one of the functions of distinctive songs of *Dendroica* is reproductive isolation.

As Marler indicates, the less species-distinctive song, given later in the season, is probably a much better indicator of relationships — e.g., the cases of the Blue-winged and Golden-winged Warblers (Saunders, 1951), the Nashville and Tennessee Warblers (Saunders, 1951), and several species of *Dendroica* and the American Redstart (see p. 112-114).

It seems likely that the later, less distinctive song is the more primitive of the two (see Saunders, 1951, for comments on this in *Vermivora),* since it would be difficult to imagine selective forces favoring the independent evolution of such similar songs in different species. The later (nesting) song was inexplicably retained and is undoubtedly functional, the two songs now differing in context (see p. 112-114) and hence reflecting motivational differences, at least in the case of the Chestnut-sided Warbler and American Redstart.

When there is more information, both visible and audible agonistic displays may be useful in the taxonomy of warblers. It is also possible that courtship displays may be useful at the generic level.

Parkes (1961) has suggested that the American Redstart is more closely related to *Dendroica* than to the Painted Redstart and *Myioborus.* The close relationship of the American Redstart and *Dendroica* is supported by behavioral evidence. The call notes and song types are very similar as are courtship and visible agonistic displays. The American Redstart is probably a *Dendroica* adapted to flycatching.

The Black-and-white and Parula Warblers have song types similar to *Dendroica,* suggesting that they too may be more closely related than usually supposed.

The Yellow-breasted Chat shows behavior differing from other warblers in the apparent absence of a distraction display, in its distinctive courtship activities, and in its vocalizations. Also, it is the only warbler lacking natal down (Bent, 1953). These facts suggest that it may not be properly classified as a parulid, although there are other warblers *(Chamaethlypis, Granatellus)* connecting it with more typical parulids (Ridgway, 1902).

The Ovenbird shows divergences from the typical warbler pattern in its tail movements, distraction display, and courtship display, all of which resemble those of the emberizines more closely than those of most warblers.

Tordoff (1954a) postulates that the warblers are derived from emberizine finches and Beecher (1953) places the emberizines as a subfamily of the Parulidae. Emberizine and warbler displays warrant comparison. This is facilitated by recent work on the behavior of emberizines by Andrew (1956, 1957, 1961).

Courtship displays of both emberizines (Andrew, 1957) and parulids involve fluffing (particularly of the rump), wing vibration or other wing movements, and tail spreading (in some emberizines). However, most emberizines also have bill raising and lowering as components of courtship displays. These are apparently lacking in warblers (except the Ovenbird). A moth flight near the female occurs in both groups. Courtship feeding occurs in some warblers, but apparently in only one emberizine (Lack, 1940). Although there are similarities in courtship in the two groups, there are also marked differences.

Bill Snapping occurs in many warblers, but has been reported in only one emberizine (Andrew, 1957). Chips are found in some emberizines, as are Zeep calls. Bill lowering occurs at territorial boundaries in some emberizines (Andrew, 1961), but apparently not in warblers. Male Soliciting in agonistic situations occurs occasionally in both groups. Tail flicks of most warblers are down-up, those of most emberizines up-down (Andrew, 1956).

Thus the present behavioral evidence indicates that parulids and emberizines are distinct, but probably closely related groups, with the Ovenbird showing the most behavioral similarities to the emberizines.

Information on warblers, though sparse, suggests that the common ancestor of warblers was probably largely ground adapted. Clues pointing to this possibility are: 1. The prevalence of ground- or low-nesting among arboreal forms (except in *Dendroica).* 2. The prevalence of distraction displays, even in arboreal forms and the hole-nesting Prothonotary Warbler (Grimes, 1936). In other passerines, distraction displays are common only in ground-nesting species. 3. The presence of flight songs in forest-dwelling warblers. Flight songs in passerines show a correlation with open habitats (Van Tyne and Berger, 1959).

More behavioral information will undoubtedly add greatly to an understanding of the evolution (and hence taxonomy) of this group. The interested amateur can contribute greatly by making careful observations of warbler behavior. More information is needed on all phases of warbler behavior, particularly in the areas of tail movements, head-scratching, agonistic displays, and courtship. The type of tail movements and head-scratching in most North American species might be determined in the course of a single season if a sufficient number of observers were to watch for it.

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Scientific Names of the Wood Warblers Mentioned in the Paper

From the AOU "Check-list of North American Birds" (fifth edition, 1957) and "The Warblers of America" (1957) by Ludlow Griscom and Alexander Sprunt, Jr.

Mniotilta varia	Black-and-white Warbler
Protonotaria citrea	Prothonotary Warbler
Limnothlypis swainsonii	Swainson's Warbler
Helmitheros vermivorus	Worm-eating Warbler
Vermivora chrysoptera	Golden-winged Warbler
Vermivora pinus	Blue-winged Warbler
Vermivora peregrina	Tennessee Warbler
Vermivora celata	Orange-crowned Warbler
Vermivora ruficapilla	Nashville Warbler
Vermivora crissalis	Colima Warbler
Vermivora luciae	Lucy's Warbler
Parula americana	Parula Warbler
Peucedramus taeniatus	Olive Warbler
Dendroica petechia	Yellow Warbler
Dendroica magnolia	Magnolia Warbler
Dendroica tigrina	Cape May Warbler
Dendroica caerulescens	Black-throated Blue Warbler
Dendroica coronata	Myrtle Warbler
Dendroica auduboni	Audubon's Warbler
Dendroica virens	Black-throated Green Warbler
Dendroica cerulea	Cerulean Warbler
Dendroica fusca	Blackburnian Warbler
Dendroica dominica	Yellow-throated Warbler
Dendroica pensylvanica	Chestnut-sided Warbler
Dendroica castanea	Bay-breasted Warbler
Dendroica striata	Blackpoll Warbler
Dendroica pinus	Pine Warbler
Dendroica kirtlandii	Kirtland's Warbler
Dendroica discolor	Prairie Warbler
Dendroica palmarum	Palm Warbler
Leucopeza semperi	Semper's Warbler
Seiurus aurocapillus	Ovenbird
Seiurus noveboracensis	Northern Waterthrush
Seiurus motacilla	Louisiana Waterthrush
Oporornis formosus	Kentucky Warbler
Oporornis agilis	Connecticut Warbler
Oporornis philadelphia	Mourning Warbler
Oporornis tolmiei	MacGillivray's Warbler
Geothlypis trichas	Yellowthroat
Chamaethlypis poliocephala	Ground-chat
Icteria virens	Yellow-breasted Chat
Granatellus spp	Red-breasted, Gray-throated, and Rose-breasted Chats
Euthlypis lachrymosa	Fan-tailed Warbler
Cardellina rubrifrons	Red-faced Warbler
Wilsonia citrina	Hooded Warbler
Wilsonia pusilla	Wilson's Warbler
Wilsonia canadensis	Canada Warbler
Setophaga ruticilla	American Redstart
Setophaga picta	Painted Redstart
Myioborus miniatus	Slate-throated Redstart
Basileuterus rufifrons	Rufous-capped Warbler
Basileuterus fulvicauda	Buff-rumped Warbler

SEXUAL BEHAVIOR IN THE CANADA GOOSE

ROBERT B. KLOPMAN

Most waterfowl give conspicuous displays before and after copulation, but precopulatory behavior is the most useful character from the standpoint of the evolutionist. A comparison of this behavior across family lines can be misleading and tend toward oversimplification. Nevertheless, let us introduce the sexual behavior of the Canada Goose *(Branta canadensis)* by comparing its precopulatory behavior with that of other large groups of waterfowl.

Copulation in many species of dabbling ducks *(Anas* spp.) is introduced by Neck-pumping (Heinroth, 1911; Lorenz, 1941). On the other hand, all members of the subfamily Anserinae, which includes whistling ducks, true geese, true swans, and the Coscoroba Swan (Delacour and Mayr, 1945), give Neck-dipping before copulation (Johnsgard, 1960). Lind (1959) and Heinroth (1911) find complete diving under these circumstances in the Shelduck, but most Tadornini (subfamily Anatinae) conform to the typical anserine pattern (Johnsgard, 1960).

The sea ducks (Aythyinae) usually show neither Head-pumping nor Neck-dipping, but the female, during copulation, remains prone on the water, and they have mutual drinking and preening sessions before copulation. Although Myres (1959) indicates that the eiders are probably distinct from both sea ducks and species of *Anas,* McKinney (1961) describes rather typical sea-duck pre-copulatory activity for the European and Pacific eiders *(Somateria* spp.).

Certain exceptions to these generalizations have been described by Lind (1959) for the Red-crested Pochard *(Netta rufina),* by Martin Moynihan (in litt., Johnsgard, 1960) and Helen Hayes (pers. com.) for the stiff-tailed ducks (Oxyurinae), and by Johnsgard (1961) and Myres (1959) for the mergansers (Merginae). The sexual behavior of the Canada Goose has been described by Balham (1954) and by Collias and Jahn (1959). My purpose is to give a more detailed account of the sexual behavior of the Canada Goose and to provide a basis for comparing its sexual behavior with other behaviors in the species' repertoire.

Methods of Study

At Holkham Park, Norfolk, England, I had the opportunity to study a semi-wild concentration of Canada Geese. Although descendants from introductions of both *B. c. canadensis* and *B. c. interior,* these birds were said to "resemble completely" the former (Delacour, 1954). Of the nearly 150

Canadas in the area, most were paired and more than a majority appeared to be in breeding condition. Habitat on the estate was a simulated parkland consisting of short-grass meadow, seeded to a commercial mixture, and occasional stands of mixed hardwoods surrounding a lake about 300 by 100 yards in greatest length and width. Nests in the park were concentrated on three small islands and several bank areas.

My observations, totalling about 300 hours, were made from mid-April to mid-May in 1957, 1958, and 1959. During these periods I gathered 22 complete records of copulation. I took notes in shorthand code and used a 7 x 50 binocular on a tripod mount.

Precopulatory Behavior

Neck-dipping (Lind, 1959) is generally initiated by the male (Table 1). With his neck fully extended upright but curved backward like a shepherd's crook, he sweeps his neck down through a sigmoid curve into the water. The head and neck appear to dip just below the surface until the neck is almost fully extended under the water. He then draws the neck out of the water, employing the same movements in reverse, until the initial position is attained. At this point his breast appears to rise high out of the water. The female gives a display (Figure 1) which appears identical to that of the male but both birds do not usually perform synchronously. Mutual Neck-dipping has a definite rhythm, especially in adult pairs, and may become noticeably faster (more so in the male) just prior to copulation (Collias and Jahn, 1959). Even though in sessions of Neck-dipping one dip quickly follows another, there is a perceptible pause at the upright, crooked position of the neck.

TABLE 1

Variability in Copulatory Behavior of the Canada Goose, Based on 22 Sequences

	Activity	*Number of observations*
1.	Male initiates Neck-dipping	15
	Female initiates Neck-dipping	3
	Unknown	4
2.	Female continues to Neck-dip as male prepares to mount	15
	Female stops Neck-dipping as male prepares to mount	7
3.	Mounting or grasping attempted only when female ceases to move away from male	22
4.	Mounting precedes grasping	8
	Grasping precedes mounting	1
	Unknown	13
5.	Postcopulatory display by male	20
	Postcopulatory display by female	4
	Absence postcopulatory display by male	1
	Unknown	1
6.	Male emits groan with postcopulatory display	3
	Female emits groan with postcopulatory display	2
	No call detected from either	17
7.	Bathing of female follows copulation	20
	Bathing of male follows copulation	0
	Unknown	2
	Total observations	158

When the male begins Neck-dipping he usually receives a similar response from his mate, but as she does so, she swims slowly away from him or occasionally makes a series of turns. The turning of the female may result in the birds facing each other during Neck-dipping, although this is not the most common orientation. In most cases he follows close behind her and sometimes slightly to her side. Should she swim far ahead of him and/or stop Neck-dipping, the male may stop displaying. Although mutual Neck-dipping usually lasts only a few minutes, it occasionally continues for about 15 minutes. In fact, if the male receives only sporadic Neck-dipping from his mate, he may Neck-dip intermittently for as long as half an hour. In most cases, however, the female's pace slackens after about 90 seconds of continuous Neck-dipping. Shortly thereafter she no longer swims away from him (Table 1), though she continues to display. The male then swims quickly alongside his mate, ceases to display, and prepares to mount. The transition from Neck-dipping to mounting occurs quite suddenly, and is not accompanied by the prone position of the female as is the case with *Anas* spp. Although I kept no record of the number of unsuccessful mountings, they were definitely associated with the termination of sexual activity in the female.

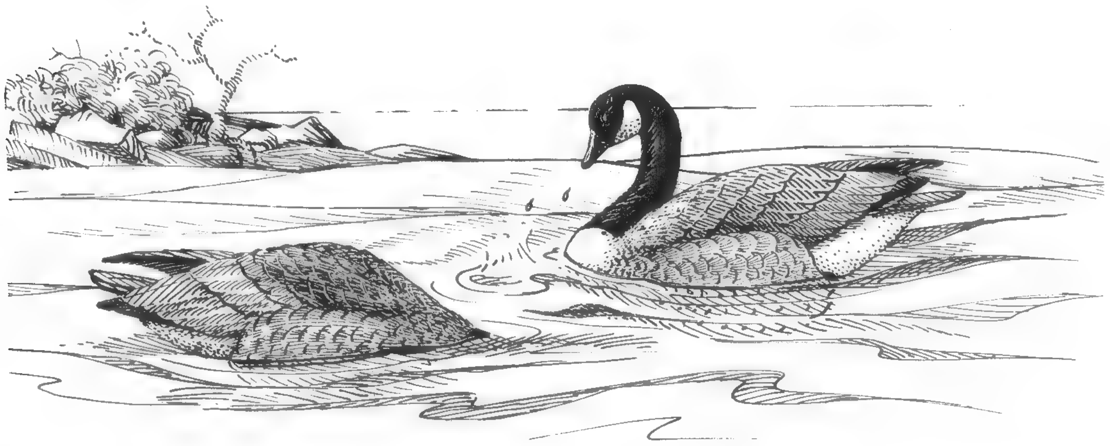

Figure 1. Precopulatory Neck-dipping, showing the female in the bowed upright position, and the male dipping his head and neck under water.

An adult male usually grasps the female's feathers a few inches below the nape and, at the same time, steps on her back, first with one foot and then the other (Figure 2). Meanwhile, her body, and often her head, becomes submerged as if the male had forced her head under water. When the female's head goes under water, her rump rises, thus facilitating cloacal contact. The male then moves his rump under and perpendicular to hers as cloacal contact is made. As in most waterfowl, copulation consists of a single vigorous thrust by the male. During this activity, the male's wings droop slightly and are extended laterally. Immediately after copulation, and sometimes earlier, the male's primaries often droop so markedly that they enter the water. Copulations last about 15 to 30 seconds and appear to be terminated by the female. She usually raises her head from the water, and her rump drops to its normal resting position. The male seems to topple from her back, releases her nape feathers (usually when alongside her) and raises his primaries to the position typical of postcopulatory display (see below).

Postcopulatory Display

The postcopulatory display, described by Heinroth (1911), consists of four components: (1) Breast raised out of the water, (2) neck extended upward but inclined backward slightly, (3) closed bill directed almost vertically

Figure 2. Canada Geese copulating.

upward, and (4) partially-closed wings which are arched laterally away from the body (Figure 3). Generally the male, occasionally the female, assumes this display immediately after he dismounts (Table 1). Johnsgard (pers. com.) suggests quite correctly that the female's postcopulatory display is not as highly ritualized and vigorous so that perhaps these data reflect differences in kind of display rather than the presence of it. Usually the male faces the female in the postcopulatory display, and sometimes gives a soft, wheezy groan. The female gives this vocalization nearly as often. Normally no calls can be heard (Table 1).

After the male dismounts, the female usually turns away from him and commences vigorous bathing followed by profuse preening. The male, on the other hand, usually follows the postcopulatory display with simultaneous stretches of both wings, a series of wing-flaps, and then vigorous bathing and preening. Preening sessions after copulations are generally concluded in unison, whereupon the pair swims to a feeding area.

Discussion

Sexual behavior may be observed at any time of day, but I saw it most frequently during the morning from 7:00 to 10:00. Collias and Jahn (1959) found that more than half of all copulations occur before 10:00 AM. These authors also found sexual behavior mostly restricted to the pair's defended area, while I found these activities to occur normally just *outside* of what I presumed to be defended waters. Unfortunately this cannot be supported by numerical data, but it persistently reoccurs in my notes. If this is actually the case, one might logically ask whether the displaying geese were disturbed, but I found only one threat upon a pair displaying sexual behavior and one overt attack out of many such observations. However, both disturbances lead to an immediate cessation of sexual activity. I conclude that, while these geese performed mutual displays and sexual behavior (specifically, copulation) just outside their defended areas, they were probably not encroaching upon the defended area of neighboring pairs.

Neck-dipping, like many other goose activities (bathing, preening, feeding, etc.), may have a "contagious" effect on near-by geese, thus causing them to show similar behavior. This is reported common by Collias and Jahn (1959), but was recorded in only seven out of 22 cases in the present study.

Such facilitation of Neck-dipping seems to have a stronger effect on unpaired geese than on paired individuals.

I also found little evidence of promiscuous sexual behavior (Neck-dipping and copulation with geese other than their mates), but I have found, as has Lorenz (pers. com.), frequent evidence of sexual promiscuity among crowded captive geese. Occasionally I saw a male Neck-dip with a bird other than its own mate, but only once did I see attempted copulation under these circumstances. I observed "attempted rape," so often reported for certain duck species (Geyr, 1924; Dzubin, 1955; Weidmann, 1956), only once in wild Canadas. Mutual Neck-dipping and mounting attempts may occur among yearlings and two-year-olds as well as among sexually mature birds (see also Collias and Jahn, 1959). Furthermore, young pairs of captive birds are often homosexual (see Dilger, 1960, re: *Agapornis*). While these conditions may also prevail in the wild, there is yet no evidence that they do.

Lorenz (1959) reports the frequent formation of "trios" among captive geese and describes their unusual behavior. Trios of sexually mature Canadas appear to be rare in the wild. Of the two trios I observed of unknown sex, in different years, each was composed of a mated pair and a goose I judged to be at least two years old (age estimated by breast contour and the absence of the yearling's strident vocalizations). In each case, the single birds did not perform Greeting or sexual displays with the pair. Such birds usually stayed on land within a few feet of the nest sites of a pair and sometimes fed with them.

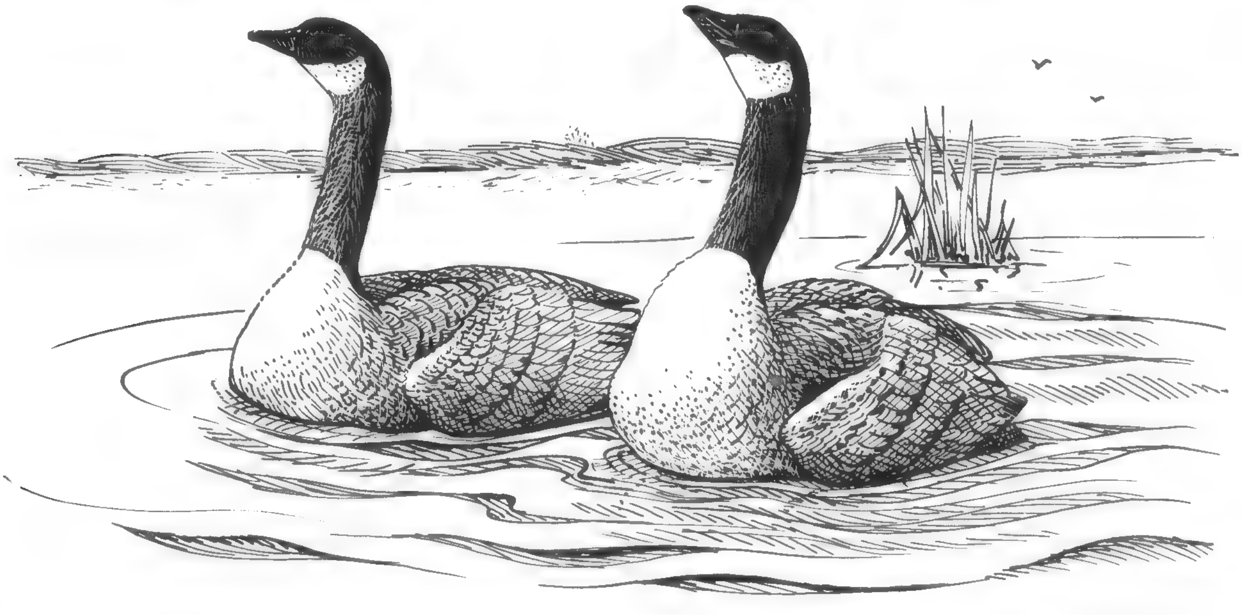

Figure 3. Postcopulatory display by Canada Geese.

Another detail of sexual behavior should be pointed out. Captive Canadas kept away from water may occasionally show Neck-dipping. Naturally this is aberrant, because Neck-dipping and copulation in geese are normally conducted on water.

The similarities and differences between Neck-dipping and bathing should be examined because Collias and Jahn (1959) report a resumption of mutual Neck-dipping *after* copulation. These activities appear to be similar mainly because they involve dipping the head into the water. During bathing, the neck is *not* extended but kept fairly close to the body. The movements are *not* the up-and-down movements of Neck-dipping, but rather back-and-forth swings of the head. Furthermore, the breast during bathing is usually held high as the head is drawn from the water, with the result that when the neck is pulled low over the back, water droplets can easily be observed falling on the back and wings. The position of the wings also differs. Whereas in Neck-dipping the wings usually remain in their "pockets," in bathing they are held out laterally and are often quivered.

Important also is the relationship between sexual activities and the Greeting ceremony (Heinroth, 1911; Lorenz, 1959), which involves a stereotyped posture, vocalization, and orientation, and can be observed in pairs as well as in groups of geese. Greeting occurs in several behavioral situations, but most often is seen after a vigorous fight between displaying individuals. Evidence from many sources reveals that this is a complex pattern of social, aggressive, fearful, and sexual motivations (Klopman, 1959, 1961). At the conclusion of this display in spring, the male commonly grasps at the female's nape although the female usually pulls away so that he then nibbles only at her scapulars and flank. Identical behavior is often observed after aggressive calling by the pair at the nest site. In one instance after Greeting in spring, I observed not only the male grasping for the nape but attempting to mount. The nibbling of the female's plumage is perhaps what Lorenz (1959) alludes to when he states that there are "remnants of sexuality" in the Greeting display. Sexual motivation of the male at least is seemingly not restricted to the sequence of behavior involving copulation.

Further support of this belief is found in a spring vocalization of the male. In winter, during agonistic encounters, either sex may utter the Hucka (the female's call is higher pitched). Females normally will use this call during aggressive situations in the spring, but the male's spring calling changes to *a-wa-a-a-aw-a-a-a*. This is usually given loudly and moanfully when intruders approach the general area of the nest site. It may also be given by the male of a pair on a feeding area, should the territory be violated during his absence. The Aw-a of the male probably has elements of sexual motivation because it has the same "groaning" quality characteristic of the soft call that is frequently a component of the postcopulatory display.

Sexual displays are expected during the pair formation of most vertebrates. Certainly this holds true for most duck species (Hochbaum, 1944; Johnsgard, 1960; and many others) and a few of the true geese (Lorenz, 1959, for example, reports an "angular neck ceremony" during the pair formation of the Graylag Goose, *Anser anser*). No homologue of this display has been observed in the Canada Goose, although Heinroth (1911) and Lorenz (1959) contend that the Triumph ceremony or Greeting serves an important role in the pair formation of *all* geese. They fail, however, to show the unique character of Greeting in this situation as opposed to Greeting found in many other contexts (Greeting among brood mates or flock companions). Pair formation, at least in the Canada Goose, usually appears spread over a period of months and may be vitally affected by early associations established in family groups and combined broods and flocks of sexually immature birds that form during the breeding season. One presumes, nevertheless, that the process of pair formation may be accelerated when pairs lose their mates early in the hunting season. As yet, however, the subtle association between pair formation and sexual behavior has not been discovered.

Acknowledgments

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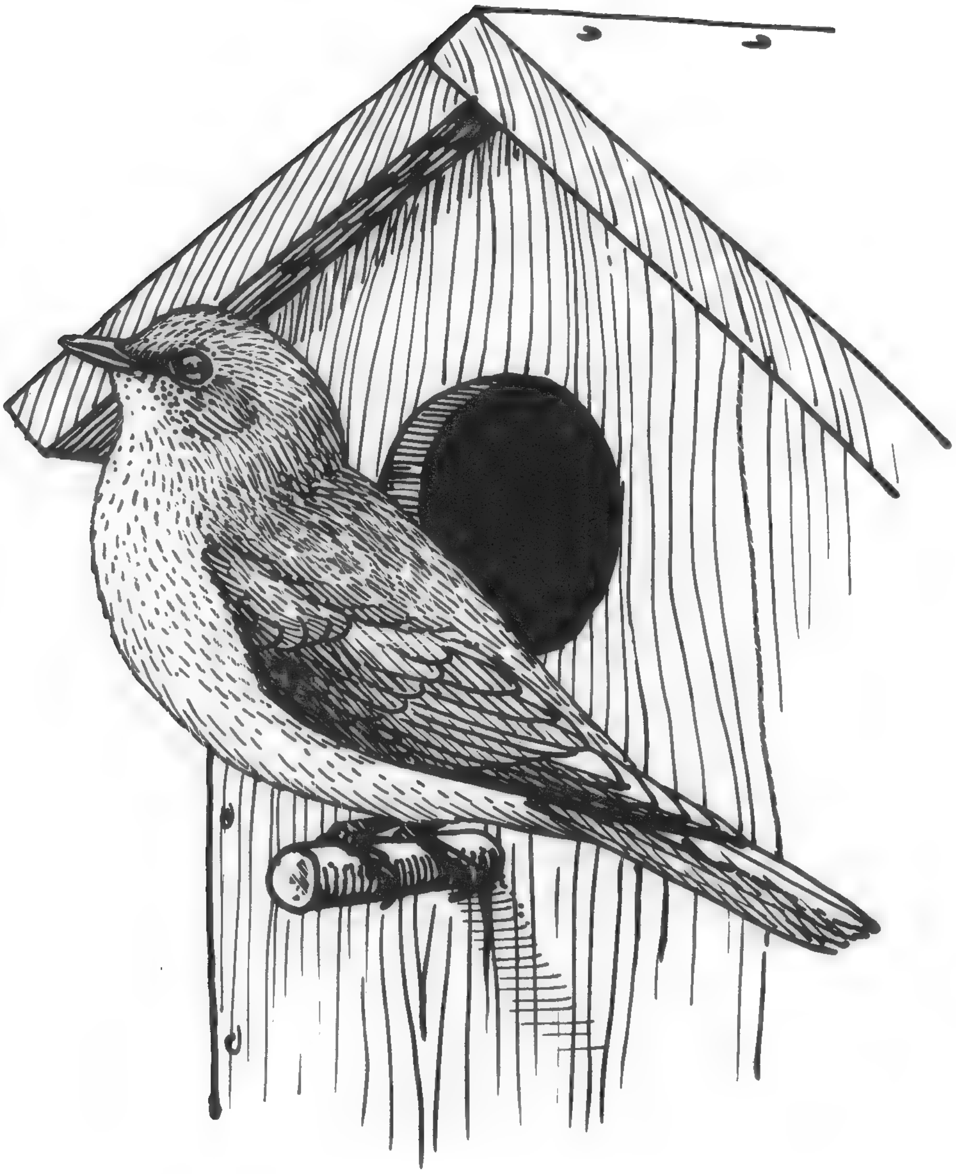


BEHAVIOR OF THE EASTERN BLUEBIRD AT THE NEST

JAMES M. HARTSHORNE

In the course of my investigations on the vocalizations of the Eastern Bluebird *(Sialia sialis)* in the region of Ithaca, New York, I paid considerable attention to the bird's behavior at the nest. This was necessary in order for me to understand fully the species' entire behavior — a prerequisite to determining the function, biological significance, causation, and development of the Bluebird's calls. The results of the behavioral aspects of my study at the nest in both field and laboratory are presented in this paper.

Materials and Methods

Tape recorders were used not only to record the vocalizations of the birds but for practically all my note-taking in the field and laboratory. This practice allowed more accurate and detailed notes because I could obtain uninterrupted behavioral sequences.

Most of the field data I obtained with the aid of special observation nest boxes and blinds; the remainder were acquired in conventional fashion either from a cloth blind or while exposed to view within 10 to 20 yards of the nest site. Birds taken into the laboratory were placed in Hartshorne Sound Isolation Chambers located in a sound-isolation room, and subsequent observations were made directly from these chambers. All eggs taken from the field were collected within a few days after being laid, and were transferred to an incubator in the same sound room.

The special field-observation nest boxes and blinds were designed to permit recording the vocalizations of the young from the time of hatching, as well as adult vocalizations associated with the young and with one another while in the nest cavity. These nest boxes had one side consisting of a removeable glass panel. Other less obvious refinements included a built-in microphone for tape recording the vocalizations within the nest box and an electronic strobe light for photography.

After a pair of birds had taken over one of these modified nest boxes, a special rigid blind was gradually moved up next to the box. Eventually the box was affixed directly to the blind (see Figure 1) so that its glass side overlapped a cutout in the blind. This arrangement enabled me to watch the wild birds within a few inches.

Figure 1. Special field nest box and blind used to obtain behavioral data at a Bluebird's nest. Circular holes provide ventilation for the interior of the blind and connect with internal light baffles. Square hole in the blind over the nest box contains "one-way glass," which permits observing the behavior of birds on the roof of the nest box.

Figure 2. Hartshorne Sound Isolation Chambers, showing method of observation (through "one-way glass"), sound monitoring, and recording of data.

Since the inside of the blind had to be kept totally dark to prevent the birds in the box from seeing me in the blind, the ventilation of its interior posed somewhat of a problem. Two systems of ventilation were employed: Forced-air ventilation was used where electricity was available; otherwise, light-tight ventilation ducts were built into the blind, so as to provide air circulation from outside.

Each sound isolation chamber (Figure 2) used in the laboratory consists basically of two more-or-less air-tight shells, one within the other. Each shell contains a rubber-gasketed door with a viewing window. The animal cage rests at the interior of the second, or inner, shell. Each sound chamber unit has its own lighting and ventilation systems, a microphone for sound monitoring and recording, a speaker to feed sounds to the birds, and electronic strobe lights for photographing their behavior.

During the breeding season simple nest boxes with one glass side were placed inside the sound chambers so that the glass side of the box faced the viewing window of the chamber. This arrangement permitted good visibility of the behavior both outside and inside the nest boxes within the sound chambers. Through the use of "one-way glass" built into the viewing windows of the chambers, the birds were kept free of any observational disturbances.

These investigations were made during a four-year period. Using the special observation boxes and blinds, I studied two pairs of wild birds in 1959 and two other pairs in 1960. From 1957 through 1960 I obtained additional data on well over two dozen wild pairs and many individuals outside the nest cavity. For information on Bluebirds in the laboratory, I studied nine different pairs as follows: Two, 1958, 1959, 1960; three, 1958, 1959; four, 1959, 1960. All were housed in sound isolation chambers with one pair to a chamber.

Pre-Nesting Behavior

Due to the extreme caution that had to be exercised in setting up the field-observation system I have described, it was not possible to observe the behavior of wild birds on the nest prior to late incubation. In the laboratory, on the other hand, this was easily possible because the birds were in chambers where they had lived since the time they were hatched and could be kept under close scrutiny through all stages of nesting. Thus my observations preceding the incubation period are based largely on birds maintained in the laboratory, supplemented by data from field observations made by me and others near but outside the nest cavity.

In her study of the life history of the Eastern Bluebird, Thomas (1946) emphasizes the importance of the nest site, particularly the entrance, throughout the year. Just before nest-building a pair makes frequent trips to the nest site and peers into the entrance hole. Before a cavity has been definitely selected, the male is likely to precede the female to a hole, though closely followed by her. Either bird is excited by the other looking into a hole. Males are particularly excited when their females "check" the hole before nest-building. Such excitement is evidenced by wing-waving and vocalizations. At its peak the vocalizations change to high-pitched squeals. Wing-waving may involve one or both wings (see Plate IA), but the performer does not appear to orient to its mate.

Although either bird may go into the nest cavity during these visits, by far the greatest number of visits simply terminate with "inspections" of the hole. Bits of nesting material are sometimes carried to the cavity by either sex during this period; if the cavity is entered, the material may be left behind. If old nesting material remains in the cavity, one of the birds is likely to remove

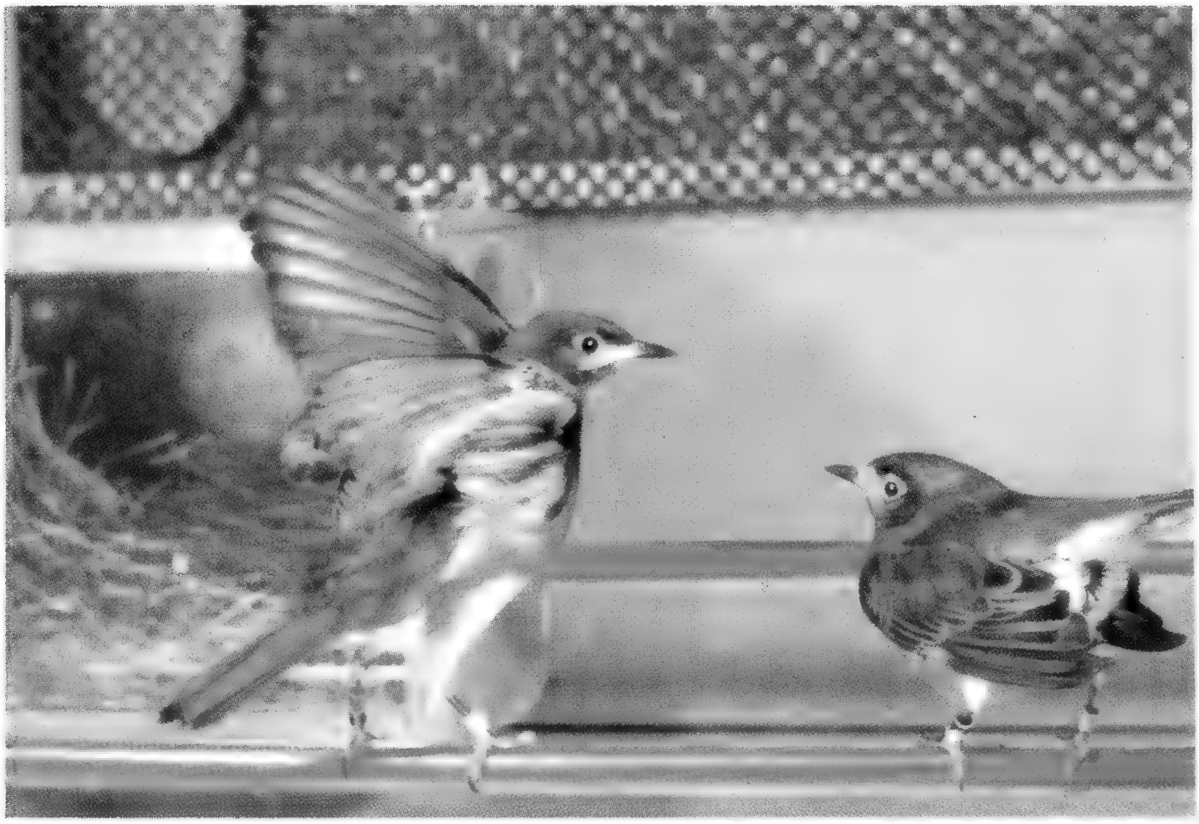
Figure 3. Copulation of Bluebirds in a sound chamber during the egg-laying period. The nest contains four eggs.

a piece or two and mandibulate it for a short time on some perch outside before letting it drop to the ground. My observations in the laboratory indicate that during this early period the birds may simply look about the interior, peck at one thing or another, or sometimes go through preliminary nest-shaping movements. Although the last mentioned are more characteristic of females, this behavior was performed in sound chambers by two males. I watched these males, plus one from another chamber, go through nest-shaping movements in the corners of their cages or food bins before nest boxes were provided.

An important part of the normal sequence of events before nest-building is courtship feeding in which the male feeds the female. This may continue well into the nestling stage (see Plate IB) when its main function changes from mutual stimulation to food transference, with the young acting as the final recipients. The male may initiate the behavior without any apparent signal from the female, but there are times when the female obviously stimulates this response from the male by assuming the begging posture typical of the young. This involves a crouched body held more or less horizontally, fluttering wings, peeping sounds, and gaping.

Copulations may begin before nest-building, but unlike courtship feeding, terminate part way through the incubation period. Successful copulations are usually initiated by the female which first assumes a soliciting posture. This closely resembles the posture used in begging for food. She crouches, holds her body in a more or less horizontal position with bill in line with the body, keeps her wings fairly still and slightly drooping with their tips below the base of the tail, depresses the feathers on the crown and back, and holds the tail from in line with the body to about 45 degrees upward (see Plate IA). Meanwhile she utters peeping sounds, similar to those used in food-begging.

During copulation the male is directly over the female, with his body in line with hers and his wings outstretched for balance (Figure 3). I saw one of my laboratory males peck at the head of the female during this act, but I did not see this in other Bluebirds. Copulation normally takes place on some perch



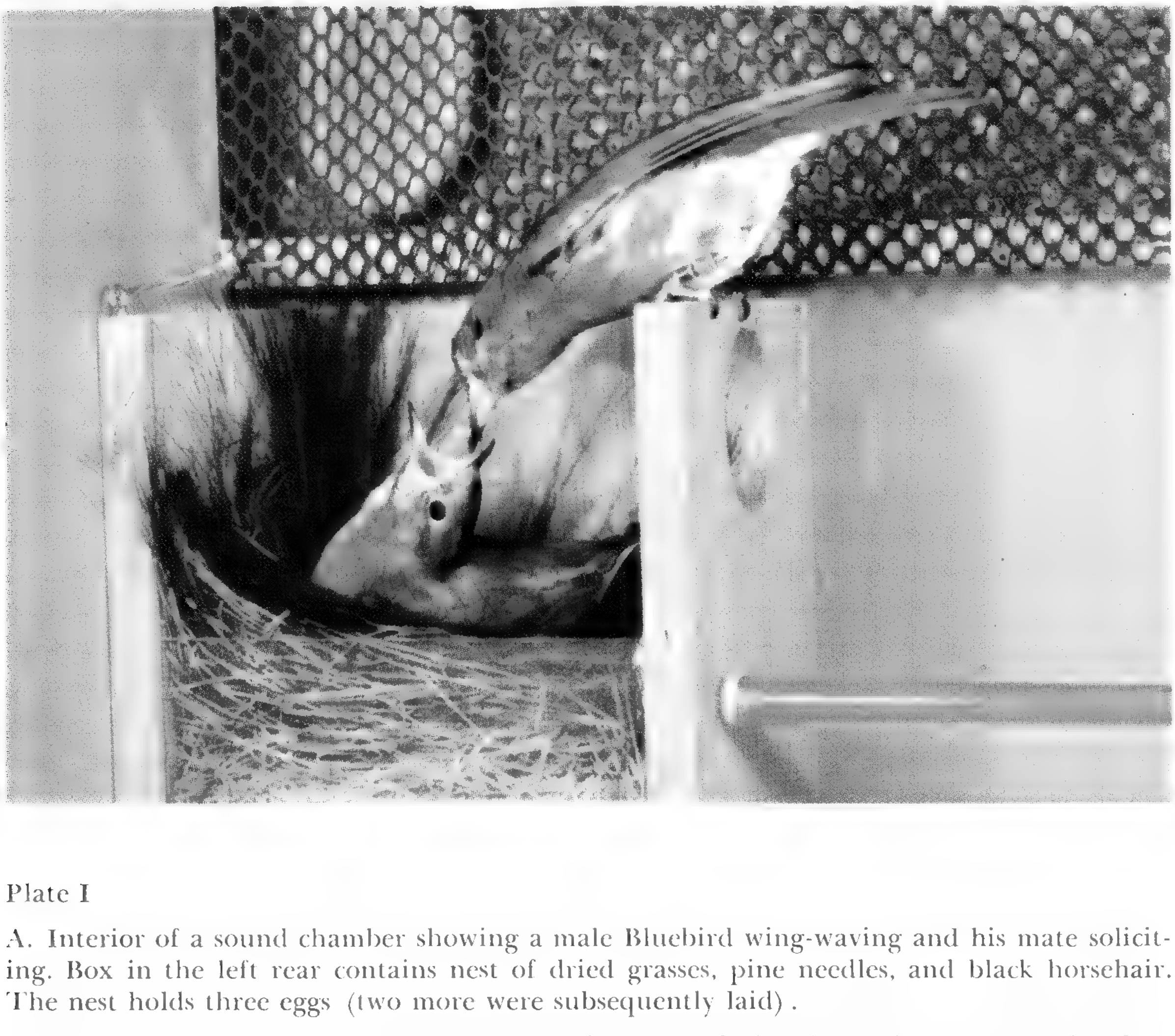


Plate I

A. Interior of a sound chamber showing a male Bluebird wing-waving and his mate soliciting. Box in the left rear contains nest of dried grasses, pine needles, and black horsehair. The nest holds three eggs (two more were subsequently laid).

B. Male Bluebird feeding his mate on nest in a sound chamber. The nest contains four 2-day-old young. (Top of box has been removed and the glass side cut down to facilitate entry and egress of adults.)

outside the nest cavity. However, I have observed at least two copulation attempts by a male while the female was incubating, but they were quite unsuccessful as the female made no effort to respond.

Nest-Building

Bluebirds have been known to start nests in a wide variety of cavities from hollow gate and fence posts, drain pipes, empty tin cans and jars, rotten stumps, and cannon barrels to the more usual tree cavities and man-made nest boxes (see Bent, 1949). Almost any cavity that these birds can squeeze into is a potential nest site even though many are far from being ideal or even suitable.

It is often incorrectly implied or stated (e.g., Bent, 1949; Hamilton, 1943; Knight, 1908) that the male and female normally share in the construction of the nest. Thomas (1946) is more accurate, stating that "An occasional male takes grass to the box at the start of construction, but as a rule the female does all the building."

Probably most observers, on seeing a sprig or two of nesting material taken into the nest cavity by the male, have been led to believe that the male assists in nest construction. I have seen only one wild male carry any substantial amount of nesting material into the nest cavity, but I have frequently seen wild males with some nesting material in the bill before and during nest construction.

Such male behavior — carrying nesting material — is probably the result of low motivation for nest-building, because he usually drops the material after some mandibulation while perched in a tree or on the nest box or while on his way into the nest cavity. Sometimes he eats the material. At other times he may enter the nest cavity with empty bill and come out with a piece which he may mandibulate before letting it drop to the ground. It was not unusual to see males come out with the same piece of material taken into the cavity.

Although breeding males in my sound chambers often carried bits of nesting material and some even performed nest-shaping movements, not one contributed to the actual construction of a nest.

In the case where one wild male carried a substantial amount of material into the nest box, he at least contributed considerable material to the cavity, though I did not determine whether he actually used it in construction, as I was not watching activities in the interior of the box at the time. My data reveal that this male was not as persistent in his carrying as the female and frequently joined her at the box with empty bill, as do most wild males, when she arrived with her load.

Nest construction by wild birds normally takes four or five days, although as few as two days (Mousley, 1916) and as many as 12 days (Smith, 1937) have been reported. Subsequent nests in a season are built progressively more quickly. It is rare for a female to use more than part of a day in construction. One female built a nest in two days in the laboratory. The first day she worked rapidly and completed the bulk of the nest. The second day she was less active and rather leisurely put the finishing touches to the main structure and added the lining.

Bluebird nests in the wild are nearly always rather loose structures, with or without a distinct lining. The main part of the nest is ordinarily made of dried grasses although pine needles are commonly used when readily available. The lining, if present, usually consists simply of finer grasses, but horse hair and an occasional feather may be used. The cup dimensions are fairly consistent, but the outside dimensions vary widely depending on the size of the cavity chosen. In the laboratory I provided Bluebirds with essentially the same materials, and the resultant nests conformed generally with those in the wild.

Egg-Laying Period

The eggs of wild Bluebirds are usually laid by mid-morning. I found that clutches in the Ithaca area ranged from three to six eggs, with four and five being the most common size. The second clutch tended to average one egg less than the first.

During the egg-laying period in the laboratory, females frequently sit on the nest, spending from a few minutes to 20 minutes each time. The total amount of time sitting on the eggs from the laying of the first egg to the last is considerable, especially in the case of the eggs first laid. No sittings are accompanied by the usual settling movements and spreading of abdominal feathers that are normally associated with incubation. Since I could not see whether a female opened her feathers to expose the brood patch or determine whether she warmed the eggs sufficiently to start embryological development, I cannot say definitely that incubation did not occur. I can only point out that the eggs always hatched at about the same time, strongly suggesting that these sittings do not result in incubation.

Figure 4. Wild female Bluebird performing a tremble-thrust. The nest contains five 8-day-old young.

A behavior that I call the "tremble-thrust" consists of the adult thrusting its bill with a trembling motion straight into the nesting cup (see Figure 4). Sometimes the thrust is delivered above the eggs (or young in later stages), at other times among them, but it is always confined to the nest cup. Most thrusts are given with conspicuous force, the bill penetrating to the bottom of the nest where it may be heard vibrating the floor of the box.

I first noticed tremble-thrusts in the wild shortly after the first observation box and blind were installed at a nest, which contained young at the time. Later I saw it during the nestling period of every nest observed. In the laboratory the earliest tremble-thrust was seen shortly after the first egg was laid and was noted in other sound chambers by the end of the egg-laying period. Owing to the fact that all breeding females in the chambers exhibited tremble-thrusts during early incubation, I am inclined to believe that all wild females do the same from the start of incubation, perhaps earlier.

During incubation, tremble-thrusts presumably function to turn the eggs. Thereafter, when there are nestlings, they take on other possible functions which I shall discuss later in this paper.

Wild males were never seen to give tremble-thrusts at any time during the nesting period. In the laboratory, however, a male in one sound chamber began doing tremble-thrusts the morning his mate laid her fifth and last egg. From this time on he performed this act, along with "bill-probing" the eggs, quite regularly when the female was off the nest. Strangely enough, his mate was not seen to give tremble-thrusts until the fifth day of incubation, whereas breeding females in other chambers showed this behavior earlier, in the egg-laying period. Although this female's frequency of performance was relatively low to begin with, by the end of the incubation period she was giving tremble-thrusts about as often as the other females.

Incubation Period

Wild Bluebirds generally start incubating with the laying of the last egg. Once begun, the amount of time that the female spends on the nest at any one sitting varies considerably and is apparently influenced by the weather. The incubation period is ordinarily from 13 to 15 days although extremes of 12 and 16 days have been noted.

Courtship feeding continues through incubation. I observed it a number of times in the wild although Thomas (1946) recorded it only twice. I saw it more frequently in the laboratory, possibly because of the inforced proximity of the pairs or my keeping them under closer surveillance, or both. Feedings took place as often on the nest when the female was incubating as they did out of the nest box.

It has been asserted by numerous authorities (e.g., Bent, 1949; Knight, 1908; Smith, 1937) that male Bluebirds incubate. To my knowledge, these statements are not based on seeing males sitting on eggs, but rather on seeing males enter nest cavities, as they commonly do for short periods when females are off the nests. My observations reveal that males entering nest boxes do not actually incubate.

While watching nesting pairs in my field observation boxes and sound chambers, at no time did I see males settle down on the eggs. Usually their visits to the nest boxes were quite short, from less than a minute to several minutes or more. In one of the sound chambers a male was seen to stay on the nest for eight minutes on the fifth day of incubation. The very next day he got on the nest for six minutes. During most visits to the nest, males simply look around as if they were on a "tour of inspection." Occasionally they peck at the nesting material and eat a piece or two on the nest or remove some from the box. I have only seen one male touch the eggs. In this case he not only performed tremble-thrusts, as mentioned earlier, but also probed the eggs, an act that was characteristic of all females watched.

In making spot checks of the nest boxes in the wild during the late evening hours when the birds had settled down for the night, I have occasionally discovered both male and female on the nest, during the incubation as well as the nestling period.

My checks on one nest in 1961 indicated that the male was a regular occupant of the box at night. On 14 July, with eggs about three days from hatching, I found him at 8:30 PM standing on the nest alone. At 9:10 PM I found both the male and female on the nest. They were in the process of shifting their positions when I looked in, so I could not determine which one was on the eggs before I arrived. Examining both of them for brood patches, I found that the female showed a distinct patch, the male none. On 16 July at 9:00 PM both birds were in the box again, the male crouched over part of the eggs, the female huddled in the corner in apparent fear. Finally, on 17 July at 8:45 PM the male was seen sitting on the edge of the nest with the female in the cup covering the three young and one pipped egg.

Under somewhat unusual circumstances, a laboratory male was once observed sitting on a nest. I had removed the top from a nest box in a sound chamber containing this male and his mate with four young and one pipped egg. Usually the male settled down for the night on the top of the nest box. But this night, as the lights were being dimmed prior to being put out, the female headed straight for the box and settled down on the nest while the male remained sitting on one of the perches. After the lights had been extinguished, I heard a commotion in the chamber through my sound monitoring system. Checking the interior with a flashlight, I found the male sitting in the cup and the female beside him on the edge of the nest. The next morning, when the lights first came on, both birds were found in the same positions.

With the lights out, the male, in attempting to take up his usual position on the top of the box, which was no longer there, landed on the female directly below. This no doubt startled the female, causing her to move out of the cup. The subsequent jockeying for a position on the nest resulted in the male getting the female's place. The last egg hatched overnight. In the morning, after the lights went on, all the young were found cold. This suggests that males are incapable of providing sufficient warmth for the normal development of either young or eggs, and that the few cases in the wild where males were seen nearest the eggs may have been the result of disturbances by the observer.

The female turns her eggs in various ways. Her most efficient method is to stand over the eggs with spread legs while raking her bill through them toward a point midway between the legs. A more frequent method is to probe the eggs gently with her bill. Tremble-thrusts, which are one of the most common acts performed at the nest by the female, serve at times to turn the eggs slightly but at other times simply to displace them.

Wild males were never seen to probe eggs, give tremble-thrusts, or even touch eggs with the bill while on the nest. None of my laboratory males, except in the case already noted, showed any interest in the eggs.

While incubating during the day, females may preen, stretch, and yawn. If there are no disturbing influences, a female may close her eyes, with the appearance of sleeping. Such periods of calm usually do not last more than a few minutes at a time, since the slightest sound will cause her to open her eyes and appear alert. Females frequently mandibulate some nesting material while sitting on or standing over the eggs, and occasionally, as in the case of males, will swallow a piece or two. On several occasions I noted adults regurgitating nesting material some minutes after it was ingested. When this takes place in the field outside the nest box, no attention is given to the pellet as it is generally lost to sight. In the laboratory, the pellet may be picked up again and reswallowed, sometimes after first pecking it apart.

The Hatching Process

In most cases young Bluebirds emerge from their shells unaided by their parents. However, I have observed wild females speed the hatching process by pecking at the shell and forcefully removing the young.

Within a very short time after a bird has hatched, the female disposes of the shell by flying off with it and dropping it some distance from the nest, or by eating it directly on the nest (Plate IIA). The following is an account from my notes on a wild female on 23 May 1959:

"At 7:02 AM the female stands up and starts nibbling on the crack that has developed in one of the two remaining eggs (three young have already hatched). She keeps pecking and nibbling at little bits of shell from around this crack and, as she does so, the latter becomes more pronounced. She draws a little blood during this procedure and eats this as she continues. From time to time she tears off bits of the underlying membrane which she also eats. She keeps this up for another minute and then performs a tremble-thrust into the nest cup right next to this egg. This appears to roll the egg slightly. The female now settles back down on the nest.

"At 7:07 AM the female stands up again and starts pecking around the edge of the crack that is now well developed. She eats some more pieces of the shell and membrane and occasionally pulls at the wet down that protrudes from the crack. She continues this until the egg is split well open. She now rolls the egg over with her bill and tries to pick it up while eating away on the membrane. Finally, at 7:10 AM she succeeds in picking up the whole shell as one half drops into the other. She appears to begin eating the shell, but perhaps she's just adjusting it in her mouth as she then flies out the hole with it."

Between the above and the following accounts each parent made a trip to the nest with food and the female once again settled down on the nest.

"At 7:25 AM the female stands up and gives a tremble-thrust down into the cup near the last remaining egg. The egg breaks in half during this process. She picks up one half of the shell and, with head and bill movements, works the piece well up between the mandibles. She breaks off a large chunk and starts to eat it. She repeats this on another piece and by 7:26 AM she has finished the whole egg shell. The female now settles back down on the young like a rocking boat and soon closes her eyes."

In many cases the eggs will hatch within a few hours of one another, but commonly one or even two eggs, particularly in larger clutches, may hatch on the following day.

Nestling Period

The period of nestling life of wild Bluebirds has been recorded as 14 to 16 days (Hamilton, 1943). If the young are disturbed two or three days before they would normally fledge, they may leave the nest prematurely. Perhaps the lower figure for nestling life results from such disturbances, as my data show that young will most often remain in the nest for 17 or 18 days — the same figures given by Thomas (1946). I have extreme records of 16 and 19 days. Even in the laboratory (see Plate IB), where the top of a nest box was removed and one side cut down to the point just high enough to retain the nest (inadvertently making it easier for the young to leave prematurely), the first young did not leave the box until the 17th day.

Feeding

Both parents in the wild normally feed the young throughout the nestling period although the male may actually contribute the larger amount of food. This is because much of the female's time is involved brooding during the first week and, if another nest is to follow, starting her new nest before the current young have fledged. Between these extremes, each contributes about equally to the feeding of the young.

Figure 5. Transference of food from a male Bluebird to his mate (on nest) via the entrance hole of nest cavity. The young are 12 days old.

Figure 6. A 36-day-old fledgling Bluebird feeding a grasshopper to a 26-day-old fledgling which is still unable to feed itself.

If the female is already in the nest cavity when the male arrives with food, he will invariably transfer the food to her (Figure 5) and she in turn will feed the young. However, if the male is in the nest cavity when the female arrives, I have never seen her transfer the food to him. The male will rarely force his way into the cavity, when the female is already there, and try to feed the young. When food is transferred to the female, she always makes an attempt to feed the young before eating it herself.

Both parents vocalize to the nestlings if not met with gaping mouths. This is particularly true of the early stages when the young are not too alert and their eyes are still closed, although it may happen at any time throughout the nestling period, if the young are unresponsive to the arrival of the parents. When the young fail to react to calling, the parent usually swallows the food and then leaves. I have seen parents in the laboratory probe the bills of the young when they did not respond.

Nestlings may be fed anytime after hatching, there being no definite time lapse between hatching and the first feeding. Young will gape immediately upon breaking out of the shell, if stimulated by the proper parental call.

In the early stages of the nestling period, the parents go into the nest cavity to feed the young on the nest. As time goes on the adults gradually begin to feed the nestlings at the entrance hole, going into the cavity only to pick up the fecal sacs which cannot be reached from the hole. During the last day or so of nestling life, the young are so eager for food that they may crowd the entrance hole, sometimes making it difficult for the adults to secure a perch at the hole before feeding them.

So strong is the adult's drive to feed a gaping mouth that it will usually keep trying until the young bird closes its gape. I once substituted eggs of a Starling *(Sturnus vulgaris)* for the non-viable clutch belonging to a pair of sound-isolated Bluebirds. The female fed her foster young with great persistence for about a week after they hatched. Thereafter, to keep the young Starlings from starving, I had to remove them from the nest and hand-feed them. Because a Starling's mouth is so much deeper than a Bluebird's, the female Bluebird could not easily reach far enough into the young Starling's mouth to release the swallowing reflex. Thus the female was forced to make several tries at each feeding, and the young Starling, often unable to swallow the food proffered, would finally close its mouth presumably from exhaustion.

Certain stimuli in the nest cavity sometimes inhibit the drive to feed nestlings. For example, if upon arriving at the hole with food, a parent spots a foreign object on the nest or is in some way frightened, it will often swallow the food even though the young are gaping. The foreign object may be nothing more than a conspicuous fecal sac.

Hamilton (1943), Laskey (1939), Nice (1931), and Wetherbee (1933) have reported fledglings (i.e., young birds out of the nest and able to fly) feeding birds of a younger brood. Neither Thomas (1946) nor I noted this in the wild although I have observed it in the laboratory. On the morning of 25 August 1959, a 36-day-old female, which had only begun to feed herself a few days before, was placed in a sound chamber with two 26-day-old Bluebirds. The younger birds had not yet acquired the ability to feed themselves. That evening I saw one of the younger birds beg food from the older one, which had picked up a grasshopper. The older then fed the younger just as an adult might have done except that it lacked dexterity in handling the food (see Figure 6). During the next few days, until the younger birds were completely on their own, the older bird periodically fed the other two.

The youngest laboratory fledgling I have seen feed itself was at 21 days of age. Even after being able to feed itself, a young bird will still beg for food, either from parents or from other young.

A reduction in the frequency of feeding young usually takes place the last day the young are in the nest, and is not accompanied by a corresponding increase in the amount of food brought by the parents. This drop in the number of feedings is especially pronounced after one or more young birds have left the nest. In some cases the parents do not feed them in the nest during this period, although they will feed them immediately upon leaving.

Orthoptera (chiefly grasshoppers, field crickets, and katydids) constitute at least 50 per cent of the young Bluebird's diet, once the nesting season is well under way in the Ithaca area. However, lepidopterous larvae (caterpillars) as well as other small, soft, succulent animals, such as spiders, form the bulk of the young nestling's food at the beginning. The parents continue to bring these items throughout the nestling period but soon begin to supplement them with berries, moths, beetles, grasshoppers, and other harder foods. Some of the more interesting animals that I have seen fed to the young are centipedes, millepedes, "hairy" caterpillars, praying mantises, and a spring peeper *(Hyla crucifer).*

Brooding

Only the female broods, although the male, as in the incubation period, occasionally sits on the nest alongside the female at night. I have never seen a male actually covering the young, but in a nest box outdoors, in 1958, I noted the male with the female nearly every night throughout the nestling period.

The amount of brooding by females is governed to a large extent by air temperature. Except in extremely hot or cold weather, females normally brood parts of the day each day during their nestlings' first week. In the next two or three days the time they spend on the nest gradually decreases and finally ends. Brooding of the nestlings at night generally continues for another two to four days, although some females stay on the nest every night for almost the entire period of nestling life. In these cases I suspect that the females do not actually brood but simply use the nest as a roost. In spot checking at night, I usually found them sitting near the edge of the nest.

Nest Sanitation

(1) Removal of Fecal Sacs.

Nestlings generally void a fecal sac shortly after being fed, while the parents, adapted to this behavior, wait for five to ten seconds. If no sac is then forthcoming, the parents either leave the nest box or, in the case of females with small nestlings, proceed to brood. Parents are alert to their nestlings' intention movements preceding defecation and not infrequently take the sac directly from the anus before it can touch the nest (see Plate IIB).

In the first few days of nestling life almost all of the fecal sacs are eaten on the spot by the parents. By about the fifth and sixth day there is a gradual transition from eating the sacs to carrying them out of the nest cavity; by the seventh or eighth day most sacs are carried away.

Fecal sacs removed from a nest cavity in the wild are usually taken as far as 20 to 50 yards before being dropped. The drive to carry the sacs this distance is evidently quite strong in the Bluebird and is not suppressed by confinement. I first noticed this when a parent, leaving a nest box with a fecal sac in its bill, flew into the chamber's walls and viewing window, as if trying to go through them. This happened repeatedly. With each fecal sac, several tries were made. There was little abatement of the behavior throughout the remainder of the nestling period.

Plate II

A. Wild female Bluebird eating an egg shell just after the hatching of a young bird. Note its wet down. The two remaining eggs are infertile.

B. Wild male Bluebird removing a fecal sac directly from a 6-day-old nestling.

The behavior was common to all the laboratory pairs. Sometimes, when a parent dropped a sac, the other picked it up and tried to get out of the chamber. Frequently the drive continued until one of the parents ate the sac, even though the time had passed when the sacs were normally eaten. Unless they were carrying fecal sacs, the adults rarely flew into the walls or viewing window. It is interesting that the conditions of confinement were adequate for normal reproductive activities, except when carrying fecal matter, suggesting that the only serious limitation imposed by confinement was insufficient distance for carrying fecal sacs.

The nest is normally kept clean, but there are exceptions. If the cavity chosen has much less than about 16 square inches in floor area, the adults may have difficulty getting onto the nest to clean it properly, especially after the young have attained appreciable size. An extreme example involved a pair occupying a chickadee box with a hole large enough to allow their entrance and a floor area of only nine square inches. The pair kept the nest fairly clean until the young were about six or seven days old. Thereafter they paid progressively less attention to nest sanitation, and on the tenth day two of the five young died. I found a quagmire of filth covering the nest. The plumage of the young was matted and caked, and the young themselves were sickly and weak.

As I have mentioned, the frequency of feedings drops off markedly in most nests the last day or so before the young leave, and the frequency of parental visits to the nest also declines. Furthermore, defecation becomes less rigidly associated with feeding, with the result that droppings start to accumulate on the nest. The parents still remove fecal sacs on the few feeding trips they make, but, because of the great lapses of time between such feedings, they are no longer able to keep up with production of feces. At this time too the young are so alert to the arrival of the parents that they crowd the hole, tending to block the entrance so that the parents have difficulty retrieving the droppings.

(2) Removal of Foreign Objects.

Because of the efficiency with which parents rid the nest of fecal matter, I planned a series of experiments in the field to see how far the adults would go in keeping their nest free of foreign objects. Pieces of wax crayons of various shapes, sizes, and colors were placed on the nest. In every case the male or the female removed the foreign object. Several pieces of red wax were shaped to resemble berries and placed in the nest cavity with the idea of fooling the birds — they had been feeding red berries to the young earlier in the day. These were removed rather than fed to the young even though the difference between the wax berries and the real ones could hardly be visually distinguished by humans.

(3) Removal of Infertile Eggs.

Until it was possible to observe nesting behavior closely, it was difficult to determine why some birds left infertile eggs in the nest long after the young had hatched while others obviously disposed of them. In one nest where a special observation box and blind had been installed, five eggs were present. Three of the five eggs subsequently hatched; the remainder were infertile. The two infertile eggs were left in the nest cup in the hope that further observation would produce information on egg removal. Six days later these eggs still remained, along with three healthy young. I removed one egg from the cup and placed it on the nest where it would appear conspicuous to the parents. On the next trip back to the box, the female fed one of the nestlings and then picked up the exposed egg in her bill, turned around, and flew out with it.

Figure 7. Wild female Bluebird removing an infertile egg from the nest. The nestlings are 6 days old.

Figure 8. Wild female Bluebird removing a dead Bluebird from a nest containing 8-day-old young. This is the most characteristic way dead young are lifted from the nest.

If the female would remove the egg from the top of the nest, why should she leave it in the cup? It appeared that the young, now six days old and over two-thirds the size of the adults, effectively shielded the eggs from the parents. I next moved the remaining egg to the side of the cup, still keeping it within the latter, so that it could clearly be seen from above. On the very next trip to the box the female fed one of the young, picked up the egg as before (see Figure 7), and flew out with it. The biological advantage of removing infertile eggs from the nest is probably to avoid the noisome consequences, should they become broken. The female will abandon the nest when an egg is broken during the incubation period, but not in the later stage when young are present.

The above experiments were continued, using the same nest, in order to witness the male's reaction to similar situations. He made no effort to pick up the eggs, or even touch them, although he sometimes appeared to gaze at them.

At one point a Starling's egg (twice the volume of the Bluebird's) was placed in the cup to see if the female would change her method of picking up an egg, perhaps piercing it with her bill in the manner of a wren, since it was apparent that she would have trouble getting it in her bill. This was not the case, however, for the female tried again and again to wedge it in her open mouth with a jabbing motion. She worked for half an hour, except for a little time off to make two quick trips with food for the young. I finally removed the egg as it was obvious she would not succeed.

(4) Removal of Dead Young.

Prior to observing the Bluebirds in the nest cavity, I suspected that the parents did something with their dead young. Although predation could account for the disappearance of young from some nests, it did not explain disappearances from others. Nine separate experiments involving three different nests were carried out in which a dead young Bluebird was placed in a nest containing live young. In one experiment the dead bird was placed on the nest; in the others the carcass was put in the cup itself along side the live young. In every case the dead bird approximated the weight and stage of development of the live young in whose nest it was placed.

In six of the nine experiments, the female removed the dead bird from the nest. In the other three, the experiment had to be terminated before the carcass was discovered. In the test with the dead bird on the nest and not in the cup, response by both the male and female occurred rather quickly. In the other tests with the carcass placed in the cup of the nest along with the live young, detection proceeded much more slowly and then apparently only by the female.

From these experiments there is reason to suspect that the parent "recognizes" these carcasses as young. When the carcass was placed on the nest and not in the cup, it was quickly removed from the nest as would any foreign object not blending with the nesting material. The fact that the male did not remove the dead young placed on the nest but removed other foreign objects placed in similar places is not too significant, because this particular setup was tried only once, with the male not allowed sufficient time to act before the female removed the carcass. On the one trip that he made to the nest before the female altered the situation, he stopped in the hole with food in his bill, saw the carcass, reached down from the hole and appeared to probe it. The female, on top of the box then approached the hole with the result that the male left the box still holding food in his bill.

When a carcass was placed in the nest cup with live young, the males paid no apparent attention to it. The females, though reacting slowly, sooner or later discovered the carcass and then diligently set about removing it (see Figure 8).

Although a dead bird in the nest among live young is conspicuous to humans, it apparently does not appear so to Bluebirds. The shortest time taken by a female to detect a carcass was five minutes; the longest time was more than an hour. In the last instance, the female made several feeding trips to the nest and spent much of the remaining time brooding both the carcass and the live young. From this and other similar cases, one wonders whether the relatively cold body of the carcass, in comparison to the warm bodies of the live young, presents the female with any significant stimulus while she is brooding.

In all Bluebird nests observed, I noticed that the females peck and poke the young periodically. This behavior starts as soon as the young have hatched and continues throughout most of the nestling period. It may take place during a brief visit to the nest after feeding the young, or during brooding. While the female is brooding for a period of, say, half an hour, she may get up a half dozen times and "inspect" the young. This may only involve standing over the young and looking down at them but may frequently be followed by tremble-thrusts and pecking at the young. Pecking is usually done rather lightly. If a young bird does not respond, the female will deliver somewhat harder blows. The nestling will invariably alter its position in an attempt to move away. The female then goes to another. If she chances upon a dead nestling, she pecks more forcibly. Soon the pecks become tugs and she lifts the carcass from the nest.

Each time a female discovers a dead young, her apparent "intent" is to drag the carcass from the nest cavity. This may or may not be successful, depending on the size of the dead bird. Dead Bluebirds ranging from 2.5 grams (newly hatched) to 18.5 grams (little more than half the adult weight) have in most cases been successfully removed. The female has no more trouble handling the lighter carcass than a good-sized fecal sac. With the heavier bodies, females have more trouble and are not always able to remove them. The problem seems to be size more than weight. A female can lift and even carry a large carcass short distances. The difficulty is getting both the carcass and herself through the entrance hole. Normally the female carrying an object exits head first. I noted two cases when large carcasses, each from a different nest, were successfully removed. In both cases the female had managed to lift and drag the dead bird to the entrance hole and, after struggling for some time to go through the hole with her load, abandoned the task temporarily to obtain more food for the young. On returning to the nest cavity with food and sighting the dead body below the hole, she swallowed the food, reached down and grabbed the carcass, dragged it through the hole, and flew off with it.

No dead Bluebird carried away was ever found closer to the nest than 18 yards. This case involved one of the heaviest carcasses and apparently presented the female with some difficulty in flight.

Tremble-Thrusts Throughout the Nesting Period

Tremble-thrusts are performed after the start of egg-laying and are continued well into the nestling period. The age of the young in three field nests, when this behavior was last noted, was 12, 13, and 16 days. An adult may give more than one tremble-thrust at a time. The maximum number given by the female in any one bout was 13; the maximum number of bouts in any one hour of observation was 10.

Tremble-thrusts occurred on the average of 2.8 bouts per hour during the first 16 days of nestling life in one nest in the wild. These data were drawn from 25 periods of daytime observation of not less than a half hour to not more than four hours each. This same nest averaged about four to six bouts per hour through the first week of the nestling period and not more than two bouts per hour for the remainder of that period.

The tremble-thrust produces a sound that is easily identified by the human ear. In the laboratory at 10:30 one night, after the lights had been turned out and the birds had gone to roost, two sound chambers, each containing a breeding pair of Bluebirds, were monitored simultaneously for tremble-thrusts. One chamber contained a nest with two day-old young, the other contained a nest with five eggs. Both females were on their nests. In the next three-quarters of an hour the female with young performed tremble-thrusts on nine different occasions, the female with eggs only once.

During the nestling period the tremble-thrust is given with greater frequency than during egg-laying and incubation, but its function is more obscure. After analyzing its immediate effects on the nest and young, I believe that it may have the following possible functions: Through its vibratory motion, it may serve to keep the nest clean by shaking nest parasites, such as the blood-sucking maggots (Protocalliphora larvae), and fine debris (e.g., fragments of sheaths) to the bottom of the nest; it may serve to enlarge the cup for the growing young by displacing the wall outward; it may serve to rearrange the young (the value of which is not understood), since the young will move away from the source of stimulation and reshuffle themselves in the nest.

Leaving the Nest Cavity

There is much variation in the time taken by a brood in leaving the nest. Often the young will leave within an hour of one another. Sometimes they will take several hours. Occasionally a young bird may lag behind the others by as much as a day, or (less frequently) precede its siblings by a day.

Young birds in the wild give location calls as soon as they leave the nest. Not infrequently these calls are detected an hour or so before the first bird leaves. In the laboratory, hand-reared Bluebirds invariably utter location calls as soon as they jump out of their nesting bowls for the first time.

Many young Bluebirds can fly 75 to 100 yards upon leaving the nest cavity and even gain altitude to reach the tops of tall trees; but, they are unable to sustain flight for any great length of time and tire rapidly if kept moving from perch to perch without intervals of rest.

As time of departure arrives, the parents make few trips to the nest, though they tend to stay near by, frequently giving location calls. After the first young bird leaves the nest, the parents, apparently preoccupied with its feeding and care, pay little attention to the young left behind until they in turn leave the nest cavity.

Summary

Through the use of special observation nest boxes and blinds in the field and the Hartshorne Sound Isolation Chambers in the laboratory, the behavior of the Eastern Bluebird *(Sialia sialis)* was observed and studied within the nest cavity at close range.

(1) Most of the Bluebird's pre-nesting behavior takes place near the nest cavity and is directly associated with the entrance hole.

(2) Courtship feeding, wing-waving accompanied by vocalizations, copulations, and frequent visits to the entrance hole constitute typical pre-nesting behavior.

(3) Copulations extend into the incubation period, and courtship feedings may extend well into the nestling period.

(4) Males rarely take part in the actual construction of the nest, although they may frequently carry bits of nesting material into, as well as out of, the nest cavity.

(5) Females alone incubate. Males may occasionally enter the nest box during this period, but have never been seen to sit on the eggs.

(6) Egg-turning may be done three different ways.

(7) The young usually emerge from their shells unaided by parents, but females may peck at the crack in a pipped egg, hastening the hatching process, and then forcibly remove the young from the shell.

(8) The female may eat the egg shell at the nest or carry it away.

(9) The male and female normally share about equally in the feeding of the young.

(10) Although Orthoptera constitute over 50 per cent of the nestling's diet once the nesting season is well under way, the nestling may be fed such things as centipedes and millepedes.

(11) Immediately upon hatching, young birds gape in response to the feeding call of the parents and may then be fed.

(12) A laboratory fledgling was seen to feed itself as early as the 21st day of life.

(13) A laboratory fledgling 36 days old fed two other 26-day-old fledgling Bluebirds for a period of several days until they learned to feed themselves. The older bird had learned to feed itself a few days earlier.

(14) Only females brood, although males occasionally sit on the nest alongside females.

(15) Both males and females dispose of fecal sacs. In the early stages of nestling life the sacs are eaten; later, they are removed from the nest cavity and carried from 20 to 50 yards before being dropped.

(16) Normally, both parents keep the nest cavity free of droppings and foreign objects.

(17) Females remove infertile eggs, when visible to them, within a few days after hatching of the young.

(18) Females remove dead young birds from the nest cavity.

(19) Females frequently perform "tremble-thrusts" (i.e., thrusts delivered into the nest cup with a trembling motion of the bill), which begin shortly after the eggs appear in the nest and continue almost to the end of the nestling period. This behavior was never seen performed by wild males, but one laboratory male showed this behavior regularly during the period in which it is performed by the female. Tremble-thrusts may serve to turn the eggs. Later, during the nestling period, they have other possible functions, such as shaking Protocalliphora larvae to the bottom of the nest.

(20) Nestlings in the wild, about to leave the cavity, often give location calls for an hour or more before their departure. Hand-reared Bluebirds invariably gave location calls immediately upon leaving their nesting bowls.

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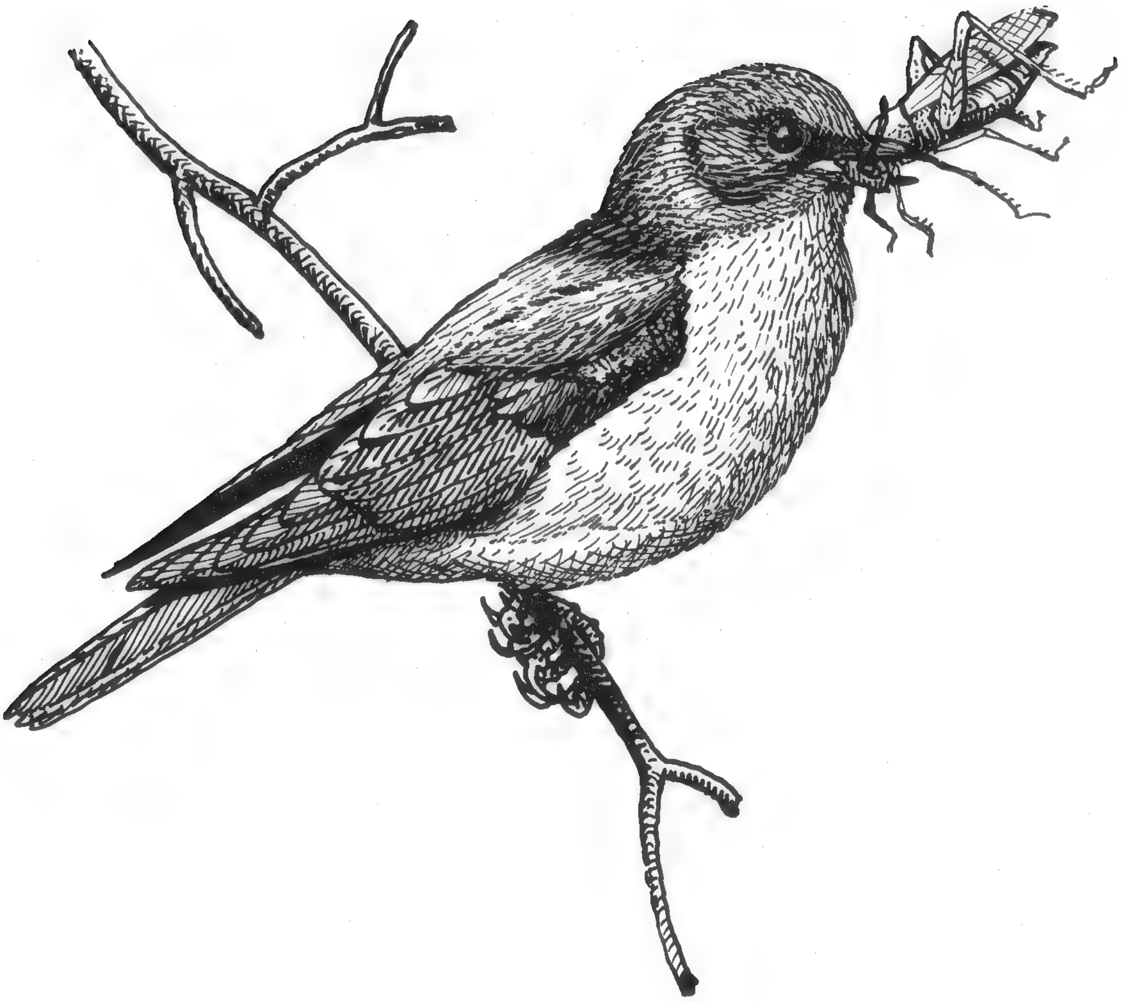

HOW THE BARN OWL LOCATES PREY BY HEARING

ROGER S. PAYNE

It has long been known that the ears of many species of owls are asymmetrical, usually one ear opening above and the other below the horizontal plane. Several investigators, intrigued by this asymmetry, have suggested the possibility of its being associated in some way with the ability of owls to locate prey. As indicated by Dice (1945), the vision of owls is inadequate for seeing mice moving in the leaf litter of a heavily-shaded forest floor when the nights are cloudy and moonless. Since many such nights normally occur during the year, it seems probable that owls, to survive, must hunt their prey by still another means, which may be based on hearing, perhaps associated in some way with the asymmetry of the ear openings.

To determine whether hearing is involved, I tried the following experiment on a Barn Owl *(Tyto alba)*. At the Laboratory of Ornithology, Cornell University, I constructed a light-tight building (floor, 12 by 42 feet; height, 6 to 8 feet) with a perch at each end, spread dry leaves over the floor, and introduced an owl. Turning out the lights to achieve total darkness, I put a mouse on the floor where it rustled the leaves whenever it moved. This experiment, done many hundreds of times during a period of four years, showed that a Barn Owl is capable of locating and striking a mouse in total darkness with an accuracy of at least one degree in both the vertical and horizontal planes.

The figure of "one degree" is only approximate and I do not have space here to discuss the various conditions and assumptions on which it is based. More data will be needed before I can state confidently the exact degree of accuracy of a Barn Owl. I can only say that I have made every effort to disprove what seems to be truly incredible accuracy and I now have sufficient data to suggest that the accuracy is much greater than one degree — on the order of a few minutes of arc.

Proof That Sounds Alone Are Sufficient

The Barn Owl need only hear the sound of a mouse rustling in leaves in order to locate and strike the animal. This fact I determined in the following way. A mouse-sized wad of paper was tied to a thread, thrown into the leaves on the floor of the room which was in total darkness, and dragged through them. The owl immediately caught the wad of paper. Because the lights were out, the owl could not use vision. Because the paper had no heat above that of its surroundings, the bird could not use infrared sensitivity. Because the paper had no mouse-like odor, the owl could not use a sense of smell.

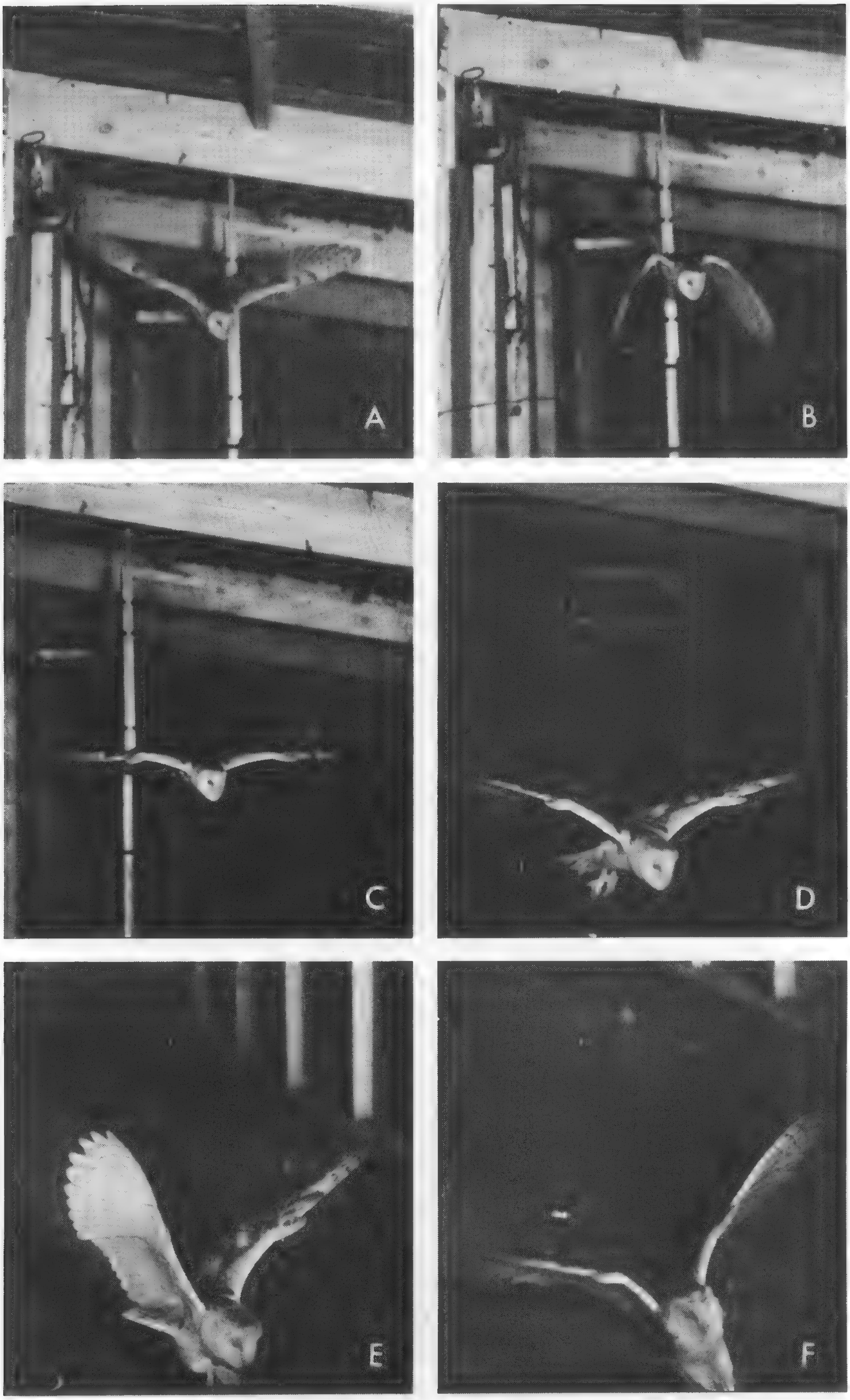

Figure 1. Barn Owl striking at a mouse in light. Leaving the perch, the bird takes one stroke with its wings (B) and then glides toward the mouse (C,D). Just before striking, it raises its wings and brings its feet forward (E). At the moment of impact its eyes are closed (F).

How then did the owl locate its prey? There are two possibilities: 1. Echolocation (the technique of producing sounds and locating objects by means of the echoes from them). 2. Homing on the source of the sound. Curtis (1952) was unable to detect that Barn Owls have any ability to echolocate. As further evidence against echolocation, I noted that Barn Owls regularly struck at a loudspeaker which broadcast mouse-like sounds while buried under two inches of leaves. This leaves the second possibility, namely, that the owl locates its prey by the sounds made by the prey.

Dependence of Owl on High Frequencies

In attempting to prove that sounds made by the prey are used by the owl, I wanted to be sure at the outset that the owl did not receive addiional information after leaving its perch — in other words, that the owl could not make corrections by using sounds heard during flight. Consequently, I buried in the leaves a loudspeaker which broadcast a recording of leaf-rustles. A switch on the owl's perch turned off this loudspeaker when the owl flew. Responding to the broadcast, the owl located its source as it did the wad of paper described above. When I filtered out frequencies above 8,500 cycles per second (the highest audible octave for humans), the Barn Owl's angular accuracy in locating the sound source was only about five to seven degrees in both the vertical and horizontal planes. When all frequencies above 5,000 cycles per second were removed, the owl refused to attempt to strike. This showed that the Barn Owl's accuracy in locating a sound source depends upon the presence of high frequencies.

Behavioral Differences Between Strikes in Light and Darkness

I photographed the owl flying at mice in the light. Then, by aiming the camera with a sniperscope (a device for transforming invisible infrared light into visible light) and taking motion pictures on infrared sensitive film, I photographed the flight of a Barn Owl in "total visible darkness." When I compared these two films, some extremely significant differences were noted.

Let us first look at the flight of an owl in the light (Figure 1). When the owl first saw or heard the mouse, it turned its head to face the mouse. The bird then crouched down and leaned forward. It pushed off from the perch while taking one stroke with its wings and then glided towards the mouse without further wing flapping. Its feet were held well back. Just before striking, it raised its wings, brought its feet forward, and threw its head back. At this point it presented the appearance of a projectile with its claws as the tip of the projectile. At the moment of impact its eye were closed. On long glides, the owl sometimes accelerated just before impact by means of a single hard stroke with its wings.

The same owl, striking in the darkness (Figure 2), performed somewhat differently. When the mouse first rustled the leaves, the owl turned its head towards the mouse exactly as it did when it could see the mouse. Once the owl faced the mouse, it had to hear at least one additional sound before striking. It again leaned forward and flew. However, this time it did not glide smoothly but, instead, flapped its wings quite violently and continuously all the way to the mouse and, with each stroke, its feet swung back and forth beneath it like a pendulum. When it was just over the mouse, it again brought its feet way forward and threw its head back, thus bringing its widely spread talons into the same path that its head was taking a moment before.

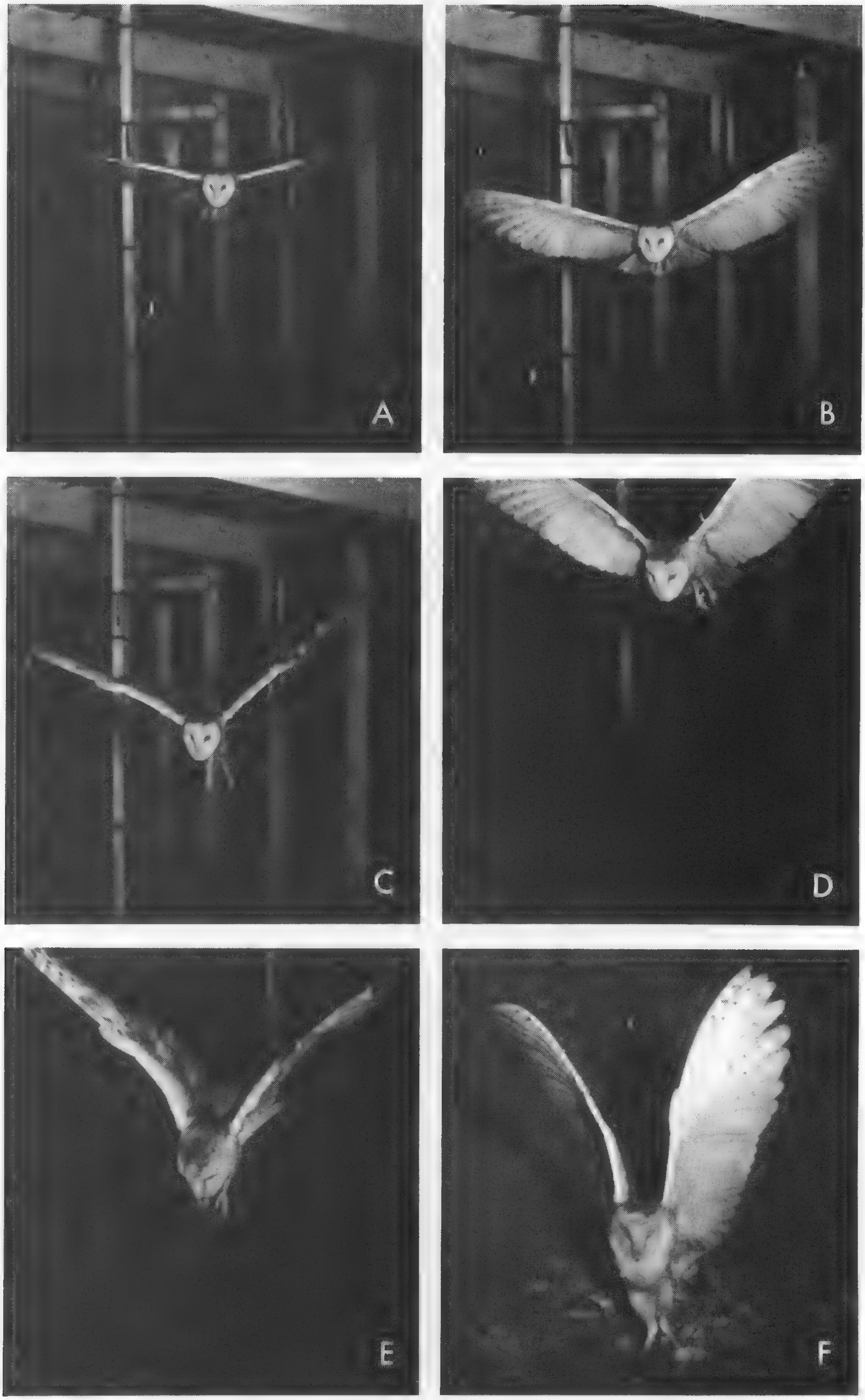

Figure 2. Barn Owl striking at a mouse in darkness. Leaving the perch, the bird flaps its wings continuously (B,C,D). With each stroke, its feet swing back and forth. Just over the mouse (E), it brings its feet forward, thus bringing its widely spread talons into the path that its head was taking a moment before. At the moment of impact its eyes are closed (F).

Avoiding Correction for Parallax

Since the owl makes the calculation of the position of the sound with its ears and yet must strike it with its feet, it should have to make a correction for parallax. The owl's accuracy is sufficient to warrant such a correction — particularly at short distances. The owl neatly avoids having to make this correction by flying at a mouse along the line between ears and mouse and then replacing the path taken by the ears with its widely spread talons at the last moment.

Maximizing the Strike Pattern

The owl also maximizes the chances of getting a talon into a mouse by maximizing the area which its talons cover. Figure 3 shows a constellation of dots made by light shining through eight holes punched in a piece of paper that had been laid over a loudspeaker. The holes were made by the talons of a Barn Owl at the moment of impact. The resultant oval pattern, if bisected perpendicular to the long axis, shows four holes to the left (the talon marks of the left foot) and four holes to the right of the line of bisection (the talon marks of the right foot). The spacing between the holes is quite uniform. This implies that the spacing between the feet is held the same as the spacing between any two talons. The resulting oval, encompassing a mouse-sized area, also maximizes the strike pattern.

To insure getting the maximum number of talons into a mouse, the owl should strike with the long axis of the oval of his strike pattern parallel to the long axis of the mouse, and this is exactly what it does. The strike is so oriented even in total darkness. In other words, the owl can determine the direction in which the mouse is headed and orient its strike accordingly. He makes this calculation acoustically by hearing the mouse move from one place to another.

The Owl Cannot See in Infrared

I include Figure 4 (taken like those preceding it from an infrared motion picture film) as proof that the owl could not see under the conditions that I was using to observe and photograph it. I used sand instead of leaves in this case in order to be able to track the exact point of impact of the owl in relation to the mouse. On the mouse's tail I fastened a leaf to make a sound when the mouse moved. The owl struck at the mouse and missed. This was a good indication that the owl did not see the mouse because never once did I observe a Barn Owl miss a mouse in light though I have watched hundreds of such strikes. The owl actually hit the leaf and knocked it off the mouse's tail. During the next few seconds the mouse moved away and in so doing collided with another leaf. The owl's back was turned. The bird whirled to face the sound but the mouse had then cleared the leaf and was running noiselessly on sand. The owl now faced the mouse directly from a distance of a few inches (Figure 4C) but could not see or hear it, as is evidenced by the fact that it did not strike. The mouse moved on with impunity (Figure 4D). The owl turned away (Figure 4E), searched the few leaves that were on the floor (Figure 4F), and then stopped all searching. Following this, I turned on the lights and the owl struck the mouse immediately.

Information Available to Owl from Sounds Made by Prey

We have seen something of what the owl can do. The next question is: How does the owl do it? In other words, what information is available to the bird from a complex sound, such as rustling leaves, and how does it use this information to determine the position of the mouse?

Figure 3. Holes made in a piece of paper by the talons of a Barn Owl at the moment of striking.

Because of the peculiar asymmetry of the external ears of the Barn Owl, one might guess that sounds on their way to the eardrums are affected by the external ears. If this were true and one could calculate the effect of the external ears, some clue might be gained as to the means used by an owl in locating the position of a sound source. Since the owl has no control over the sounds which it uses for acoustic location and can never predict their form, we can assume that there are only three types of information which the ears can extract from a sound wave: 1. Component frequencies. 2. Relative time of arrival or phase differences between the sounds at each ear. 3. Relative intensities of sounds in each ear.

Since reflection or refraction from, or by, solid structures, stationary in relation to a sound source, cannot change frequency, the first, frequency changes by the external ear structures, need not be considered. Because the Barn Owl must face the mouse directly before making a final orientation, and because, in that position, differences in time of arrival or phase would be too slight for an owl to appreciate with enough accuracy to explain his minimum angle discrimination, the second, differences in time, is probably useless to an owl in making final fine calculations, though such differences may be of help in initial, rough location. The third possibility — changes in intensity varying with the angle from which the sound is received — seems fruitful.

Three Dimensional Polar Diagrams

The problem is how to get an owl to tell us how loud it hears a sound in each ear when a sound of constant intensity is presented from different angles relative to it. I approached this problem by implanting a microphone in each of the owl's ears and measuring sound intensities at the site of the eardrum while broadcasting sounds of constant intensity from various angles to the owl. When such experiments are performed on other animals, data on intensity variations versus angle of presentation are usually taken only in the horizontal plane. The graphs from such data are called polar diagrams. Barn Owls, however, unlike most animals, are capable of at least equal accuracy of location in the vertical and horizontal planes. Therefore, one must construct polar diagrams in three dimensions by presenting sounds not just from a loudspeaker running on a horizontal, circular track but from a loudspeaker that can broadcast sounds from any point on the surface of a sphere. Without going into either a lengthy description of my procedures, or a detailed examination of the rather complicated graphs which resulted, I will merely mention some of the trends I observed and conclude by presenting a theory to explain how Barn Owls may use these three dimensional, polar-sensitivity patterns to locate a sound source.

Nulls in Relation to Frequency

Perhaps the most striking features of the Barn Owl's polar-sensitivity plots are the sudden drops in intensity which occur over narrow angles as one gets within about one octave of the owl's high frequency limit of hearing. Such sudden drops are called "nulls." Rough tests in which I implanted electrodes on each inner ear and recorded the cochlear microphonic response of the Barn Owl showed that the upper frequency limit of hearing is about 20,000 cycles per second. At about 5,000 cycles per second each ear has a broad region of maximum sensitivity directed forward with the sensitivity falling off gradually as a sound is directed at either side of the head. As the frequency is raised the region of maximum sensitivity becomes narrower and then is divided into two regions by a horizontal, equatorial band of poor sensitivity. At the same frequencies a crescent-shaped region of poor sensitivity, half circling the line of sight on the same side of the head as the ear being tested, begins to appear. By 11,000 cycles per second crescent-shaped and horizontal null regions are very pronounced in each ear and they have moved closer to the line of sight. Any further increase in frequency makes the null regions more extreme. In other words, the rates of cut-off, or the rate of change of intensity versus angle of presentation, are more extreme. As frequency is increased to about 15,000 cycles per second and beyond, a host of additional null regions appear at various angles, scattered about seemingly at random with the crescent-shaped and horizontal nulls still present and moving closer to the line of sight.

Throughout the spectrum of the frequencies audible to the Barn Owl, one area surrounding the line of sight will always receive sounds at maximum intensity. The general trend is for this area of maximum intensity to become smaller and smaller due to the movement towards the line of sight of the bordering null regions. Thus, if the owl adjusted the position of its head to hear all the frequencies in a complex sound at maximum intensity, either simultaneously or in sequence, it might get the following results: Let us assume for the sake of simplicity that the owl is listening to one frequency and then another. At a frequency of 5,000 cycles per second, it could make a rough and rather hazy location of the sound by turning the head to receive a maximum intensity in both ears. Should the owl then switch its concentration to some higher frequency and maximize its reception by adjusting the head position, the owl would improve its previous location of the sound source, since higher frequencies have narrower regions of maximum sensitivity due to the impingement of the bordering null regions. The owl could continue to concentrate on ever higher frequencies and further refine its location of the sound source with each new frequency by continuing to orient its head to hear equal and maximum loudness in each ear. By the time the limit of its hearing range is reached, the owl would be confined to listening in sufficiently small regions of maximum sensitivity bounded by sufficiently abrupt cut-offs to give it a theoretical minimum angle of sound location of a fraction of one degree.

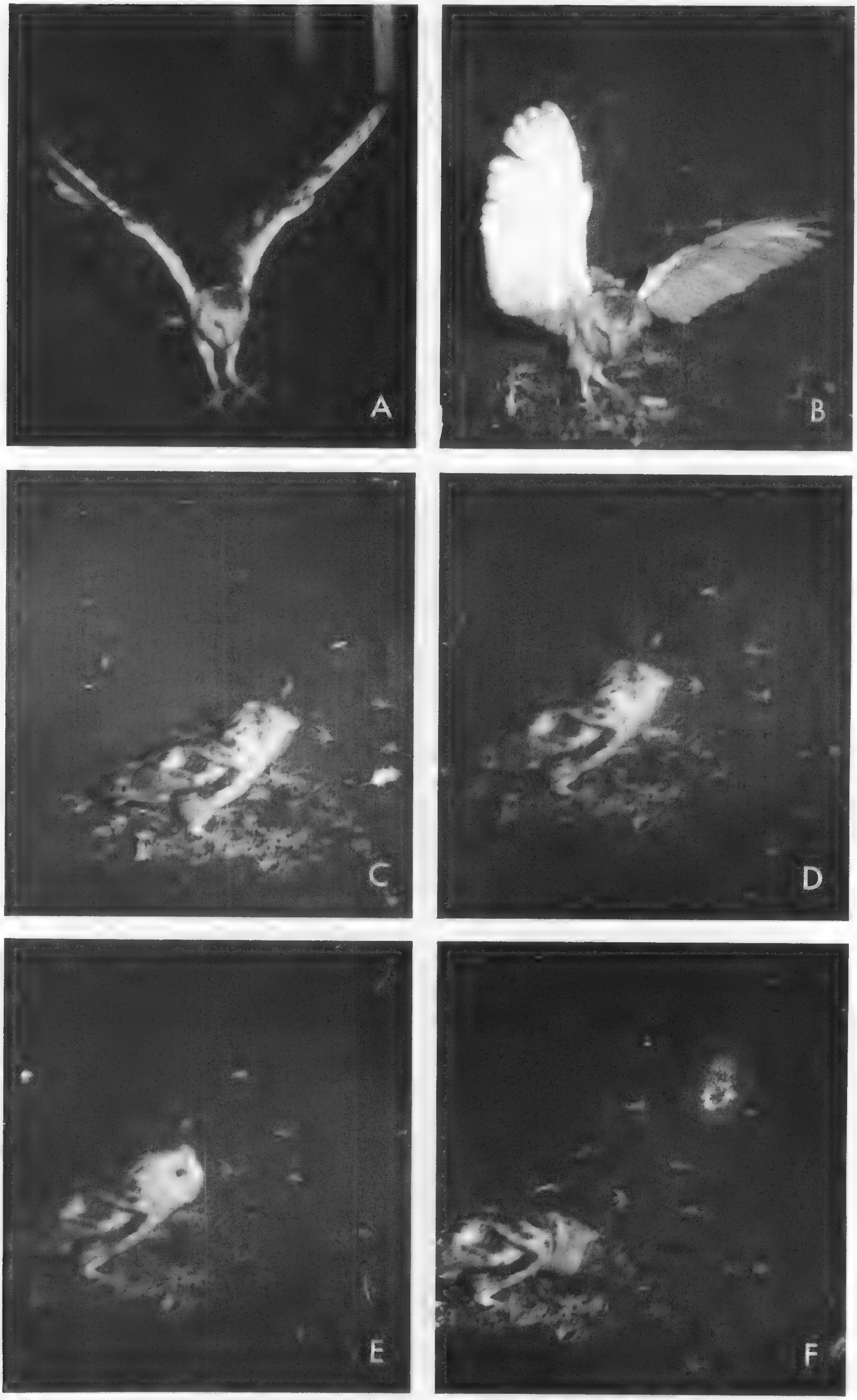

Figure 4. A Barn Owl, striking at a mouse in darkness, fails to see it. Just before striking, the bird spreads its talons (A) to cover as wide an area as possible, but misses the mouse (B). The mouse moves away (C,D,E,F) unseen or unheard by the bird, which finally stops searching.

The technique I have described would also work if the owl moved the head to receive all frequencies at once at the highest intensity in each ear. One might imagine that from the owl's "point of view" it would be moving the head in order to hear with equal loudness in each ear the most "hi-fi" reception possible. Using either technique, simultaneous or sequential treatment of a complex sound, the only position in which the owl could hold the head in the end would be within a fraction of a degree of facing the sound directly.

Further Considerations

There are two important, additional aspects of the polar sensitivity plots which I obtained: 1. Though at first glance all features of polar diagrams at any one frequency appear to be mirror images for the left and right ears, all features in the right ear occur about 10 to 15 degrees higher than their mirror image complements for the left ear. This is undoubtedly linked with the asymmetry of the ears. 2. Since crescent-shaped nulls near the line of sight are semicircular and do not surround the line of sight in either ear and because of the vertical asymmetry of polar patterns just mentioned, a sound, which is moved away from the line of sight while the head is stationary, will decrease with extreme rapidity in one ear while it decreases with extreme slowness or even increases in the other ear.

Thus: 1. Differences due to incorrect orientation of the head are amplified by differential reception in the two ears when the owl tries to match intensities in the two ears. 2. One ear is available (i.e., always available in a region of high sensitivity) to monitor the other ear when its signal at any given frequency is disappearing as the sound is directed at a null region.

Theory

My theory, then, puts only one demand on the owl, namely, that it orient the head in such a way as to hear all frequencies, audible to it in a complex sound, at maximum intensity in both ears. When it has achieved such an orientation, it will automatically be facing the source of the sound with a theoretical accuracy of less than one degree.

Acknowledgments

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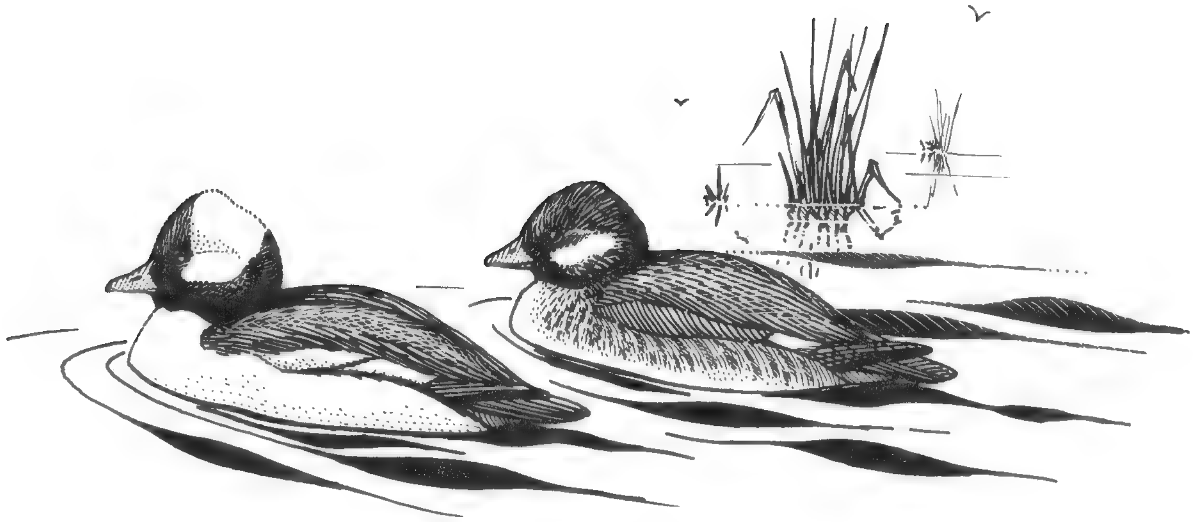

FORMER GRADUATE STUDENTS WITH MAJOR WORK IN THE LABORATORY OF ORNITHOLOGY

Degrees Awarded and Thesis Titles

ADAMS, HEMAN. Ph.D. 1961. A study of the rate of ossification in Passeriformes from the time of hatching to the time of fledging.

AMADON, DEAN. Ph.D. 1949. The Hawaiian honeycreepers (Family Drepanididae).

ARNOLD, JOHN R. Ph.D. 1938. The systematic position and natural history of the Northern Blue Jay, *Cyanocitta cristata bromia* Oberholser.

BALL, KATHLEEN E. Ph.D. 1949. A study of the Ring-necked Pheasant on Pelee Island, Ontario.

BARBOUR, ROGER W. M.S. 1939. A study of the life history of the Red-eyed Towhee *(Pipilo erythrophthalmus erythrophthalmus).*

BAUMGARTNER, FREDERICK M. Ph.D. 1937. A study of the American Horned Owls *(Bubo virginianus).*

BECKER, EDNA E. M.S. 1940. Plan B.*

BENSON, DIRCK. M.S. 1937. Studies in the ecology of the Black Duck (*Anas rubripes* Brewster).

BENSON, MARY. M.S. 1939. A study of the American Redstart (*Setophaga ruticilla* Swainson).

BENNETT, ESTHER. Ph.D. 1961. Aspects of vocalization in the Red-winged Blackbird (*Agelaius phoeniceus* (Linnaeus)) as determined by audiospectrographic analysis.

BENTON, ALLEN H. M.S. 1949. Plan B.

BEYER, LEONARD K. M.S. 1935. A study of the Bank Swallow, *Riparia riparia* (Linn.).

BIBBEE, PAUL C. Ph.D. 1947. The Bewick's Wren, *Thyromanes bewickii* (Audubon).

BUCHANAN, FOREST W. M.S. 1947. Plan B.

BUMP, NELSON GARDINER. Ph.D. 1948. Wildlife habitat changes on the Connecticut Hill Game Management Area over a twenty-year period and their effect on certain species of wildlife.

BURNETT, FRANCES L. Ph.D. 1955. The application of sound recording to museum natural history exhibits.

BUTTS, WILBUR. Ph.D. 1929. A study of the Chickadee and White-breasted Nuthatch by means of marked individuals.

CAMERON, AUSTIN. M.S. 1948. Plan B.

CASSEL, J. FRANK. M.S. 1941. Plan B.

COLES, VICTOR. Ph.D. 1928. Studies in the life history of the Turkey Vulture, *Cathartes aura septentrionalis* Wied.

COMPTON, DOROTHY M. M.S. 1930. A study of the Downy Woodpecker, *Dryobates pubescens medianus.*

CROUCH, JAMES E. M.S. 1931. A study of the Cedar Waxwing, *Bombycilla cedrorum.*

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DILGER, WILLIAM C. Ph.D. 1955. Ecological isolating mechanisms, reproductive isolating mechanisms, and relationships of the avian genera *Hylocichla* and *Catharus.*

EATON, STEPHEN W. Ph.D. 1949. The genus *Seiurus*: A comparative study of the species.

EDEBURN, RALPH. Ph.D. 1938. A study of the distribution of breeding birds in a typical upland area.

EDMINSTER, F. C., JR. M.S. 1930. A study of ornithological terms in common use.

EDWARDS, ERNEST P. Ph.D. 1949. Birds of the Patzcuaro Lake Basin.

ELMORE, LARUE J. M.S. 1935. A study of the sexual behavior of the Ruffed Grouse (*Bonasa umbellus* Linn.).

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FICKEN, ROBERT W. Ph.D. 1960. Behavior of the Common Grackle, *Quiscalus quiscula* (Linnaeus).

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FISCHER, RICHARD B. Ph.D. 1953. Studies in the breeding biology of the Chimney Swift, *Chaetura pelagica* (Linnaeus).

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GOLLUP, JANE BERNARD. M.S. 1949. Plan B.

GOODWIN, ROBERT. Ph.D. 1960. A study of the ethology of the Black Tern, *Chlidonias niger surinamensis.*

GORDON, KENNETH L. Ph.D. 1936. The application of the laboratory type of experiment to field studies of the behavior of chipmunks, winter birds, and some nesting birds.

GOULD, VICTOR E. M.S. 1932. A history of the Bob-white in New York State with particular reference to restocking.

GRINNELL, LAWRENCE I. Ph.D. 1947. A study of the Common Redpoll, *Acanthis flammea flammea* (L.).

GRISCOM, LUDLOW. M.S. 1915. The identification of the commoner Anatidae of the Eastern United States in the field.

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HALDEMAN, DORIS W. M.S. 1929. A study of the Song Sparrow, *Melospiza melodia.*

HAPP, GEORGE. M.S. 1935. A study of the Flicker (*Colaptes auratus* (Linnaeus)).

HARPER, FRANCIS. Ph.D. 1925. A faunal reconnaissance in the Athabaska and Great Slave Lakes Region.

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HENSLEY, MARVIN MAX. Ph.D. 1951. Ecological relations of the breeding bird population of the desert biome in Arizona.

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HOWELL, JOSEPH C. Ph.D. 1940. A study of the American Robin (*Turdus migratorius* Linnaeus).

HOYT, J. SOUTHGATE Y. Ph.D. 1948. Further studies of the Pileated Woodpecker, *Hylatomus pileatus* (Linnaeus).

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JOHNSON, ROBERT A. Ph.D. 1936. A study of the life history of the Atlantic Murre *(Uria aalge aalge).*

KELLOGG, PETER PAUL, Ph.D. 1938. A study of bird sound recording.

KELSO, LEON H. M.S. 1938. A study of the Screech Owl *(Otus asio).*

KENYON, KARL W. M.S. 1941. A study of the old nest as a visual stimulus to the renesting of the Baltimore Oriole, *Icterus galbula* Linnaeus, including supplementary life history observations.

KESSEL, BRINA. Ph.D. 1951. Investigations on the life history and management of the European Starling *(Sturnus vulgaris vulgaris* L.) in North America.

KINGSBURY, ELIZABETH W. Ph.D. 1933. The status and natural history of the Bobolink, *Dolichonyx orizivorus* (Linnaeus).

KNAPPEN, PHOEBE M. M.S. 1926. A census of the birds nesting on the Cornell campus in 1926 compared with a similar census made in 1913.

KUTZ, HARRY L. Ph.D. 1940. Studies on the inhibiting influence of captivity upon reproduction in wild ducks. Effect of light and various gonadotropic hormones.

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LEISTER, CLAUDE W. Ph.D. 1929. The food and feeding habits of the ducks of the Cayuga Lake Region.

LEWIS, HARRISON FLINT. Ph.D. 1929. The natural history of the Double-crested Cormorant (*Phalacrocorax auritus auritus* (Lesson)).

LOETSCHER, FRED W. Ph.D. 1941. Ornithology of the Mexican State of Veracruz with an annotated list of the birds.

MENG, HEINZ K. Ph.D. 1951. The Cooper's Hawk, *Accipiter cooperii* (Bonaparte).

MERRY, KATHERINE. Ph.D. 1941. A study in the life history of the Eastern Phoebe, *Sayornis phoebe* (Latham).

MOSER, E. RANDOLPH. M.S. 1943. Plan B.

MUIRHEAD, PEGGY. M.S. 1943. Plan B.

ODELL, THEODORE T. M.S. 1926. The food of orchard birds with special reference to the Pear Psylla.

OWEN, OLIVER S. Ph.D. 1950. The bird community of an elm-maple-ash swamp in Central New York.

PALMER, RALPH S. Ph.D. 1940. A behavior study of the Common Tern, *Sterna hirundo* Linnaeus.

PARKES, KENNETH C. Ph.D. 1952. The birds of New York State and their taxonomy.

PAYNE, ROGER S. Ph.D. 1962. The acoustical location of prey by the Barn Owl *(Tyto alba).*

PETRIDES, GEORGE A. M.S. 1940. A study of hedgerows in winter and their relation to wildlife in Central New York State.

PETTINGILL, OLIN S., JR. Ph.D. 1933. The American Woodcock, *Philohela minor* Gmelin.

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PICKWELL, GAYLE B. Ph.D. 1927. The Prairie Horned Lark.

PIRNIE, MILES D. Ph.D. 1928. The plumage changes of certain waterfowl.

RAND, AUSTIN L. Ph.D. 1932. The distribution and habits of Madagascar birds.

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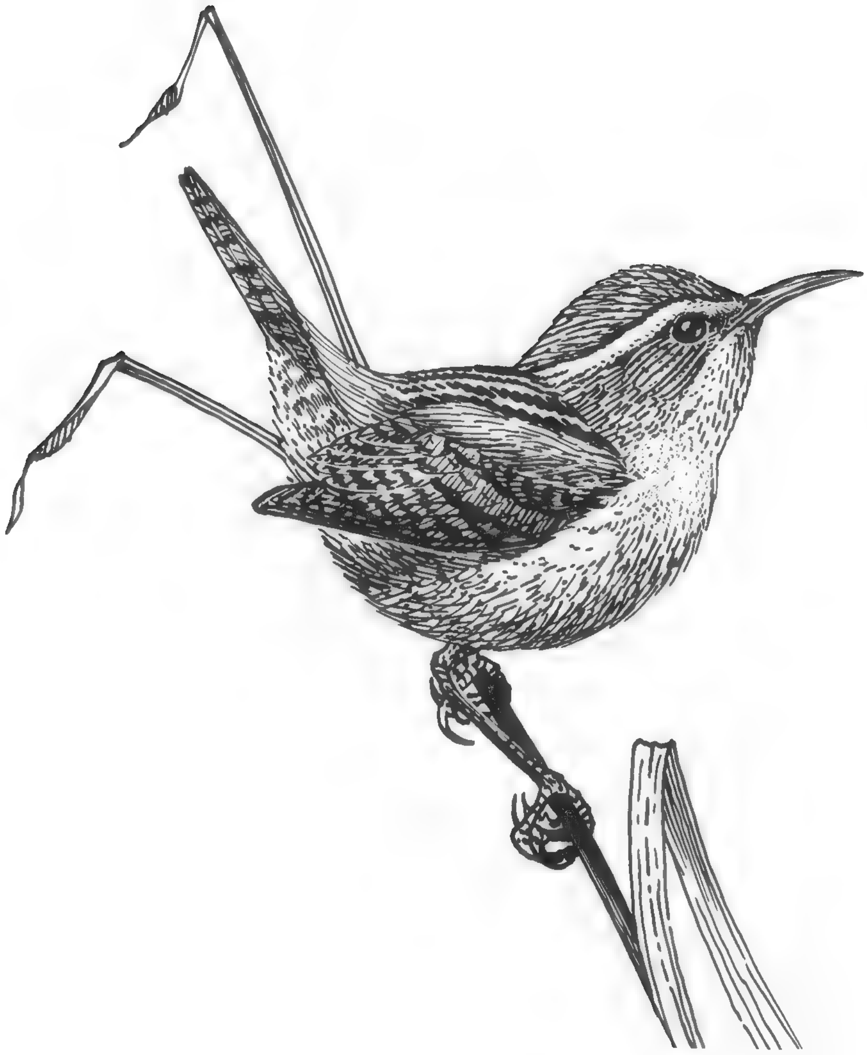

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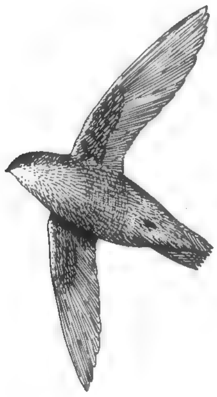

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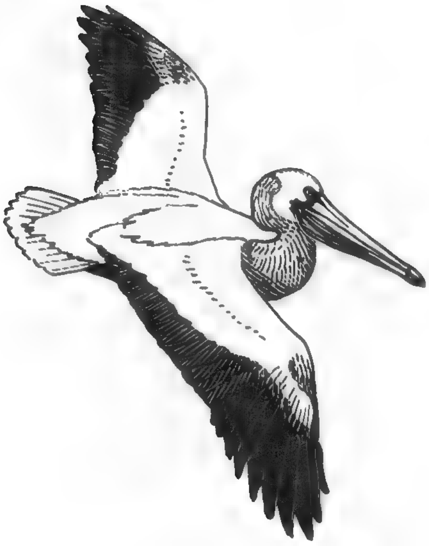

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All line drawings by William C. Dilger unless otherwise indicated

Cover illustration of the Mountain Trogon by Don Richard Eckelberry

Female Violaceous Trogon digging her nest in a colony of paper wasps.

SOME REMARKS ON TROGONS WITH SPECIAL REFERENCE TO THE MOUNTAIN TROGON

Don Richard Eckelberry

Trogons are lethargic birds. You are likely to see one sitting well up in a tree, hunched over a branch with wings slack and tail drooped, putting what energy it has into a series of throaty notes. After a time it slips from its perch in a sweeping glide and hovers before a cluster of ripening fruit, plucking its choice, or before a leaf where it snatches a large insect. Then it is back on a branch again where, with its tail now inclined a bit forward under its body and jerking slightly, it repeats its call. Finally it drops into the air and, with deeply-undulating flight, disappears into the forest to join its mate in digging a nest.

Trogons, which comprise the family Trogonidae, have short, blunt bills, rounded wings, long, broad tails, and extremely small feet with first and second toes directed backward. The bills, despite their small size, are the trogons' principal equipment for digging nest cavities, usually in tree stubs spongy with decay, or in termitaries or wasps' nests which, though harder, can be flaked off. Some trogons use old woodpecker holes or natural cavities when such are available.

Of the thirty-four currently-recognized species of trogons, the greater number live in tropical America, the others in Africa and south Asia. The discovery of trogon remains in the Miocene deposits of France indicate that in a warmer period the family was more widespread. Only one species, the Coppery-tailed Trogon *(Trogon elegans)*, reaches the United States in southern Arizona and Texas, but there are seven other species as near as Mexico. One, the Violaceous Trogon *(Trogon violaceus)*, ranges from Tamaulipas south to the Amazonian region of South America. Shown on the opposite page is the female of this species digging her nest in a colony of paper wasps.

Male trogons are among the most splendidly colored birds in the world. Their basically complementary colors vary, although not greatly, and there seems little reason to recommend one species over another, so handsome are they all, until you have seen the Quetzal *(Pharomachrus mocino)*—that ruby and emerald jewel set in the dripping cloud forests of the Central American mountains. It is hard to say why these potent colors achieve a quality, a refinement, which on parrots they never attain. Perhaps it is due largely to the simple pattern of color, so remarkably constant throughout the group, and to the textures of the feathers. Yet, at the risk of being branded an anthropomorphist, I think the pleasing effect of all these birds is in no small part due to the gentle nature of the birds themselves. In temperament the Quetzal seems a strange symbol for the Aztecs to adopt, even if combined with a serpent. Quetzalcoatl's apotheosis by the Toltecs into a god of peace, wisdom, culture, and prosperity was evidently the Nahuatl equivalent of the Mayan god Kukulcan. It is not surprising that after being adopted by the all-conquering Aztecs, Quetzalcoatl was gradually transmogrified and lost popularity to the hummingbird war god Huitzilopochtli. I have always thought that, gram for gram, hummingbirds were a better symbol for aggression and combat than eagles.

The Mountain Trogon *(Trogon mexicanus)* ranges in the highlands from northern Mexico to Honduras. The male of the species appears on the cover of this issue of THE LIVING BIRD. Alexander F. Skutch has chronicled its life history (see *The Auk* for July, 1942), and there is little one can add to this detailed account except that the bird is readily decoyed by an imitation of its notes. Ludlow Griscom in his "The Distribution of Bird-Life in Guatemala" *(Bull. Amer. Mus. Nat. Hist.,* Vol. 64, 1932) quotes A. W. Anthony as saying that neither he (Anthony) nor the Guatemalan Indians were able to distinguish between the spaced notes of the Ferruginous Pygmy-Owl *(Glaucidium brasilianum ridgwayi)* and this trogon. The pattern is the same, but if memory serves, the owl gives higher pitched, more whistled notes which are apt to run on indefinitely. It may be that the species of owl is mistaken here (I am not familiar with the calls of other members of the genus) for *G. brasilianum* is a lowland species ranging up to 4,000 feet elevation while the Mountain Trogon begins its vertical range at about 3,000 feet and is a common (and usually a solitary) bird in humid pine-oak woodlands and the still higher and colder fir belt to 11,000 feet. I have never tried to call up a Ferruginous Pygmy-Owl and had a trogon respond or vice versa. The species of trogons I have heard show no great range in voice, though they do vary sufficiently in pitch, duration, speed of delivery, and the like to make sympatric species readily separable with a little experience.

On the female Mountain Trogon the metallic green upperparts are replaced with dull brown, the red of the underparts is reduced in area and intensity, and the outer pairs of retrices are barred with black and white along their lateral edges. The eyes of the female are parenthetically enclosed by white crescent-shaped marks and there is some white also on the brownish wings.

180 WOODSOME ROAD, BABYLON, NEW YORK

Male Quetzal

NESTING AND PRODUCTIVITY OF THE RED-WINGED BLACKBIRD IN RELATION TO HABITAT

NEIL A. CASE AND OLIVER H. HEWITT

The Red-winged Blackbird *(Agelaius phoeniceus)* is generally considered a marsh-nesting species. In recent years reports of Red-wings nesting in habitats other than marshes have become common (Bent, 1958). The widespread use of "new" nesting habitats seems to be associated with a recent population increase (Dykstra, 1960; Cardinell and Hayne, 1944).

In 1958 the United States Fish and Wildlife Service initiated a contract with the Agricultural Experiment Station at Cornell University, Ithaca, New York, whereby basic research on the Red-winged Blackbird would be conducted. The first objective of that research was to determine the productivity and extent of different nesting habitats for Red-wings. Observations were made on arrival in the nesting area, territory establishment, and nesting.

Study Areas

The areas selected for nesting studies were:

(1) Spencer Marsh; 18 miles south of Ithaca; about 105 acres of heavy cattail *(Typha* sp.*)* and bulrush *(Scirpus acutus)*, with 50 per cent open water; lying in a valley at an elevation of 1,024 feet.

(2) Airport Marsh; 2 miles north of Ithaca; 5 acres of cattail with some flooded shrubs; on a plateau at about 1,060 feet above sea level.

(3) Inlet Valley Marsh; 2 miles south of Ithaca; a small cattail pocket occupying about one acre; close to a main highway in the valley at 440 feet elevation.

(4) Upland habitat comprising about 180 acres of forage crops, alfalfa and timothy, and fields left to weeds and brush and bordered by woodlots; upland habitat at elevations of 1,200 feet with little water and 500 feet with several streams.

(5) An area of about 160 acres at the Cornell University Biological Station at Shackelton Point on Oneida Lake; upland habitat of fields grown up to weeds, grass, and brush at 380 feet above sea level.

During spring migration, observations were made at the Inlet Valley and Airport Marshes and adjacent upland fields and at another marsh called the Boathouse Marsh. City development has eliminated most of the once extensive marsh at the head of Cayuga Lake and only a few small tracts of dense cattail are left. The Boathouse Marsh is one of those remaining tracts and has an area of about one acre.

Arrival on Nesting Areas

In 1959, flocks totalling several hundred adult male Red-wings arrived at Ithaca in the last week of February. These birds were seen in small marshes and cultivated fields for a few days, then disappeared, acting as the "vagrants" defined by Allen (1914). Toward the end of March the first true migrant flocks of adult males were seen. Some birds left the first flocks and established territories, but the majority remained in flocks and moved on. As the migration season progressed, the later flocks included some immature males. Many migrants roosted in the Boathouse Marsh and other small marshes near by.

By the first of April most territories which were later used for nesting were defended. At night the territorial birds remained in their territories.

During the first week in April the first females arrived in flocks also containing immature males. Females appeared to follow the pattern of the earliest males, some leaving the flocks and taking territories, others continuing to migrate. By the middle of April most females that nested near Ithaca were mated and were showing the first signs of nesting activity, defending territories against other females and carrying nest material.

By the end of April both adult and immature female Red-wings were engaged in nesting, and nearly all of the Red-wings still in flocks were immature males. The immature males continued to roost in the Boathouse Marsh and other Cayuga Lake marshes used by earlier migrants. These marshes had very few nesting Red-wings and were not heavily used for roosting after mid-July.

In 1960 and 1961 there were no vagrants in the Ithaca area, but the rest of the migration proceeded as in 1959.

Territory

Nero (1956b) defined the territory established by an adult male Red-wing as "a clearly circumscribed portion of the breeding grounds from which he repels Red-wing males, females other than his mates and, at times, even fledgling Red-wings."

Establishment and Behavior

In 1960 the first flocks of Red-wings were seen near the Inlet Valley Marsh on 27 March. On 1 April there were six territorial males in the marsh. On 1, 2, and 3 April all six were trapped and banded. On 22 April four of these males were retrapped in the same territories in which they had originally been banded. The other two territorial males present in the marsh on 22 April wore bands and presumably were the other two males banded the first few days of the month.

In 1961 flocks of Red-wings were first seen near the Inlet Valley Marsh on 21 March. By 1 April there were again six territorial males in the marsh. On 9 April one of the territorial males of the previous year was recaptured in approximately the same territory he had occupied in the marsh in 1960. An adult female also captured on 9 April was recaptured on 20 April in the same territory in which she was originally captured. The male defending the territory along the highway south of the marsh was killed by a car in July 1961, and was the same male banded in that territory in 1960. The identity of the other four males was not determined.

The adult male's territory serves all of the functions ascribed to territory by Armstrong (1947). Outside of the territory, but near its boundary, an alien elicits threat displays from the territory occupant. Within the territory an intruder elicits threat displays and attack. By observing the action of a territorial male when another Red-wing, other than his mate, approaches, territory boundaries may be clearly determined.

Song-spread and Bill-tilting threat displays (Nero, 1956a) were directed at any alien approaching a territorial boundary. Two adult males on adjoining territories would sometimes perch within a few feet of each other, both giving threat displays, but neither crossing the territorial boundary to attack.

An intruder entering an established territory might or might not be attacked. Territorial defense by a male seemed to depend on the state of the nesting cycle and on individual aggressiveness. When the territory was first established, intruders evoked Song-spread and Bill-tilting, but were seldom chased or attacked. As the season progressed intruders were more often chased and attacked more vigorously. Once a female took up residence in a male's territory, intruders were usually chased upon appearance. Occasionally an intruder was followed out of the territory. When this occurred, males from territories being crossed by the chase often joined in the chase and the intruder was followed to the edge of the marsh or field where the territorial birds broke off the chase and returned to their respective territories. Rarely the chase continued beyond the limits of the marsh or field.

Threat displays and chasing were common, but actual conflict between male Red-wings was seen only three times. On two of these three occasions the fight was very brief, one male fleeing after a few seconds, but on one occasion the antagonists flew together about ten feet above the ground, grappled with their feet, and fell to the ground. They lay where they fell, pecking and scratching for twenty minutes. At times one bird raised a wing over the fray, but they did not separate until the fight ended abruptly with one bird fleeing and the other in close pursuit. Territorial males from adjoining territories and males flying over were attracted by the fight and landed on the ground within a few feet, watched for a few minutes, and then either returned to their territories or flew on. At one time eight males surrounded the antagonists like spectators. There were no threat displays or antagonism evident in the observing Red-wings. After the fight over forty body feathers were picked up from the site, an area of less than one square foot.

Before females established territories, males frequently left their territories during the middle of the day. From the time resident females arrived until the nesting season neared its end, adult males seldom left their territories except when chasing intruders or when engaged in sexual chase. This change in territorial behavior is also reported by Nero (1956b) and Orians (1961).

Song-spread display of the male Red-wing.

Although other Red-wings were the most frequent intruders which provoked threat displays, several other species of birds elicited these actions. Territorial male Red-wings would hover over, then dive toward an intruding mammal. Intensity of aggressive behavior varied between individual birds, but increased through the nesting cycle. Before nesting started a male Red-wing usually hovered over a man entering his territory, but seldom dived. Aggressive behavior became more intense through the period of nest construction, laying, and incubation, and particularly as the young grew older. It reached a peak at fledging.

Although this behavior increased as nesting progressed for every territorial male observed, there was great variation between individuals. Many adult male Red-wings dived viciously but only three were observed to actually strike. In each of these instances, the nest held nestlings old enough for banding at the time of the attack, and each nest had been visited three days previously without eliciting such vigorous defense.

The breeding female established a smaller territory within the territory of her mate and including the nest. In this area the female gave the same threat displays as the male and occasionally assisted the male in chasing and attacking an intruder. As with the male, the vigor with which the female defended her territory increased as nesting progressed and varied with individual birds. Once the nest was constructed, the female's territory became the immediate vicinity of the nest. Nero and Emlen (1951) moved the nests of female Red-wings and found that the females followed their nests, even out of the male's territory.

The territory of a female is used for nesting and rearing young, and for roosting. Female prenuptial display, pairing up and maintenance of the pair bond, and coition are usually conducted in the territory of the adult male. Allen (1914) and Nero (1956a) both describe sexual chasing which may move outside of the male's territory, the participants returning to their territory at the conclusion of the chase. The female leaves the territory to feed, often travelling some distance.

Size of Territory

The size and shape of adult male territories varied greatly and were influenced by pattern of the vegetation, presence and distribution of high song perches, and pressure from other males. Aggressiveness of the individual male also had a direct influence on territory size, but it was apparent that the number of females within one male's territory had little influence on size of the territory. Nero (1956b) also found this to be true.

Figure 1 shows the size and shape of the six territories in the Inlet Valley Marsh in 1960. Number of females, locations of nesting attempts, and successful nests are indicated for each territory.

Maximum, minimum, and average sizes of male territories are summarized in Table 1. In general, territories were smaller in marsh habitat, where 51 averaged 0.17 acre, than in upland habitat, where 49 averaged 0.54 acre.

Territorial size in our marsh habitats is similar to those reported by Nero (1956b) and Orians (1961). The latter found denser populations and smaller territories where cattail was broken up, producing greater edge effect.

In all areas except Spencer Marsh, the limits of individual territories were determined by observation and outlined on maps.

The greater size of territories in the two small marshes compared to those in Spencer Marsh, and the greater size of upland territories compared to all

TABLE 1

Size of Territories of Red-wing Males

Location	*Number of territories*	*Territory size (acres)*		
		Maximum	*Minimum*	*Average*
Airport Marsh	14	1.12	0.06	0.26
Inlet Valley Marsh	6	0.40	0.26	0.33
Spencer Marsh	31	—	—	0.10
Upland (500 feet elevation)	20	0.99	0.19	0.57
Upland (1,200 feet elevation)	29	0.94	0.03	0.52
All marshes	51	1.12	0.06	0.17
All uplands	49	0.99	0.03	0.54

marshes is apparently due to lower population density, the density in uplands being much less than that in marshes. The two small marshes studied were surrounded by upland habitat suitable for Red-wing nesting, and territories included area surrounding these two marshes.

One territory at the Airport Marsh was exceptionally large, 1.12 acres, compared to 0.56 acre for the second largest territory in the marsh. This territory included a large expanse of open water with high song perches on each side of the water.

Nesting

While Red-wings commonly nest in marshes and in uplands in habitat suitable for Meadowlarks *(Sturnella* sp.) and Bobolinks *(Dolichonyx oryzivorus),* population density was much less in uplands investigated than in marshes. From this it might be inferred that decreasing marsh habitat and increasing populations forced more and more Red-wings to take up territories away from marshes. It follows that fields near marshes would be the first occupied by Red-wings, and as distance from the marsh increased, population density would decrease. This may have been the case when Red-wings first started nesting outside of marshes in any numbers, but is not true in Tompkins County today. The upland habitat at 500 feet elevation which was studied was adjacent to several small marshes used intensively by Red-wings. The upland habitat at 1,200 feet elevation was several miles from the nearest marsh. Yet population densities in the two areas were about the same. There was as much variation in numbers of Red-wings between individual fields in each area as between the two areas. Male territory size averaged about the same, 0.52 acre and 0.57 acre, for the two areas. Population density was far from maximum in either area with little friction between adjacent territorial males and with much unoccupied ground between territories.

Census data obtained by the road count method (Hewitt, 1963) revealed average densities of breeding males to be about 16 per 100 acres in marsh habitat, and 11 per 100 acres in upland habitat.

Sex Ratio

During the 1960 nesting season there were 13 female Red-wings and six territorial males in the Inlet Valley Marsh, an average of 2.17 females per male. Actual pairing in the marsh consisted of one male with a single female, three males with two females each, and two males with three females each (see Figure 1). In uplands where nesting density was low and individual birds could be identified by location, four territorial males with a single mate each and 22 with two females each were observed, an average of 1.85 females per male. In the Airport Marsh there were 14 territorial males and observation indicated between 21 and 30 territorial females.

The maximum number of active nests per day is a good indication of the number of females in a marsh. In the Inlet Valley Marsh in 1960 this was 13 which coincided with the known number of females. In the Airport Marsh the maximum number of active nests in 1960 was 27, giving a ratio of 1.86 females per male.

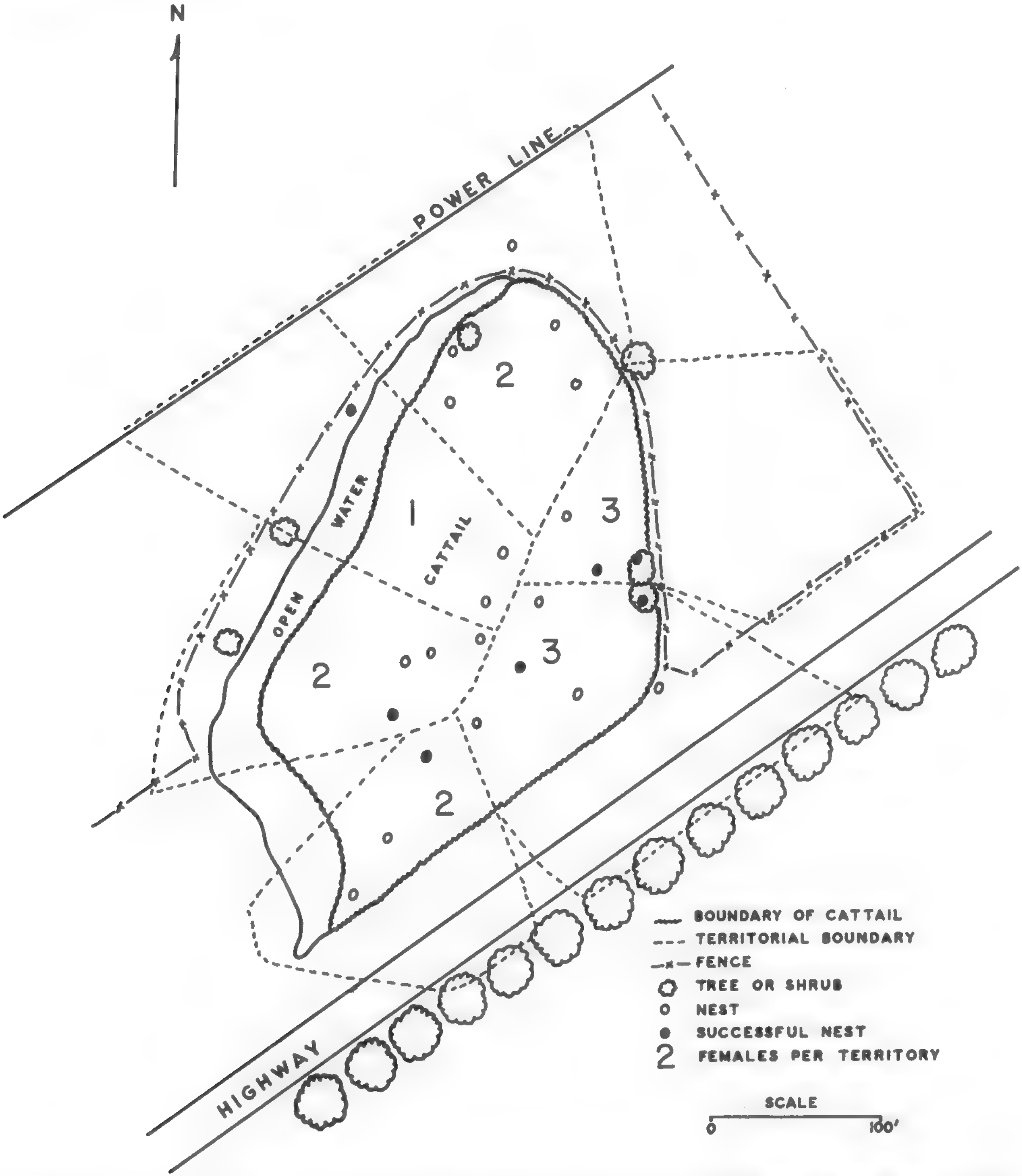

Figure 1. Map showing size and shape of the six Red-wing territories in the Inlet Valley Marsh, with the numbers of females, nests, and successful nests in each.

In 1961 there were again six territorial male Red-wings and a maximum of 13 active nests per day in the Inlet Valley Marsh. There were 16 territorial males and a maximum of 39 active nests in the Airport Marsh, a ratio of 2.44 females per male.

Meanley (1961, unpub.), in a three-year study of eight Red-wing nesting colonies in Chesapeake Bay tidal marshes, found a sex ratio of about one male to two females. Smith (1943), Nero (1956a), and Orians (1961) report averages from 1.6 to 3.7 females per male. Williams (1940) reported a sex ratio in nestling Red-wings of about 50:50. The difference between actual sex ratio and the unbalanced sex ratio of polygamous breeders is explained by the fact that many females breed when one year old, but few yearling males apparently are able to establish territories, even though capable of breeding (Orians, 1961).

Females began pre-nesting behavior during the second week of April. Actual nest construction did not start until two weeks later. The earliest nests were completed in the first week of May, with egg-laying and incubation beginning the next week. Earliest hatching took place in the last week of May.

Nest construction is done entirely by the female and there are no dummy nests, although many nests are deserted before they are completed or before they receive eggs. The time of early nest construction appeared to coincide remarkably for all females in an area. In 1960 the first egg was laid in a completed nest in the Inlet Valley Marsh on 7 May. On that date there were 11 other nests either being constructed or recently completed in the marsh. This was one nest less than the number of females known to be in the marsh.

Early in the season and during the peak of nesting, nests were constructed in five or six days. Some later nests were completed in three days. Egg-laying usually started the day after the nest was completed, although in some cases one day elapsed between the time the nest was completed and deposition of the first egg. In two cases observed, more lining material was added to the nest after the first egg had been deposited.

Nest Location

Red-wings are highly adaptable and their nests have been found in many locations. During this study Red-wing nests were found in 30 different species of plants. The most unusual Red-wing nesting site was a small red pine *(Pinus resinosa)* plantation, where trees were spaced about twelve feet apart, and from six to ten feet tall. Six Red-wing nests were located near the tops of the trees, three near the center of the stand, and three within a few rows of the edge. None of the nests were in outer rows.

Although Red-wings apparently will nest in almost any species of plant which will support their nests, around Ithaca a few species were most often selected, and preference changed as the season progressed. Marsh nests constructed in May were found in cattails and small bushes. In June and July more nests were found in bulrushes. In uplands most Red-wing nests in May were built in yellow rocket *(Barbarea vulgaris),* while nests constructed in June and July were located in goldenrod *(Solidago* sp.).

Clutch Size

The average size of clutches in 926 nests from three breeding seasons, 1959-61, was 3.5, with a range of 1 to 5 eggs per nest. Only those nests in which incubation was known to have occurred were used in determining clutch size. This precluded eggs and nests which were deserted before clutches were complete. Nests found after the eggs had hatched were not included, because the adults usually removed any egg that failed to hatch with the others.

No significant difference in average clutch size was found among the various habitats studied in 1960 and 1961 (Table 2).

Allen (1914) reported the usual complement of eggs in a clutch to be "three or four, the one number being as common as the other." In 840 completed clutches, we found 38 per cent comprised of 3, and 53 per cent of 4 eggs. Meanley et al. (1959) obtained an average of 3.3 eggs per clutch in 896 Maryland nests. Beer and Tibbitts (1950) found an average clutch size of 3.7 in 153 Wisconsin nests.

TABLE 2

Number of Red-wing Nests Used in Determining Clutch Size and Average Clutch Size for Each Location Studied in 1960 and 1961

	1960		1961	
Location	*Number of nests*	*Average clutch*	*Number of nests*	*Average clutch*
Airport Marsh	37	3.43	57	3.44
Inlet Valley Marsh	18	3.61	8	3.50
Spencer Marsh	233	3.42	277	3.60
Upland (500 feet elevation)	20	3.70	51	3.86
Upland (1,200 feet elevation)	13	3.15	72	3.65
Shackelton Point	129	3.46	—	—
Totals	450	3.45	465	3.61

Incubation and Care of Nestlings

Incubation started with the laying of the last egg and was done entirely by the female. The usual incubation period was 11 days, although both 10 and 12 days were recorded.

The female normally did all the feeding of the nestlings while they were in the nest. One male was observed making regular trips to a nest and feeding nestlings, and another male was seen making occasional trips. In each of these cases, a female was also feeding the nestlings.

A female in search of food for nestlings might travel some distance, often leaving the marsh or field in which her nest was located. In travelling to and from her nest, the female flew in a straight line. If there was a disturbance or alarm in the vicinity of the nest when she returned, she landed on a prominent perch or joined the male in hovering over an intruder; otherwise she returned directly to the nest.

If disturbed, nestlings left the nest on the 9th day after hatching. If undisturbed, the stronger nestlings left the nest on the 10th day, and weaker and smaller nestlings left on the 11th or 12th day. In inclement weather, many nestlings remained in the nest up to 14 days.

Peaks of Nesting Activity

The peak of nesting activity of Red-wings was determined for each area studied in 1960 and 1961 by plotting the number of active nests per day for each location. For this purpose, an active nest was defined as a nest containing eggs or nestlings, and not deserted. Graphs of the number of active nests per day for each area are shown in Figure 2.

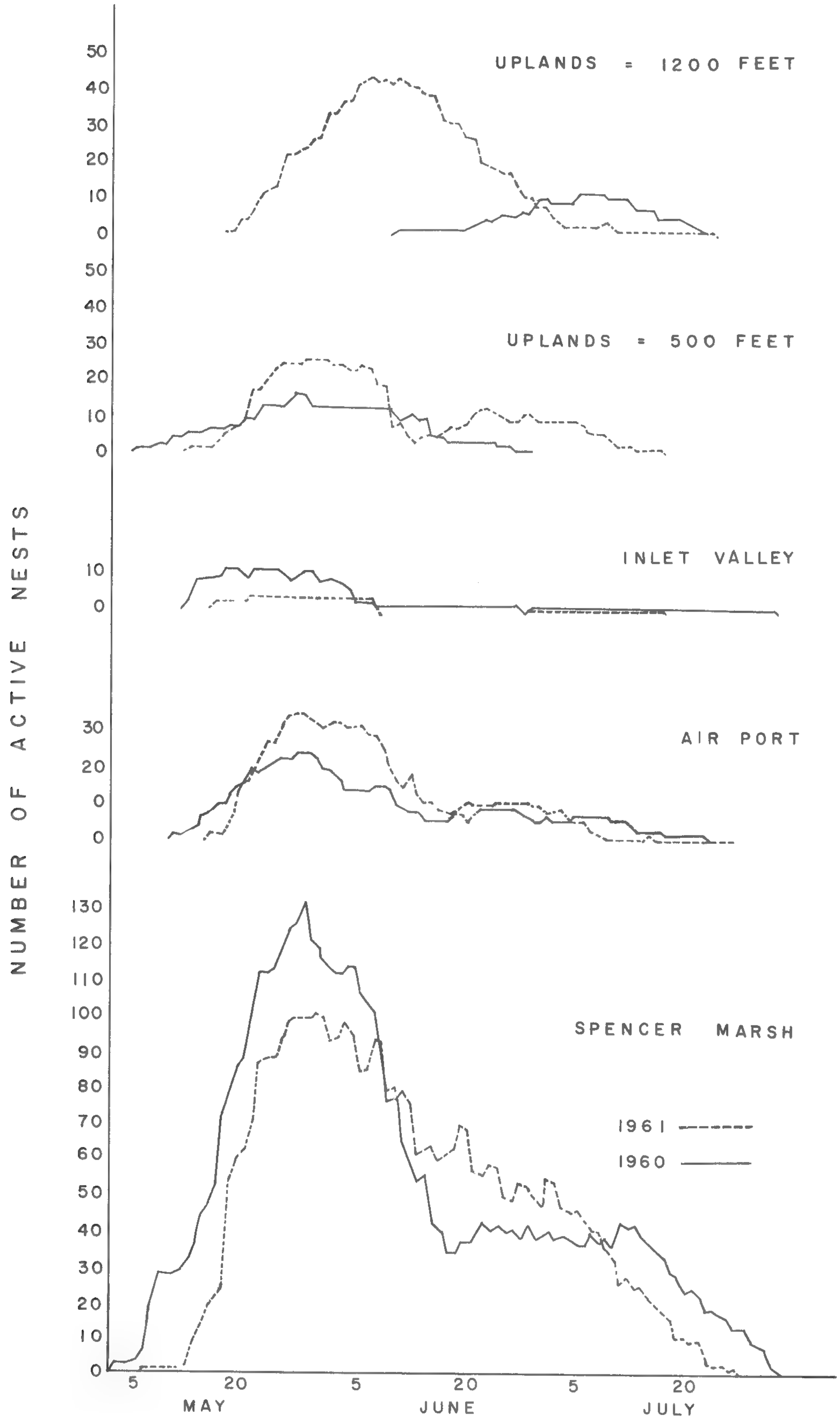

Figure 2. Number of active Red-wing nests per day in each study area, 1960-61.

The peak of nesting activity for each year at Spencer Marsh, the Airport Marsh, and uplands at 500 feet elevation came during the last week in May and coincided nearly to the day. The number of active nests in the Inlet Valley Marsh was too small to give a clearly-defined peak, but the figures suggest that the peak was the same each year and also came near the end of May. In 1960, observations in uplands at 1,200 feet elevation were not begun until the middle of June so the peak on the graph is not the peak of nesting. In 1961, study in uplands at 1,200 feet was started at the same time as in the other locations investigated. The peak of nesting activity in upland habitat in 1961 occurred a week or ten days later than in the other locations.

The dates of peak nesting activity correspond remarkably with observations made at Ithaca in 1914 by Allen.

Nesting Success and Productivity

To determine nesting success of Red-wings, nests were classified as successful, broken up, or deserted. A nest was considered successful if one or more nestlings reached the flying stage and left the nest. A nest which was torn down, had eggs broken, or had eggs or young disappear was considered broken up. A deserted nest was one which was started but never finished, completed but never had eggs, or abandoned with eggs or young. The number and per cent of nests in marsh and upland categories for 1960 and 1961 are given in Table 3.

In 1960, nesting success in all marshes was markedly higher than in uplands. This difference in success was due, in part at least, to upland nests being destroyed by mowing. Eight of the 36 nests broken up in uplands in 1960 (22 per cent) were destroyed when the fields in which they were located were mowed. In 1961, 16 of 99 nests broken up in uplands (16 per cent) were destroyed by mowing.

TABLE 3

Number and Per Cent of Red-wing Nests Successful, Broken Up, and Deserted, by Location

Location	*Year*	*Successful*		*Broken up*		*Deserted*	
		Number	*Per cent*	*Number*	*Per cent*	*Number*	*Per cent*
Airport Marsh	1960	28	47	14	23	18	30
	1961	29	48	23	38	9	15
Inlet Valley Marsh	1960	7	30	3	13	13	57
	1961	2	11	7	39	9	50
Spencer Marsh	1960	173	42	104	25	137	33
	1961	115	21	226	42	195	36
Upland (500 feet elevation)	1960	10	24	24	57	8	19
	1961	14	15	47	51	31	34
Upland (1,200 feet elevation)	1960	7	28	12	48	6	24
	1961	34	30	52	46	28	25

TABLE 4

Condition of Red-wing Nests Deserted in Spencer Marsh

Condition	1960		1961	
	Number	*Per cent*	*Number*	*Per cent*
Incomplete or complete but empty	96	70.1	165	84.1
Containing eggs	28	20.4	25	12.8
Containing young	13	9.5	6	3.1

Incomplete nests, and nests that were complete but did not yet have eggs, were frequently deserted. Since the search for nests was begun as soon as any sign of nesting was noted and every nest found was marked and revisited, nest desertion was undoubtedly higher in areas studied than in undisturbed habitat. As the nesting cycle progressed at a nest, the probability of its being deserted decreased. Nests containing eggs were much less apt to be deserted than incomplete nests, and nests with young were rarely abandoned. The number of nests in each condition that were deserted in Spencer Marsh in 1960 and 1961 and the per cent of the total number of nests deserted each year in each category are listed in Table 4.

The numbers of fledglings which left the nest in each area studied in 1960 and 1961, and the number of fledglings per nest found and per successful nest are summarized in Table 5.

The numbers of fledglings produced per successful nest may give a misleading concept of productivity. For example, the number of fledglings per successful nest in Spencer Marsh in 1961 was 2.48 as compared with 2.51 for 1960. This comparison indicated that productivity was about the same in each

TABLE 5

Red-wing Fledglings Produced

Location	*Fledglings produced*		*Fledglings per nest*		*Fledglings per successful nest*	
	1960	1961	1960	1961	1960	1961
Airport Marsh	85	69	1.42	1.13	3.04	2.38
Inlet Valley Marsh	21	3	0.91	0.17	3.00	1.50
Spencer Marsh	435	285	1.05	0.53	2.51	2.48
Upland (500 feet elevation)	28	41	0.67	0.45	2.80	2.93
Upland (1,200 feet elevation)	16	84	0.64	0.74	2.29	2.47
Shackelton Point	191	—	1.09	—	2.89	—

season. However, the proportion of nests successful was much less in 1961 than in 1960. Comparing the number of fledglings produced per nest found in 1961, 0.53, with the number of fledglings per nest in 1960, 1.05, indicates the decrease in productivity in 1961.

Disturbance caused by construction next to the Inlet Valley Marsh is believed to have caused the decrease in nesting success there in 1961 as compared to 1960. At Spencer Marsh nesting success decreased greatly in 1961 as compared to 1960, while the number of nests broken up increased greatly. In 1960 eggs disappeared from 49 per cent of the nests broken up. In 1961 the proportion of nests broken up from which eggs disappeared increased to 61 per cent. Reasons for this increase were not determined.

Red-wing fledglings, about nine days old. Photograph by David G. Allen.

In the Airport and Inlet Valley Marshes, where the population density was determined, the number of fledglings produced could be related to the number of nesting Red-wings. The number of fledglings produced per territorial male, per nesting female, and per breeding adult in 1960 and 1961 for these two areas is listed in Table 6. Meanley (1961, unpub.), in his three-year study of Red-wing nesting colonies in Chesapeake Bay tidal marshes, found "approximately 4.0 birds fledged (reaching flying stage) per female or 7.5 per male."

Renesting and Second Broods

If a Red-wing nest was destroyed or deserted during April or May, the female would usually start a new nest in the same area within a few days. In June some females would still renest, but the number decreased as the month passed and by the end of June most females whose nests were destroyed deserted the nesting territory.

TABLE 6

Number of Fledglings Produced Per Territorial Male, Per Nesting Female, and Per Breeding Adult Red-wing

Number of fledglings	*Airport Marsh*		*Inlet Valley Marsh*	
	1960	*1961*	*1960*	*1961*
Per territorial male	6.00	4.31	3.50	0.50
Per nesting female	3.15	1.77	1.62	0.23
Per breeding adult	2.05	1.25	1.11	0.16

Every nest found during the study was revisited throughout the nesting season or until destroyed. No nest which had been deserted or broken up was ever reused. In one instance a new nest was constructed on top of a nest which had been deserted.

Red-wings are generally credited with raising two broods in a season (Allen, 1914; Mayr, 1941; Beer and Tibbitts, 1950; and others). Some Red-wings did raise two broods in a season in the areas studied, but the majority did not. That it was impossible for even half of the Red-wings to have raised two broods is shown by the graph for peak nesting activity at Spencer Marsh (Figure 2).

A conservative time limit for one nesting period is 27 days—6 days for nest construction and egg laying, 11 days for incubation, and 10 days for feeding nestlings. Two broods would take at least 54 days unless a female constructed a second nest while still feeding young in the first nest—a contingency which was never witnessed. Referring to the data from Spencer Marsh in Figure 2, the maximum number of birds which could have had active nests over a period of 54 days in 1960 was 36. At the peak of nesting there were 131 active nests in the marsh. In 1961, 30 birds could have had active nests over a 54-day period and there was a peak of 100 active nests. Probably many more females attempted to raise second broods and were unsuccessful.

Summary

The first flocks of migrant male Red-wings arrived at Ithaca toward the end of March. The earliest flocks of female Red-wings arrived the first week in April. Some immatures were seen in all flocks, but the number increased as the season progressed.

Some of the first males to reach Ithaca established territories and the number of territorial birds increased rapidly. Most territories were occupied by the end of the first week in April. Females started entering territories of the males upon arrival.

The territory of a male Red-wing is easily delineated by the threat displays the occupant directs toward intruders. Male territory size averaged 0.17 acre for 51 territories in marshes and 0.54 acre for 49 territories in upland habitat.

Upland habitat several miles from any marsh was as readily used by Red-wings for nesting as upland near marshes.

The sex ratio in breeding areas investigated varied from 1.86 females per male to 2.44 females per male. The sex ratio of nestlings is believed to be 50:50 and the higher ratio of females per breeding male is due to the fact that most yearling males do not breed.

Nest construction, began the last week in April, usually took six days, and was done entirely by the female. Although nests were constructed in many species of plants, they were most frequently located in cattails and bulrushes in marshes, and in yellow rocket and goldenrod in uplands.

Clutch size averaged 3.5 eggs for 926 nests and ranged from one to five.

Incubation took 11 days and was done entirely by the female. With two exceptions the female also did all the feeding of nestlings while in the nest. Fledglings usually left the nest the 10th day after hatching, earlier if disturbed, later in inclement weather.

The peak of nesting activity, based on maximum number of nests containing young or eggs per day, occurred the last week of May in marshes and uplands at 500 feet elevation. The peak of nesting activity in uplands at 1,200 feet was a week or ten days later.

Nesting success, judged by per cent of nests from which fledglings departed by themselves, ranged from 11 to 48 per cent for the different locations studied. Marshes were generally more successful than uplands. In the majority of cases of nest failure eggs disappeared from the nest.

Fledglings produced in the sites studied ranged from 0.17 to 1.42 per nest found, and 0.16 to 2.05 per breeding adult.

During April and May most females renested if their nests were destroyed, the number of renestings decreasing rapidly in June. Less than half of the nesting females raised two broods in a nesting season.

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THE LIFE CYCLES OF THREE AUSTRALIAN PARROTS: SOME COMPARATIVE AND POPULATION ASPECTS

JOHN LE GAY BRERETON

The life cycle is generally thought of by ornithologists as the series of events and actions in the life of a pair of birds either from their separate emergences from the egg until their deaths, or from the beginning of one breeding season to the next. The life cycle might also be thought of satisfactorily as the life of a *population* of a species. This would permit our tracing changes in fecundity and survival curves and the mean length of a generation. Data of this sort are still much too rare but when we have them in sufficient quantity we should be able to see how these variables are juggled in order that a population can survive without becoming so dense or so sparse as to put its own existence in jeopardy.

Most any population, which oscillates between overpopulation and underpopulation, would soon be close to extinction and have a low probability of survival. This probability could be prevented, however, if the breeding population were regulated so that it would not be too dense and would be composed of individuals which are neither very old nor very young. One way the population could be regulated would be by a reserve "pool" of medium-aged birds from which individuals could be drawn to replace breeding stock.

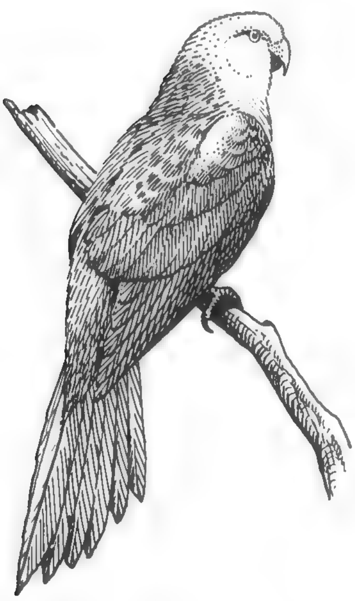
The study of the life cycle is not simply the description of events and actions and their correlation to environment and seasonal change, but also the study of behavior, the function of which is to ensure that the breeding core of a population is not endangered by competition or over-exploitation (Brereton, 1962; Wynne-Edwards, 1962). The purpose of this paper is to consider the life cycle of some Australian parrots with this point of view in mind.

Three Types of Parrot Life Cycles

(1) The King Parrot *(Alisterus scapularis)*

This species is one of three in the genus whose range is from some eastern islands of Wallacia through New Guinea and south to northeastern Australia. It is a bird of lowland rain forest.

The plumage of the male is bright and distinctive while that of the female and juveniles is much duller. No courtship preening or social preening is known, but courtship feeding occurs. The main food of King Parrots appears to be berries and fruit, but they like corn which they take from the plant or ground. The food is transferred from the bill to the foot while they are perched in trees. When flocked they vocalize in flight and after landing. During feeding periods they show aggression and may vocalize too.



King Parrot

In the autumn and winter in eastern New South Wales, King Parrots, in flocks of up to 30 individuals, move out of the rain forest to feed on corn. Later, they appear in pairs, and still later, during the incubation period, the male perches in a tree near the one in which the female is sitting on eggs. Juveniles and immatures have not been noticed in the vicinity of breeding pairs.

Although the details of the King Parrot's life cycle are not known, it may be assumed to be as follows: In the autumn and winter the species occurs in flocks, each probably composed of one large family party, or several closely-related family parties. At the beginning of the breeding season the adult pairs disperse from the flocks and move into the rain forest where they seek out suitable nest-holes. After their young fledge, the family party rejoins other such parties and remains with them until the next breeding season. In view of the long life of these parrots, such flocks could become very large in a number of years, but this is not known to happen.

(2) Eastern Rosella *(Platycercus eximius)*

This species lives in tree savannas from the Queensland border to eastern South Australia. Although it feeds typically on the ground, it frequently searches in trees for the fruit of the eucalyptus and mistletoe. In such situations it often transfers the food to the foot while eating the pieces.

Since 1958 a capture-recapture study has been under way at Armidale, New South Wales. Since the work is still in progress, a full report is impossible, but the results to the end of 1961 are worth presenting here because of their bearing on the problem under discussion.

Trapping is undertaken each month during the winter at three trapping points. The recapture rate is high—292 (63 per cent) of the 465 captures have been recaptured. Furthermore, the 465 captures at the three points represent only 231 individuals of which 172 were not recaptured. Thus the large number of recaptures has accumulated from taking over and over again only 59 individuals.

The life cycle and behavior of the Eastern Rosella has been studied at the same time by means of field and cage observations, combined with the capture-recapture data. In the autumn the Rosella is seen in groups of about eight birds. They feed on the ground in the morning and evening, and sit quietly.

When roosting they gather in larger groups of 12 to 25 individuals. At their roosting sites — eucalyptus trees and saplings or melalenca thickets — they usually land in the smaller branches and, with frequent noisy disturbances and changes, climb into the outer twigs where they become deeply enmeshed in the dense mass of leaves in this part of the tree. The attachment of these parties and flocks to certain trees is very strong. If they are disturbed and fly out, they quickly and repeatedly return to the same trees.

As winter approaches they may be seen feeding in flocks of about eight to twenty-five. In cold weather, flocks may become large — seventy to several hundred birds — but when such a feeding flock is disturbed it breaks up in flight into parties of about twenty. Feeding may occur in the middle of the day in unusually cold weather. Not infrequently the Eastern Rosella, in these circumstances, feeds with the Red-backed Parrot *(Psephotus haematonotus).*

Early in the spring, family parties tend to separate from the flock. They frequent patches of timber with large eucalyptus trees which have knot-holes and pipes used as nest-sites. The parent pair examines various trees over an area of about a hundred acres, followed by the juveniles of the party. The male leads, flying up to a tree, giving the Tail-wobble, looking into the hole, and moving a short distance away. In such circumstances the female peers into the hole, and later enters it for short periods. She may place her culmen against the wood near the hole as if testing its firmness. As she goes down into the hole the male gives a distinctive piping call. If another Rosella flies too close, the male utters the Beak-clatter. Should the intruders not move off, this may elicit a flying attack, accompanied by the Tail-wobble and a distinctive vocalization during which the tail is spread, revealing the light-colored distal parts of the lateral rectrices. These affrays often involve several birds and are extremely noisy. Should a predator appear while the female is in the hole, the male gives the A-Chut-Cha vocalization — presumably a warning signal.

Eastern Rosella

Cage studies show that fairly early in the spring the female Rosella changes from roosting in the open to roosting in a chosen nest-hole. She spends some time scratching and cleaning out the hole with her feet and bill. Later, shortly before eggs are to be laid, courtship feeding is performed, either on the ground during general feeding, or in trees away from the nest-hole, or in the tree near the nest-hole. Courtship preening, on the other hand, has not been observed in the Eastern Rosella. The female does all the incubating, leaving the hole about twice per day to be fed by the male and usually returning almost immediately. The same procedure is more frequent after the young have hatched. Once they pass the pinfeather stage, the male commences to enter the hole—doubtless to feed them. The fledglings fly from the hole one at a time after much displaying by both parents. Immediately afterwards, courtship feeding, having been absent during the period when the male was feeding the young, recommences. This is followed within a day by copulation. Both parents have been feeding the fledglings but, from now on, feeding is continued chiefly by the male until the fledglings are independent.

The Eastern Rosella generally has two broods, the second following immediately upon the first, which could produce as many as twelve young birds. We have too little information on what happens after fledging, consequently the following events are mainly postulated.

On the average, about four young-of-the-year appear to remain with the parents during the production of the first brood. These juveniles, now almost twelve months old, keep in the vicinity of the parents during incubation, but with the emergence of the first fledglings of the year and the male's occupancy in feeding them, the relationship between juveniles and parents becomes more distant. On the fledging of the second brood, the earlier brood tends to amalgamate with the juveniles, which comprised the second brood of the previous year, and to move as a separate group although at the same time following the parental group. Meanwhile the fledglings of the second brood move closely with their parents. In this way we should expect juveniles and fledglings to make up small parties of eight to twelve birds, and parents and second-brood fledglings parties of six to eight individuals. These parties come together at roosting time, making up flocks of fourteen to twenty individuals. As mentioned earlier, in winter three or more such flocks may join together for feeding, making larger flocks of seventy-five or more birds. With the onset of spring, closely related parties return to the breeding area, where again the parents continue to dominate the group, searching for nest-holes and finally choosing one, often the same one used the year before. The "lower-status" party no longer moves closely with the parental group and may remain flocked. Its chances of survival may be much poorer than its parents'.

This hypothesis is not inconsistent with our trapping results. In the first place, we have an indication that first-year birds disappear. Of the 231 individuals trapped for the first time, 172 were not seen again. Some of this apparent loss may actually be due to the loss of bands, but much of it may be the result of mortality. In the second place, by being able to age the birds, we know that the older ones continue in the population for long periods. Some of the 57 individuals which we retrap cannot be less than five years old. Thus a severe loss of the younger individuals seems to be taking place, yet we have very little understanding of how it occurs.

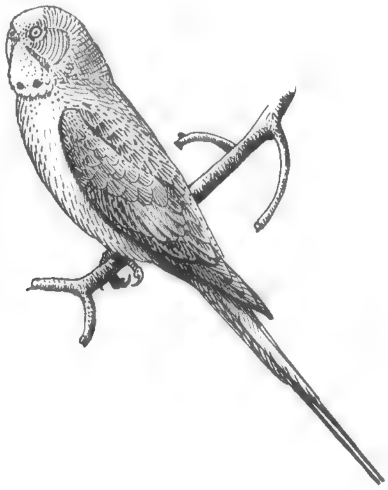
(3) Budgerigar *(Melopsittacus undulatus)*

This species occurs in flocks scattered throughout the arid zone of central and western Australia. In severe droughts it moves farther south and toward the coast. Generally considered nomadic, at least in northwestern New South Wales, it appears each summer near water holes and rivers bordered by eucalyptus trees with suitable nest-holes. It feeds almost entirely on the ground where it takes seeds from tall grass. Food is never held in the foot.

Although the Budgerigar is well known in aviaries, its life cycle and general ecology have not been studied. Its water balance, so nicely adapted to aridity, has been investigated by Cade and Dybas (1962), and its general behavior has been described by Brockway (1962). I have made a preliminary study of the population life cycle in caged birds and will summarize it here.

Two populations were followed. Each was housed in a two-cage system, a small hole allowing movement from one cage to the other. Food and water were kept in both cages, three nest boxes in one of them. At the start each population comprised three adult males and three adult females taken at random from stock cages where the sexes had been kept separate. The two populations were placed beside each other and were the only birds in the room. Light was fluorescent and controlled by a time-switch set for a 12-hour day. Air temperature ranged between 60° and 80°F.

When the cages were first arranged, all the individuals stayed in the same cage, and this was the one nearer its neighbor. For several days the birds kept silent, and perched so as to allow an individual distance of about 15 inches. Feeding occurred mimetically.



Budgerigar

When Loud-warbling (Brockway, 1962) of the males commenced, it was associated with their attempts to courtship-feed the females. At first the females responded aggressively, but this behavior gradually decreased and courtship feeding proceeded. At this point a male moved to the nest-box entrance, frequently followed by a female. In due course a female entered a box for short to increasingly longer periods, as was found also by Brockway (1962). On leaving the box she was often courtship-preened by the male at the entrance, but she was more often courtship-fed. The female was very apprehensive in or near the box in the early stages, and the presence of another female disturbed her greatly. By incipient copulation, courtship preening, and courtship feeding, the male "attempted" to bring about her return to the box. In the early stages she left the nest-box area apparently from fear—later it was clearly an aggressive tendency. She showed little or no concern toward males. On the other hand, the males showed distinct aggression toward other males.

All the incubation was done by the female, the male never entering the nest-box until the young had hatched. He did, however, feed the female by poking his head through the hole of the nest-box. After the fledglings left the nest-box, the male, but more often the female, occasionally fed them, though this was unusual. The fledglings occasionally courtship-preened and courtship-fed.

In both populations a single pair dominated the nest-box area, taking up one box for themselves and denying use of the other two to the other pairs.

Failure of the subordinate males to get near the nest-holes resulted in a failure of their mates to enter nest-holes. Consequently these two females reverted to spending the greater part of their time perched, asleep, or preening, in the "non-reproduction" cage. When their mates or other males attempted to courtship-feed them, their response was aggressive, with the result that their mates tended to turn their attention to the dominant female. This usually produced an aggressive Bill-thrust from the dominant female, and aggressive chasing of the challenging male by her mate. However, when the young neared fledging, the dominant female sometimes allowed subordinate males to feed her. The food-begging calls of the young released a marked tendency for both subordinate males and females to attempt entering their nest-box, but this was resisted by the parents. After the first brood fledged, the parents increased their courtship feeding and preening, copulated, and the female re-entered the nest-box to lay. The fledglings now spent most of their time in the non-reproductive cage, while the subordinate pairs showed more readiness to breed, one pair laying one egg by the time the young of the second brood emerged. Both females took possession of nest-boxes but their capacity to breed successfully was greatly reduced.

The events described above applied to both populations, but there were marked differences. In the second population the two superior males and their mates were evenly matched; the dominance of one over the other passed back and forth almost daily. Only one chick was reared, while one adult male died. His death was the result of constant chasing and finally, as he weakened and his head and wings drooped, of being mounted repeatedly by the aggressive, sub-dominant male. Owing to the lack of social organization of the kind found in the first population, this second population's capacity to increase, and even to survive, was greatly lowered.

While it is clear that these experiments need to be run several times and for longer periods, it is worth while to attempt to interpret them in terms of what is known of the ecology of the species and its life cycle.

The Budgerigar has a high social index (Brereton, 1963). This has been correlated with its migratory way of life, and compared with the even higher social indices of the brush-tongue parrots (Lorriidae) which are nomadic. The degree of social cohesion is so very strong that individuals do not leave the flock. Thus the fledglings and juveniles remain close to their parents during breeding. This could lead to a powerful tendency toward unrestricted increase in numbers and, ultimately, intense and even damaging competition for the limited number of nest-holes at a breeding place. It seems likely that a hierarchial system, which inhibited breeding without physical aggression, would be advantageous to the population. Furthermore, it seems likely that, when the population grows too large for individuals to be able to recognize new members, the low-status, younger element may "bud off" and attempt to exploit as yet undeveloped breeding places.

Discussion

The three species discussed here illustrate three markedly different life-cycle types, each being found in a different vegetational formation. In the first, the King Parrot, we have a sedentary species of lowland rain forest. It has a limited development of social behavior with a social index of 37. The parental pair appears to remain united over the years, but the young seem to lose contact with the parents when they take up their breeding area. In the Eastern Rosella we again find a sedentary species with a low social index (40), yet with the juveniles associating much longer with their parents. It is found in a rainfall area, rarely subject to droughts, but in an open type of woodland. It feeds chiefly on the ground but has a well-developed ability to obtain food in trees and shrubs. Lastly we have the Budgerigar of the arid interior, feeding exclusively on grass seeds and unable to hold food in the foot. It is a nomadic species with a high degree of sociality (83), the young remaining with the parents throughout their lives, except for the occasional budding off of flocks of lower-status individuals.

In all three types I suggest that there exists a reserve, non-breeding population which, in the sedentary forms only, joins with the long-lived breeding group in the winter when flocking takes place. However, in the migratory Budgerigar, the reserve population always travels with the breeding population. In this way both populations can exploit good conditions at any time during their wanderings, but will return each summer to a relatively fixed number of breeding sites.

These three types of life cycles fall into a series, and may serve as a basis of comparison for other species of the order. However, I am tempted to list at least two others, examples of which are not known but which may exist or may have existed. The first type would be a species in which the young and the parents lead solitary lives, the parents being together only briefly for copulation and the initial rearing of the young (Type 1). A second type would be one where the parents remain together but there is no flocking in the winter (Type 2) . The third type is that of the King Parrot where flocking does occur in the winter (Type 3). Next we have the example of Eastern Rosella where flocking occurs and some of the young remain with the parents throughout a part of the breeding season (Type 4). Lastly, we find the situation, as in the Budgerigar, where the young move for an indefinite time with the adults (Type 5).

It may be argued that the life cycle of a species is a unified whole and is characteristic of a species. In this sense it is as good a taxonomic character as any, making comparative studies of life histories fully as meaningful as studies of comparative morphology (Cole, 1954). Now that I have described a means of categorizing parrot life histories, consideration may be given to comparative details of parrot life cycles.

Table 1 summarizes the distribution of courtship preening and feeding, participation of male and female in incubation and feeding young, and other life-cycle characteristics, together with life-cycle type and social index, among 19 different kinds of parrots. (The families to which the species are assigned follow Brereton, 1962.) I must point out that, while courtship feeding or courtship preening may be absent in certain species of parrots, in none of the parrots in Table 1 are both absent. When courtship feeding is absent, both parents take part in incubating. Feeding of young is undertaken by both parents, but in the Budgerigar and the family Platycercidae, the male only assists in the later stages of rearing the young. In the African genus *Agapornis* we see two clear-cut groups in terms of social index and nest-spacing. Although there appears to be no other change in the elements of the life cycle studied here, numerous correlated differences exist when the behavior of these species is examined in detail (Dilger, 1960; and pers. com.). Differences of a greater magnitude are known in the Platycercidae.

It is shown in Table 1 that courtship preening is absent in Eastern Rosella and *Neophema bourkii*. While the Rosella holds food in the foot, this is absent for the more distinctly grassland forms, *Psephotus haematonotus* and *Neophema bourkii*. The genus *Lathamus* has a life cycle much more like that of a

TABLE 1

Summary of Life-Cycle Characteristics in 19 Species of Parrots

	Court. preen.[1]	*Court. feed.*[2]	*Sex incub.*[3]	*Sex feed.*[4]	*No. broods*	*No. eggs*	*Nest spac.*[5]	*Mobility*[6]	*Veg. Form.*[7]	*Type l. c.*[8]	*Social index*[9]
CACATUIDAE											
Calyptorhynchus spp.	p	p	f?		1?	1-2	m-d	s-m	rf, f	4	79
Cacatua galerita	p	a?	mf?	fm?	1?	1-2	m	s-m	rf, f	4	76
C. leadbeateri	p	a?	mf?	fm?	1?	1-2	dd	s-m	w	3	57
C. sanguinea	p	a?	mf?	fm?	1?	1-2	cl	s-m	w	4	80
C. roseicapilla	p	a?	mf?	fm?	1?	1-2	cl	s-m	w	4	67
LORIIDAE											
Trichoglossus sp.	p	p					m	n	f	5	100
Glossopsitta sp.	p	p					m	n	f	5	100
MICROPSITTIDAE											
Loriculus galgulus	p	p	f	?	1	3-4	d		f, sv		57
Agapornis cana	p	p	f	fm		4-8	m-d	s?	sv		44
A. pullaria	p	p	f	fm		3-5	m-d	s	sv		52
A. taranta	p	p	f	fm		3-5	m-d	s	sv		46
A. roseicollis	p	p	f	fm		3-5	cl	s	sv	3	74
A. personata	p	p	f	fm		3-5	cl	s	sv		85
MELOPSITTACUS											
Melopsittacus sp.	p	p	f	f-m	many	6	cl	m	sv	5	87
ALISTERIDAE											
Alisterus scapularis	a	p?					d-dd	s	rf	3	37
Nymphicus sp.	p	a?	mf	fm			m-d	s-n	sv	4	66
PLATYCERCIDAE											
Neophema bourkii	a	p	f	f-m	2	6	cl?	s-n?	sv	4	c.60
Psephotus haematonotus	p	p	f	f-m	2	6	cl	s	sv	4	60
Platycercus eximius	a	p	f	f-m	2	6	m-d	s	w	4	40

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[1] Courtship preening: p, present; a, absent.

[2] Courtship feeding: p, present; a, absent.

[3] Sex(es) incubating: f, alone; mf, male and female equally.

[4] Sex(es) feeding young: fm, male and female equally; f-m, female at first and later also male.

[5] Nest spacing: cl, more than one nest per tree; m, nests within 220 yards of one another; d, within 220 to 1,760 yards; dd, over 1,760 yards apart.

[6] Mobility; s, sedentary; m, migratory; n, nomadic.

[7] Vegetational formation: rf, rain forest; f, forest; w, woodland; sc, scrub; sv, savanna.

[8] Type of life cycle: see text for 5 different types.

[9] Social index: A series of numbers from 1 to 100 used to express the degree of sociality. The higher the number, the greater the degree (see Brereton, 1962).

loriid. Thus we get some inkling of those parts of the life cycle which are plastic and those which are more rigid.

Although the data do not allow us to present any firm conclusions on the adaptive advantages of these various life-cycle patterns and the components which have been listed, it does allow us to see that a fuller knowledge of this sort of material can throw light both on the evolution of life cycles and social behavior and on the relationship of the life-cycle patterns to population regulation. Much more could be done in this field if aviculturists and bird watchers would collect and publish more data of this kind.

Conclusion

It is conceivable that the reproductive capacity of a species might become so great that it might endanger the survival of the species (Cole, 1954; Brereton, 1962). Examined here is the possibility that the life cycles of the three parrots described include a mechanism for reducing the capacity to increase and for providing an adequate reserve supply of individuals in cases of catastrophy. Attention is also drawn to the species and family specificity and to the variation in the life cycle. It is suggested that further work along this line will throw light on the evolution of social behavior and population regulation.

Acknowledgments

Aspects of this paper were discussed with Dr. W. C. Dilger, and all the data concerning *Agapornis* and *Loriculus* were made available by him. It is indeed a pleasure to acknowledge his aid, that of his students, and of all the staff of the Laboratory of Ornithology at Cornell University where the author was visiting Research Fellow during 1962.

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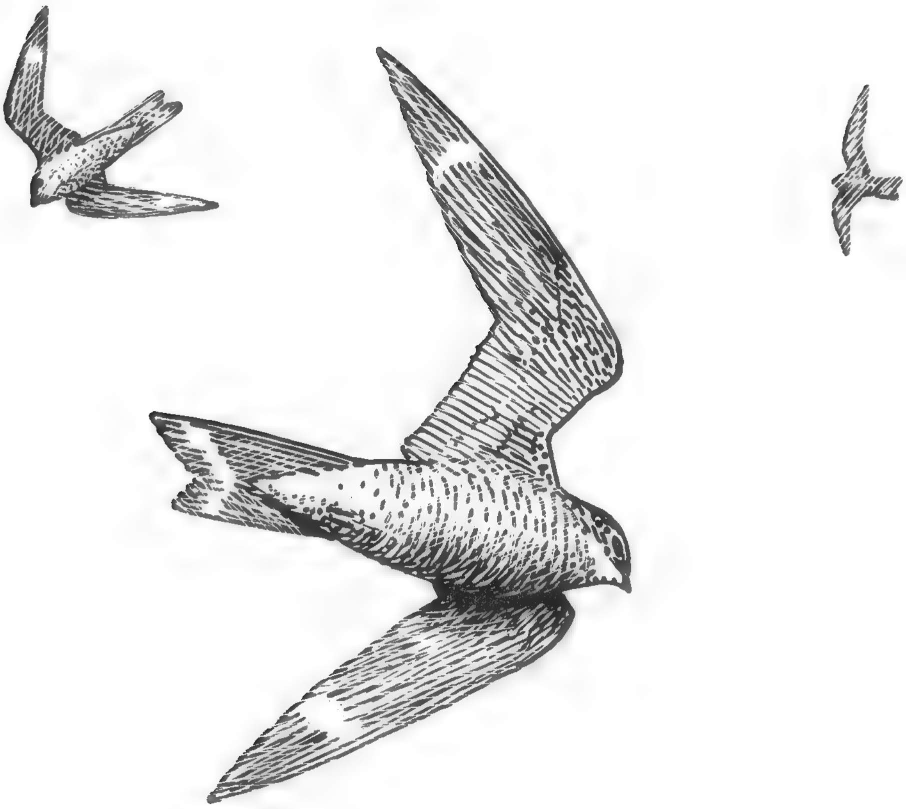

NOTES ON THE BEHAVIOR OF COMMON NIGHTHAWKS IN FLORIDA

CHARLES A. SUTHERLAND

While at Key Largo, Monroe County, Florida, on 6 June 1962 I located 16 pairs of Common Nighthawks *(Chordeiles minor)* nesting remarkably close to one another. Three of the pairs were identified on the basis of vocalizations as belonging to the Caribbean race, *C. m. vicinus;* the others were of the Florida race, *C. m. chapmani.* From 6 to 11 June, I made numerous observations on the different pairs and devoted 46 hours to watching one pair, with two young, of the Florida race. The results of this work are reported here and compared with the literature on both the Common Nighthawk and the Lesser Nighthawk *(C. acutipennis).* References to the literature pertain to the Common Nighthawk, unless otherwise indicated.

The Nesting Area

I found the Nighthawks nesting at the north end of Key Largo on a 26-acre coral flat. Though without houses, it was interrupted by a road, a boat basin, and a marl pit surrounded by an eight-foot dike. In the vicinity were canals, a causeway, a few houses, mud flats, and some mangroves.

The coral flat consisted of bare coral with widely scattered small plants. Nesting in the area were Ground Doves *(Columbigallina passerina)* and Least Terns *(Sterna albifrons).* A cat and one rat were the only other vertebrate animals seen on the flat.

Methods of Observation and Equipment Used

Since the nest-site of the family I chose for concentrated study could be viewed from my car, I used my car as a blind, driving it to a suitable position and away again without flushing the brooding female. My presence and movements in the car did not appear to interfere with parental care of the young. I checked the nest at night by using a spotlight and a 7x,50 binocular. On three evenings I made observations from sunset to total darkness and on two mornings from total darkness to sunrise.

To record vocalizations of the Nighthawks I used a battery-operated Nagra III tape-recorder. In obtaining the sounds of the adults and young at the nest I placed the microphone close by the nest and then monitored the sounds with earphones and tape-recorded them in my car.

Proximity of Nests

Seldom are nests of Nighthawks concentrated in one area as they were on Key Largo. When I walked over the coral flat, one male after the other took flight to defend his territory. It seemed that no sooner had one male, whose territory I passed through, settled on the ground when another male was in the air to take his place. The 16 nests averaged about 80 yards apart. Gross (1940) quotes E. A. Samuels as having found nests on a rock ledge "every four or five rods." Warren (1890) found Nighthawks in Pennsylvania breeding within a few yards of each other, and Rust (1947) found nests in the open country of Idaho, 52 and 210 yards apart.

Audible Displays

I distinguished eight types of calls, all of which were recorded on tape and are now in the Library of Natural Sounds of the Laboratory of Ornithology at Cornell University. The calls and accompanying behavior described below refer to the Florida race. Although the vocalizations of the Caribbean race were recorded, they are not brought into the discussion.

Peent — This was given by the male in conjunction with a series of four or five quick wing-beats (one Peent to each series) and appeared to announce territorial ownership. Neither Eugene Eisenmann of the American Museum of Natural History (pers. com.) nor I have found evidence of the female giving this call.

Kit — This call, rapidly repeated, I heard twice, (1) by a male in pursuit of another Nighthawk and (2) by a male in response to my entering defended territory. Gross (1940) describes a similar call given by a male while chasing an unidentified Nighthawk as a series of *yap-yap-yap-yap* sounds in rapid-fire succession. He also found that when males chased each other during courtship season they gave sharply-accented, rapidly-uttered calls resembling *dick-a-dick-a-dick-dick-dick-dick-dick*. Bent (1940) mentioned notes heard from the western race of Common Nighthawk, *C. m. hesperis*, as sounding like *click-click-click-click*, rapidly repeated. When Weller (1958) walked into a Nighthawk's territory, the male uttered a *cho-ic* or *che-wip* intensely and rapidly until Weller left. While all these calls are clearly similar, they are not well enough described to be compared adequately.

Booming — This was a characteristic display of the male when he finished a dive with suddenly down-flexed wings. The resulting rush of air caused a loud vibration. Miller (1937) observed the Lesser Nighthawk performing short dives during courtship displays but producing no sound. He suggested that the display may be a form of relict behavior. Weller (1938) noted that Booming was largely restricted to the nest area, and this I found to be true at Key Largo. Rust (1947) remarked that he could determine the approximate locations of nests merely by watching where males were diving.

Peep — Except when frightened or hungry, the chicks gave these notes any time they were active. These were undoubtedly the "faint peeping notes uttered by the youngster" of which Gross (1940) speaks.

Long Peeps — The chicks studied on Key Largo gave these more intense, drawn-out calls in response to Hissing (see below) by the female and to Peent notes of the male prior to his descent from the air to feed the chicks.

Hissing-growl — The female gave this sound each time the male flew over her and Peented, just prior to feedings at dusk. With each pass her responses grew louder and longer until the male landed to feed the young. Bowles (1958) reported that the female occasionally remains silent when the male lands with food. Gross (1940) mentions a female answering the male at feeding but did not describe the call. Weller (1958) thought the call of the male to be a signal to the young of his approach. In regard to the Lesser Nighthawk, Pickwell and Smith (1938) wrote: "The female arrived in the vicinity of the nest, flying about, and the male responded while continuing to brood the young. The male shortly arose and flew toward the calling female." They did not describe the calls.

Short Growl — This short, low, purring growl was heard usually only at feeding time when both adults were on the ground. The male's version sounded slightly deeper than the female's. Weller (1958) reported a similar sound: When the male landed near his mate he called a low, nasal *nar-r, nar-r,* to which she responded with a gutteral *kra-a* but did not leave the nest. This may also be the call Gross (1940) described when he wrote that the female uttered "a purring, pacifying note" while brooding the young.

Chucking — This was given by the female when encouraging the chicks to follow her on her return after being flushed. Weller (1958) may have been referring to calls of this nature when he wrote about the female moving toward the nest and giving a low nasal *kurr* or *kra* at the rate of one per second, while the "young followed her, resting periodically until they reached the nest site." Pickwell and Smith (1938) speak of *whunk* and *hrunk* notes of the female Lesser Nighthawk that are seemingly used to attract the young.

Hiss-ticking — Hissing plus a ticking sound are given, as part of the female's distraction display, with mouth completely open and wings quivering and outstretched on the ground. Sutton and Spencer (1949) wrote of this performance: "Her hissing was almost incessant. The odd sound was broken or roughened by a curious popping or snapping." Dexter (1952) also heard the clicking sound along with the hiss. He thought that the clicking sound was the result of bill-snapping, but a captive Nighthawk in my possession always gave the call with its mouth completely open, and there was no bill-snapping. I find no reference to hissing by the Lesser Nighthawk when flushed from the nest. Pickwell and Smith (1938) have this to say about the distraction display in the Lesser Nighthawk: "The bird [female] got up not two or three feet in front of him [human intruder] and went fluttering over the ground for a distance of 50 feet, flicking the pebbles with her wing tips. She made no audible sound other than that caused by the wings." In another observation, Pickwell and Smith (1938) noted that when the female stood her ground "she opened her eyes more widely, spread her tail, raised her wings, lifted her throat feathers, and gave a deep, throaty, rasping hiss. The hiss was not very loud but very decisive." During the night of 9 June at Key Largo, with a spotlight and binocular, I observed nearly identical Wings-up threat behavior in the female of the family studied when a cat threatened her nest. Gross (1940) has also written of this defensive behavior.

Territorial Occupation and Defense

The male of the family I studied was usually absent during the day, though most of the other males remained on their respective territories from shortly after sunrise until late in the afternoon. I was never able to find his diurnal and nocturnal roosts. Pickwell and Smith (1938) speak of some male Lesser Nighthawks roosting within their respective territories and of others roosting near one another in an area where no nests were known.

Roberts (1936) commented on Nighthawks when agitated as sometimes alighting crosswise on a limb. One of the males at Key Largo often rested during the whole day in that position on a dead branch three inches in diameter and three feet above the coral. At times he, too, rested on the ground. Six males in the colony occupied territories with no perches available and consequently rested on the coral flat itself.

Any Nighthawk at Key Largo that passed over a territory other than its own was immediately chased by the resident male. Due to their relative positions, territories had to be crossed in order to reach the feeding grounds; therefore, it was inevitable that chases occurred during the morning and evening foraging hours.

A male calling from high above his territory dived steeply toward an intruder with wings held obliquely above the horizontal. Just above and behind the intruder, the male then suddenly flexed his wings downward and produced a loud, low-frequency vibration (=Booming) as he pulled sharply out of the dive. Depending on the relative speeds of the birds the attacking male (1) returned to a position high over his territory, (2) dived again from some lesser height, or (3) continued after the intruder in level flight. These chases usually ended at the male's territorial boundary.

Once just after sunrise I heard and then tape-recorded a series of calls given during an unusually long chase. For several minutes the male pursued a second bird (probably a male) in a great circle over the mud flat and through at least three territories. The pursuing bird gave a series of short, sharp, metallic squeaks sounding like Kit rapidly repeated. As the distance between the birds increased, the rate of repetition decreased and a few Peent notes were added.

Whenever I crossed a male's territory he took wing, called (Peent), and periodically dived, Booming a few feet above and behind my head. If I remained long enough, the bird usually returned to a resting spot on the ground. On one occasion the Kit call was given instead of the usual Peent.

Nesting Habits

Nighthawks lay their eggs on bare ground. The location chosen may be a sand dune, a gravel-covered arroyo, or a flat, gravelled roof-top. There is usually little vegetative cover. Many authors (Woods, 1924; Pickwell and Smith, 1938; Bent, 1940; Gross, 1940; Sutton and Spencer, 1949; Weller, 1958) have noted that Nighthawks often move their eggs or young within their territories. The young of the family I studied at Key Largo moved several times each day. When heat became intense in the late morning, the female led her chicks into partial shade provided by bits of vegetation. Invariably the chicks moved a foot or more each time she flushed and returned. Her Chuck notes attracted the young to her when she returned to them. The trio then settled where they met. Morning and evening feedings caused moves of five feet or more at a time. If disturbed while brooding, the female usually led her chicks to some new location 10 to 15 feet away.

Flushing and Distraction Behavior

The nesting females at Key Largo showed wide variation in their reaction to my approach. Tomkins (1942) reported this, too, in his observations in Georgia.

Frequently when I flushed a female Nighthawk from the nest, her mate chased her, silently. During such chases the pair usually remained near their territory. When the disturbing factor was no longer a threat, the female returned to her nest. If the female landed elsewhere on the coral flat, the male dived and Boomed over her. At such times she either preened her breast and shoulder feathers or sat motionless. In her subsequent return to the nest she ordinarily bobbed her head, looked about, took wing, and flew over the nest once or twice. Landing near her nest, she then sat quietly for a moment, stood, bobbed, looked about, and walked to the nest, Chucking as she went. In the Lesser Nighthawk, Pickwell and Smith (1938) heard a *thunk-unk* sound accompanying head-bobbing motions, but I did not hear it accompanying such motions in the Common Nighthawk nor have I found it reported in the literature.

Figure 1. Distraction behavior of a female Common Nighthawk. Photographed on a gravelled roof-top at Bowdoin College, Brunswick, Maine, by Olin Sewall Pettingill, Jr.

On one occasion I crawled within four feet of the family I studied in order to photograph them. The female flushed, but quickly returned to her chicks when I gave a few squeaks. Thereafter, sudden motions caused her to flush only about six feet and she returned each time.

On several occasions when I flushed a female Nighthawk she showed typical distraction behavior. (See Figure 1.) This was identical to Tomkins' (1942) description which he divided into three parts. The female (1) flew directly away with her tail spread and pointed at the ground, (2) landed some distance away with wings and tail spread and cowered, quivering, and (3) opened her mouth and hissed, her eyes fastened on the intruder. Behavior roughly comparable to the first two parts have been observed in both sexes of the Lesser Nighthawk by Pickwell and Smith (1938). I have found no references to any such behavior in male Common Nighthawks.

Reaction to Wind

Late in the afternoon of 8 June a thunderstorm passed just west of the coral flat at Key Largo. Though there was no heavy rain, strong winds blew for half an hour, reaching a velocity of about 25 mph—strong enough to rock my car. When I began observations at 6:45 PM (the sun a few degrees above the horizon) the female of the family I studied was initially sitting perpendicular to the wind. Then in sequence she assumed positions (1) facing, (2) perpendicular to, and (3) tail to the wind. While back to the wind she was twice lifted by wings and tail and dumped forward. The chicks crawled back under her each time. The male stayed aloft throughout the storm which was over by 7:30 PM.

While a brooding Nighthawk might cope with a strong wind best by facing her streamlined form into it, perhaps the back-to-the-wind position assumed by the bird allowed more adequate shelter for the young. Also, since Nighthawks do not tuck their heads under their feathers, the position may have given greater protection to her face. The only reference I have found in the literature to the behavior of Nighthawks in storms is by Gross (1940) who stated that during rainstorms the female never left her chicks even though it meant depriving them of food.

Reaction to Heat

Changes in the location of the chicks belonging to the family I studied seemed to follow a pattern. After their evening feeding, the chicks were on plant-free coral. With feeding at dawn they moved only slightly. When heat in the morning became intense, the female waddled to shade under thin tufts of vegetation. As long as she gave Chuck notes, the young followed her. Once in the shade all three remained there for the day. During extreme heat the female panted and held her contour feathers away from her body; the chicks remained under her. With cooler afternoon temperatures the chicks came out, sat in the open, pecked at their parent's bill, and climbed over her back. The female remained quiet all the while.

Woods (1924) noted that a female Lesser Nighthawk moved her eggs into partial shade on hot days, returning them to the open when the heat abated. He wrote: "It seems probable that the lights and shadows thus produced supplement the protective coloration of the birds." This suggestion might apply to the Key Largo birds.

The female I studied usually faced away from the sun. On one occasion her chicks sat in front of her exactly in the shadow of her head and shoulders. This type of orientation away from the sun was described by Weller (1958) in studies of Nighthawks in Missouri.

During periods of intense heat, the female opened her mouth and performed what Cowles and Dawson (1951) have called "gular fluttering" in the Lesser Nighthawk. This consists of rapidly fluttering the throat or gular area. Cowles and Dawson found this action to be a cooling mechanism in a manner analogous to panting. I have no doubt that this action has the same function in the Common Nighthawk.

Precocity of Young

The two chicks in the family I studied were about three days old (estimated from descriptions by Gross, 1940) when first found and were already able to stumble over the coral in response to their parent's Chucking. Bowles (1921) observed a newly-hatched chick that was strong and alert enough to leave the nest at his approach and to return when he stepped away. Chicks of the Lesser Nighthawk have been seen to crawl to their calling parents when less than two days old (Pickwell and Smith, 1938).

Nocturnal Eyeshine

When I put my spotlight on the brooding female I noticed that her eyes shone red. Sutton and Spencer (1949) and Pickwell and Smith (1938) have observed red eyeshine in breeding Common and Lesser Nighthawks, respectively, but van Rossem (1927) noted that wintering Lesser Nighthawks in El Salvador "gave only a pale green reflection, which was easily overlooked and not visible beyond a few feet." He speculated that the color change may be correlated with breeding activity.

Feeding of Young

I watched feeding behavior in the family I studied at five different periods—three evenings and two mornings. Except in the last period (the second morning) only the male brought food. In each of the four evening periods the male returned from foraging at mid-dusk. His usual procedure before landing was to make three or four slow, level passes over the female, wings flapping slowly and uttering each time one sharp Peent which elicited the Hissing-growl from the female. The chicks also responded to the Peent with their intense Long Peeps. In succession the male (1) landed a short distance from the nest; (2) the female waddled toward him, the chicks following part way; (3) the parents moved toward their young; (4) the male fed his young while the female rested a few inches away; (5) the male took flight; and (6) the female resumed brooding for the night. In these cases total darkness was just approaching when the male left.

In both morning periods objects on the ground were just barely discernible to me when the male first arrived. In the second morning and last period the male fed his offspring while the female was away foraging. Later she returned and also seemed to transfer food to the young but I could not be sure. In any case, head-pumping motions accompanied the action. Both adults appeared to place their bills inside the mouths of the young.

The female is known to feed the young, as Gross (1940) has reported. Possibly my presence on the territory at Key Largo may have caused the female to guard her chicks so closely that she would not leave to obtain food. Feeding the young was therefore left to the male.

Gross (1940) noted how variable Nighthawk feeding behavior can be when he found a male that did not feed the young at all. Pickwell and Smith (1938), during their many observations on the Lesser Nighthawk, recorded "not more than one or two definite feedings by the female, . . . the male being the chief carrier of food for the young." They suggested that the imbalance in parental feeding was due to the observer's presence. Data presented by Bowles (1921) indicate that the adults share feeding duties almost equally.

On one occasion I saw the female place her bill inside the chick's. Bowles (1921) has observed the following three different methods of food transfer: The female (1) placed her bill far down her chick's throat and fed with a violent pumping motion. Then (2) she allowed the young to pick food remnants from her open mouth. On another occasion the male (3) crouched and opened his mouth, allowing the young to put in their heads for the food.

Nearly all feeding by parents at Key Largo was in the hours at dusk, after sunset, and before dawn. Feedings just after nightfall may have been the result of the adults being disturbed earlier. In the Lesser Nighthawk, Pickwell and Smith (1938) noted that feeding activity seemed to be "strikingly crepuscular." They obtained no evidence that the young were fed at night.

Brooding Behavior

Only the female brooded the young and this she did almost constantly. When she left the nest for a short period in the early morning or evening, presumably to feed, the male might or might not remain on the territory. In their studies, all more detailed than mine, Bowles (1921), Gross (1940), Tomkins (1924), Rust (1941), Sutton and Spencer (1949), Dexter (1952), and Weller (1958) also found that the female alone brooded the young. The only time the male I watched associated with his offspring was to transfer food to them. Pickwell and Smith (1938), however, reported that males of the Lesser Nighthawk brooded their offspring for short periods of time just after feeding.

Summary

At Key Largo, Florida, a five-day study was made of 16 pairs of Common Nighthawks nesting on a coral flat. The distance between nests averaged about 80 yards. Altogether 46 hours were devoted to intensive observations on one Nighthawk family. The behavioral data gathered are presented, together with a review of similar data reported by other authors on both the Common and Lesser Nighthawks.

(1) Eight types of audible displays are described.
(2) The males show a marked territorial defense.
(3) The young move several times each day.
(4) The females show wide variation when flushed from their nest; a few give an entire three-part distraction display.
(5) The brooding females show definite reactions to wind and heat.
(6) The young can leave their nest-site within three days of age.
(7) Nocturnal eyeshine is red in breeding females.
(8) The males assist the females in feeding the young.
(9) The feeding of young takes place at dusk.
(10) Food is transferred to the young by the adult putting its bill in the chick's throat.
(11) The males do not brood.

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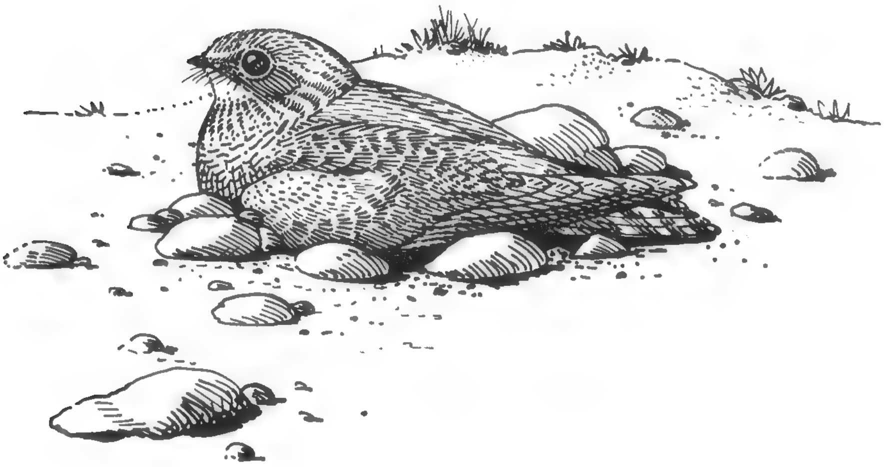
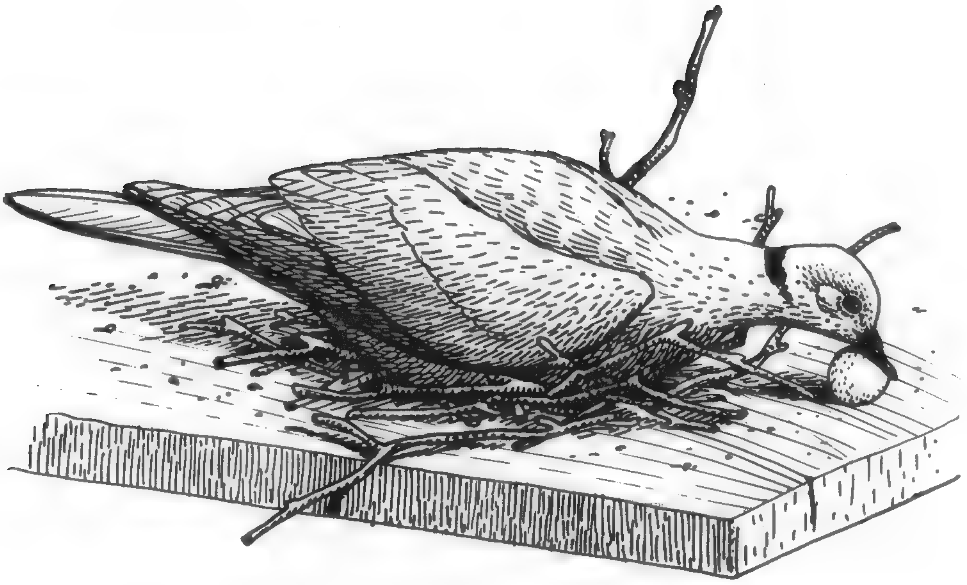




THE INFLUENCE OF THE NEST-SITE ON INCUBATION IN MOURNING AND RINGED TURTLE DOVES

RONALD J. HOCK

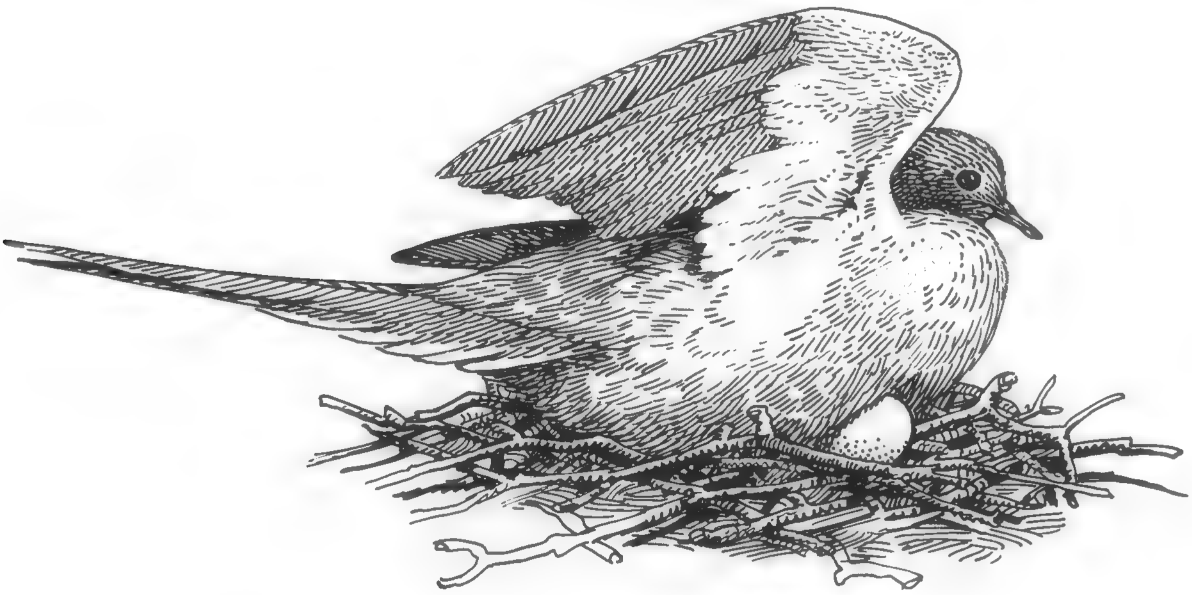
Is the bird's nest-site a greater stimulation for incubation than its eggs? Part of the answer may be found in how the bird reacts to its own eggs that have been placed just outside the nest and to different eggs in the nest. Being interested in this question, I performed a series of experiments on captive Mourning Doves *(Zenaidura macroura)* and Ringed Turtle Doves *(Streptopelia risoria).*

General Information About Both Species

Mourning Doves are widespread in North America and adapt well to captivity. Ringed Doves, Old World in origin, are a domesticated species, living in a wild state locally in such places as Los Angeles, California, and Miami, Florida.

Wild Mourning Doves, as a rule, construct their nests in trees 10 to 25 feet above ground, although they have occasionally been reported nesting in low shrubs and even on the ground (see Bent, 1932; McClure, 1943). The nest consists of a crude platform of twigs, weed stems, and other fragments of vegetation with a shallow cup, molded to fit the birds and well supported by a crotch or wide branch of a tree. Sometimes the Mourning Dove will use an old nest of a Robin *(Turdus migratorius),* Common Grackle *(Quiscalus quiscula),* and other species (Nice, 1922; McClure, 1943), occasionally modifying it by adding more nesting material. The male collects the material and presents it to his mate which arranges it to form the cup (Nice, 1922). Two eggs, always white, constitute the normal clutch; and are laid from 12 to 24 hours apart. They require, according to McClure (1943), an incubation of 13.9 days with a variation of only 0.2 of a day over a three-year period. The captive female I observed, incubated from between 4:30–5:30 PM to 8:30–9:30 AM the following day, at which time the male replaced her. This corresponds to the times given by Whitman (1919). The number of broods reared per year is two or more. In Iowa, McClure (1943) found that as many as five brood attempts were made during the breeding season. While incubating or brooding, captive Mourning Doves will often remain on the nest when approached, assuming a defense posture by rising, elevating the wings at the shoulders, and occasionally giving a low cooing sound.

Ringed Doves lay eggs, normally two, almost anywhere in their cage, but ordinarily incubate only if they can lay on elevated platforms. The nest consists of a few twigs and similar materials haphazardly thrown together in a manner sufficient to prevent the eggs from rolling off the nest platform. Both sexes share in incubation, the length of the attentive periods and the times of change-overs being almost identical to those of the Mourning Dove. Ringed Doves are much tamer than Mourning Doves, rarely displaying the defense posture when approached on the nest.



Nesting Mourning Dove in defense posture.

Methods and Materials

For my experiments I used two pairs of Mourning Doves and two pairs of Ringed Doves. I kept them in a wire flight cage, 8 feet by 16 feet by 8 feet high, in a field near the Cornell Laboratory of Ornithology, Ithaca, New York. One side of the roof was covered by wooden boards which provided some protection against weather and helped to keep the food dry. I fed the birds French's Parakeet Mixture and Conditioning Food.

For nest-sites I supplied wire cages, 2 feet by 2 feet by 4 feet high, with large openings, which permitted the birds to enter freely: the bottoms of the cages were covered with straw. All these cages were attached vertically to the sides of the flight cage four feet above the ground.

One pair of Mourning Doves and the two pairs of Ringed Doves nested. Eventually there were two young Mourning Doves from the first brood in the flight cage. A fully-fledged young Rock Dove *(Columba livia)* was kept in the flight cage during the latter half of my experiments.

The straw in the bottom of the nest cages was sufficient in quantity so that the birds brought no nesting material from elsewhere. They simply made a slight depression in the straw and deposited their eggs therein. Both pairs of Ringed Doves occasionally nested in the same nest cage. They were much less aggressive at their nest-sites than were the Mourning Doves which never permitted any of the other birds (except their recent offspring) near their nest.

I devoted 14 days to each species during a period between 30 June and 10 August, and made all my observations while concealed in a blind at one side of the flight cage.

I conducted two experiments on both pairs of Ringed Doves and the one nesting pair of Mourning Doves. The first experiment consisted of displacing the two eggs of each pair about four inches outside the edge of the nest. The second experiment included this procedure plus putting in the nest five eggs of the Peach-faced Lovebird *(Agapornis roseicollis)*. These eggs are also white but much smaller than dove eggs. I colored each egg differently (orange, green, yellow, blue, and white with purple spots) with a felt-tipped pen. Being smaller and colored, these eggs provided different tactile and visual stimuli within the nest. The experiments were performed on both species on two successive clutches of eggs, and were carried out on each clutch twice daily for seven consecutive days. They were run beginning at about 10:00 AM and 5:00 PM so that both sexes could be studied. The eggs were displaced together in random directions and were replaced in the nest after one-half to two hours of observation. Colored eggs, when used, were removed at the end of the observation period.

Results and Discussion

When the two eggs being incubated by the male Mourning Dove were placed outside the nest, he invariably returned to the nest and turned all the way around in the depression several times. He then proceeded to retrieve one egg by stepping to the rim of the nest, extending his neck forward, bringing his bill over the egg, and rolling or raking the egg with his bill toward his body while simultaneously making rapid balancing movements that functioned to prevent the egg from escaping to one side. Taking two or three steps backward and continuing to roll the egg, he soon had it back in the nest. After a brief interval in which he turned around once or twice in the nest, he retrieved the other egg. He repeated the performance in five out of the seven times I ran the experiment. The female retrieved both eggs similarly in seven out of seven times. Wickler (1961) mentions egg-rolling in "tree-nesting pigeons."

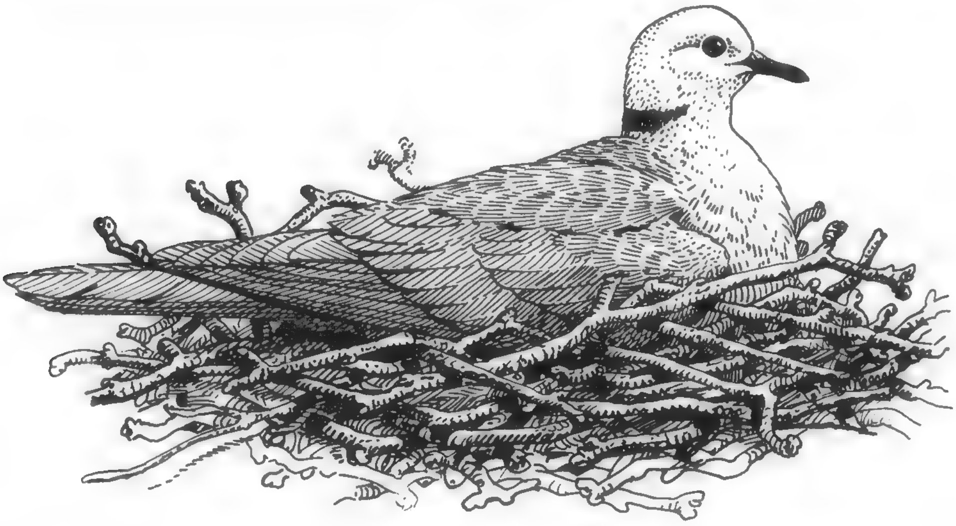
When the colored eggs were placed in the nest, the male refused to incubate for the first three days. During that time, after the male had been away from the nest between 5 and 10 minutes, the female went to the nest and incubated. She was often on the ground when the male left, and, as observed by Goodwin (1952), was evidently induced to fly to the nest by seeing the male away from the nest. My total observations on the female Mourning Dove are as follows:

1. She sat on the colored eggs (4 times), paying no attention to her own displaced eggs.
2. She sat on the colored eggs, then retrieved both her own displaced eggs (1 time) and one of her own eggs (3 times).
3. She first sat on her own displaced eggs and then later sat on the colored eggs in the nest (1 time).
4. She first sat on her own displaced eggs and then later rolled them in to the nest and sat on all seven eggs (1 time).
5. She sat on the colored eggs, then on her own displaced eggs, and finally rolled in one egg (1 time).

Three of the above reactions were observed when the female went to the nest as a result of the abnormal absence of the male. After the first three days the male always returned following a disturbance and (4 times) sat on the colored eggs in the nest during his normal period for incubation.

In one instance the young Rock Dove disturbed the incubating male Mourning Dove by pushing him out of the nest and sitting on it. The Mourning Dove, failing to drive away the Rock Dove, then mounted him in his attempts to remain on the nest-site.

If the male Mourning Dove was disturbed or chased from the nest as much as an hour and a half before his normal leaving, he was usually replaced by the female, which proceeded to incubate, remaining on the nest for the night. But when the male was disturbed earlier—e.g., at noon—the female sat for a while, and then the male took over and sat for a longer period, causing the afternoon change-over to take place much later. If the female was disturbed in the early morning, she almost always returned immediately.



Ringed Turtle Dove incubating.

The Ringed Doves were more variable. When the normal eggs were moved out of the nest, one of the males first sat on the nest, and then left to sit on the normal eggs (6 times). His movements while on the empty nest suggested that he left because he could not sense the eggs beneath him. In two of the above six instances, he sidled an inch or two toward the empty nest taking the eggs with him, probably by rolling them along with his feet. He sat on the nest, then on the eggs, and finally, after a long time, rolled one egg into the nest (1 time). This particular male rolled his eggs a few inches out of the original site (once or twice for each of his clutches) in the same manner that the Mourning Dove rolled his in. He was the only bird that defecated in his nest, and the feces may have prompted his moving. His mate sat on their eggs wherever they were placed without first sitting in the nest (7 times). If an egg was taken away from a Ringed Dove while he was rolling it, he immediately stopped the performance, including the raking movement. This is in contrast to the observations by Lorenz and Tinbergen (1957) on Greylag Geese, *Anser anser,* which under similar circumstances stopped the balancing movement but continued the raking movement. The Ringed Dove tried egg-rolling only when the situation made it possible, or when the eggs were placed not more than an inch or two from the nest regardless of the situation. The eggs were never noticed to slip away from the bill while being rolled, even when rolled over a sloping area.

The other male Ringed Dove sat on the empty nest (4 times), sat on the nest and then retrieved an egg (1 time), and sat on the eggs (2 times). His mate sat on the normal eggs (5 times), and in the empty nest (2 times).

In the colored-egg experiment, the first male sat in the nest of colored eggs and then on his normal eggs (5 times), and sat in the nest on the colored eggs without leaving (2 times). His mate sat in the nest and then on the normal eggs (1 time), and on the normal eggs (5 times) without first sitting on the nest of colored eggs. She remained in the nest on the colored eggs (1 time).

The second male sat on the colored eggs (5 times) and on the normal eggs (2 times). His mate sat in the nest of colored eggs (4 times) and on the normal eggs without stopping at the colored eggs (3 times).

Whitman (1919) performed similar experiments with somewhat different results. He displaced the eggs two inches to one side of the nest. In the now-extinct Passenger Pigeon *(Ectopistes migratorius)* he noticed that the experimental bird always abandoned the nest thereafter. His Ringed Doves either abandoned both eggs and nest or retrieved one egg, and his Rock Doves usually retrieved both eggs. Although he supposedly performed the experiments on more than one individual of each species, he does not provide any quantitative results.

Tinbergen (1953) states that, when the eggs of a Herring Gull *(Larus argentatus)* are moved a foot away from the nest, the nesting bird usually returns to the empty nest and occasionally retrieves one of them. When he filled the nest cup with sand, the bird still returned to the nest-site, disregarding the displaced eggs. When an artificial nest was made under the displaced eggs and the former nest destroyed, the bird usually chose the nest rather than the old nest-site. He found some individual variation in these choices, however, depending on the type of nesting terrain. For example, it was easier to lure a bird away from its nest-site if the environment were monotonous, without conspicuous land marks.

Doljnik (1960) mentions that in passerine birds the nest is three times stronger in stimulating incubation than is the clutch, whereas in lower orders of birds which build primitive nests the eggs are the chief stimulator.

Conclusions

The Mourning Dove has a much stronger tendency to incubate in the nest than the Ringed Dove. This may have evolved because the Mourning Dove normally nests in trees, where there are few opportunities to change its nest-site without building a new nest. The Ringed Dove, being a domesticated bird, is more accustomed to incubate on platform-like situations, such as shelves. This has resulted in its accepting a much larger nest-site.

Egg-retrieving in the tree-nesting Mourning Dove suggests that this species may have evolved from a ground-nesting ancestor.

Ringed Doves, although they also retrieve eggs occasionally, more often sit on the empty nest or on displaced eggs. This suggests that the Ringed Dove, through conditions due to domestication, has lost much of its drive to retrieve eggs.

Both Mourning and Ringed Doves are less likely to retrieve or sit on their own displaced eggs when abnormal eggs similar in shape, although smaller and differently colored, are substituted in their nests.

The incubating drive in Mourning Doves is aroused more by their own eggs than abnormal eggs, but most of all by the nest-site. The combination of abnormal eggs and nest-site provided the minimum stimulus necessary to keep the incubating bird from going to its own displaced eggs.

The presence of a Mourning Dove away from the nest will induce its mate to go to the nest even if it cannot see the untended nest. This highly developed reaction must be of significant survival value, especially in the later stages of incubation.

Mourning Doves, when disturbed close to their natural afternoon-time for exchanging places on the eggs, will usually exchange earlier in the day. The mate away from the nest is evidently ready to incubate for an hour or two before the sitting bird normally leaves. In most change-overs the approach of the mate coincides with the departure of the sitting bird.

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ALL-DAY OBSERVATIONS AT A ROBIN'S NEST[1]

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At the University of Michigan Biological Station near Pellston in northern Lower Michigan a pair of Robins *(Turdus migratorius)* nested in the crotch of a birch tree eight feet from the ground and six feet from a window of the cabin in which my wife and I lived for the summer. As the nest could be easily viewed through the window from the inside and the normal behavior of the nesting birds readily observed, we chose to make three all-day records of activities at the nest. Taking turns at two-hour watches from daybreak to darkness, we chronicled every prominent action at the nest, the time of day (Eastern Standard Time) when the action began, and (in many cases) the amount of time consumed in the action. Although a footpath, along which many people moved during the day, passed close to the nesting tree, the Robins were used to the traffic and only rarely left for a few moments when a human noise or action was unusually disturbing.

Schantz (1939) reported on a detailed study of a pair of Robins nesting on the porch of his home in Columbus, Ohio. He used an electrical apparatus for recording arrival times at the nest. Later he (1944) published a brief summary of an all-day record of direct observations on a Robin's nest in a tree that was viewed from his window under circumstances as convenient as ours. Very few such uninterrupted all-day watches of nesting activities have been conducted on any bird species. In summarizing our data here I intend to show how all-day observations give a fuller picture of a species' nesting activities than random observations of a few hours each day or mechanical methods that simply record the moments of entering and leaving a nest.

History of the Nest Studied

The female Robin started building the nest early on 9 July and completed it by the afternoon of 11 July. She laid the first egg at about 10:00 AM, 12 July, and I marked it later in the day. (The two eggs that were to follow I also marked soon after they were laid.) That evening she returned to the nest and stayed on it all night. She was gone early the next morning but returned at about 9:00, remaining on the nest nearly an hour. During this period she laid the second egg. At about 7:30 PM she began sitting on the nest and stayed on it for the night. The third and last egg was laid at about 11:00 AM, 14 July. Except for short (inattentive) periods away, she was on the nest all day. Incubation was obviously well under way.

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[1] Contribution from the University of Michigan Biological Station.

The first and second eggs hatched on 25 July between 7:30 AM and noon, and the third on 26 July between 1:30 and 5:00 PM. Nestlings 1 and 2, which I color-banded after hatching, and Nestling 3 left the nest on 3 August.

From the above history the following information may be derived:

1. The nesting was late in the season and was quite likely a second or even third such nesting of this pair.
2. The time required to build the nest was about three days. This is the minimum amount of time cited by Young (1955), although two or three days was found by Howell (1942) to be "the average amount of time" for a late nesting.
3. The first egg was deposited the day following the nest's completion. Schantz (1939) determined the interval between completion and laying of the first egg to be five and three days, respectively, in a March and a May nest of one pair of Robins. It seems evident that in successive nestings during a season the interval becomes progressively shortened.
4. The eggs were laid in the morning at 24-hour intervals. Howell's (1942) findings were virtually the same ("usually . . . about 10:00 AM").
5. The incubation period (i.e., the period beginning with uninterrupted incubation to the hatching of the first egg) was 11.9 to 13.1 days duration. Actual time intervals between the laying and hatching of each of the eggs were as follows:

First Egg:	309.5 to 314 hours	(12.9–13.1 days)
Second Egg:	285.5 to 291 hours	(11.9–12.1 days)
Third Egg:	290.5 to 294 hours	(12.1–12.3 days)

   The above figures differ with those obtained by other investigators, in some cases by as much as one and a half days, owing partly to a normal variation in the amount of time required by eggs to hatch and partly to different methods in measuring incubation periods. Thus, Schantz (1939) stated that, without exception, incubation began the evening after the second egg was laid and "lasted for about" 13 days, but he did not indicate whether he considers incubation as ending with the hatching of the first or the last egg. Howell (1942) found that the incubation period (the period starting with uninterrupted incubation and ending "when the young Robin breaks free of the egg shell") of 17 eggs at Ithaca, New York, ranged from 12 to 14 days; and Young (1955) determined the incubation period ("the time between clutch completion and hatching") of 40 eggs at Madison, Wisconsin, ranged from 10 to 14 days with an average of 12.4 days.

6. Nestlings 1 and 2 were nine days old and Nestling 3 eight days old when they left the nest. No doubt we caused them to depart prematurely by weighing them earlier on the day that they left. Usually the time spent by young in the nest is 13 days with a range of 9 to 16 days (Howell, 1942).

Activities During Two Days of Incubation

Our first all-day observation was on 20 July, the seventh day of incubation. The weather was clear and windy, with temperatures ranging from 53°F at 6:00 AM and 73° at 9:00 AM to 78° at 3:00 PM and 71° at 6:00 PM. The second all-day observation was on 22 July, the ninth day of incubation. Weather conditions differed from those on 20 July by being clear and windless in the morning, cloudy and breezy in the afternoon; temperatures were nearly the same, ranging from 60°F at 6:00 AM and 69° at 9:00 AM to 74° at 3:00 PM and 77° at 6:00 PM.

On 20 July the female first left the nest at 4:33 AM and returned for the night at 8:30. During the day she was inattentive (i.e., away from the nest) 28 times for periods of 1 to 15 minutes duration. On 22 July her first departure was later, at 4:58 AM, but she returned for the night at 8:50. Her inattentive periods on this day totalled 24 with extremes of 1 and 19 minutes. A summary of her periods of attentiveness (i.e., times on the nest) and inattentiveness is given in Table 1. Included in Table 1 is the all-day record by Schantz (1944), made on a clear day (April 24, the tenth day of incubation) with temperature ranging from 56° to 72°F. The female was inattentive 32 times for periods of 1 to 10 minutes duration.

TABLE 1

Attentive and Inattentive Periods of Incubating Female Robin at Nest

	Michigan		*Ohio*
	20 July	*22 July*	*24 April*
Attentive Periods			
Total number	27	23	31
Extremes, in minutes	2-136	4-69	6-45
Average time in minutes	32.4	32.13	20.6
Percentage of time	80.12	77.73	79.
Inattentive Periods			
Total number	28	24	32
Extremes, in minutes	1-15	2-19	1-10
Average time in minutes	6.85	8.83	5.6
Percentage of time	19.88	22.27	21.

It will be seen in Table 1 that the amount of time spent on the nest during all three days was nearly the same. This is to be expected, as the weather conditions on these days were about the same. Had one of the days been cooler or stormy, or been closer to the day when the eggs were to hatch, she might well have been more attentive.

The shorter periods of attentiveness on both days in Michigan were more numerous in mid-morning and mid-afternoon and the longer in the early morning, around noon, and toward evening. (See Figure 1.) Doubtless the coolness of the early morning and evening hours and the increased heat of mid-day were factors causing the longer periods. Several of the shorter periods were caused when human activities on the path below the nest frightened the female off.

During her periods of attentiveness the female we observed was rarely still for longer than a few minutes. Her movements were usually associated with the following actions:

1. Standing, sometimes over the eggs or on the edge of the nest. This often preceded departure from the nest, or followed arrival, but occasionally it took place when the bird simply hopped to the edge of the nest, remained there a few moments, and then hopped back onto the eggs.
2. Turning in the nest, sometimes as much as halfway round.
3. Preening, more often the feathers on the underparts than those of the wings, rump, and tail.
4. Turning the eggs either with the bill or with a rocking motion of the body over the eggs. Poking at the nesting material occasionally preceded or followed this action.

The distribution of these actions through both days is shown in Figure 1. It will be seen that the actions occurred in almost any attentive period at any time of the day. Two, and occasionally as many as three, actions succeeded one another. There was no rule in the order, although the last-mentioned action, turning the eggs, frequently followed any of the other actions. At no time did we notice the bird sleeping. Her eyes were open and she was constantly alert through the days.

We recorded a total of 143 actions on 20 July and 118 on 22 July, as follows:

	20 July	22 July
Standing	25	22
Turning body	61	53
Preening	29	18
Turning eggs	28	25

In his all-day watch Schantz (1944) noted that the Robin "changed positions" 70 times and turned the eggs 22 times. He did not give totals of other actions.

As shown in Figure 1, all the actions we recorded are rather scattered throughout the attentive periods. There is no correlation of actions with time of day. The fewer actions on 22 July are to be expected in view of the lower percentage of time (see Table 1) spent in attending the nest.

All in all, the actions of the incubating Robin indicate considerable activity by the bird on the nest. Just how this would have compared with its nocturnal activity on the nest we do not know, although I suspect that some activity, such as turning the eggs, must have taken place. Odum (1944) was impressed with the nocturnal activity of the incubating House Wren *(Troglodytes aedon)* on which he (1941) once reported. "Sometimes the bird even left the eggs for short periods to move to the edge of the nest or to the front of the nesting box" (1944: 49). Odum (1944) went on to postulate that activity on the nest at any time, day or night, while serving obvious functions, may also serve to relieve physical discomfort resulting from circulatory congestion. Experiments have shown that when the bird's body is at rest the reduced arterial pressure and absence of the kneading action of the skeletal muscles tend to produce restriction of circulation and, in turn, discomfort. Smaller birds, such as passerines ("song birds"), which have a more rapid heat loss and heart rate, are more susceptible to circulatory congestion. The urge to relieve the consequent discomfort may therefore be one of the factors accounting for their greater activity on the nest and the shorter attentive periods.

On 20 July the male appeared at the nest or in the vicinity 11 times. Four of these times he came to the nest when the female had just left or was absent. His longest stay was 30 seconds. In three of these instances he stayed on the nest's edge and peered into it, then departed. In the fourth instance he dropped into the nest and sat on the eggs for about two minutes. Three of these times he came while she was present and in all three instances fed her. His longest stay was 22 seconds. In one of these instances the female pushed the food received at one of the eggs in an effort to feed it. The remaining four appearances of the male consisted of perching in a near-by tree and calling. In two of these instances the female reacted by merely lifting her head and looking in his direction, in a third instance she paid no attention, and in a fourth she got up from the nest and left to join him.

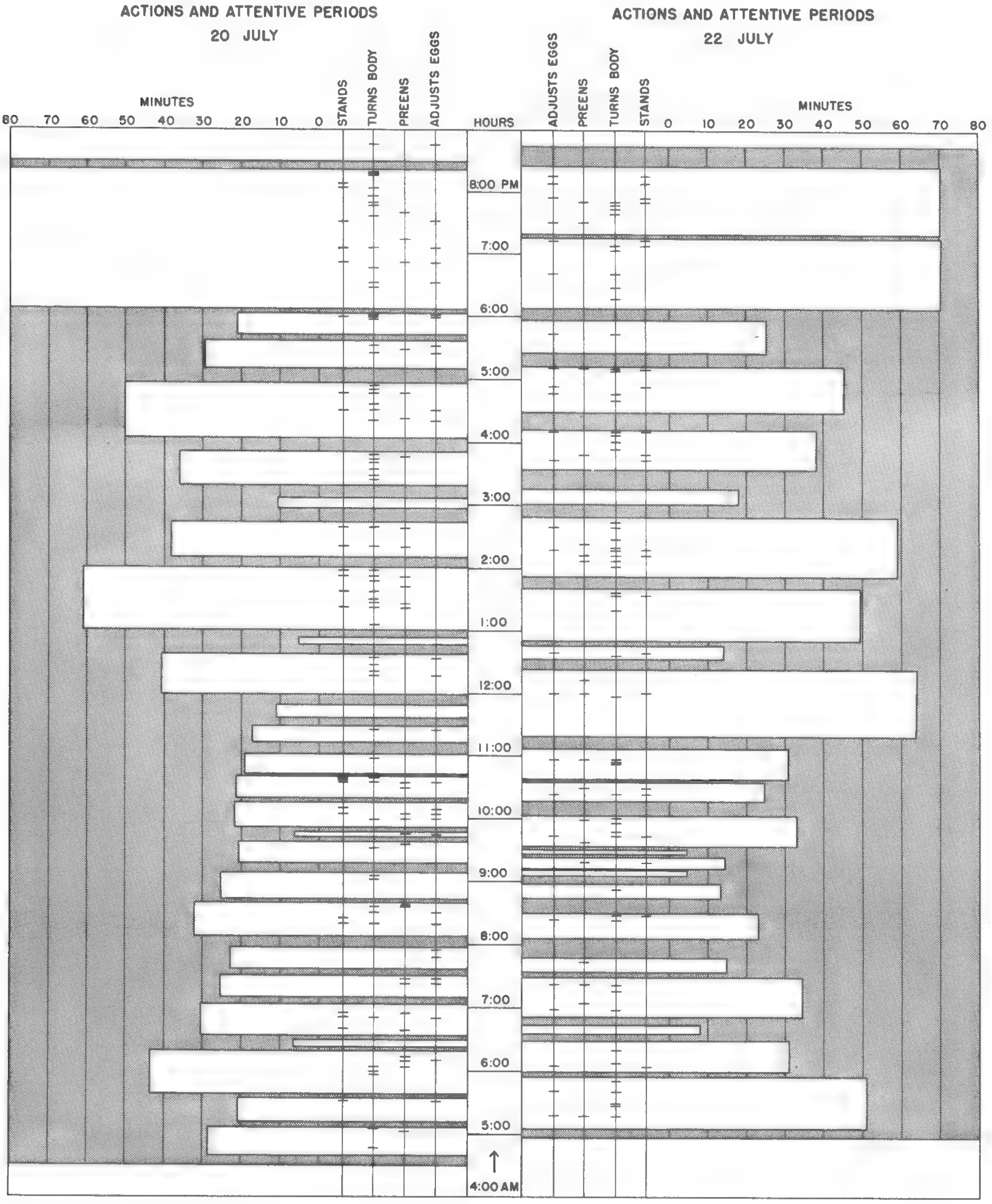

Figure 1. The actions and periods of attentiveness of an incubating female Robin in Michigan on two days, 20 July and 22 July. A one-minute inattentive period, beginning at approximately 9:45 AM, 20 July, is not shown.

TABLE 2

Feeding Visits by a Pair of Robins on 28 July

Both Sexes		
Total visits in 15 hours and 30 minutes	79	
Average number of visits per hour	5	
Minimum number of visits per hour	1	between 6:00 and 7:00 AM
Maximum number of visits per hour	10	between 6:00 and 7:00 PM
Intervals between visits	78	
Average number of intervals per hour	4.5	
Average length of intervals	11.6	minutes
Minimum length of intervals	0.5	minute at 5:09 AM
Maximum length of intervals	54	minutes between 12:48 and 1:42 PM
Female		
Total visits	43	
Average number of visits per hour	2.7	
Minimum number of visits per hour	0	between 1:00 and 2:00 PM
Maximum number of visits per hour	7	between 6:00 and 7:00 PM
Intervals between visits	42	
Average length of intervals	20.5	minutes
Minimum length of intervals	3	minutes between 6:05 and 6:08 PM
Maximum length of intervals	86	minutes between 12:48 and 2:14 PM
Male		
Total visits	36	
Average number of visits per hour	2.3	
Minimum number of visits per hour	0	between 6:00 and 7:00 AM
Maximum number of visits per hour	4	between 2:00 and 3:00 PM
Intervals between visits	35	
Average length of intervals	21	minutes
Minimum length of intervals	2	minutes between 8:24 and 8:26 PM
Maximum length of intervals	93	minutes between 12:09 and 1:42 PM

On 22 July the male appeared at the nest only three times. In the first of these instances he arrived while she was absent, stayed 15 seconds on the edge of the nest, then departed. In the second, he arrived as she departed, stayed 35 seconds. In the third, he arrived and immediately fed her, whereupon she departed and he remained for 60 seconds. All three of these instances occurred early in the morning, at 5:06, 5:58, and 7:07. I am unable to account for the male's failure to appear the rest of the day.

Schantz (1944) reported the male at the nest 16 times, "often coming immediately after his mate had left," and spending a total of 68 minutes at the nest.

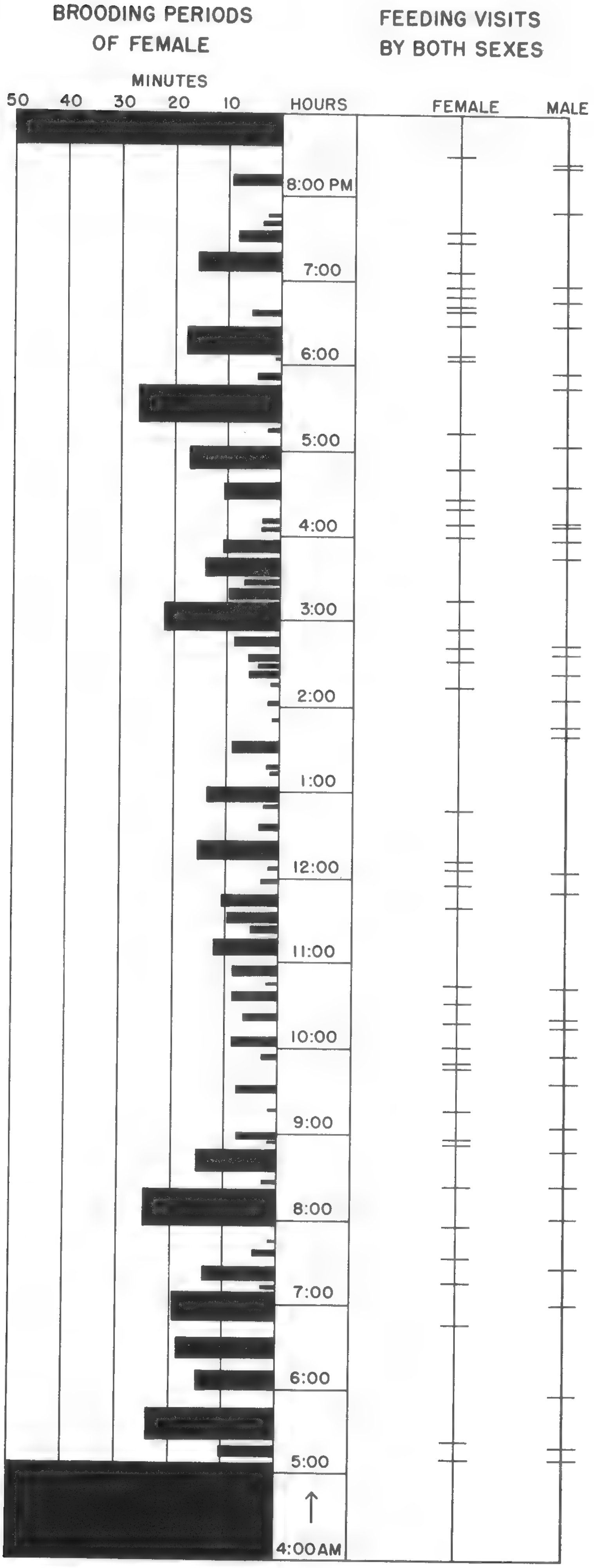

Figure 2. The brooding periods of a female Robin, and the number of feeding visits to the nest by the same female and her mate, in Michigan on 28 July.

Once, while the male was at our Michigan nest, another Robin appeared in the vicinity. He immediately pursued it, driving it away. On another occasion a female Robin alighted in the nesting tree. The incubating female, spotting her quickly, left the nest and pursued her beyond our view. An Ovenbird *(Seiurus aurocapillus)* and a Red-eyed Vireo *(Vireo olivaceus)*, appearing at different times in the nesting tree within several feet of the nesting female, were completely ignored.

Parental Activities During One Day

One all-day observation was undertaken on 28 July when two of the nestlings were three days old and the other was two. The day began clear with no wind, but by noon the sky had become overcast and the wind began reaching velocities between 15 and 20 miles per hour. Temperatures ranged from 64°F at 5:00 AM and 73° at 9:00 AM to 78° at 3:00 PM and 73° at 6:00 PM.

The female left the nest at 5:07 AM and returned for the night at 8:37 PM. During the day she returned to the nest 76 times. (See Figure 2.) In 63 of these instances she remained to brood for an average period of 7.42 minutes (extremes 1.29–26) or for 52.4 per cent of the time between her first departure in the morning and return at night. Her brooding periods averaged shorter between mid-morning and mid-afternoon and were more widely spaced in the early afternoon.

The female fed the young 43 times, the male 36 (see Figure 2). Their rate of feeding per hour was similar (see Table 2). They fed the young more often after 1:00 PM than before, and the least often before 7:00 AM, between 11:00 AM and 1:00 PM, and after 7:00 PM. As a rule, the female brought food each time she returned from an inattentive period, gave it immediately to the young, then brooded them. In only eight instances, all in the late afternoon, did she feed without brooding thereafter. Sometimes the female was present when the male returned, sometimes not. When she was on the nest, she either stood up to let him feed the young or left the nest as soon as he perched on it. At no time did he feed her.

The male never stepped into the nest to brood the young. Invariably he perched on the rim of the nest from which he delivered the food. Except on six occasions, all after 3:00 PM, when he lingered on the rim of the nest after feeding for 3 to 13 minutes, his visits to feed ranged from a few seconds to no more than a minute.

Once when the female returned she found a Black-and-white Warbler *(Mniotilta varia)* peering into the nest and on another occasion, while she was brooding, a Baltimore Oriole *(Icterus galbula)* alighted in the tree within four feet of her. Both times she took after them, her crest feathers lifted and calling loudly. The intruders retreated hastily.

Figure 2 shows the distribution of brooding and feeding periods in the course of the day.

Summary

Three all-day records of activities were made at a Robin's nest in Michigan, two during incubation and one during the dependency of the young.

Incubation was performed by the female, except for one two-minute attempt by the male. Time spent by the female at the nest during incubation was nearly the same on both days, being about 80 and 77 per cent of the time (27 and 23 attentive periods) between her departure from the nest in the morning and her final return in the evening. Her shorter periods of

attentiveness were more numerous in mid-morning and mid-afternoon. While on the nest she was rarely still for more than a few minutes. Her movements were usually associated with four different actions: standing, turning the body, preening, and turning the eggs. On the two days a total of 143 and 118 actions was recorded. There was no correlation of actions with time of day and there was no evident sequence of actions. The female was not observed to sleep during the day. On each of the days the male appeared at the nest, or in the vicinity, 11 and 3 times for short periods. In four of these instances he fed the female, and the female, in one of the instances, pushed the food received at one of the eggs.

The female spent 52.4 per cent of the time (63 periods) brooding the young during the day. The brooding periods averaged shorter between mid-morning and mid-afternoon and were more widely spaced in the early afternoon. The male did not brood the young.

The female and male fed the young 5 times per hour (the female 2.7 and the male 2.3 times). The length of intervals between feeding visits averaged 11.6 minutes (by the female 20.5 and the male 21 minutes). The young were fed more often after 1:00 PM than before, and the least often before 7:00 AM, around noon, and in the evening after 7:00.

While incubating, the female ignored the close approach of an Ovenbird and Red-eyed Vireo, but later, while caring for young, drove away a Black-and-white Warbler and a Baltimore Oriole which came near the nest. During the period of incubation the female and, on another occasion, the male pursued another Robin which appeared in the vicinity of the nest.

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Donaldson's Touraco. Painting by Louis Agassiz Fuertes.

THE TOURACOS: AN AFRICAN BIRD FAMILY

James P. Chapin

Drawings by the author, Francis Lee Jaques, and Helen Ziska,
courtesy of the American Museum of Natural History.

Among the many groups of interesting birds to be found in Africa there is but one family with numerous species wholly restricted to that continent — the Musophagidae. These attractive and often very colorful birds, the touracos or plantain-eaters, do not occur anywhere north of the Sahara nor even in Madagascar, though they are represented on a few islands close to the African coasts. In length they vary from about fourteen to twenty-eight inches. Their nearest relatives are probably the cuckoos, yet the touracos are less markedly zygodactylous. The fourth toe may curve backward over a perch, but after death it points forward. The feet are well suited for resting on boughs or for running rapidly along them. The couas of Madagascar show a vague resemblance to the touracos, but plainly belong among the cuckoos.

As a vernacular name for the Musophagidae I should greatly prefer to use "touracos" rather than "plantain-eaters." Touraco stems from a native name in West Africa and is reminiscent of their voices. Plantain-eater would intimate that the birds commonly eat plantains or bananas. In the wild state I have never known one to eat these cultivated fruits, which are regularly harvested while green. Neither have I known any to eat the wild bananas that grow here and there in Africa. Isert was plainly misguided when in 1789 he named one of the birds *Musophaga*.

In 1800 Cuvier latinized touraco and made the species *persa* the type of the genus *Turacus*. Kluk, to be sure, in 1779 had used Tauraco for the same bird, misspelling the word that had been in common use for decades before, but Kluk's name was overlooked for 154 years, and should never have been revived. I shall continue to use *Turacus* for nearly all the species with red in their wings.

One of the most attractive of this group is Donaldson's Touraco, the subject of a striking painting (see opposite page) by Louis Agassiz Fuertes, the last he ever did, since it was made only eight days before his death on 22 August 1927. Miss Mary Young recently presented it to the Cornell Laboratory of Ornithology.

Several other familiar names besides touraco are often used for some birds of the family. Certain grayish species have long been known as go-away birds, because one of them in southern Africa often utters an alarming *go-weh!* The use of the word lourie for others with considerable greenish color arose probably through the Boer settlers confusing them with the lories, allied to parrots, in the East Indies. The native name, Bulikoko, for the Great Blue

Touraco, *Corythaeola cristata,* in the Lower Congo has been adopted by Europeans in much of the Congo, while in West African pidgin English it is known as The Peacock. Names for touracos in native languages are legion.

The family Musophagidae consists of 22 species, of which 16 have the plumage largely suffused with melanin and often lustrous. These forms all have large areas of red in the remiges, due to a very special pigment, turacin, with an appreciable component of copper. A second unusual pigment, turacoverdin, gives a greenish color to many species. (Völker, 1944; Keilin and McCosker, 1961.) The six species that lack turacin are largely grayish, except the giant *Corythaeola cristata* which is of a rather light blue above, not because of any blue pigment, but as a result of feather-structure. The touracos are readily divided into three main groups: the 16 species with red in the wings, 5 grayish species, and the one Great Blue Touraco.

The beaks of all touracos are relatively short and stout, their bases often hidden by feathers that cover the nostrils. The culmen is usually decurved, but in no case is there any resemblance to parrots. Heads are mostly crested, the wings rather short and rounded, tails relatively long and rather square at the tip.

With such a compact family it is not easy to arrange the species in any linear order suggestive of a trend in evolution. The typical touracos with red in the wings may seem the most highly evolved with respect to plumage, yet the Great Blue Touraco because of size and proportions might likewise be regarded as farthest from any hypothetical ancestor (Moreau, 1958a).

Figure 1. Great Blue Touraco.

Great Blue Touraco

For a general exposition it may be simplest to begin with this outstanding species (Figure 1). *Corythaeola cristata* is abundant and conspicuous in the rain forests of western and equatorial Africa, from the Casamance River to the western fringe of Kenya, as well as on Fernando Po (Figure 2A). It is likely to be the first touraco noticed by a traveller ascending the Congo River. Associating in parties of five or six, it frequently gives its resounding series of rolling *coos.* From tree to tree the great birds go, several wing-beats being followed by a brief sail on set pinions, with slight loss of altitude. Much of their food consists of the fruit of the parasol tree, *Musanga smithii,* so characteristic of second growth in western Africa. In addition to other fruits, tender green leaves, soft shoots, and flower-buds are often eaten.

The nest of *Corythaeola* is the largest built by any touraco; it is composed mainly of dry sticks freshly broken off by the builders. Some may be three feet in length. The nest is set in forking branches, perhaps 20 yards or more

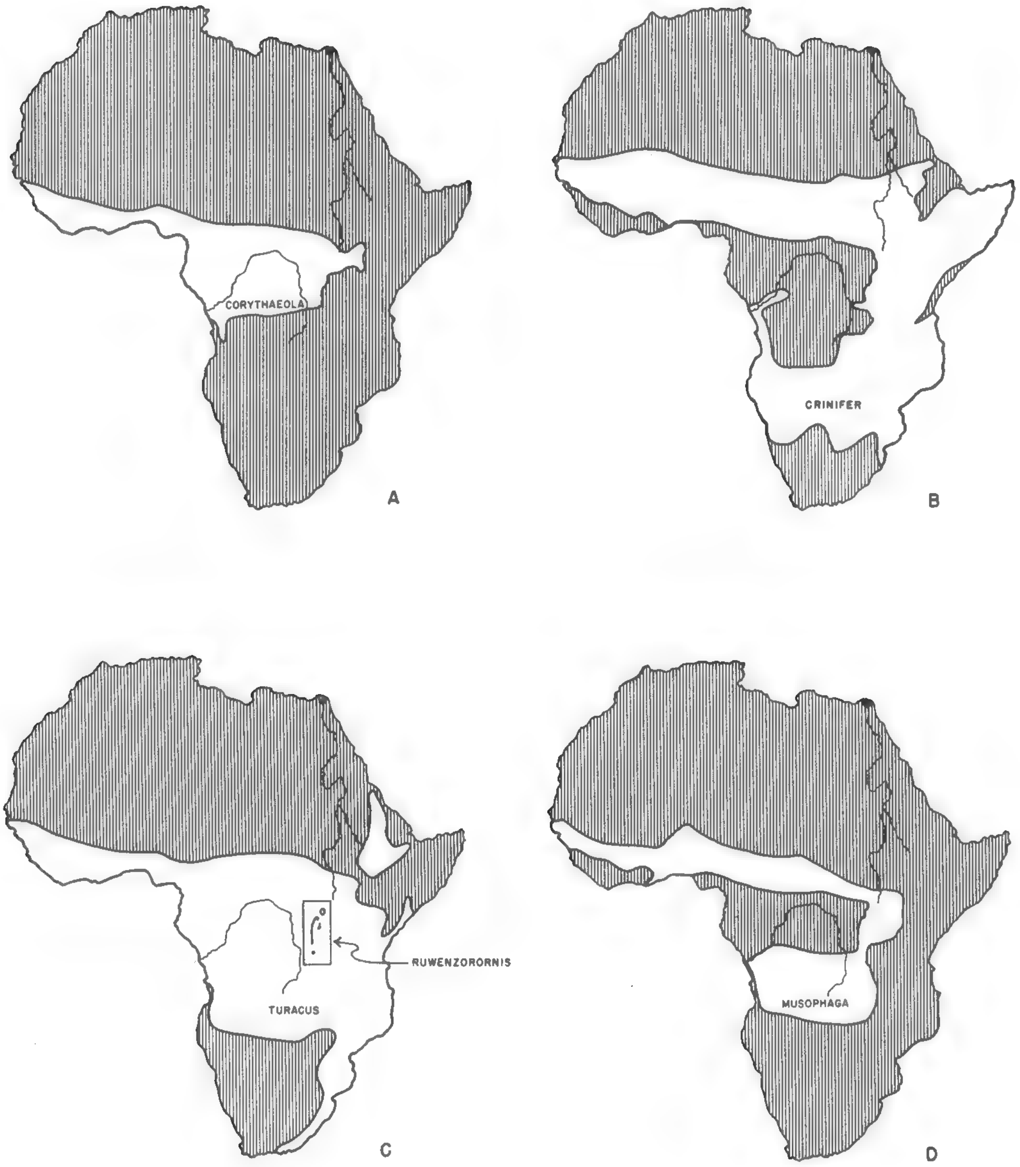

Figure 2. Ranges of the five genera of touracos. A, *Corythaeola.* B, *Crinifer.* C, *Turacus* and *Ruwenzorornis* (in box). D, *Musophaga.*

above the ground; its upper surface is concave, but has little or no soft lining. In it are laid two rounded eggs, pale blue-green in color. Nestlings have blackish down.

This brief description would fit the nests of all the other touracos, allowance being made for their markedly smaller size. Some may be flatter or less substantial, and the eggs vary slightly in color, from dull creamy white to bluish white, or pale ivory-green. They are always of rounded form. Some of the nests may be built within 12 feet of the ground, but usually they are placed higher up. Nestlings of *Turacus* are also clothed with blackish down; those of *Crinifer* with light gray.

In the forests near the equator, with little or no change of season, nests of *Corythaeola* and the species of *Turacus* living there may be found in virtually any month. In regions with a long dry season, however, various forms of *Turacus* cease nesting when the rains have ended, whereas the gray go-away birds usually prefer the drier months for breeding.

Go-away Birds

The five go-away birds may all be included in the genus *Crinifer,* although one with a bare face has often been kept separate. They inhabit open countries,

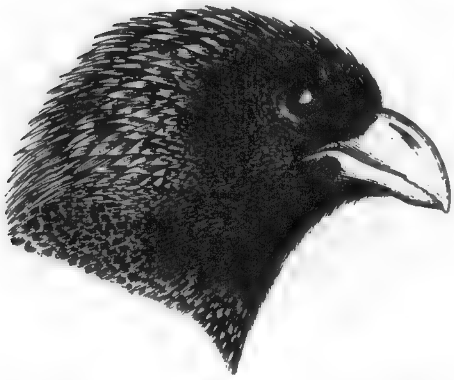

Figure 3. Band-tailed Go-away Bird.

even arid ones. (See Figure 2B for geographical range.) All have exposed nostrils. *Crinifer piscator,* the West African Go-away Bird, ranges from Senegal to Lake Chad and the Shari River Basin, reappearing south of the equator near the middle Congo River and Stanley Pool. It has no conspicuous crest, only long lanceolate feathering on the hind-crown, and the tail is uniform blackish brown beneath. To the eastward, from near the Shari River to Eritrea, and then southward around the eastern side of the Congo and on to the Lualaba River, lives *Crinifer zonurus,* the Band-tailed Go-away Bird (Figure 3). It differs in having the crown-feathers less narrowed and a whitish cross-band showing beneath the tail.

These two species are to be found in grasslands with scattered trees, particularly along some watercourse. They travel in small groups of three to five. The voice of *zonurus* sounded to me like laughter. A loud *kwah* might be followed by a short series of *how,* with the tone changing to a curious falsetto at the end. In flight a low *ka* might accompany each wing-beat. In the northeastern Congo nesting was in progress from December at least until March. The nests I found held two bluish white eggs, but *C. piscator* is reported to lay either two or three grayish white eggs.

Crinifer leucogaster, the White-bellied Go-away Bird, differs markedly from the foregoing species by its long and blunt-ended, blackish crest. Below the gray chest its underparts are white, while back and wings are clear gray, the wing-coverts with black tips. The range of this go-away bird is long and narrow, from Somaliland and the Rift Valley in Ethiopia, only in very dry country, south to central Tanganyika. Its calls are described as a sheep-like bleating—*ha-haaa.* In its nests, placed 10 to 20 feet up, either two or three eggs are to be found, pale bluish and glossy.

The Southern Go-away Bird, *Crinifer concolor,* is uniformly gray, with a long, loose crest. Its home is in southern Africa from Zululand and the Transvaal to northwest Angola, and to the Rufiji River on the east. It is

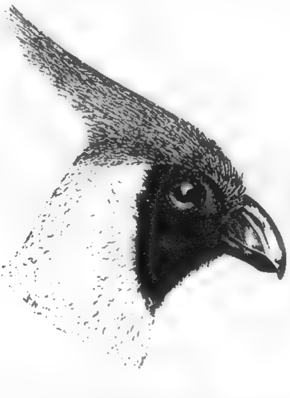

Figure 4. Bare-faced Go-away Bird.

addicted to bushy or acacia-grown savannas. Small parties will fly one by one from tree to tree. Their best-known call is a vigorous *go-weh!* but a loud grunt and other notes have also been reported. The diet, like that of other go-away birds, is of berries and other fruits. Nests are to be found in any season, including the dry months, and eggs may be two or three, white or pale greenish blue.

Last of the go-away birds is *Crinifer personatus,* the Bare-faced Go-away Bird (Figure 4), very similar in behavior and form to *C. concolor,* but with a bare blackish face, whitish neck and upper chest, the latter smudged with green. The bare face seems scarcely enough to justify its generic separation as *Gymnoschizorhis.* The range of *C. personatus* is split in two parts, its nominate race dwelling in southern Ethiopia, the other from Lake Edward and the Kavirondo district to Masailand and north of Lake Nyasa. It frequents trees near stream beds, and often repeats double notes like *go-ah, go-ah* in a way suggesting hollow laughter. Its whitish eggs may number either two or three.

Red-winged Touracos

Turning next to the genus *Turacus* we find its thirteen species all more deeply colored and lustrous, with large areas of red in their wings. The gloss on bodies and wings varies in color from species to species, and even among some geographic races. Eyelids are often red and "beaded," beaks vary from black to yellow and even red. The coloration of heads and the shapes and patterns of crests are most diagnostic; these are the features I shall emphasize.

The species of *Turacus* live in heavy forests, galleries, and sometimes wooded savannas. (See Figure 2C for geographical range.) The majority are primarily lowland birds, yet a few are restricted to mountain forests, especially those surrounded by dry areas. Their nests are built of sticks, and the sets of rounded eggs are almost invariably two. Reproduction goes on mainly in the rainy months. Space will not permit much discussion of races; only the salient characters of a species can be pointed out.

We may begin with *Turacus macrorhynchus,* the Deep-billed Touraco, ranging through West African forests from Sierra Leone to Fernando Po, western Cameroon, and the Lower Congo. In the Upper Guinea race the feathers of the rounded crest are narrowly tipped with whitish and black, in the Lower Guinea race with dark red. It utters a series of loud, rolling *coos.* The nest is built of dry twigs in the tops of low trees; the two eggs are creamy white.

Turacus persa, the Guinea Touraco, with wholly green crest, higher and more angular, is distributed in forests from the Gambia to the vicinity of the lower Ubangi River, the Lower Congo, and northwestern Angola. The white stripe below the eye is a variable feature. Its usual calls are a resonant series of rolling *khaws,* a little less harsh than those of *T. macrorhynchus,* and its two creamy white eggs are just a trifle smaller.

In equatorial forests to the east of *T. persa* lives *Turacus schüttii,* the Congo Touraco (Figure 5), with a slightly lower crest tipped with white. It extends from the Upper Congo forest and northern Angola to Uganda and a few mountains in neighboring Sudan. The color of the back changes from violet in the west to brassy green near the eastern limit. When calling, this touraco gives a series of resonant syllables like *khraw, khraw, khraw,* etc., low in tone. Less often there is a long, hoarse grunt, or a rapid succession of sharp notes like *quick! quick! quick!* The diet is mainly of fruit, very often that of *Musanga,* the parasol tree; but once I found 17 small snails as part of a meal. Two white eggs are laid in the usual stick nest.

Figure 5. Congo Touraco.

Still farther to the south and east dwells *Turacus livingstonii,* Livingstone's Touraco, from Angola to Burundi and southwestern Kenya, the coast of Mozambique, and coastal Zululand. Though closely related to *T. schüttii* it has a much more pointed crest, tipped with white. The height of the crest varies geographically, reaching its maximum in Angola, its minimum in southern Mozambique and Zululand. The situation in Tanganyika is more complicated, with one race restricted to a few isolated mountain forests. The voice of this species is much like that of *T. schüttii.*

Still farther south *Turacus corythaix,* the South African Touraco, ranges from the interior of Zululand to the Knysna Forest in Cape Province, and has a rather isolated bluer-bodied race in the eastern Transvaal. Its white-tipped crest is higher than that of *T. schüttii* and not pointed. Some have held that *livingstonii* must be conspecific with *T. corythaix,* but no intermediates are known. The latter species occupies such forests as it can find, behaves much like others of its genus, feeds on wild figs and other fruits. Its eggs are usually two, white and smooth.

Along the coast of East Africa, from Usambara and Zanzibar Island north to the lower Juba River, lives *Turacus fischeri,* Fischer's Touraco, with a crest of very different coloration. The crown-feathers are green at the base, turning gradually to deep red and then to blackish toward the tip. The longer feathers of the crest and nape are narrowly tipped with white. The dark red color continues to the back of the neck.

Angola, too, has a red-crested species, *Turacus erythrolophus,* the Angolan Red-crowned Touraco, with a more rounded crest, its feathers but faintly tipped with white. The whole facial area is largely whitish, the nostrils concealed by feathers, as in all the foregoing species of the genus. It extends northward from the Benguella region to the upper Kwango River and the left bank of the lower Congo River, and prefers savanna woods to heavy rain forest.

In one small region north of the equator near the Banso Mountains in the Cameroon there is another red-crested species, *Turacus bannermani,* Bannerman's Touraco, which might be regarded as a race of *erythrolophus* did it not have a somewhat swollen beak with exposed nostrils. The facial area is distinctly grayer, and the red crest shows no white tips (Serle, 1950).

Most members of the genus *Turacus* discussed thus far have been inhabitants of the lowlands, though some of them may ascend to 7,000 feet or even higher on forested mountains. In Ethiopia, however, lives a beautiful species, *Turacus leucotis,* the Ethiopian White-eared Touraco, which is largely restricted to forested mountain areas between 4,000 and 8,000 feet. It is plainly characterized by a white crescentic marking near the rear edge of the ear-coverts. There is also a conspicuous white spot just before the eye. Nominate *leucotis* has a blackish crest of moderate height, not pointed. It lives on most of the Ethiopian plateau country, but is replaced in a relatively restricted area on the east, in the mountains of Arusi, by *T. l. donaldsoni* with crest-feathers green at the base but then turning to red.

Donaldson's Touraco was the subject of the last bird painting by Louis Fuertes, only a week before his tragic death. We can imagine his enthusiasm in 1926 when first he encountered this splendid red-crowned bird, some six weeks after landing at Djibouti. He and Wilfred Osgood had been travelling south from Addis Ababa, the capital of Ethiopia, for three weeks, had crossed the dry Awash Valley and climbed out of it into the mountains of Arusi. On 19 November they entered a fine forested country with cedar and *Podocarpus* trees, the Wadago forest near Mt. Albasso. The rains had not ended and they made camp there. The very next morning Fuertes set out before breakfast. Uphill only a few hundred yards from camp he caught sight of this lovely bird, gliding along the leafy branches and turning its head to watch him. This first example had to be collected, and a few others were sacrificed during the next five days. By 3 December Fuertes and Osgood crossed the canyon of the Webbi River and entered Bale Province. From then on they saw only the black-crested nominate *leucotis* (Fuertes and Osgood, 1936).

In his diary Fuertes did not attempt to describe the voice of this touraco, to which I have listened in a zoo where there was a *T. persa* in an adjacent cage. When *persa* called, it seemed to stimulate the red-crested *donaldsoni.* The latter bird kept its waxy scarlet beak a little more open than did *persa,* moving the mandible slightly up and down and swelling its throat. The hoarse rolling *coos* were not so loud as those of *persa,* and were almost run together. They reminded me slightly of the calls of *Musophaga rossae.*

Close to the southern limit of *T. leucotis* in Ethiopia lives another beautiful touraco, *T. ruspolii,* named in 1896 from a single specimen which came to the Museum of Genoa. The type remained unique until 1942, when a few more were collected at Arero, about 100 miles southeast of Lake Abaya in an isolated juniper forest at 6,000 feet (Benson, 1945). Prince Ruspoli's Touraco differs from *T. leucotis* in lacking the white crescent near the ear and in having a longer loose crest, which is grayish white distally, shading to pinkish at the base. Lores, cheeks, and throat are plain grayish green.

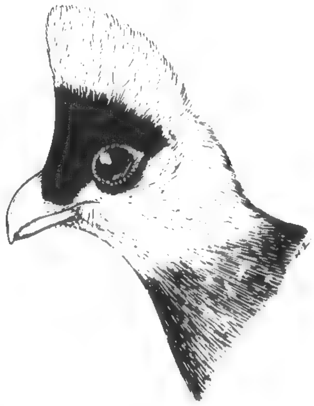

Figure 6. White-headed Touraco.

Another touraco with a white crest but not closely related to *ruspolii* or *leucotis* is *Turacus leucolophus,* the White-headed Touraco (Figure 6), living in savannas from the eastern edge of Nigeria to the vicinity of Mt. Elgon in east-central Africa. Avoiding the heavy equatorial forest it occupies the gallery

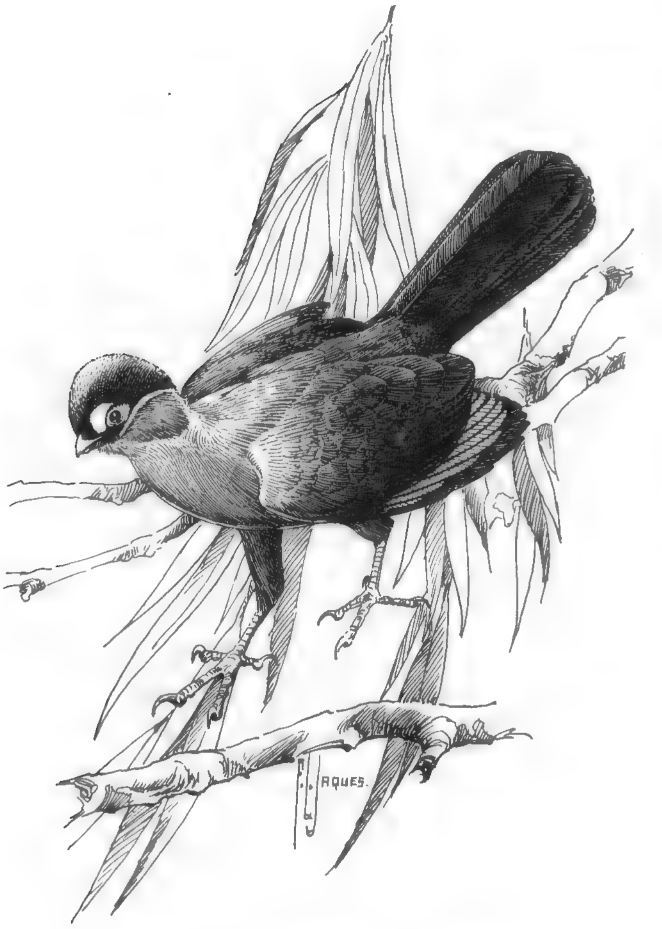

Figure 7. Hartlaub's Touraco.

forests near its northern edge and often ventures out into the smaller trees amid the grass. Its whole head is white, except for the blue-black forecrown and area above the eyes. These touracos are usually found in parties of a half-dozen, and their calls are lower and less resonant than those of *persa* or *schüttii*. The succession of hoarse grunting notes like *kraw—kraw—kraw*—are introduced by a higher initial syllable. The food as usual consists mainly of berries and other fruits, but once I found a fair-sized snail had been eaten, and again a small flower-head. Touracos in captivity have frequently been seen to devour small leaves.

Among the few species of *Turacus* that are wholly restricted to mountain forests is *hartlaubi* (Figure 7), an inhabitant of highlands in East Africa from the south end of Lake Rudolf to Elgon, Kenya, and West Usambara. The head of Hartlaub's Touraco bears a high, rounded crest of blue-black, with a large spot of white in front of the eye and a white stripe below it. One of its varied calls has been written *quar, quar, quarck, quarck,* and its nest holds two white eggs, or sometimes only one. Usually only a pair is seen, but sometimes parties gather to feed on wild figs or other fruits (van Someren, 1956).

The last species of *Turacus,* the Purple-crested Touraco (Figure 8), has often been placed in a separate genus, *Gallirex,* because its nostrils open somewhat farther out on the beak than those of *T. bannermani*. Yet otherwise *Turacus porphyreolophus* diverges very little in plumage and behavior from its congeners. It has a rather rounded purple crest and no white near the eye. Its range extends from Natal along the coast northward to Mombasa, and westward in lowlands to the Loangwa Valley. Southern representatives show a reddish flush over the otherwise green breast. Mainly an inhabitant of evergreen gallery woods, this touraco ascends occasionally to 6,000 feet on wooded mountains. Its nest holds either two or three white eggs.

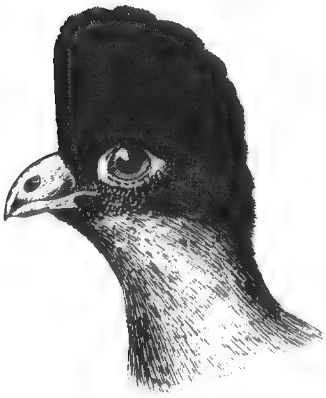

Figure 8. Purple-crested Touraco.

Johnston's Mountain Touraco

Still another touraco with exposed nostrils has a better justification to generic separation as *Ruwenzorornis johnstoni.* Its beak is relatively narrow, the culmen decidedly elevated toward the forehead (Figure 9). On the back of the neck there is a distinct patch of red, and the nominate race has the orbital skin bare. (See Figure 2C for geographical range.) A second race on the high mountains farther south in the Kivu and Rwanda has the whole orbit feathered.

Perhaps I am prejudiced in favor of this monotypic genus, which has given me much pleasure in its homeland, at altitudes from 7,000 to 12,000 feet. Though rather like a *Turacus* in behavior, *R. johnstoni* has some very distinctive calls. Single loud chirps of unusual resonance may run into an accelerating series of similar notes, diminishing again at the close. A different call is a resounding *ch-k-k-krowng!* suggestive of some monkey. Lastly, a single hoarse *kaw* may be delivered. As might be expected, the food consists of small fruits gleaned from the trees. The nest is like that of other touracos, and may sometimes be placed as low as 12 feet (Chapin, 1939).

Helmet Touracos

The two species of the genus *Musophaga* differ still more from *Turacus* by their beaks. The maxilla is inflated, extending back on the forehead, and rounded at the rear. These birds occupy only the fringes of the heavy Guinean forests, and range far outward in gallery forests. (See Figure 2D for geographical range.) *Musophaga violacea,* the West African Violet Touraco, is thus distributed from the Gambia to the northern Ubangi country. It has a

Figure 9. Johnston's Mountain Touraco.

low, red plush-like crown-patch and a white stripe beneath the eye. *Musophaga rossae,* Lady Ross's Violet Touraco (Figure 10), with no white on the face, a larger bare orbital patch and a well-developed, upright red crest, encircles the forest of Lower Guinea. From northern Cameroon it extends eastward to Mt. Elgon and the Nandi District of Kenya, then southward from Lake Victoria and the eastern Congo to Northern Rhodesia, finally veering west to Angola and the Lower Congo.

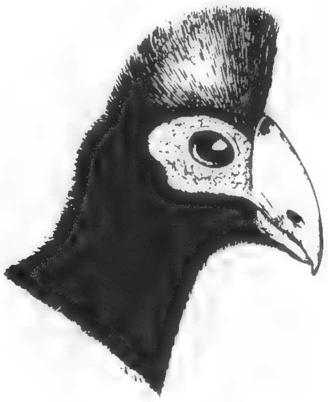

Figure 10. Lady Ross's Violet Touraco.

Primarily a lowland bird, *Musophaga rossae* ascends occasionally to 6,000 or even 8,000 feet. It often goes in parties that may number as many as twelve individuals. The calls they utter are different from those of most species of *Turacus.* The rhythm is less regular, two or more birds seem to be calling together, and there is a slight suggestion of the more rolling notes of *Corythaeola cristata.* In stomachs of *M. rossae* I found only fruit. Breeding continues all through the rainier months; the two eggs are rounded and white.

In Summary

Beyond question the touraco family is notable not only for being distinctively African, but also for its pleasing styles of coloration, its adaptation to such varied habitats, and its attractive ways of life. The characters that distinguish some nearly related species are not deeply significant, and are shown mainly in the region of the head. Complementary ranges of some species make them seem little more than races, until some abrupt change is found in one or more characters. On the other hand the races of one species may diverge in the color of the body from green to violet, or in that of the crest, from red-tipped to black.

Such differences will lead a taxonomist to wonder just where the limits of species are to be drawn. The *persa* group forms a wide band of related forms ranging from the Gambia all across tropical Africa to Mozambique and the eastern Cape Province. These I consider as representatives of four species, though others are tempted to unite them in one. But we need not know the intricate details of classification to share the admiration of Louis Fuertes for Donaldson's Touraco, one of the most beautiful of the whole family.

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The Bulikoko, or Great Blue Touraco.

BIRDS IN ART AND ILLUSTRATION

DON RICHARD ECKELBERRY

It is curious that discussions of bird art should appear in an ornithological journal, but that very fact bears out much of the thesis presented in the first (1962) volume of this annual. "Techniques and Problems in Bird Illustration" might be a more appropriate subject for me, but since my friend, mentor, and colleague, George Miksch Sutton, has had his say and I have been invited to have mine, the opportunity to express opinions, seasoned now by time and experience, is too great to let pass merely for the sake of being practical. That can wait. The purpose of this analysis is to invite that public which is interested in bird painting to look at it with a more critical eye, hopefully with a fresh view, and to demand more of it. If and when this comes to pass, bird painting may not suffer the equivocal position which—not without justification—it finds itself in today.

Realism, Art, and Craftsmanship

A case can be made that all art, by its very nature, is an abstraction. Every painting perforce removes space, removes the peripheral limits of vision with a frame, removes a large portion of light intensity through the limitations of pigments, removes movement, removes all but one angle of vision, removes many sorts of detail. Whole schools have been founded upon attempts to reinstate the illusion of one or another of these.

A case can also be made that all art is realistic by its very nature. Even when abstraction is carried to the non-objective point of lines, colors, and masses, you are still painting lines, colors, and masses. You cannot abstract from red. Mondrian made his mark by carrying this process about as far as he could go: only vertical and horizontal lines, only primary colors and black and white. And it is effective. But this type of self limitation also reduces the orchestration of painting to the equivalent of the fife and drum, and after a little time one tires of it. The problem of synthesizing what we commonly call reality into a fully integrated picture is the difference between climbing that very highest mountain from which such artists as Van Gogh and El Greco flew their flags and trimming the mountain to a mole hill in the Mondrian manner.

No one considers the chirp of a cricket, the roar of a lion, the song of a bird, or the rumble of a volcano to be music which the composer should carefully attempt to duplicate in his compositions. Why then do people persist in thinking that to reproduce accurately the visual appearances of these same things is to create graphic art?

I do not believe that art has anything to do with visual appearances. It is not what is seen but *what is felt* in what is seen that counts; in other words, not sight but insight. An artist perceives the aesthetic component of nature which can be expressed but not defined, something we might call *subjective realism*. And it is real because we experience it—as real as taxonomy, as temperature, as anything. All this applies to art in its purest sense, whether it is expressed in music, painting, or literature. These are all art forms or media to convey anthropocentric realities. As has been mentioned, music escapes from the distractions of visual realism and thus is, to my mind, the purest or most immediately sensed art medium.

All this does not mean that "realistic" painting is not art, but only that it is not necessarily art. If the artist wishes to use visually realistic objects, he must build them into a picture in relation to one another. This selection and relationship must apply to every pictorial element, so that the finished painting has a designed architectural completeness. A painting ought to have such unity that nothing could be added or taken away or moved without damaging the effect.

There are so many latent truths, so many realities in nature, that the artist must decide which of these truths he will express. He makes his statement clear by exaggerating what he wants to say and by playing down everything else. This is what led Edgar Degas (who would certainly be considered a realistic painter) to say, "A picture is something which requires as much knavery, trickery, and deceit as the perpetration of a crime. Paint falsely and then add the accent of nature. The artist does not draw what he sees but what he must make others see."

Craftsmanship is that command over the mechanical difficulties of a medium which every artist needs to facilitate his expression. Oftentimes this "means to an end" is taken for the end itself by the artist, by his audience, or both. Thus virtuosity or technical competence is often confused with art. Craftsmanship is an accomplishment in its own right. It is satisfying to see a thing well executed. There is a sensuous delight in seeing textures perfectly imitated or an object so convincingly reproduced that it seems really to "come alive." But it is in the extent to which the artist goes beyond this in his expression and his design of the picture, which determines its aesthetic value.

The painter Segantini puts it thus: "The rendering of reality existing and remaining outside of us is not art. It is not and cannot have any value as art. It is not and cannot be anything more than a blind imitation of nature and therefore a mere material reproduction. Matter must be worked on by the mind to attain lasting form."

And this is accomplished through design. Design is rhythmic order. We can detect it everywhere behind the surface chaos of nature. The gyrations of the planets, the procession of seasons, the ebb and flow of tides, our breathing and pulse-beat, all pronounce this rhythmic order. Man seeks order and balance in the universe. He classifies animals and plants. He aims for political order on an ever larger scale. He divides his work and sleep and play to the tick of the clock or the list of the earth. But as man seeks order in variety, so does he seek variety in order. Constant repetition is unbearable to him. He ornaments his home, his person, and his expression. He elaborates or orchestrates simple themes. So we have this tension in balance, this rhythmic order of unity in variety and variety in unity. And this is the stuff that art is made of — these relationships brought down to particulars within their own frame of reference. As John Dewey says, "The first characteristic of the environing universe that makes possible the existence of artistic form is rhythm."

When the painter looks at nature, he is confronted with a confusion of colors, values, and shapes. His picture is composed through his way of seeing—his individual point of view. And from all this complexity he chooses a few things with which to make a picture that will convey, he trusts, something of the feeling which impelled him to paint. This is rarely fully realized, but it is the carrot which keeps the artist on the path.

It follows then that subject matter, birds or whatever, has nothing to do with art. If the subject matter is sacrosanct, not to be distorted, forced, or otherwise tampered with (an illusion anyway), the painter is essentially a craftsman, an illustrator. This is not disparagement; it is fact. And while I have drawn a sharp line between the two up to this point for the sake of clarity, there is still to be considered that band of overlap which we might call the area of the inspired interpreter. Putting it in musical terms, some virtuosos bring such feeling to their interpretations that they intensify the aesthetic experience even though they neither wrote nor feel entitled to take too many liberties with the original. The best bird illustration and the lesser bird art probably fall within this area. The purpose here is to distinguish between this fringe area and unquestioned art, so far as we can, but not to make the distinction invidious. We have no problem in identifying the uninspired or the incompetent.

Ways of Seeing

If the aesthetic component may be called *subjective realism* (seeing into the subject matter), there remain two other basic views of reality involved here, ones concerned with observation as such and not the emotional response to it, though in practice all three may be variously combined. At the risk of sounding like those scientific writers who try to impress their public by their labors in the coinage of new terminology (moving then to methodology and winding up with the admission that the data are inconclusive), I would call these two other elements *intellectual* and *objective realism.*

The intellectual realist paints what he knows to be there whether one is likely to see it or not. Through the use of local color, detail, and crisp delineation he paints as though he always saw his subjects under ideal circumstances. He is never really at home with the full background because it inevitably conflicts with the foreground if the treatment is consistently maintained.

The objective realist is just as rarely at home in the decorative field for he is essentially a painter of light. He shows what the eye sees in the transient moment of perpetually altering conditions of value, color, and definition which light dictates.

There is no room here to go into such further distinctions as stylization and conventionalization, or into personal style and the influence of media upon style. But having discussed subjective realism, I am using the following examples along the intellectual-objective spectrum to further clarify the matter and make it relatively easy for the reader to place published contemporary work. I say "published" because I have little doubt that the best contemporary work is often unpublished for the simple reason that such pictures were not painted with any utilitarian end in mind.

Audubon, an Intellectual Realist

John James Audubon's birds have a look of arrested motion about them similar to action photographs taken at high speed but doubtless stemming as much from dramatizations in the Romantic tradition as from observation.

Brown Pelican, by Audubon. This small reproduction of an adult in full breeding dress conveys Audubon's great skill as a designer but gives little of the power and exquisite detail of the life-sized original. The bird is shown in red mangrove with seedlings emerging from the fruit. Audubon was no purist. He freely mixed watercolor, ink, chalk, or just about anything, to produce the effect he was after. This is, of course, not evident in the Havell engravings.

In the field I have tried to see these transitional attitudes. Naturally our eyes have a better opportunity to register the postures of birds at rest, but I have broadened my concept of what constitutes a "natural" position.

To a person knowing nothing of ornithology, Audubon's birds in his monumental "Birds of America" (1860-61) are more convincingly wild and alive than those of most bird painters largely because he stressed these vivacious gestures. However, many of his subjects are shown in very characteristic poses—the Brown Pelican (reproduced here), the Chats (also reproduced here), the Yellow Warbler (plate 95), the Nashville Warblers (plate 89), and the Grackles (plate 7) are good examples. And while many of his birds lack the individual character, or more precisely the species-character that later bird painters have been able to give them, some are extremely expressive of the birds' "personalities." His Mockingbirds (plate 21) and Crow (plate 156) are typical.

The more I examine Audubon's paintings, the more I admire them. First and foremost he was a great designer. It is amazing how, in the precise execution of the part, he escaped the common tendency to lose control of the whole. We usually see the entire arrangement as an organized picture first and details later. He made the bird a part of the picture and subservient to the design. Sometimes he became so interested in the design that he made the bird almost incidental—*e.g.*, the House Wren (plate 179). Even plates which have little accessory material show birds beautifully placed on the paper. Look at the wonderful poise and balance of his Swallow-tailed Kite (plate 72) which bespeaks all the natural grace of the bird.

Audubon was a powerful draftsman with an almost oriental sensitivity to line. He obtained the illusion of form almost entirely by linear methods, and when he did introduce light to give roundness, it was in a rather arbitrary manner—*e.g.*, his Purple Martins (plate 22). There was no timidity in his drawing, no fumbling, no fear of trying a new position. The few portraits he did to finance his travels show that he could have become an excellent painter in this field if he had so desired. His occasional excursions into oil painting were less successful, as that is a medium less adapted to the linear approach. I should think that Audubon would be highly regarded in the Orient where bird painting has unquestionably reached a position of high art without any of the doubts and qualifications which still nag it in the West.

Audubon selected the plants and other accessories for his birds with evident concern for color harmony as well as for their natural relationship to the birds, and he possessed to an unusual degree a feeling for textures—moss and lichen-coated limbs, dry wood and scaling bark, elastic webbed feet, sparkling eyes and soft feathers. Joseph Mason and others have been given a good deal of credit for the floral accessories. Young Mason was only eleven years old when he joined Audubon as pupil-assistant for less than two years; this "contribution" to the master's work cannot be taken seriously. Robert Havell, the engraver of "The Birds of America," had a much greater influence.

The quality of Audubon's work varies considerably. Some of the western species toward the end of the series are mere conglomerations of birds, Havell being left to assemble them as best he could. The water birds which tend to require more by way of scenic background were, in general, less successful. It is in such instances that the mushy, pseudo-atmospheric treatment, so common among his contemporaries, creeps in. Used to working in great detail, Audubon was at a loss as to how to fit this with the broader treatment required for the illusion of depth. Some of his plates feel pinched for space. The Yellow-

Yellow-breasted Chat, by Audubon. The authenticity of this painting is attested to not only by Audubon's selection of a wild rose as a nest location but by the following quotation from "Birds of the Colorado Valley" (1878) by Elliott Coues: "the brooding bird assumes her patient place, and presses down her golden breast upon her hopes. Then this strange bird goes fairly wild with joy; . . . he rises on the wing, and in mid-air above the nest, with fluttering pinions, down-stretched legs, and open beak, he poises, hovers, and performs a thousand antics in the sheer abandon of his eccentricity."

billed Tropic-birds (plate 262) and the Long-tailed Jaegers (plate 267) are laid on the paper as though placed in a shoe box. His Horned Owls (plate 61) are cross-eyed to no advantage and his Cooper's Hawk (plate 141, figure 3) has a perpetually wet tail. But every artist paints poor pictures and every artist has a right to be judged by his best work. A good Audubon painting is a thing of rare beauty and power and is art without demeaning adjectives.

Fuertes, an Objective-Intellectual Realist

The bulk of the ornithologically-minded, after paying lip-service to Audubon, turn to the work of Louis Agassiz Fuertes with real affection. Two of his earlier wash drawings are reproduced here, while his last painting, of Donaldson's Touraco, has been reproduced to accompany Dr. Chapin's article in this issue of THE LIVING BIRD.

Aaron Moore Bagg, in an evaluation of Fuertes' work, wrote in *Bird-Lore* (May-June, 1938): "It was in 1897 that Fuertes set forth upon his career as an artist of nature, especially the birds. Immediately that outstanding ornithologist, Elliott Coues, stated, 'I say deliberately, with a full sense of my words, that there is now no one who can draw and paint birds so well as Mr. Fuertes, and I do not forget Audubon himself when I add that America has not before produced an ornithological artist *of equal possibilities.*' (I have italicized that last phrase because, from a speculative point of view, I find it of revealing significance.) This was the situation. Fuertes found himself an artist of increasing ability and genius; he already was accepted as such. Now, two roads were open to him: he could paint pictures which would be considered things of beauty by the general public; or he could confine his work to the specialized field of contract illustrations for nature magazines and books. He chose the latter course . . ."

I would add here that Mr. Bagg might have considered the possibility that this decision was less free and Olympian than his words suggest. Economics may well have dictated that decision, and growing responsibilities may have held him to it.

Mr. Bagg goes on to say, "Fuertes, therefore, is best known as a contract painter. The birds and animals he painted are amazingly perfect in structure, color and pose. In this respect he has never been surpassed. But this is specialized work: Fuertes' paintings are, first and foremost, excellent textbook illustrations for the professional and amateur nature-lover. They are intended to serve as an aid to field identification, and, as such, of necessity they must be representations of birds or animals as one would see them at close range, and uncomplicated by the natural play of light and shadow. Furthermore, in these paintings of Fuertes, the particular subject is the focal point of the whole painting, and for the most part the backgrounds are merely incidental, something by way of context to give an idea of the subject's size and usual habitat."

Though Fuertes was the inspiration which drew me into bird painting, and for whose work I still have the highest regard, there is little I can object to in this assessment.

George Sutton has a considerably different attitude, one reflecting perhaps a more general opinion within the ornithological field at least, when he speaks of his teacher's work *(Audubon Magazine,* November-December, 1941) in these words: "Looking at Fuertes' plate of the Long-crested Jay I cannot help thinking: How is it that in a simple, dignified portrait of this bird there is more real life than in any drawing Audubon ever made? Fuertes' bird does not need to have its wings spread, or be scratching its ear with its foot, or be

Northern Shrike, by Fuertes. This wash drawing and the one of the Winter Wren on the opposite page, both done by Fuertes early in his career, display the artist's rare gift for capturing typical attitudes and essential "character" of his subjects as well as his free handling of the medium (watercolor).

leaping from twig to twig with crest lifted in excitement or pressed flat with fear. Fuertes' jay-bird is just as much of a clown, just as naughty an egg-thief, just as rowdy and robustious as any jay-bird Audubon ever did, but all this characterization is effected not by the gymnastic attitudes of half a dozen birds on as many branches, but by the glint in one bird's bright, intelligent eye!"

Now, with all due respect, I do not believe that you can express in the glint of a bird's eye anything more than the glint. I will admit that by throwing the pupil off center, as Audubon often did, you can instill a certain look of intentness or even fright if combined with an appropriate pose; that by partly closing the eyelids a bird assumes a sleepy appearance; that the brow ridge of a hawk lends it a frown; or that the large dark eyes of the Woodcock, or of thrushes and goatsuckers, gives them a peculiarly mellow expression. But the attribution of such subtleties of expression as my colleague suggests seems to me a case of reading into the picture one's own knowledge and experience. This is possible because Fuertes painted far more objectively than did Audubon.

After some brief initial difficulties with proportion, Louis Fuertes produced a vast body of work of astonishingly consistent quality. The transparent watercolor technique of his plates for "The Birds of New York" (1910) and his opaque handling of the illustrations in "The Birds of Massachusetts and Other New England States" (1925-27) are equally fine. His Abyssinian field sketches—those marvelously fresh, direct watercolors done shortly before his death—carried his craftsmanship to absolute perfection. Only in his rare efforts in oils did he sometimes find himself in technical difficulty.

Fuertes' drawing was as strong and sure as his brushwork. His color, if not inspired, was at least not objectionable. But his sense of design, one must admit, was very weak. In identification plates this is of no great importance, but in the few paintings where he tried (and successfully) an unbridled use of light and a fully realized background, such as his "Prairie Falcons of Pyramid Lake" or "The Golden Eagle of Catalina," there are grave compositional faults. The *birds* are faultlessly done, but remain portraits against backgrounds which would require severe cropping by way of partial compensation for areas not structurally tied into the picture.

It was Fuertes' desire, unfortunately never carried out, to give up illustration to paint not just bird portraits but paintings with birds in them. It is possible that if he had been able to do this, his interest would have gravitated from illustrating the individual bird to a synthesis of bird with background.

Winter Wren, by Fuertes.

Eagle and Hare, by Liljefors. Despite the incipient action, this splendid oil, dated 1904, of a Golden Eagle swooping in on a hare, is rather a quiet picture compared with that shown on page 80. The difference resulting from the softer, more texturally varied treatment has an almost Rembrandtian chiaroscuro. Note that in both cases the mood dominates the subject matter.

It is perhaps unfair to wish that he had gone beyond his considerable achievements to a more creative expression when he left such a notable contribution to ornithology. As it is, his influence in this country has been great. Not only has his work instructed and conditioned the eye of the contemporary bird illustrator, but that of the ornithologically-minded public as well. Both Roger Tory Peterson and George Sutton have pointed out that there is a "Fuertes school of thinking."

As Roger Peterson puts it *(Audubon Magazine,* May-June, 1942), this influence "extends down to the tyro who goes out on Sunday with a pair of binoculars. He sees a bird through his glasses, perhaps not too well, and his mind immediately goes to a Fuertes drawing of that bird. This mental image fills in the gap. He sees the bird as Fuertes drew it, not as it actually looked in the brief moment it perched before him." This is certainly true and is no small tribute to Fuertes' work. For the bird illustrator, however, it is not a very healthy situation. Such convincing renderings are apt to come, through no fault of Fuertes to be sure, between the illustrator and his personal, hence creative, observation. Or, his unorthodox—i.e., non-Fuertesian—approach may even be held against him.

Liljefors, an Objective Realist

In contrast to both Fuertes and Audubon, Bruno Liljefors, the Swedish wild-life painter, bathed his pictures in natural light and paid little attention to the local ("actual") color of objects. Two of his paintings are reproduced here. With light to give form, line is no longer necessary and Liljefors dispenses with it. Fuertes had, for his purposes, to retain local color. This meant that he could only use light in an arbitrary way to suggest form. Otherwise, it would strongly affect color. With Fuertes it was still necessary to employ line to hold objects together, though in a much more modified way than with Audubon. A glance at their works will show this transition from line without light (Audubon) to arbitrary line and light (Fuertes) to light without line (Liljefors). It is also interesting to note that this transition, as it gains in atmospheric effect, shows a progressive loss of "decorative quality."

In Liljefors we have a painter who has achieved a complete synthesis of bird (or mammal) and habitat. No other wild-life painter has shown birds in foreground, middle distance, or background more convincingly. This is no small accomplishment. In fact, I believe it is the greatest accomplishment of all. Any painter knows how much more difficult this is than serving the bird and foreground up on white paper or, even more, than simply presenting the bird and suggesting its habitat. It is one thing to omit or suggest, and quite another to really carve depth into that stubbornly flat white surface where the picture is to be.

Like Audubon's, Liljefors' work is usually well composed and sometimes has a definite Japanesque flavor—not in line, however, but in pattern (as in Degas' compositions) and in proportion (though horizontal rather than vertical). Sometimes the emphasis is on texture and atmosphere rather than upon any defined arrangement. Color was, so far as one can judge from poor reproductions, perhaps his weakest point. Occasionally, especially in the early years, his canvases (he was strictly an oil painter) were confused and smacked of what used to be called "German realism," but usually he achieved simplicity and directness of statement. His working methods were very much like those of Winslow Homer in Maine and resulted in the same authenticity. The works of both show the same progessive elimination of all superfluities. In his oils

Sea-Eagles, by Liljefors. This canvas, dated 1912, of a pair of White-tailed Eagles chasing an Eider, is a typical example of the artist's "sketchy" style. Compared with the Golden Eagle (see page 78), the treatment here is slashing and rough, enhancing the violence not only of the birds but of the heaving sea and boiling sky. Liljefors repeated this theme many times, yet each picture captured the drama differently.

Homer was never quite able to achieve the vitality of the sketch, that directness and immediacy which sings out of his Bahaman watercolors (which are as good as anything in the medium). Liljefors somehow managed this in oil, though the mood and content is very different. In "Det Vildas Rike" (Stockholm, 1943) there are some examples in what I take to be small oils (no sizes given), reproduced in color. One, a painting of a Goshawk pinning down a Hooded Crow in the snow with other crows flying in to mob the hawk, is a very exciting and economical work, as is his Siskins dated 1933. Of two undated landscapes in the same late style, one is a smear of frost-covered trees, the other simply hare tracks in snow, disappearing into a stand of young pines. I do not know what artist could do more with unimpressive scrub landscape than Liljefors did in such paintings as that, from the same volume, of two hen Mallards rising before a wind-whipped copse.

Liljefors had as complete an understanding of his subjects as did Fuertes. But more than that, Liljefors' waterfowl have weight and displace water which also has weight; his eagles are great, heavy birds and one feels the strength required to keep them in the air. Eagles were favorite subjects. One of several similar canvases reproduced here, a Golden Eagle skimming the ground to intercept a hare, shows the way the elongated feathers of the hindhead form a puffy loose collar in flight. Yet nothing is put in which would not logically be seen under the condition of light which bathes the whole picture.

The painters of light naturally prefer the large birds which are better adapted to use with scenery. The painters of line are apt to like the "dickey-birds" just as well, but I do not think that they have either the size or angularity best suited to background pictures of power, and they do not, on the whole, lend themselves to flying groups. Although Liljefors said that he considered himself an animal portraitist, he was not that in the sense that Fuertes truly was, for Liljefors' pictures were of the whole time of day, the feel and mood of a place, even more than of the subjects he portrayed. They are really landscape paintings with animals in them, however simple the background treatment might sometimes be.

A gunner himself, Liljefors often did pictures of hunter and hunted. It is the same basic idea as an eagle after a hare, but somehow with man in the picture it does not come off as well. Much of the art of his time was really painted literature, and precious little of that kind of thing holds up. I would not place any of this genre with his best.

One of my favorite Liljefors paintings shows two swans in cold gray-green water. One feels the heave and swell of the water, and the swimming action is wonderfully conveyed in the arch of the foremost bird's neck. Another great picture, much darker in key, is more abstract. At first one sees only the pattern of light and dark, and then later such details as a female eider flying in the foreground.

Liljefors did numerous paintings of snipe, curlew, and other birds in grass so similarly colored that they might well be called studies in camouflage.

About the turn of the century, when Liljefors was 40, the banker Ernest Thiel made an agreement with him, to again quote Aaron Bagg, "to do twenty paintings of wild life as he saw it, for which Mr. Thiel would pay him an average price of approximately $525 apiece. Through this compact during an important period of his life, Liljefors was enabled to devote himself to creative work without any worries of a material nature." It would appear that we, as well as Liljefors, owe much to Thiel. A large number of the artist's works now hang in the Thiel Gallery in Stockholm. It is unfortunate that he is so little known here and that the Swedes, who regard him so highly, do not provide us with a book of really good color reproductions and an English text.

In Summary

This paper attempts to define the aesthetic and scientific components of bird painting and, by way of examples, the spectrum of approaches to it. Had space permitted, it would have been instructive to consider photography in the same way, for, while much more limited in scope because it is a less plastic and selective medium, it should not be discriminated against. I would not go so far as one of our naturalist-critics has in handing the future to the camera, not quite yet. There is no question but that some bird photography is artistically superior to some bird painting. The only area in which it can at present outfunction painting is in the new way of seeing it as found in stroboscopic techniques, a new "evidential realism"—not what we feel or know or see, but what the camera tells us is there. In all other areas, if painting cannot do better, it does not deserve to survive. And if it does not, that does not really matter, for then the artist's eye will move behind this new kind of brush and he will select raw quality from quantity and go into his darkroom to practice the same old magic.

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LOUIS FUERTES REVISITED

FREDERICK GEORGE MARCHAM

The Man

Fifty years ago the name Louis Agassiz Fuertes meant "painter of birds," for he was the best known painter of birds in the United States. To many persons who were qualified to judge he was not merely the best known but the most accomplished painter of birds of all time. He made his living by illustrating bird books, by serving as official artist to biological expeditions, and, at the very end of his life, by selling his drawings to commercial companies for use in advertising. Sometimes on commission and sometimes for his own pleasure he worked in oils and produced more formal and elaborately executed pictures of birds. In his short but busy life few were the periods when he was not observing or hunting or skinning or sketching birds; consequently the volume of his work was immense. By good fortune most of it exists today.

Fuertes was born in 1874 the son of Estevan Fuertes and Mary Perry. His father was professor of civil engineering at Cornell University; the son was graduated from the College of Architecture at Cornell in 1897. He went to work at once as a painter and illustrator in Ithaca, New York, which remained his home and headquarters throughout his life. In 1904 he married Margaret Sumner, member of an Ithaca family; they had two children, a son and a daughter.

Fuertes took part in the whole range of community life in Ithaca, not as councillor or alderman but as choir singer, lecturer, and raconteur, and as a continuous helper to wild life and conservation groups, Boy Scouts, and young people in general. The children enjoyed particularly his drawings (sometimes comic) and his skill in imitating animal sounds ("make like a pig, Uncle Louis"); the adults his genial conversation, good spirits, and fund of stories. He kept not so much open house as open studio. Those who came to him were mostly members of Cornell families—persons who admired his pictures and knew by his reputation that he was a master, but appreciated him even more for his wit, his warmth, and his sense of fun. In 1921 when Livingston Farrand became president of Cornell he said that "he had known only two things about Ithaca; that it was the home of Cornell and the home of Louis Fuertes." He was surprised and distressed to find that Fuertes was not a member of the Cornell faculty and he offered him a professorship. In 1922 Fuertes accepted the invitation to give an annual series of lectures at Cornell and so restored the formal relationship that had broken when he was graduated in 1897.

Of his lecturing Dr. A. A. Allen has said, "During my fifty years at Cornell I have at no other time nor in any other classroom seen such a spontaneous response from students and from colleagues as that which followed Louis

Fuertes' lectures. His early death robbed Cornell of one of the greatest teachers it has ever known, as well as the greatest bird artist." Louis Fuertes died instantly in an accident in 1927. In 1956 his daughter Mary (Boynton) wrote "Louis Agassiz Fuertes: His Life Briefly Told and His Correspondence Edited" (Oxford University Press). I have taken the quotations used above and the extracts to be discussed below from this book, which I regard as one of the most brilliant and delightful collections of letters ever written by an American.

His Ability to Portray the Living Bird

Most persons who knew Louis Fuertes or who have studied his paintings and drawings single out for praise one gift of his above all others, his ability to portray the living bird. This gift was in him as in other artists the fruit both of knowledge and of the power of expression. He knew what he wished to put on paper and canvas, and he had what he called "the technical ability to paint." When he spoke about these two qualities of his, the knowledge and the power to express it, he gave knowledge first place; and rightly so. He was first and foremost a practicing ornithologist, one who from childhood wished to know about birds. Indeed, writing of himself—"this boy" he calls himself—he said: "it was not the natural ability to draw which established this boy in the painting of birds, but rather the opposite: his desire to learn accurately developed him in his crude and unlearned handling of his medium." So he began with the wish to know. His life was a continuing period of learning. He spent months in field and forest, he collected and skinned tens of thousands of birds, and, while he painted, his eye was on the living bird or the skin. George Sutton said of him: "He held the phoebe skin while he worked, turning it this way and that, looking at it closely, counting its feathers with his pencil, blowing at it to make it fluffy, going to the window once or twice to examine its gape or eyelid or rictal bristles in a stronger light." For him knowledge, exact knowledge, came first.

He had a great knowledge of birds and quite properly he said so whenever a critic challenged him. "The hawk is all right," he wrote to Chapman, who questioned one of his drawings. "I have watched practically all *genera* shown and all do as I have shown *accipiter,* carry the prey at almost leg length and slightly back. Sparrow hawks carry mice that way. Ospreys invariably carry fish (vide Abbott), Roughlegs carry even field mice that way, and peregrines, doves. In all the cases I have ever seen of a hawk or eagle carrying prey it has always been carried away from the body."

His Skill As a Writer

His knowledge was great; but what of his powers of expression? In one sense the answer is obvious and simple: all who have studied his paintings and drawings agree that he was a master craftsman, some say the very first among all the world's painters of birds. And so, in a sense there is no more to be said about his powers of expression — they were superb. But to say this is not enough. Great as his skill was with brush and pencil, he expressed himself, in my judgment, even more fluently as a writer. And in my judgment an appreciation of his power of expression as a painter gains much from the study of his letters, particularly of the letters describing scenes and people. The letters, so admirably presented by his daughter Mary, are for the layman a simpler subject for study than the paintings: the layman knows more about words and the effects they produce than he does about brush strokes. What do we learn from the letters?

He Used Words As He Used the Brush Stroke

We learn first that he was wide awake to the use of words, as he was to the use of the brush stroke. Different words, different patterns of words, produce different effects. He spoke of suffering from "advanced years and ill-timed shortage of sleep and longage of hours;" these, he said, made him "easy prey to the prowling streptococci of the Lehigh sleeper. Or thereabouts. Which, slipped into words of one syllable, means that I've had a bad cold in my Bronix." He played with words. "I already wish that I was back at Sheldrake, splashing in the pellucid shallows with the playful perch. But I ain't. I'm sweltering in the shimmering sunshine with the shrinking sunflower." He made fun of arty words and phrases. "A ray of hope steals up over the purple evening horizon, while naught but the contralto quaver of a belated mole-cricket disturbs the sad, serene quietude of the tropic crepuscule." Perhaps remembering "Greenland's icy mountains" he wrote "from Old Chilalo's chilly slopes." And he threw in an occasional epigram: "Life is one B.V.D. after another with a splash of Red Sea water between."

He used words in this way, with awareness of their "literary" effect, only occasionally, when his mood changed or he moved from one topic to another. More often his writing flowed on, in the informal manner of a letter writer, without thought of effect. Much of his writing was narrative and descriptive. He was away from home, perhaps in Alaska, or Africa, or South America, and he wrote to tell his wife or a friend about something that had happened to him or that he had seen.

When he wrote to tell a story or describe a scene, his role as letter writer-artist was much the same as his role when he painted a bird. Sometimes, as with the phoebe skin, the object lay before him. "Looking out just now I see the forest half a mile back, then nearer a broad savannah. Then a shallow stretch of shining water, and, about 200 feet away a flat sandy bar in the river. On it are nine crocodiles—three big ones—and among those, on one end, about 50 dozing black skimmers, and over the whole thing, and quite near, floats on outspread wings and in the glaring light a beautiful, pink roseate spoonbill."

Word-Painting from Memory

But direct description of this kind was rare. More often he wrote from memory and described what he had seen in the day or two preceding his letter writing. So from memory he wrote: "The marsh is the most beautiful place at all times, but, at sunset and the hour following it, it is beyond description. Just now a perfectly full moon, almost blue-white, begins like a ghost to show in the east, just as the glow from the west begins to reflect across. Then it brightens as the sunset progresses and the serene and calm violet east and the flaming red and orange west both seem too beautiful to be real. The flat blue-black horizon of sparse trees, the ruddy beds of quill reed and the rustling rushes that the boat glides past, and the vibrant and brilliant air cut everywhere with the swift steady flight of ducks, ducks, ducks, some sifting straight overhead, silent except for the icy whisper of their wings, only heard for a second or two when they are nearest, others lining their straight course into the sunset—the darting teal going as if they were hurled out of a gun—the frosty marsh smell everywhere and a cool wind in your neck, all gets to you in a wonderful way. Then, when it is almost dark, suddenly there is a waving, rushing splash, all over in less than a second, and dimly against the darkening sky a broad line of velvet, silent birds deploys, rises, and falls into formation and melts into the sky beyond."

Fuertes painting an American Flamingo. Photograph taken aboard the "Estrella" in the Bahamas, May 1902, by Frank M. Chapman.

"Whole Sense Outfit" Used in Word-Painting

This is a simple word-painting and yet it has remarkable qualities. The early part is easy enough with its account of colors and things seen. But Fuertes goes on to describe things heard, and smelled and felt—the "cool wind in your neck." To adopt a phrase of his, he was using his "whole sense outfit." And his language too is striking: "Some sifting straight overhead . . . others lining their straight course into the sunset." And what a care for detail! Each phrase does a job, conveys an impression. And yet he is never confused, never in a hurry. Every part of the picture is in place and the whole is precisely executed in less than 250 words.

Descriptive passages of this kind abound in his letters. Sometimes a single phrase tells the whole story. "We passed all morning like fleas along an elephant's belly, along the steep flank of bare or grass covered mountains." He speaks of a scene where all is "sheltered under a lovely orchard-like growth of gnarled old live-oaks and nut pines, as still as a church on week-days." And of another when the mist prevails; "when it is foggy all the infinitely complicated background is lost in gray and you get the most beautiful silhouettes of enormous trees, isolated more or less from the great forest mass, and see the wonderful grace and form-beauty of the host tree and all its beautiful parasitic decoration."

He described a person with the same vividness. This was the cook at one of his camps. "Tall and slim, sixty plus years old, she wears for daily use as a waist a naively inadequate towel, so arranged as to be no good at all, either for purposes of warmth, concealment, or even mere decoration. When she can get one she wears a long black cigar between her bare gums, for she has no teeth that ever meet. Her lanky arms are welted and scarred so that they look like black snakes run over by a train; and her wool is cropped short." A sentence suffices for a small town. "Buenaventura is a beautifully situated place as seen from the sea, ten miles up a mangrove lined river; but once there you see a filthy, wet, bug-infested, fever-ridden collection of shacks and dobes which we're only too glad to get right out of."

Two Remarkable Word Pictures

Two longer passages have remarkable qualities. The first depicts the scene in a peasant's hut where he and his companion Geoffrey O'Connell sheltered in the mountains of Colombia. "Early to bed with numb feet, that staid so till we left. But before we turned in a pair of sad old packhorses of women came in off the trail. They couldn't be turned out on the *paramo* at night (murder, no less) so they were shown into the room. They had a taller-dip and made a pretty picture from our beds, lousing each other in the candle-light with claw-like hands, and grunting, snuffling, and hawking in the cold against the flickering background of smoked mud walls, their witch-like shadows dancing with the jumping light. By this time the dogs and cat and one of the turkeys were all in the room, and after the family had crawled into their den and the 'padron' had *tied* on the door for the night, we were all ready for a real cozy night, laughing and talking until a late hour. The poor old dames grunted into their packs and shuffled out in the cold dawn."

And finally another word-picture from the mountains of Colombia. "Last night, when we were all here and settled in the big room 'at our service,' the young woman asked us if we would like some music. Certainly, what? Well her brother had picked [up] the art of playing the guitar and sang. We hadn't seen any men around that looked like her brother, so: 'How old is your brother, senorita?' 'He's just gone five.' Well a somewhat old-looking, babyish boy was produced in a minute. She sat in the corner and held the guitar on her lap. The youngster stood beside her and played all on the neck of the guitar. He couldn't reach around it so his thumb was only a nuisance to him and he did the bass string with his little finger—never mind. I've heard the best 'tiple' player in Bogota, and perhaps a hundred others along the streets; this little kid played with *perfect* precision, and had all the tricks of mute and thumb and hush and three finger four time (that makes your whole insides dance with them) that any I ever heard could handle. Then he sang. Madge, I would have given anything in this world to have had you (just for an hour if you had wished it) in this high, square, bare, mud-floored room, lit by a candle, to see and hear the group of two in a corner. The girl was just setting. That youngster . . . sang songs to the most moving and wild accompaniments, that were such perfect embodiment of romance that words were useless (although he had 'em) and not one but was the purest, most intensely characteristic expression of these places and people you could possibly get. He had a curious trick of hushing—then singing out like a purple finch, with his head back, everything rich minor, except for an occasional line—for a question in the major. Then that goat-getting hush on the minor reply. His sister said she had helped him with the words only. He isn't a bit abnormal other ways, and when I set and baited a rat-trap in the corner he was in and out every three minutes the rest of the day."

The little guitar player comes alive as vividly as the marsh at sunset; and for the same reasons. Fuertes' senses had taken in the whole scene, item by item. He had held all of it in his memory and then, when he came to write, he had found the precise words and phrases to paint the picture.

Fuertes holding a Snowy Owl. Photograph taken outside the artist's studio at Ithaca, New York, November 1918, by Arthur A. Allen.

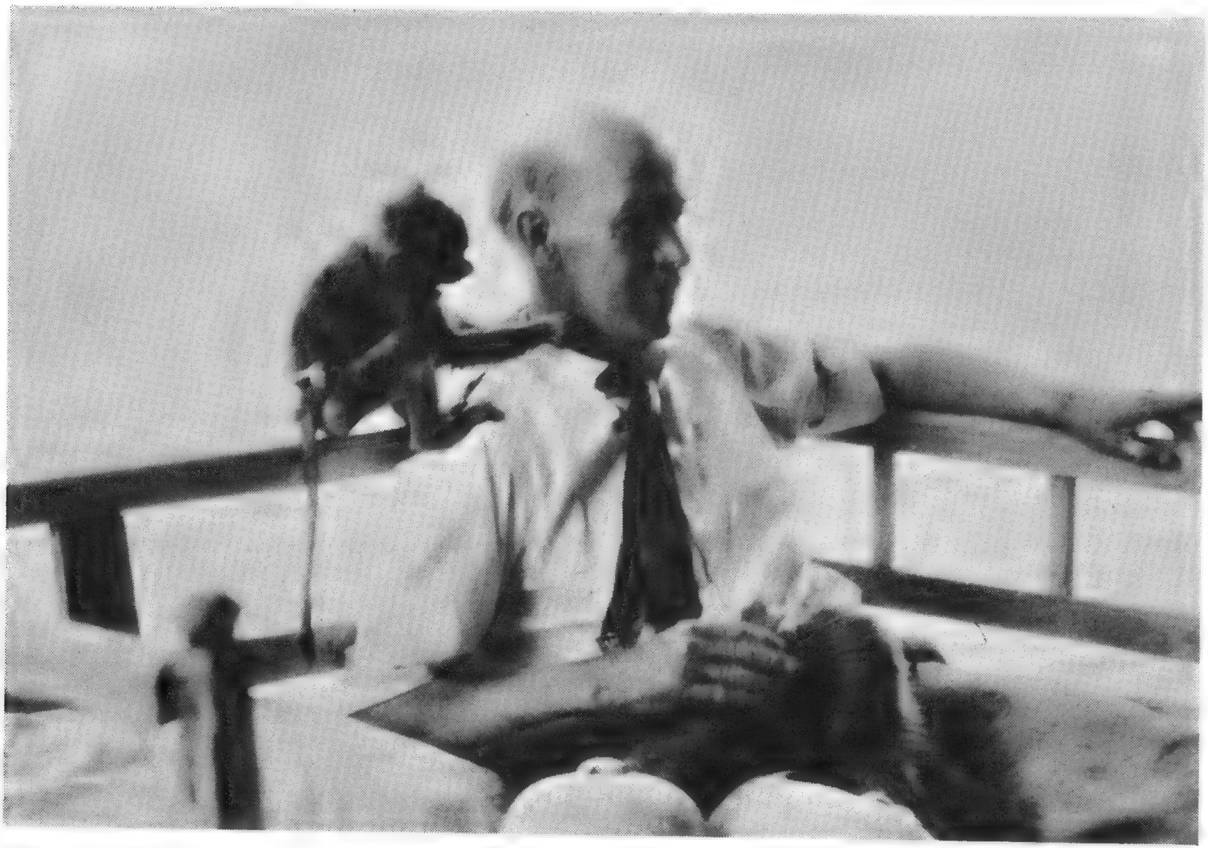
Identifying Himself with Things and People

His ability to grasp a scene in all its detail—to amass the knowledge that he later expressed in words and phrases—came, I believe, from an extraordinary power to identify himself with things and people around him. He was much more than an observer, even a keen observer. He became part of what he saw and heard. "I've had sensations that would just pick me up by the neck and shake out the gasps." A mere observer would have been pleased by this or distressed at that. Not Fuertes. His whole being experienced and apprehended the scene. Joy and grief rather than pleasure and distress were his rewards. "I lifted my head and yapped with joy, like a setter pup with the hedgehog quills at last taken out of his fool chops, when last Sunday I got on the commander's bridge of a snuff-colored mule and heard his little shoeless heels click under me." "I went down the side of the mountain today and got into a tangle that made me so mad I nearly cried."

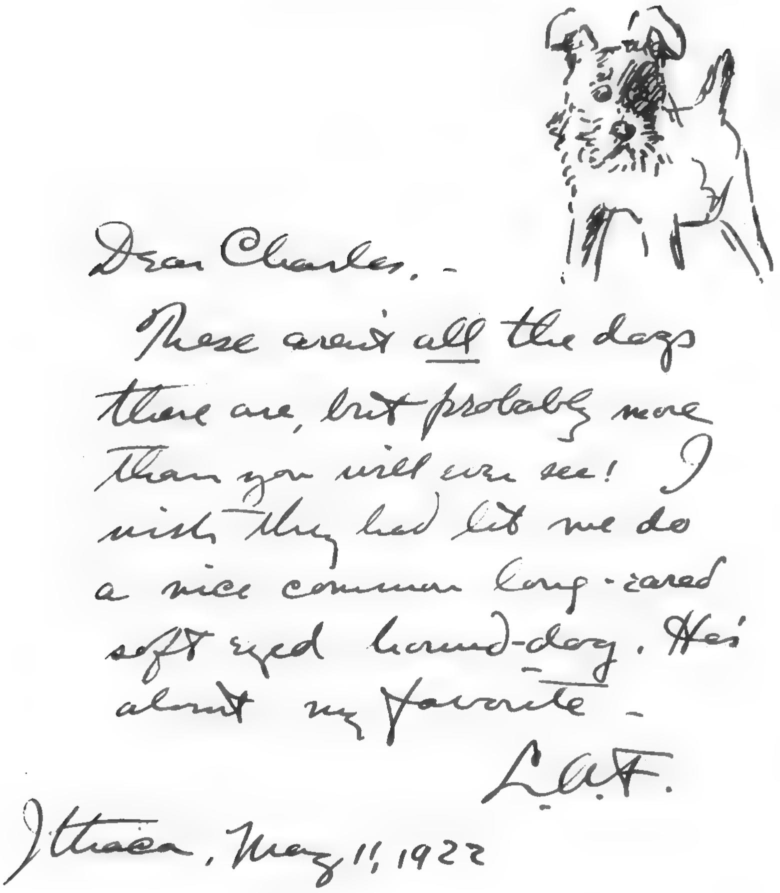
He brought to the things and people around him the zest of a child. He explored with eyes and ears and hands and nose; his response was vivid, immediate. "VRMMMMMMM. From somewhere out in the dark just then came a sawmill-like hum, and BAT, right on the side of the head, with a fine chill-bringing crescendo, landed a thing like an elephantine june bug, with a head like this (sketch). H'raus mit'm. I jumped clear across the room. Candle now so (sketch). This can't go on, for I can't hold the bug any longer, nor let go indoors—goodnight. More later." Here again his alert ear and eye transfixed the scene and he summoned up the words and phrases to describe it.

He Knew the Value of the Individual Word

Throughout his letters Fuertes' use of words and phrases is as remarkable as his powers of observation and the tenacity of his memory. That he knew something of the use of words I have already shown. But his knowledge went far beyond the little tricks of playing with alliteration, purple passages, and balanced phrases. He knew the individual word for what it was worth and when he put a phrase together he chose the right word for his purpose, as in, "the deep, frost-silvered forest." Often he needed more than one descriptive word to convey the whole range of his impressions and so he wrote "reeking, steaming, moist," or "we bumped, tossed, lurched and pitched." In a passage that called for distinguishing a variety of sounds he found the right words: "the blowing and snorting of the whales, the screaming, way out on the bay, of gulls and loons and an occasional goose, and nearby the licking of the little waves in the pebbles and the hum of a big bee, with just a thin 'ray' of a hermit's song way over across the bay by the spruces, make the part of the picture you see with your ears." Sometimes he made words fit his needs in another way. "The strangest thing to see a bright, fox-colored humming bird s-s-sing like a creeper, with a big, bumble-bee buzz — curve up into a giant forest where everything in view is vast, poise with its tail, pendulum-like, swinging under it, look around, and broooom off again, all before you quite notice it."



Fuertes with "Tinisn" during the trip to Abyssinia, his last expedition, in 1926-27. Photograph by Alfred B. Bailey.

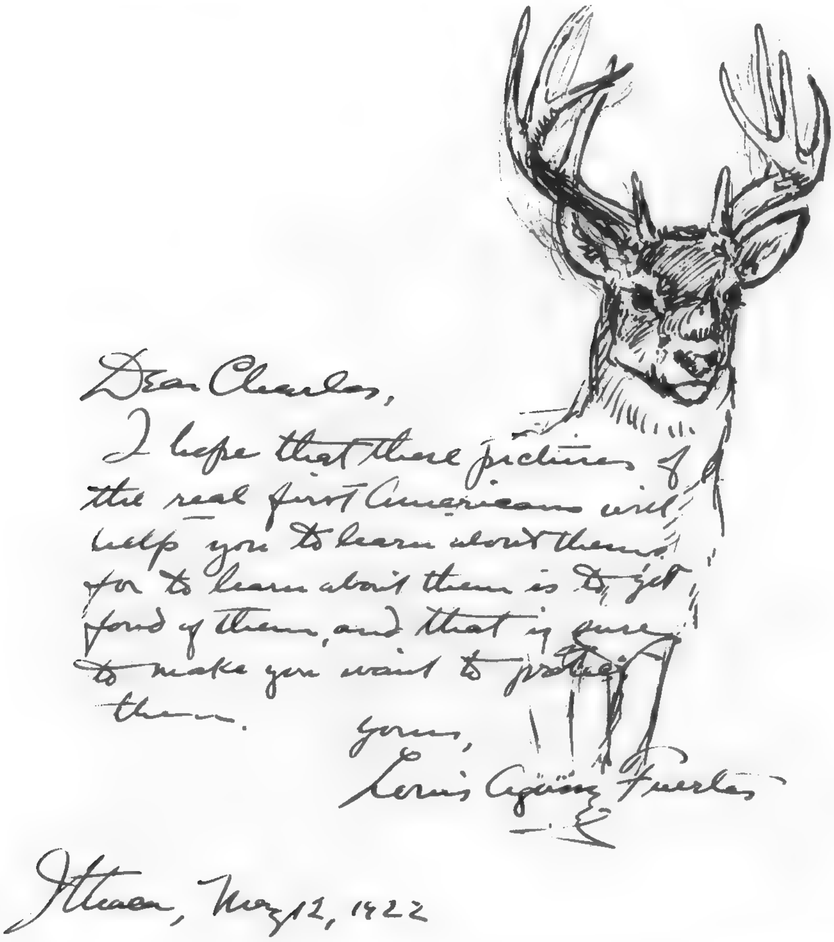


Dear Charles, -

These aren't *all* the dogs there are, but probably more than you will ever see! I wish they had let me do a nice common long-eared soft eyed hound-dog. He's about my favorite -

L.A.F.

Ithaca, May 11, 1922



Dear Charles,

I hope that these pictures of the real first Americans will help you to learn about them, for to learn about them is to get fond of them, and that is sure to make you want to protect them.

Yours,

Louis Agassiz Fuertes

Ithaca, May 12, 1922

Among the several books of the National Geographic Society which Fuertes illustrated were "The Book of Dogs" and "Wild Animals of North America." On the flyleaf of the copies presented by Fuertes to Charles S. Underhill—a young man at the time and now Librarian at the Newark (New York) Public Library—are the above inscriptions, reproduced here with Mr. Underhill's permission. Fuertes' inscriptions, like his letters, were skillfully worded and frequently enlivened by sketches.

An Ear for the Music of Words

Fuertes also had an ear for the music of words. "Along the trails rare little farms, built so steep they look like maps of farms tacked on the walls, harbor and faintly nourish a scattered people; the poorest in every conceivable sense, I think, in the world. They know of nothing, truly. They can hardly think at all and stand in a blurry daze while you pass them and probably for hours after. I have never been so touched by what man, God's creature, will do and do without to live bare life, as here in these sad, huge, resourceless desolations of the eastern Andes."

Command of Words Was Instantaneous

His skill with words was much more than the skill of the poet or essayist because his command of words was virtually instantaneous. The letters themselves, when seen in manuscript form, show that he wrote fluently, without erasures or substitutions. And remember the circumstances in which he wrote. Often he was deep in the forest or camped on the mountain-side. He wrote many of the passages I have quoted by candle-light (taller dips), when he had finished his painting for the day and was too tired to go on with his skinning. But even so the words, the right words, flowed from him: "this stuff I did not intend to shove at you, but it got out just ahead of me." And the letters themselves look, if not like models of penmanship, at least like tidy, precise examples of the letter writer's art, often with sketches in margin or text that are as lively and telling as the words and phrases they illustrate.

Here is literary expression in one of its highest forms, the direct, immediate, unbroken presentation of experience in words. The right words bring to the reader exactly what the writer saw, heard, and felt. But in writing as in painting the power to express is dependent on the power to know. What Fuertes knew was what his senses had brought him. He did not write fiction, he did not invent, he did not write philosophy or deal with the economic or historical causes of things. His knowledge was of the event before him or on the surface of his memory.

His words and phrases and descriptive passages are indeed works of beauty but they are so because they rightly expressed the intensity of his sense-experience. His senses gave him deep and exact knowledge; they perceived and separated out an almost endless variety of colors, sounds, and other experiences. The words and phrases came later. They acquired significance for him when he had a meaning, a distinct experience, to attach to them. His "original vocabulary," which Dr. Allen has commented on, was original because the sense-experience associated with it was original.

His Writing Belongs Beside His Paintings

Are the letters worthy to be set beside his paintings and drawings as testimony to his gifts as an artist? I believe so, and on two counts. They proceed from the same exactness of knowledge and the same fluency of expression as are found in his pictures of the living bird. They are alive in the same way. And what he brings to life in the narrative and descriptive letters is the world of plants and animals as well as a panorama of landscapes and human scenes; his themes are no less rich and varied than the multiplicity of his bird pictures. However freely he expressed himself with brush and pencil — "he worked rapidly putting down pencil stroke after pencil stroke without pause"—he was equally free as a letter writer.

And so to another Fuertes story; this one bearing upon the argument of my essay and, I believe, a newcomer to the great collection. I heard it from Miss Mary Hull, the sister of one of my colleagues and a native Ithaca lady, somewhat older than Louis. She told me that when he was a boy a local department store, Rothschilds, held an exhibition of his paintings and drawings. She visited it and soon after she met Louis on the street. She praised his work and asked, "Louis, how do you do it, how do you paint them so exactly?" He answered, "But that's the way they are." If you really knew the living bird you could paint it no other way.

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BIRD PHOTOGRAPHY AT SAPSUCKER WOODS

ARTHUR A. ALLEN

There was a time when I had to ask myself "What bird is that?" and later "Do we need its skin in the Cornell collection?" Now after more than sixty years of watching birds, the images of most North American species are fairly well imprinted on my mental "field guide" and the Cornell study collection is fairly complete. In the place of these earlier activities has come the urge to share with others the bird pictures I have stored away in my memory book. Had I the ability of a Fuertes or a Thorburn I probably would spend the rest of my days painting those pictures but neither pen, nor pencil, nor brush behave properly in my inadept fingers. The only means under my control is the camera which, despite its limitations, does have the advantage of realism.

One need not be an artist to learn the techniques of photography, and hunting with a camera can be a sport even more intriguing than hunting with a gun. In fact bird photography has become a very worth-while hobby to hundreds of ardent observers who have advanced a step beyond the mere bird-watching stage, and it is much more than a sport or a hobby to the observant ornithologist able to devote the time, the thought, and the ingenuity to recording his observations in this way.

To me photography has always been a means to an end. Of course, I thrill to the sport of capturing on film a flock of teal as it whizzes by—and I still get satisfaction out of being the first to photograph an Ivory-billed Woodpecker or a Bristle-thighed Curlew. But in my case the camera has always meant the possibility of portraying accurately and artistically every species of bird, in every plumage and in every species-typical activity. Long before we had color film I visualized such a collection to augment our museum collections of skins and mounted birds, and now that color film has become so versatile, the possibilities of such a marvelous assemblage seem endless. Indeed after 25 years with a color camera, I have succeeded in photographing only about 500 of the species and subspecies of North American birds and for most of them I have only a few of their plumages and a sprinkling of their varied behavior patterns.

I would not underrate the magnificent work of our great bird artists who, by their own skill, are able to reproduce a species in all the brilliance of its color, in all the appeal of its contours, and in a perfect composition so difficult to capture with a camera. A good photographer studies the pictures of those past masters of composition such as Fuertes and Thorburn with a desire to emulate them with his camera. On the other hand, the greatest bird artists welcome the opportunity to study the results of the camera, before undertaking to portray their subjects.

Nowadays as I drive about the country or sit at the windows of Sapsucker Woods, I see birds as through the lens of a camera. They are doing interesting things, they are gracefully perched, they are beautifully framed and nicely lighted and my mind automatically inquires: Is that photographable? Could that set-up in some way be reproduced in front of my camera? Occasionally this is easy. The bird, not very timid, is perched close to the road or to the window and my camera is ready with its long-focus lens and loaded with the right film so that I am able to preserve the fleeting moment then and there. For example, the Florida Bald Eagle, shown in this article, permitted me to stand in the open beneath its favorite perch within the city limits of Sarasota, Florida. But for the one such picture I am able to snap, I have hundreds stored somewhere in the back of my brain awaiting the auspicious moment when, through some devious method learned by experience, I can induce the bird to hold the same pose or to perform in the same manner before my camera.

We have, for example, on the cover of our sound-book, "Bird Songs in Your Garden," a color photograph of a Song Sparrow singing in the forsythia, a rather charming and appropriate photograph. I did not just run into the garden and snap that picture. I saw it several years before in a place impossible to photograph. Finally came the year when the forsythia in my garden was in bloom and a belligerent Song Sparrow was defending a territory 100 feet away, but using song perches that were neither photogenic nor photographical. I moved, therefore, a nice bouquet of forsythia to his territory in front of a photographic blind, ran an extension cord from the house to the blind, and played his recorded song back to him. In addition, I set up a miror on one side of the forsythia to engage his attention. Since I made sure there was no other convenient perch near by, I soon had him not only singing from the forsythia but also fighting his reflection in the mirror. Thus I satisfied my own craving to match the picture I had been carrying for several years as a mental image and I preserved for all time a fleeting moment in the life of a Song Sparrow giving its territorial song.

Last June I was standing at the edge of a field with Bayard Read, talking with the farmer about an oriole's nest in his front yard, when a female Bobolink flew by with a grasshopper in her bill. I watched the bird and made a mental note of where she alighted in the field. Later I asked Bayard if he would like to film a Bobolink at the nest. He seemed somewhat incredulous when, after watching the bird for awhile through binoculars, we walked directly to her nest, not at the spot where she went down with food but at the spot from which she flew up. Bobolinks and other field birds never fly directly to their nests but, after feeding the young, usually fly up from the immediate vicinity.

"Now," I said, picking up a stick and forcing it into the ground two feet north of the nest, "This will mark the spot and will probably become a preferred lookout perch for the Bobolink and her mate. We will set up this 'pop-tent' of yours about twenty-five feet to the south, leave it overnight, and tomorrow move it up to the proper distance for the lens you plan to use. Perhaps you would like to include in your film of the Bobolink some of the daisies and buttercups and hawkweed that are all about us but not in the immediate vicinity of the perch. If so, we will hang a milk bottle of water on the stick and when you are ready to photograph, you can make any flower arrangement you wish. At the same time, to avoid having the long grass in front of the nest conceal the birds while feeding the young, we will bend down the grass and catch the tips under this short board which will not show in the picture. Then, when you are through photographing, all the shelter about the nest can be rearranged."

A Bald Eagle in Florida on its favorite perch. This was a roadside snap with no planning ahead. Photograph by Arthur A. Allen © National Geographic Society.

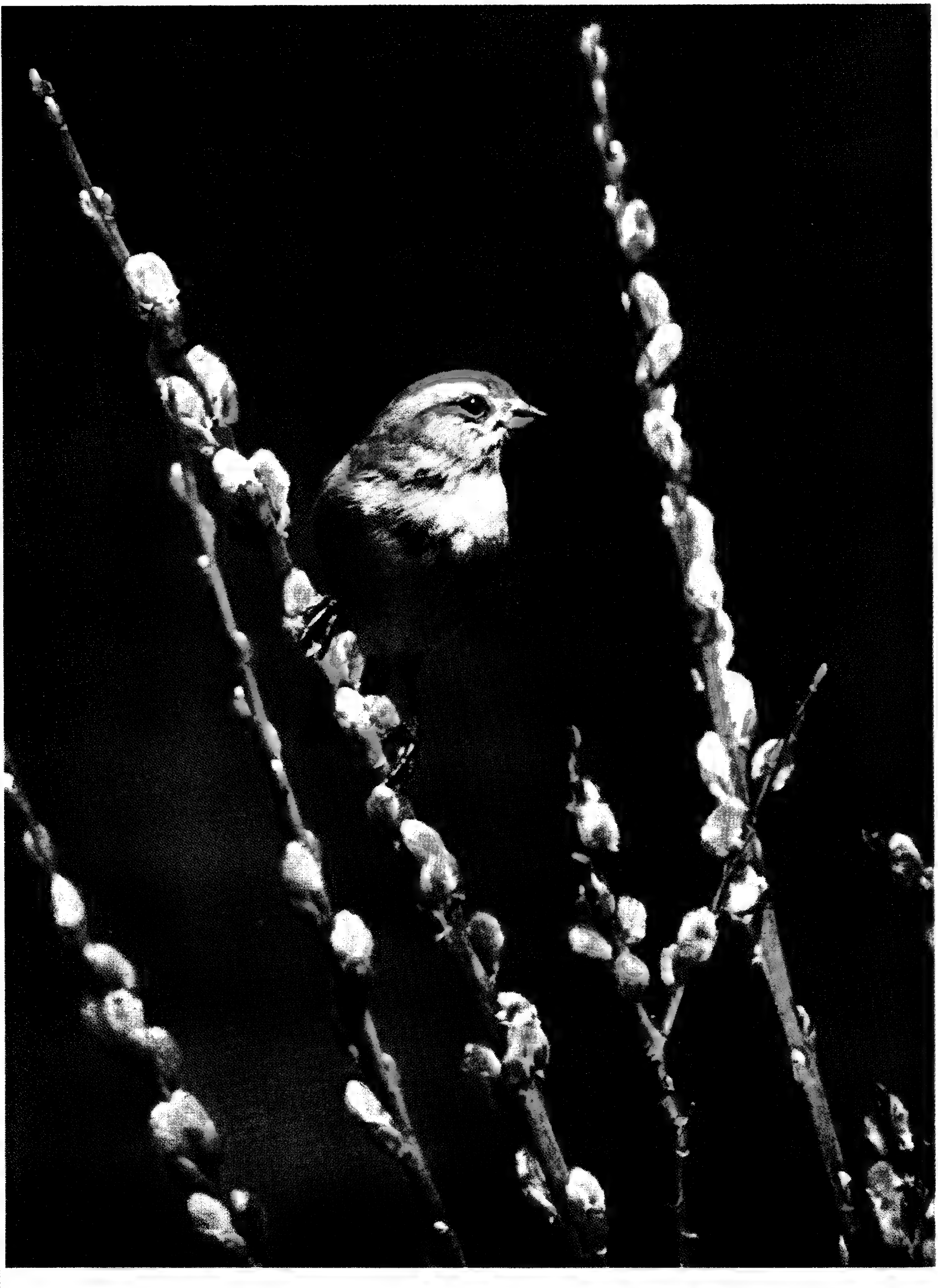
Everything worked smoothly: Bayard got his film; I sat in his blind for awhile and took the accompanying still pictures and Bayard's son "B.G.," who was just starting bird photography, got color pictures that were certainly the equal of mine. Two days later the farmer mowed his field but, since the nest was still marked, he was able to avoid it—and six young Bobolinks were reared successfully.

For nearly forty years a Peregrine Falcon nested in the gorge below Taughannock Falls not far from Ithaca. The eyrie, first discovered in 1909 by Louis Fuertes and Professor Elon Howard Eaton, may have been occupied for years previously. Often one of the birds was shot by an irate poultry man but the survivor secured a new mate and, although the exact location of the eyrie sometimes changed, seldom (if ever) was Taughannock Falls without its Peregrine until 1946. Quite a number of bird photographers, including Guy Bailey, George Britton, and Harry Knight, were able to work their way to the edge of the cliff and, with telephoto lenses, get fairly good pictures of the Falcon incubating or brooding its young — but none of the photographs indicated the grandeur of the setting so close to the spectacular waterfall. For years I carried in my mind's eye a picture of the Peregrine against the Falls and finally, when the Peregrine moved its eyrie to the south side of the gorge about 300 feet from the Falls, my opportunity came. The nesting ledge was 40 feet down the perpendicular cliff and directly below a substantial lookout where I placed my blind. From here there was a good view of the Falls but there was no satisfactory perch for the Falcon anywhere in the vicinity. So with the help of Miles Pirnie, I hauled a dead tree to the edge of the cliff about 30 feet in front of the blind and fastened it in such a way that the Falls would furnish the natural background. Returning in about a week, I could see that the bark on the perch had been disturbed by the bird's talons. I climbed into the blind and, in half an hour, secured the accompanying black-and-white photograph of the Peregrine in its magnificent setting. Some years later, after color film had become available and while the Falcons were still using the same ledge, I repeated the whole performance with Professor William Wimsatt and secured the accompanying color portrait with a longer focus lens.

And so, through the years, I have been able to reproduce with a camera a few of the mental pictures that I continually carry with me, but for every one accomplished, dozens of others fill that little space in my brain catalogue, urging to be born. With the coming of fast color film and speed lights the periods of gestation have shortened, but the possibilities of the camera have been so greatly extended that dozens of new subjects have crowded in — subjects that could not even have been considered twenty-five years ago. So there is plenty of work and in a field that is practically inexhaustible for those who have the interest, the ingenuity, and the equipment.

Now let us see what we are doing at Sapsucker Woods to help fill the empty spaces in the perfect collection I visualized. We have only 89 species of birds that actually have nested within our boundaries. The migrants which frequent our pond, our woods, and our open land at one time or another bring up the total number of species to 200. Each one of these species, with its great variety of behavior patterns, is a possible subject for the camera. Of course, one has to know his birds to understand what they are doing and what particular behavior they are expressing. Even then it sometimes takes a good deal of inventiveness to induce them to "behave" within range of the camera.

Right now, as I write, we are blessed with a superabundance of Black Ducks and Mallards, some 500 of them, that spend most of their time sleeping on the ice and waiting to be fed. Periodically, however, they take to the little



Tree Sparrow in the pussy willows—a "convenience perch" arranged near its nest. Photograph by Arthur A. Allen © National Geographic Society.

Above, a Song Sparrow rests between rounds of fighting his reflection.

Below, the set-up for the above picture with photographic blind, mirror, speed lights, and bouquet of forsythia. The blue background was not illuminated in the above photograph, so it appears black. Photographs by David G. Allen.

hole in the ice, kept open by an agitator, and start "behaving" — fighting, courting, mating, tipping, diving, bathing, scratching, giving intention movements, performing all the actions so typical of ducks. Yet many of these actions have not yet been very satisfactorily documented with a camera. Here, then, are wonderful opportunities. When the ducks come to feed, they romp over our "early American" rail-fence feeder as though it were bare ground. I never expected to see Black Ducks, or even Mallards, perched on a rail fence, picking up chick feed like House Sparrows, nor had I ever hoped to see a Trumpeter Swan handling Mallards like cordwood, picking them up by the head or the neck and pitching them to one side as it made its way through the crowd of ducks blanketing the feeding area. We installed three speed lights against the glass of my office window to illuminate properly the amusing happenings at feeding time and a couple of the photographs are offered here.

Whenever a bright day makes possible the use of color film at 1/1000 second, we often enjoy the sport of "duck-hunting with a color camera" by using Novaflex, follow-focus lenses on Nikon cameras. We sit in comfortable armchairs at the plate-glass windows of the observatory and snap the ducks as they return over the trees after having been frightened from the feeding area. It is truly duck-hunting de luxe although, in spite of the comfort, it is much more difficult to produce pictorially good, sharp, well-composed, flight pictures than most people might guess—and certainly more difficult than it would be to kill the ducks with a shot gun.

At another time, when the ducks were not quite such a nuisance, and when a covey of Bobwhites were coming regularly to the feeding station, we aimed speed lights set on tripods at a three-foot, snow-covered area and recorded, from my office window, considerable Bobwhite behavior without having to expose the camera or the photographer to the exigencies of zero weather.

When the ice leaves the pond in the spring, we anchor a short log just offshore and sprinkle it liberally with chick feed which is relished by the blackbirds and sparrows as well as by the waterfowl with their young, and even the muskrats. Surprisingly enough the goldfish, with which the pond is stocked, are also attracted by the spilled grain. The concentration of goldfish attracts the Belted Kingfishers and the herons within camera range from the windows, so the possibilities for using up color film are endless.

For photographing smaller birds coming to the feeding station, one needs only to visualize the most attractive setting in which he has ever seen each species and make just such an arrangement on the feeder — a "convenience perch," we might call it. Perhaps the memory is of early spring with a Tree Sparrow sitting on a pussy-willow branch; perhaps it is a Cardinal in flowering dogwood or a Pine Warbler in the redbud. If the setting created is also the most convenient perch for the bird coming to be fed, it is likely to use it instead of some other and the resulting photograph will be much more attractive than that of a bird merely eating from a feeder. The color plate of the Tree Sparrow in the pussy willows shown in this article was secured in this way as was that of the alert Cardinal in the dogwood. I have yet to photograph a chickadee drinking upside down from the tip of an icicle — a performance which I once observed and have carried in my mental album for years. In the case of ground feeders such as the Bobwhite, it is possible to arrange the feed so that the bird will be seen against a background matching the most attractive or most appropriate view that you have in your mental filing case for that particular species.

Male Bobolink feeding young near the "convenience perch" used by the female in the color plate, opposite page. Photograph by Arthur A. Allen.

When the nesting season arrives, it is much more satisfactory to be anchored than to be travelling. In the first place it is possible to locate the territories of most of the birds when they are giving their territorial songs early in the season and often to spot them carrying nesting material. Not that there is any distinct advantage photographically in finding nests early — it is just easier. It is foolish to start photographic work on a nest until the birds have been incubating five or six days or have young five or six days old. Birds are very easily disturbed before incubation or the care of the young is well under way. To know the exact whereabouts of many nests and the exact dates when nests were begun, however, is a great time-saver when the photographic season arrives. At Sapsucker Woods we keep a chart of all the nesting birds and the status of their activities whenever possible.

For studying and photographing birds at their nests, there is a standard procedure which, if followed, results in very few accidents and little disturbance to the birds. Photography should not start until the birds have been incubating five days. In the case of hawks and a few others, it should not start until the young are four or five days old. Then some sort of blind or dummy blind is set usually not closer than 20 feet to the south of the nest and nothing

A female Bobolink on a "convenience perch" arranged near her nest. Photograph by Arthur A. Allen © National Geographic Society.

Above, waterfowl in a hole kept open by an agitator ("Lightnin Mixer") in front of observatory windows. Photographed from the raised blind shown in the background of the picture below. Photograph by David G. Allen.

Below, waterfowl in the hole, kept open by the agitator, as seen from the observatory windows. Photograph by Arthur A. Allen.

about the nest is disturbed. The next morning, the blind is moved to the exact spot from which the pictures are to be made, and, time permitting, it is left there a second night with no disturbance to the vegetation about the nest. Not until one is ready to photograph are leaves or grasses that interfere with the view tied aside, and then only for the time during which pictures are being taken. We never leave a nest "opened up" except when we are there to protect it. The blind itself may protect the young from some enemies but not all.

The most satisfactory nest pictures are now taken with speed lights set perhaps two or three feet from the nest, because the direct sunlight never has to shine on the eggs or young, the lighting is much more even, and the short exposure of the speed lights stops all motion. If blessed with speed lights, the photographer should also use dummy lights placed at the correct distance when he sets up his blind. Dummy lights can be merely empty coffee cans that are replaced with the speed lights when one is ready to photograph. By following this procedure, the pictures of the Yellow-billed Cuckoo and the Yellowthroat nesting along the trails of Sapsucker Woods were secured without much trouble.

Nests on or near the ground are the easiest to work with, but many of our pictures are made from the tops of ladders or from blinds on platforms thirty or forty feet up in trees. The same principles, however, are followed in the set-up and the more deliberate the early activities of the photographer are, the better.

Sometimes, in the later stages of parental care, the young birds flutter from the nest at one's approach. If photographs of the adults feeding them are desired, the youngsters should be captured and placed for a couple of hours in a wire wastepaper basket where the parents will feed them while the blind and speed lights are arranged. It is imperative that all the young be captured lest the parents spend their time feeding the ones at large and neglect those in the basket. When everything is ready the youngsters can be perched on a branch over the basket and probably replaced several times before they are content to wait and be fed. In all types of photography for which a blind is used, it is desirable to have an accomplice who, when everything is ready, will walk away from the blind. We call him a "go-awayster" and the birds, since they cannot count, return to their nests or young very soon after he has left.

There are some photographers like Crawford Greenewalt (see the accompanying photograph) who dislike the confinement of the blind and prefer to sit at a distance from the nest and operate the camera shutter with a thread or an electric release. This often works just as well, especially if one has an electric rewind on the camera. Also it is somewhat more comfortable and enables one to see more of what is going on all around him. The use of the blind, however, gives one a much more intimate view of what he is photographing and, I believe, the birds behave more naturally when they can see no one watching them even at a distance.

The use of speed lights in bird photography conditions one to photographing in any weather or time of day—even at night, so that nothing is safe from the camera. The opossums and coons that patrol the feeder at night, the cottontails that enjoy the cracked corn intended for the ducks, and the Screech Owl that nests in a bird house are all fair game for the camera. One of the members of our Council, Spencer Knight, built a 25-foot tower to bring him to the level of a Long-eared Owl's nest in a pine tree, and he spent the greater part of several nights communing with owls and taking portraits of the owl family. He invited David Allen to join him and one of the results of the visit is shown in this article.

The Peregrine Falcon of Taughannock on a perch arranged for its convenience. Photograph by Arthur A. Allen.

The Peregrine of Taughannock. This photograph required considerable planning. Photograph by Arthur A. Allen © National Geographic Society.

Above, duck hunting de luxe as enjoyed through the plate-glass window of the observatory.

Below, returning Mallards as seen through the Novaflex, follow-focus lens and recorded in the Nikon camera at 1/1000 second. Photographs by David G. Allen.

Above, courtship maneuvers of a Pintail as seen through the observatory window. This is the so-called "Head-up-tail-up." Photograph by David G. Allen.

Below, another courtship maneuver is the "Grunt-whistle" here shown. Photograph by Arthur A. Allen.

Above, getting ready for the duck invasion of the "Early American Feeder." Speed lights close against the windows will give sufficient illumination. Photograph by David G. Allen.

Below, much activity in front of the speed lights. A Trumpeter Swan is removing a Canada Goose from the Early American Feeder. Photograph by Arthur A. Allen.

Above, Mallards and Black Ducks overrunning the "Early American Feeder." Speed-light photograph by David G. Allen.

Below, maintaining the "peck-order" on the top rail of the feeder, a Mallard punches a Black Duck. Photograph by Arthur A. Allen.

Above, Evening Grosbeaks fill the feeder and consume great quantities of sunflower seed.

Below, after dark an opossum takes anything that is left. Photographs by David G. Allen.

Above, an unusually adaptable cottontail climbs two feet up on the feeder for the cracked corn, a surprising feat for this terrestrial creature. Photograph by David G. Allen.

Below, how far can he jump? A Blue Jay, in his desire for sunflower seeds, mistrusts the gray squirrel. Photograph by Arthur A. Allen.

Above, a male Cardinal in the dogwood—an arranged "convenience perch" near the feeding station.

Below, a spring Bobwhite—against a background of marsh marigolds and fiddleheads of the cinnamon fern arranged at the feeding station. Photographs by Arthur A. Allen.

Above, a Yellow-billed Cockoo returns to its nest along one of the trails in Sapsucker Woods. This speed-light photograph with no artificial background gives the appearance of night.

Below, a male Yellowthroat has just fed his young in the nest near the dike. This speed-light photograph has sufficient background vegetation to catch the light. Photographs by Arthur A. Allen.

Above, a speed-light arrangement with artificial blue background for flight pictures of a Cedar Waxwing feeding its young.

Below, the Waxwing returns with a berry while the blue card gives a light background. Photographs by Arthur A. Allen.

Above, a Blue-winged Warbler feeds its fledglings. The natural background of leaves catches the light from the flash, making an artificial background unnecessary.

Below, disliking photographic blinds, Crawford Greenewalt sits in the open behind one while photographing Cedar Waxwings with his stereo set-up. Photographs by David G. Allen.

Above, Frederick Truslow, from the top of a ladder, photographs a Yellow-throated Vireo at its nest.

Below, the Yellow-throated Vireo photographed from the top of a ladder. Photographs by David G. Allen.

Above, David Allen climbs to a blind in a large oak overlooking the nest of a Red-shouldered Hawk (black arrow at extreme right) in a near-by beech tree. Photograph by Richard B. Fischer.

Below, the Red-shouldered Hawk with its young as seen from the blind in the oak. Photograph by David G. Allen.

Above, a nocturnal Screech Owl brings a night crawler to its young in a bird house.

Below, twenty-five feet up in a pine, a Long-eared Owl broods its young. Spencer Knight built a tower so that the blind, from which this picture was taken, would be on a level with the nest. Photographs by David G. Allen.

Above, low water in late summer proves a blessing in disguise by attracting shorebirds. Photograph by Arthur A. Allen.

Below, an unusual Baird's Sandpiper enjoys the exposed mud flat. Photograph by David G. Allen.

One objection to speed lights is that unless there is some background fairly close to the subject to catch the light, the picture will look as though it were taken at night. Consequently, we sometimes put up artificial light blue or green backgrounds as in the accompanying waxwing pictures. This is especially useful for photographing birds in flight when a background of natural leaves might interfere with their free flight or their use of a pre-arranged perch.

There are many other techniques employed by inventive bird photographers besides those mentioned above. Since every bird has its peculiar habits and individual responses, some knowledge of birds coupled with ingenuity are required by photographers to cope with them. Herein lies the sport as well as the satisfaction of accomplishment which one feels when a truly perfect photograph comes back from processing. And this happens infrequently, even with the experts!

Most of the photographs illustrating this article, even though reproduced here in black and white, are from color tranparencies.

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THE CONTRIBUTION OF MUSEUM COLLECTIONS TO KNOWLEDGE OF THE LIVING BIRD

KENNETH C. PARKES

"Why do you need so many of each kind?"

Few curators of large museum collections have not heard that question from laymen (ranging from high school students to trustees) on a tour "behind the scenes" in the museum. It is probably asked more frequently of ornithologists than of other curators, as most people seem more sensitive to the fact that museum specimens of birds imply the death of living creatures than to this same fact applied to mice, salamanders, or butterflies.

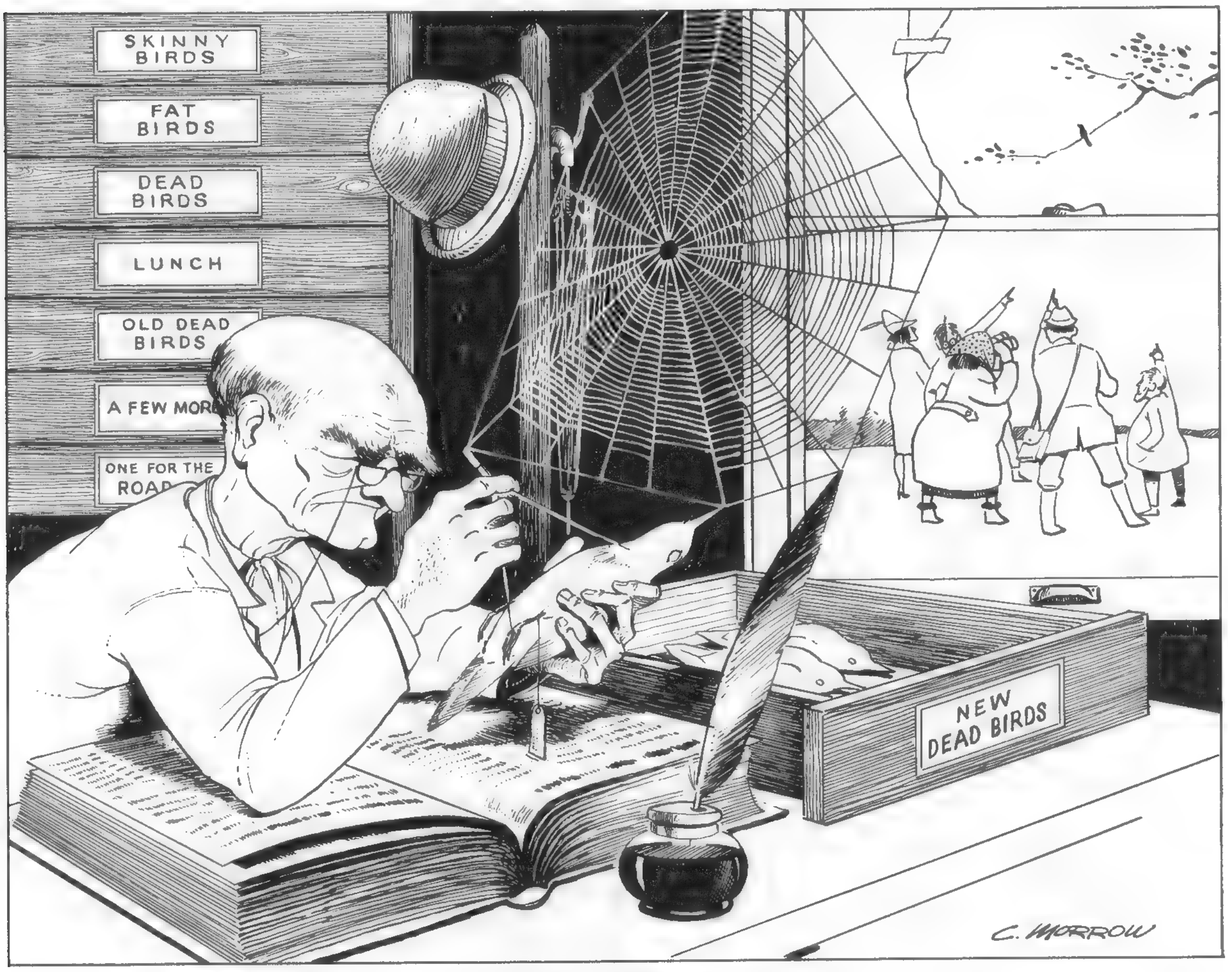
The question is usually answered with a short lecture, the success of which varies with the ability of the curator to explain his research in laymen's vocabulary, on the study of variation—seasonal, sexual, age, geographic, and individual. The visitor may not understand all of the lecture, but I think he does leave with the realization that just one Robin, one Eastern Bluebird, or one Cardinal is not "enough."

Perhaps even more difficult is the task of communication between the museum man and his colleagues who are engaged in completely different kinds of ornithology, involving the study of birds as living organisms, whether in the field or in the laboratory. Many have somehow picked up the notion that museum ornithology consists primarily of measuring beaks and tail feathers, and giving new scientific names to finer and finer subdivisions. Needless to say, formal descriptive taxonomy is still very much a part of our work, and there are (fortunately) those of us who find it more fun than analyzing sound spectrograms or taking temperatures of nestlings. Taxonomy is not quite so sterile a pursuit as some of our friends seem to believe; we are interested not only in the differences and similarities we note among our trays of dead specimens, but in the significance to the birds themselves of these differences and similarities, and how they came about.

Taxonomy as such, however, is not the subject of the present paper. What I would like to do is to demonstrate some of the other kinds of information that can be obtained from museum skins of birds, and what can be deduced about various biological processes and cycles of the living bird from such information. I am discussing only skins, omitting the whole subject of functional anatomy, with its research material (also housed in museums) consisting of skeletons and alcoholic specimens.

In the following discussion, certain assumptions about the nature of the available material will be made. First, that a reasonably large series of specimens is available of the species being studied, if only by borrowing material from all possible museums. Needless to say, some birds are so rare in collections that the total of all extant specimens cannot be considered "adequate" for many kinds of research. However, there is no shortage of unsolved problems among species for which long series *are* available, as will be quickly seen after thumbing through the first volume of the "Handbook of North American Birds" (Palmer, 1962). And many species from areas of the world other than the *relatively* well-studied Holarctic Region are represented in museum collections by surprisingly large numbers of specimens, even if virtually nothing is known of their habits in life.

The second assumption we will make, at least at first, is that the label of each specimen bears accurate data, but that these data are confined to the bare minimum of sex, date, and locality. Both parts of this assumption are subject, in practice, to qualification. Date and locality are usually accurate, subject to slips of the pen, but the museum worker soon learns to expect a certain proportion of "mis-sexed" specimens. These can usually (but not always) be detected by discrepancies in size or color, and suspected specimens discarded from further consideration. On the other hand, data supplementary to the minimum listed above are often to be found on museum labels. Whereas data on condition of gonads and skull ossification, to supplement the simple sex symbol and the notation "ad." or "imm." are most frequently found on modern specimens (though still lamentably missing on many), a gratifying number of Nineteenth Century collectors noted on their labels the colors of soft parts (eyes, bill, feet, naked skin) and the contents of the stomach. Brief mention will be made again, toward the end of the present paper, of the subject of improving label data. The experienced worker with museum collections knows that, much as he would like to have this supplementary information available for all specimens, he will in most instances have to get along without it; we will thus proceed on the premise that only the basic minimum is available for each specimen in the series.



"THE IMAGE"

In what non-taxonomic fields of ornithology, then, can the series of museum skins be of use?

Identification

The first point may seem so obvious as to be scarcely worth mentioning, but it is nevertheless of fundamental importance. The collection of museum skins is the chief basis for *identification.* We are now blessed with excellent guides to field identification of the birds of many parts of the world. It should never be forgotten, however, that much of the work of the author of such a guide (especially in areas where field identification has not evolved to the sophisticated level to be found in North America and Europe) and almost all of the work of the illustrator is based upon the use of correctly identified museum specimens. Identification is important in the laboratory as well as in the field. Whereas experimental work on birds was formerly largely confined to domestic species, more and more of the research of ethologists, endocrinologists, physiologists, and other laboratory workers is now being done with suitable wild species. Such birds are often obtained from dealers who neither know nor care about the exact geographic origin of their stock. Most workers are aware that their conclusions apply *with certainty* only to the species being studied, and sometimes only to the *population* of the species from which their experimental birds originally came. There are still, unfortunately, occasional references in the literature to studies of "the weaver finch" or "the quail." Not only is the museum collection the place to turn for verification of the identity of the species or subspecies of bird being studied, but samples of the laboratory stock may well be deposited in the museum collection as additional verification for future workers. If this is done, when later taxonomic work shows the existence of hitherto undescribed geographic variation within a species, examination of the reference specimens may indicate from which population the laboratory or aviary stock originally derived. The Bleeding-heart Pigeon *(Gallicolumba luzonica),* for instance, is a well-known aviary species, most of the captive specimens having come from the Philippine island of Luzon. I recently found (Parkes, 1962) that the population of northern Luzon *(G. l. griseolateralis)* is separable on several characters from that of central and southern Luzon *(G. l. luzonica).* Examination of numerous aviary specimens in museum collections indicates that most, if not all, of the caged stock came from within the range of the subspecies *luzonica.* Generalizations about the behavior of living Bleeding-heart Pigeons based on aviary birds, therefore, apply to the populations of southern and central Luzon, and might not be valid for those of the north.

Among birds commonly kept in captivity are several belonging to genera which include confusingly similar species. Harrison (1957) published an account of the behavior of the Dark Fire Finch *(Lagonosticta rubricata).* Fortunately he kept a reference skin of one of his birds, and this now proved to be Jameson's Fire Finch *(L. rhodopareia)* rather than the species first named. Had this skin not been available for comparison with museum material, this error in the behavior literature might not have been detected (Harrison, 1963).

Plumage Succession and Age Characters

Two major subjects of investigation with museum skins are inextricably bound together, and can hardly be discussed separately. These are the study of the sequence of molts and plumages, and the determination of characters indicative of age. The latter subject, of course, is of great interest to workers in the field of wildlife management as well as to bird-banders, both groups wanting reliable external criteria by which to age the live birds they handle.

The first step in working out age characters, through the study of plumage succession, is to find the *youngest* specimens in the museum series. Museum skins of newly-hatched birds (or birds only a few days old) are not uncommon if the chicks are downy (Anseriformes, Galliformes, Falconiformes, Strigiformes, Charadriiformes, etc.), but relatively rare of passerines and other naked or sparsely-downed hatchlings. Of the latter, however, stub-tailed nestlings are frequently available. The critical point is that the true juvenal plumage, that which succeeds the natal down (if any), be identified as such, to act as the reference point for changes to later plumages. When the characters of the juvenal plumage (which may be rather short-lived) have been determined, the next step is to find, among the series of specimens, individuals in which the plumage now known to be juvenal, is being replaced by the next succeeding, or first basic plumage (variously "first winter," "second juvenal," "immature," etc. of earlier literature; see Humphrey and Parkes, 1959). This transition, as all later molts, is detected by finding incoming, partially-sheathed feathers among those of the previous generation. Individuals in which the molt had progressed further at the time of collection will illustrate progressive stages of this first prebasic molt (always identifiable as such as long as there are recognizable juvenal feathers left), until the characters of the fully-developed first basic plumage become completely evident. The same procedure is followed in determining the characteristics of whatever plumage succeeds the first basic in the species being studied; that is, the search for incoming new feathers among the (often somewhat worn or faded) older feathers of the first basic plumage, and the lining up of individuals showing progressive stages of this molt until no further molt can be detected (in the many species with a partial prealternate molt, only a portion of the first basic plumage is replaced). The same procedure is followed to determine the transition between each identifiable generation, until finally the plumage or plumages show no further significant change from cycle to cycle, and can be conveniently called "definitive" ("adult" in much of the literature, although some species are sexually mature, hence "adult," in pre-definitive plumages).

The series of specimens can now be arranged in order of relative age, from the newly-hatched chick to the definitive plumage or plumages (depending on whether the species has one, two, or rarely three plumages in each cycle). Note that I say *relative* age. Up to this point we have not paid any attention to any of the label data except sex (in order to keep the plumage sequences of sexually dimorphic species clear). We have ignored dates. We can now, with a certain amount of confidence, state that a given specimen represents a plumage stage younger (or older) than another, but we are not prepared to say how much older or younger, nor to give an estimate of the *absolute* age of the bird.

In the world as a whole, the reproductive period of birds varies in spectrum fashion from short, discrete breeding seasons in which the reproductive cycles of all individuals of the population are virtually synchronous (typical, among others, of many arctic birds and of certain colonial species elsewhere) to an apparent total lack of breeding "season," individuals being found in any stage of the reproductive cycle at any calendar date (22 of 60 equatorial cloud forest species; Miller, 1963). For those species with little or no population synchrony in reproduction, no deductions other than *relative* age of the various plumage stages can be made; such species, in museum series, can be identified by the wide scattering of label dates on birds of corresponding plumage stage (especially the very young birds).

On the other hand, population synchrony in breeding is suggested by close correspondence in label dates of young birds of similar degree of plumage development. In a sufficiently large sample, a rough estimate of the length of the breeding season can be determined by the extreme dates of very young or newly-hatched birds. This period will, of course, probably include specimens from later nestings in multiple-brooded species, but (again, with a large enough series) it may be possible to show that dates of young specimens of such species when graphed show two or more peaks. Once it has been shown that a degree of reproductive synchrony exists, and the range of variation of this synchrony determined (for example, hatchlings collected 1 June through 18 July; thus the known range of variation in this population is fifty days), it is possible to give not only relative age but an estimate of absolute age for a given specimen. A young bird at any stage can be aged by dating its hatching arbitrarily at the midpoint of the previously determined hatching season, and counting from that date. The possible error is half the number of days in the hatching season. In the example given above, a young bird collected 25 September will be three months ±25 days of age, 25 days being the extent of the hatching season on either side of 25 June, the midpoint. With this information, the degree of population synchrony of molt can be compared to that of breeding; in some species, for instance, individuals may be found in some stage of the first prebasic molt over a period longer than that corresponding to the range of variation of actual age, whereas other species seem to molt roughly simultaneously, even though individuals from a broad range of hatching dates are involved.

The periodical replacement of the feather coat is, of course, an important part of the biology of birds. The study of the sequence of molts and plumages has traditionally used museum specimens as its research materials. From our large sample of specimens we can deduce the duration of a period of molt for the population of birds being studied, and we can work out the sequence of molt for a hypothetical "typical" individual based on a composite of the individuals in our sample. It would, of course, be desirable to know, in addition, the duration of molt for a single individual, but this cannot be ascertained from museum skins except insofar as it can be no *longer* than the duration of molt in the population as a whole, and is probably substantially shorter. Duration of molt for an individual bird must be determined from the living bird, preferably a wild bird under natural condition. This has been done by several workers by repeated netting or trapping of banded individuals, but this must necessarily involve the assumption that repeated handling of the live bird has no traumatic effect which may alter in any way the normal molt sequence.

Reproduction and Development

Certain information about the reproductive cycle can be obtained from the simple examination of museum skins. We have already seen that hatching dates are readily ascertainable when the museum material contains very young specimens. A certain amount of information on post-hatching development of young birds is also easy to obtain from skins; in addition to plumage development *per se,* this might include loss of egg tooth, approximate date of fledging based on development of remiges, and time of attainment of adult proportions. In the absence of label notations about reproductive stage of adult birds, certain deductions can still be made; the incubation patch is often evident in museum skins, especially in certain groups such as Charadriiformes, Anseriformes, and Galliformes. The timing of "defeathering" and "refeathering" of the incubation patch can be worked out, as well as the relative role of the sexes in incubation (for an example, see Parkes, 1953). Evidence of incubation is also afforded in certain large birds, especially hawks, by excessive wear of feathers of the throat and upper breast where these rub against the edge of the nest while the bird is sitting on eggs (example, Carnegie Mus. No. 114049, *Buteo jamaicensis fuertesi,* 10 miles S. of Marathon, Texas, May 23, 1933).

Migration

Another major field of ornithological study in which the museum collection may play an important part is migration. The most obvious application of museum data to knowledge of migration is in the correlation of dates with presence of the species at a given location, in the absence of data on living birds from reliable observers. Although migration dates within North America are now based largely on field observations of living birds (as published in *Audubon Field Notes* and countless local journals), the status of North American migrants south of our borders is still known chiefly from museum specimens (see, for example, Eisenmann, 1955). In addition to the simple definition of the wintering area and migration routes of a species, museum specimens may be used in other ways in connection with migration studies. Engels (1962) used museum specimens of Bobolinks *(Dolichonyx oryzivorus)* to determine the latitudinal distribution of this transequatorial migrant between August and November, in working out the day-lengths experienced by the birds during this period.

As already mentioned, most of our knowledge about sequences of molts and plumages of birds comes from museum specimens. The chronological relationship between molt and migration is also to be learned from the study of museum collections. Some migratory species molt prior to migration, some along the way, and some not until the wintering grounds have been reached. Information of this sort may be used in ways not immediately apparent. For instance, Phillips and Parkes (1955) showed that the name *Tyrannula richardsonii* Swainson, long applied to the Western Wood Pewee, could not possibly have been based on an individual of that species. Baird, who was the first to use this name for a pewee, realized that the wing formula of Swainson's type specimen (from Saskatchewan) differed from that of any pewee and resembled that of a phoebe, but attributed this discrepancy to "incomplete growth during the moulting season." However, as we showed through examination of museum specimens, the wing molt of adults of the Western Wood Pewee (now *Contopus sordidulus)* takes place on the wintering grounds in South America between December and March, a fact unknown in Baird's time through lack of specimen material. Since, for various reasons, Swainson's type could not have been a *juvenile* wood pewee, the attribution of the non-pewee wing formula to "incomplete growth" is thus shown to be erroneous.

Having already deduced the plumage characteristic of various age classes from our initial study of the museum series, we can make certain secondary deductions, using these primary deductions as evidence. For example, a preponderance of specimens exhibiting the plumage characters of birds of the year from certain areas in winter, and of older birds from other areas, is strong evidence of some sort of differential migration of age classes in such a species. Howell (1953), through censusing museum collections, found that there is differential migration of the sexes in the Yellow-bellied Sapsucker *(Sphyrapicus varius),* as well as differences in extent of migration among the four subspecies. He presents some interesting conjectures as to the possibility of sex-linked multiple genetic factors affecting intensity of pigmentation and extent of migration, since there appears to be a correlation between distance of migration and degree of pigmentation, both as to sex and to population.

Behavior and Other Topics

Although the study of behavior is of necessity restricted to observations of living birds, the specialized structures utilized in displays can be studied in detail in museum specimens. Feathers so modified as to produce sounds in flight can seldom be well observed under field conditions, but I remember as a high school student attaching several of the narrow primaries of a Woodcock *(Philohela minor)* to a cork on the end of a string and whirling it around my head. To the amazement of my fellow-conspirators (the feathers were surreptitiously detached from a mounted bird in the biology lab), a distinct whistling noise was produced. There are, of course, many species of birds well known as museum specimens but virtually unknown as living organisms. The presence of ornamental plumes, modified flight feathers, bright color patches, etc. at least gives us hints as to the possible nature of courtship displays in such species.

As mentioned at the beginning of this paper, the museum collection represents the raw material from which our entire system of naming and classifying birds is derived. Once named and classified, the museum collection becomes the research tool of students of zoogeography and of avian evolution, whose findings may range from straightforward descriptions of things-as-they-are to the wildest conjectures about how-they-may-have-gotten-there.

The reader will, with this impetus, be able to think of many other ways in which the collection of bird skins housed in a museum can lead to additional knowledge about birds as living organisms.

Improving Specimen Labels

The usefulness of museum specimens is vastly increased if the collector will record, at the time of collection, as much information as he can to supplement the minimum of date, locality, and sex. Many of the important points with respect to label data were covered in a well-known paper by the late Josselyn Van Tyne (1952). He stressed the need for unequivocal clarity in the recording of locality and date, the importance of indicating the condition of gonads and degree of skull ossification as evidence to support the sex and age given, and the value of recording weights and perishable colors. "Other matters which should be recorded on the label are the details of physical condition (*i.e.,* degree of fatness, presence of brood patches or other evidences of breeding), readily identifiable stomach contents, and an indication of the habitat." (Van Tyne, 1952: 30.) To this list can be added such additional points as a notation when known families are collected ("mate of No. 3456, parent of No. 3457 and 3458"), notes on parasites, abnormalities or injuries, method of collecting if unusual (such as diving ducks caught in fishing nets at known depths, swifts taken in caves, migrants that hit buildings or TV towers, etc.), vocalizations *(Empidonax),* nest-type *(Collocalia;* see Sims, 1961, and Medway, 1962) and, especially, molt. Although, as mentioned above, most studies of molt are carried out by examining prepared specimens for incoming feathers, such feathers ("pinfeathers") at the growing stage are much easier to detect on the inside of the skin during preparation. If only a few new feathers are appearing, these may be lost during skinning or overlooked in later examination. The preparator's notation on the label such as "trace of molt on flanks" will be of great use in later studies.

Van Tyne mentioned the fact that all of this material *can* be written legibly, using both sides of a "standard 3- by 5/8-inch museum label," using an additional blank label to add data if necessary. However, there should be nothing sacred about either the size or the format of a museum label. Any institution fortunate enough to be receiving specimens from a collector who conscientiously records all of the kinds of information suggested above is ill-advised to force him to conform to a standard small label if a somewhat larger one will offer more flexibility. An institutional tradition which demands, for instance, that one entire side of the label be left blank except for the name of the institution and the scientific name of the bird, is sterile and needlessly confining.

Under the heading "hieroglyphics," Van Tyne stressed the need for legibility, but did not go into detail. I would suggest that *all* label data be *printed* (in so-called "manuscript writing") by the collector, rather than written in his usual handwriting. I have seen labels which conform rigidly to institutional requirements as to format, but written in handwriting usually thought of as typical of physician's prescriptions.

As an indication of the kind of information now being added to museum skins by modern collectors aware of the great importance of such data, I reproduce here (Figure 1) a typical label from one of E. T. Gilliard's recent expeditions for the American Museum of Natural History. I might suggest also that collectors and students who are not used to printing their labels try to emulate the legibility of data recorded by George M. Sutton.

The bulk of this paper suggests some of the information about living birds that can be deduced from museum skins bearing only minimal data. With the addition on the label of the kinds of facts suggested in the last few paragraphs, the museum collection becomes infinitely more useful. For example, among passerine birds whose first basic plumage cannot be distinguished from the definitive basic plumage, a notation about degree of skull ossification will enable young birds to be identified as such well after the completion of the first prebasic molt. In species which may not breed their first year but do return to the breeding grounds along with sexually mature birds, the combination of age as deduced from plumage characters and gonad condition as noted on labels may help to determine the minimum age of breeding. An abnormal internal condition (such as excessive infestation by parasites) noted on the label may explain what appears to be a long-delayed molt. In areas traversed by a migrant population while the resident population is already breeding, a label notation as to reproductive condition is vital if the characters of the resident population are to be correctly assessed (migrant individuals of the northern race of Yellow Warbler, *Dendroica petechia amnicola,* have been collected near Ithaca, New York, when nesting of the local race *D. p. aestiva* was well under way). Soft-part colors are now known to vary with age, sex, and season in many species, and can be correlated with other cyclic manifestations if noted on labels. And so on.

Conclusion

Although new species of birds are still trickling into museums yearly, and the flow of newly-described subspecies may seem (especially to the non-taxonomist) to be endless, systematics of birds has progressed to the point at which it is at least *conceivable* that all valid taxa may some day have been described.

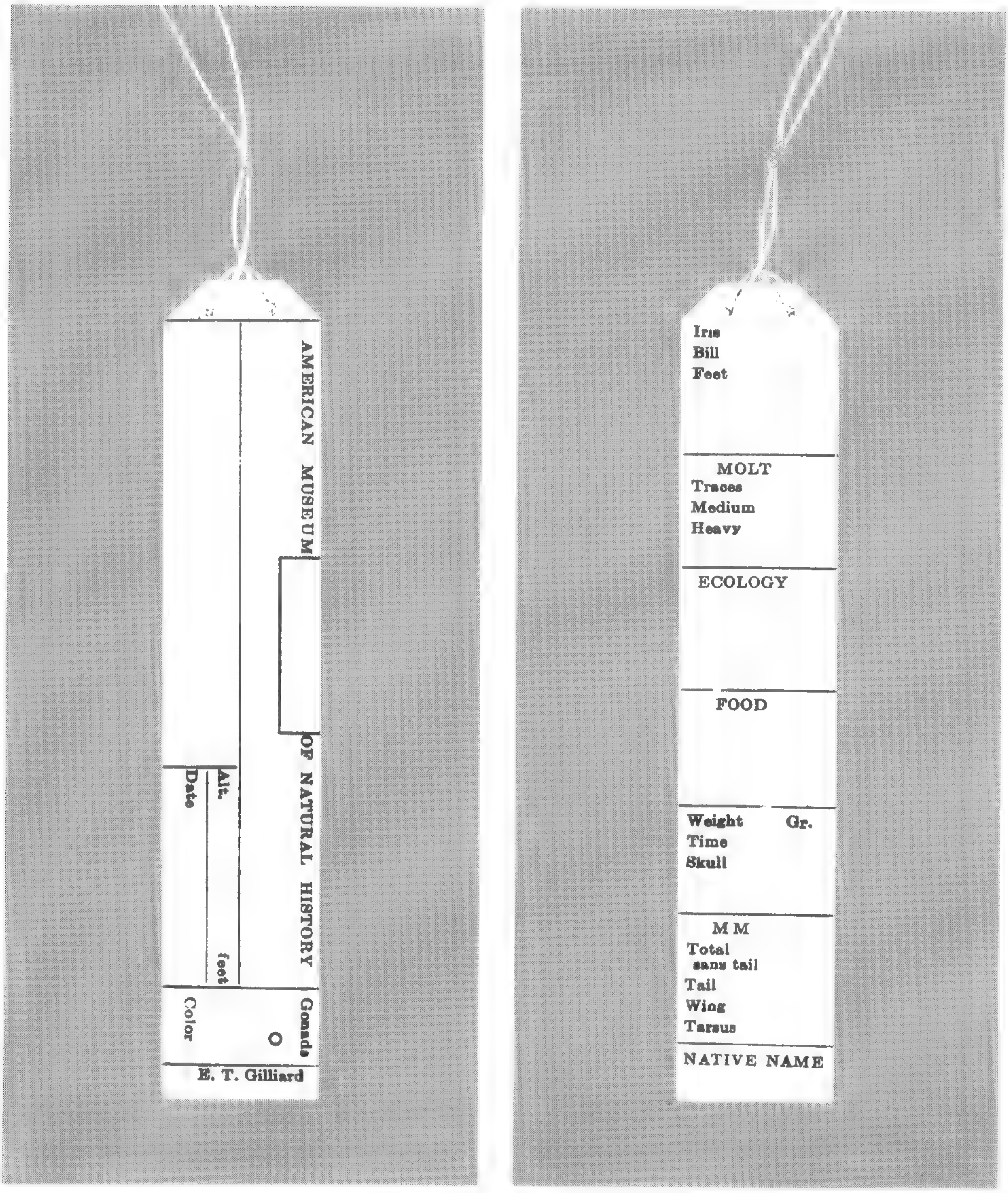


Figure 1. The type of label (both sides shown) used by E. Thomas Gilliard on one of his recent expeditions for the American Museum of Natural History.

That this will by no means call a halt to the usefulness of the museum collections should now be obvious, and, indeed, much additional museum material is needed of many of the best-known (in a taxonomic sense) species in order to understand fully such matters as molt and plumage sequences.

Acknowledgments

I am grateful to E. Thomas Gilliard for permission to reproduce one of his specimen labels, of his own design. This paper is an offshoot of a somewhat different one originally planned and outlined in collaboration with Philip S. Humphrey of the United States National Museum; much of the material on plumage sequence and age characters is derived from what had originally been intended as a joint paper, and I am grateful to Dr. Humphrey for his agreement to incorporate this material in the present paper. The cartoon was drawn by Clifford J. Morrow, Jr., Chief of Special Exhibits, Carnegie Museum.

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THE IMPORTANCE OF BIRDS IN THE ECOLOGY OF ARTHROPOD-BORNE ANIMAL VIRUSES

WILLIAM F. SCHERER

An arthropod-borne animal virus is a small intracellular parasite measuring 20-200 millicrons in diameter. In nature the virus (1) infects hemophagous ("blood-sucking") arthropods when they ingest it along with blood or tissue juices of animals, (2) multiplies in arthropod and vertebrate host tissues, and (3) is transmitted by bite to susceptible animals (see World Health Organization, 1961). These viruses, recently termed arboviruses, are composed mostly of protein, nucleic acid, and lipid and do not include viruses which are otherwise transmitted by arthropods—e.g., by contamination of mouth parts. The arthropods currently known to be involved in transmission of arboviruses are mosquitoes, ticks, certain flies, and possibly mites.

The Distribution and Number of Arboviruses

Arboviruses are distributed widely throughout the world and are important causes of human and animal diseases in both temperate and tropical climates. Among the major threats to the health of humans and horses are the arthropod-borne encephalitis viruses, which cause inflammation of the brain ("sleeping sickness") and death. In the United States, the viruses of Western encephalitis, Eastern encephalitis, and St. Louis encephalitis are frequent causes of human epidemics: Western and Eastern encephalitis viruses also cause horse epizootics. In Japan, there are several thousand human cases of Japanese encephalitis yearly; in South America, Venezuelan encephalitis causes frequent epidemics; and in Russia, various tick-borne encephalitis viruses cause considerable human disease. Death occurs in 10 to 50 per cent of encephalitis cases and often serious consequences, such as paralysis, remain after the acute phase of the disease.

Currently there are approximately 150 recognized animal arboviruses of which at least 50 cause disease in man, and five are of veterinary importance. In the Western Hemisphere, of the 68 known arboviruses, 10 cause human epidemics (Eastern, Western, Venezuelan, and St. Louis encephalitis, Mayaro, yellow fever, dengue II, Guaroa, Oropouche, and Junin) and five have produced epizootics in domestic animals (Eastern, Western, and Venezuelan encephalitis, blue- tongue and vesicular stomatitis). Human encephalitis, caused by up to six different arboviruses, occurs in at least 13 of the 24 countries in the Western Hemisphere extending from Canada to Argentina, and the failure to recognize the causes of this disease syndrome in certain other countries is

Figure 1 *(above)*. Site of a heron-egret colony in Sagiyama National Preserve near Tokyo, Japan.

Figure 2 *(below)*. Site of a heron-egret colony Shinhama Imperial Refuge near Tokyo, Japan.

undoubtedly related to the absence of virus research. Yellow fever continues to occur in an enzootic jungle cycle in tropical countries of Africa and the Western Hemisphere, and its geographic extension remains a threat to adjacent regions. In 1958, hemorrhagic fever, apparently mite-borne, rose to epidemic proportions in rural Argentina near Buenos Aires, and since a similar virus exists in Trinidad, the possibility must be considered that a more northern distribution of this disease will occur. At least 15 arboviruses produce mild to moderately severe febrile ("feverish") illness in man in 11 countries of the Western Hemisphere and many other arboviruses cause this type of disease in other parts of the world. Furthermore, it is probable that considerable human febrile disease in the tropics is caused by arboviruses. It also seems likely that there are arboviruses as yet undiscovered, and that the geographic distribution of many known arboviruses is wider than presently recognized. Thus, the significance of these viruses in human and animal health has yet to be fully evaluated.

Birds are known to be important in the natural maintenance and spread of certain arboviruses and are of suspected importance for others. Their possible functions fall into three categories: (1) as amplifiers, (2) as reservoirs, or (3) as transporters of virus. In general, the best evidence that birds function in one or more of these capacities exists for the encephalitis viruses. For certain other arboviruses, such as yellow fever, there is no convincing evidence incriminating birds in their ecology, and for a vast number of, as yet, inadequately studied arboviruses, there is essentially nothing known of their ecology, or as a matter of fact, of their importance as causes of human or animal disease.

Birds as Amplifier Hosts for Arboviruses

Birds can function as amplifier hosts for arboviruses when they occur *yearly* as large *numbers* of susceptibles and are *attractive to vector arthropods.* They then serve as hosts for virus reproduction following the bite of a transmitting arthropod, develop virus in their blood *(viremia)* for several days or at least for a sufficiently long period to infect other arthropods which ingest blood-containing virus. Usually such avian infections are not accompanied by manifest disease. Amplification occurs because an amplifier host can become infected by the bite of only one arthropod, whereas while viremic, it can infect hundreds to thousands of arthropods. Animals which can serve as effective amplifiers are usually those with large populations and rapid population turnovers. Unless the annual population of newly-born animals susceptible to virus infection is large, a host usually cannot be an effective amplifier. But with vertebrates, such as birds, rodents, and pigs in certain parts of the world, the density of infected arthropods, especially mosquitoes, can indeed be rapidly increased during the summer, and eventually produce enough infected arthropods to transmit virus to man.

It should be stressed that not all bird species of any one habitat function equally well for amplification of a particular arbovirus. For example, at two ardeid (heron-egret) colonies near Tokyo, Japan (Figures 1 and 2), infection with Japanese encephalitis virus was a regular summer phenomenon among nestlings during 1952-56 (Buescher et al., 1959). Avian infection demonstrable by recovery of virus from blood or appearance of antibody[1] in plasma was first

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[1] Antibodies are specific globulin proteins produced by lymphocytes and plasma cells of vertebrates in response to inoculation of various large molecular substances, usually proteins or polysaccharides (sugars). Virus infections cause production of antibodies which appear in blood and usually render the animal immune to subsequent infection by the same virus.

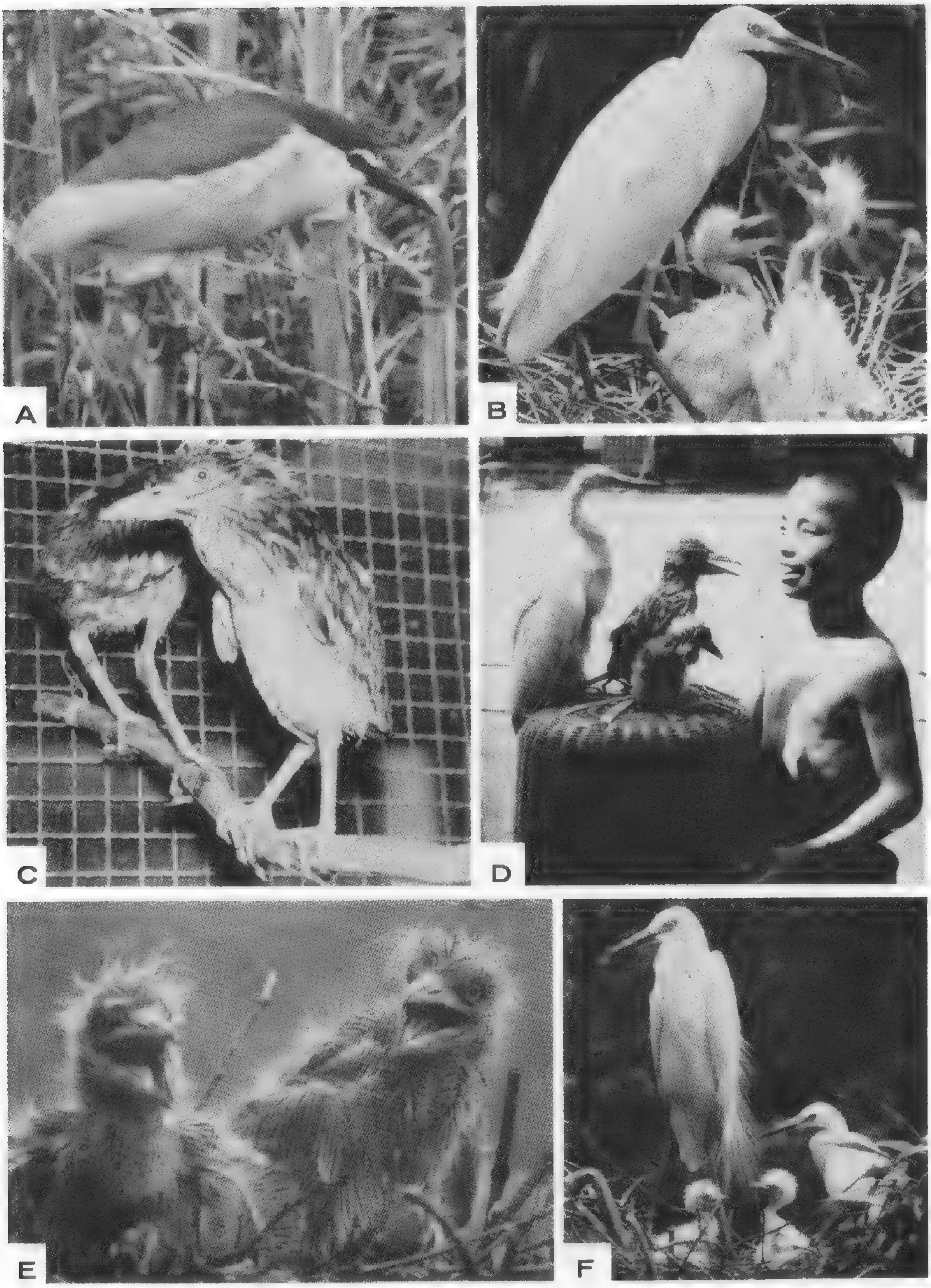

Figure 3. Herons and egrets in Japan. A, adult Black-crowned Night Heron. B, adult and nestling Little Egrets, approximately 15 days of age. C, juvenile Black-crowned Night Herons. D, juvenile Plumed Egret and young Black-crowned Night Herons. E, nestling Black-crowned Night Herons, approximately 10 days of age. F, Plumed Egrets and nestlings, approximately five days of age. (A, B, D, E, and F, photographs courtesy Tokutaro Tanaka, Kitaurawa, Japan; C, photograph U. S. Army. Reprinted from *American Journal of Tropical Medicine and Hygiene,* Vol. 8, 1959.)

found in late July and early August of each year and was, for practical purposes, coincident with the demonstration of virus in mosquitoes. Frequencies of avian infection during the period of virus dissemination (as measured by hemagglutination-inhibition antibody tests) ranged from 0.01 to 0.47, but were consistently greater in Black-crowned Night Herons *(Nycticorax nycticorax)* than in Little Egrets *(Egretta garzetta)* or Plumed Egrets *(Mesophoyx intermedia).* See Figure 3A through F. Moreover, except for Great Cormorants *(Phalacrocorax carbo),* no conclusive evidence for virus infection of other Japanese birds could be obtained, and while serologic survey of Japanese wild birds suggests wide-spread involvement with this virus (Hammon et al., 1958), the relative efficience of other bird species for dissemination of Japanese encephalitis virus remains uncertain.

Other phenomena are also important in the function of birds as amplifier hosts for arboviruses (Scherer et al., 1959). For example, maternally transferred, protective antibody[2] probably temporarily delays infection of nestlings. However, since this antibody disappears usually within several weeks of hatching, it seems unlikely that it significantly reduces the total seasonal amount of virus available in amplifier birds for infection of vector arthropods. Breeding habits of birds are important because, in the spread of virus, it is essential to have susceptible nestlings available at the time of year when vector arthropods occur.

Anatomical features also influence exposure of nestlings to mosquitoes. For example, the skin of a nestling is thin and soft and is usually covered only by loose fluffy down which is no impediment to biting mosquitoes or other arthropods. After the nestling period, however, feathers cover the skin (except on the legs and near the eyes) and thus offer some degree of protection from mosquito bites. The accessibility of nestlings to arthropods is governed in part by nest habitats and flight activities of the adults. In Japan, for example, it was found that both the incidence of ardeid infection and the density of transmitting mosquitoes were less in trees high above ground than at ground level, suggesting that the height of nests can limit spread of viruses among birds and arthropods. Also it was noted that adult Black-crowned Night Herons feeding at night left their nestlings alone in nests at a time when vector mosquito biting activity was greatest, whereas egrets feeding during the daytime tended to cover nestlings during mosquito attack.

Conceivably feeding habits of birds may be important in the spread of arboviruses. Again, to cite an example from studies in Japan, ardeid nestlings fed by regurgitation of fish (e.g., loaches), crustacea, and frogs from parents' stomachs or mouths became infested soon after hatching by endoparasites which burrowed deeply into the stomach wall and gained access to blood and tissues (Scherer et al., 1959). In doing so, such endoparasites certainly could inoculate virus or become infected with virus by injestion of viremic blood. While this facet of bird-virus ecology is purely speculative at the moment, it is a possible method of virus transmission and is worthy of further investigation.

Birds as Reservoirs for Arboviruses

The possible role of birds as reservoirs of arboviruses during winters in temperate zones, when adult vector arthropods are in small numbers or not actively biting animals and man, is a subject of much current speculation and investigation. One hypothesis is that avian hosts have chronic latent, long-

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[2] In birds, antibodies are transferred in yolk from female to young, but since these antibodies are passively acquired, they deteriorate within several weeks after hatching.

term infections which produce recurrent viremia and thus serve as a source of virus for vector arthropods. Studies of several hundred wild birds experimentally infected with Western encephalitis virus, have resulted in recovery of virus from one or more organs of ten birds at intervals of one to ten months following primary infection (Reeves et al., 1958, and pers. com., 1961). Western encephalitis virus has been recovered from bloods of a Brown-headed Cowbird *(Molothrus ater)* and a House Sparrow *(Passer domesticus)* 198 and 234 days after experimental infection (Reeves et al., 1958); St. Louis encephalitis virus 38 days after experimental infection of a Cowbird (Chamberlain et al., 1957); and Eastern encephalitis virus 14 days after infection of a Mourning Dove *(Zenaidura macroura)* (Karstad et al., 1959). However it still must be shown that birds with latent infection can serve as sources of virus for vector arthropods, and it must be learned whether physiologic changes in birds, concomitant with migration or reproduction, can induce reappearance of viremia from virus sequestered in tissues.

Birds as Transporters of Arboviruses

The possible role of migrating birds as transporters of arthropod-borne animal viruses is mostly speculative at the moment because very few specific studies of the subject have yet been done. Basis for this thesis resides mainly in the possibility that migration occurs either during the incubation period (viz., the time between inoculation of virus and onset of viremia) or during the period of active viremia. Since infection of most birds occurs without illness, their movements are probably not impeded while they are experiencing infection by an arbovirus, and they might very possibly disseminate virus on a local or long-distance basis. Also, transportation of virus might occur in arthropod ectoparasites riding with birds, and an intensive study of this possibility is now being carried out at the Naval Medical Research Unit in Egypt (H. Hoogstraal, pers. com., 1961). Conceivably long-distance dissemination of virus could occur either during long flights of single birds or by serial movements of virus by different birds which produce, at successive geographic locations, cycles of virus among local vector arthropods and vertebrates.

Studies of Japanese encephalitis virus in ardeids in Japan, for example, strongly suggest that flight activities are important in local dissemination of virus beyond heronries (Scherer et al., 1959). Local movements of susceptible breeding adults in search of food possibly result in transportation of virus in or out of colonies. When breeding ceases, mature ardeids move permanently from colonies. Since this movement occurs during August-October when birds are being extensively infected, it seems highly probable that viremic ardeids transfer Japanese encephalitis virus to various parts of the plain surrounding Tokyo or to more distant regions to the south. Whether virus returns to the Tokyo area each spring as birds migrate north has not yet been resolved.

Similar hypotheses concerning migrating birds as transporters of arboviruses have resulted from bird-virus studies, carried out in the Western Hemisphere, involving Eastern, Western, and St. Louis encephalitis viruses. During the 1959 epidemic of Eastern encephalitis in man along the eastern coast of the United States, considerable infection of birds was detected (Hayes et al., 1962), and each year, during the summer occurrence of Western encephalitis in California, bird infections occur (Reeves and Hammon, 1962). However, most studies of birds as virus vehicles are only in the embryonic stages at this time, and much more knowledge is needed on (1) birds as hosts for arthropod-borne viruses, (2) the biology of birds in relation to this problem, and (3) ecto-parasite infestations of birds. It seems likely that indisputable evidence incriminating birds as transporters of arboviruses will require collaborative investigations by workers at different points along migration routes functioning as teams of ornithologists, zoologists, entomologists, and virologists.

Currently an informal American Committee on Arthropod-Borne Viruses supported by the Rockefeller Foundation is sponsoring activity of a Subcommittee on the Relation of Birds to Arthropod-Borne Viruses, composed of David E. Davis, Joseph J. Hickey, Robert J. Newman, Maurice W. Provost, and Donald D. Stamm, Chairman (USPHS, Communicable Disease Center, Atlanta 22, Georgia). The Subcommittee's initial objectives are to improve the exchange of information and the degrees of cooperation between ornithologists, virologists, and other biologists, in hopes that such efforts will accelerate acquisition of the knowledge needed to understand fully the importance of birds in the ecology of encephalitis and other arthropod-borne animal viruses. Persons interested in participating in research related to these problems are urged to contact Dr. Stamm.

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THE CADENCE OF BIRD SONG

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Bird songs are recognized by pitch, sequence of notes, quality, volume, and rhythm. An additional feature, unconsciously recognized but not particularly noticed, is the cadence of delivery. The song of the Red-eyed Vireo *(Vireo olivaceus)* is delivered in short phrases a second or so apart, the song of the Wood Thrush *(Hylocichla mustelina)* in phrases at a more leisurely rate, four or five seconds apart. If the singing rates of these two species were reversed, one would realize it immediately.

Information on the timing of song has been published for many species, including some of those considered here. However, I have found no papers specifically emphasizing delivery rate of song as a separate phase of study.

The present work, started in 1949, discusses the rate of singing for more than 1,500 individual birds representing 52 New World species. Methods are described, results are presented, and the possible value of this information is considered.

Definition of Cadence and Methods of Study

The cadence of delivery of a song is the average length of time from the first note of a song unit to the first note of the succeeding unit throughout the whole song performance. The period timed includes that in which the song unit is heard *and the silent period between song units.* This was the system used by Borror (1956) when studying Carolina Wrens.

The song unit for the Wood Thrush is its song *phrase;* for the Indigo Bunting *(Passerina cyanea),* the *group* of paired notes; and for the Ovenbird *(Seiurus aurocapillus),* its "teacher" song.

Cadence was obtained while listening to the song in the field. As the first note of each unit was heard, the position of a sweep second hand of a wrist watch was written down. For example, while listening to the daytime song of an Eastern Wood Pewee *(Contopus virens),* I wrote the following numbers: 21, 30, 42, 55, 6, 17, 23, 32, 40, 49, 59, 10, 15, 28, 34, 44, 55. By subtracting each number from the following number, the time span for each of the 16 intervals was: 9, 12, 13, 11, 11, 6, 9, 8, 9, 10, 11, 5, 13, 6, 10, 11. These add up to 154 which, divided by 16, gives an average 9.6 seconds, and is the *cadence of delivery* of this particular song.

To obtain the cadence value for a species, individual cadence values were averaged and a standard deviation was determined to represent the variation between the individuals timed. The coefficient of variability (standard deviation divided by cadence) will be referred to occasionally in the text.

A second method of determining cadence was used for song units of rapid delivery—those faster than every two seconds. For the Red-eyed Vireo I counted the number of phrases delivered in half a minute or minute and divided this number into the time elapsed. If the bird sang 48 phrases in 60 seconds, the cadence was 1.25 seconds (60 divided by 48).

I determined cadence when the bird was in *relatively continuous* song. If the song units were at 6 to 8-second intervals and the bird stopped singing for a half minute or so or flew to another tree and continued singing, the silent periods were not considered in the calculations. Information published on song delivery often gives the number of songs per hour or per day and does not take into account the periods of silence between a series of song performances. A cadence calculated on this basis would indicate fewer song units and a larger cadence value (longer time between song units).

Many factors influence the amount or rate of singing. Thorpe (1961) discussed some of these factors which include time of day, time of year or of life cycle, temperature, humidity, rain, cloud cover or sunshine intensity, period of molt, whether or not the bird was paired, the presence or absence of one of the same or another species near by, whether or not the bird was on its territory, and whether or not it was feeding.

This is an imposing list, but results are given just as they were obtained. Except for the caprimulgids and the Wood Pewee's twilight song, the timing was done during morning daylight hours in April and May.

I timed bird songs in each of the East Coast States but most of my records are from New Jersey south. Originally the data were kept by states, but when no marked differences were found, the figures for all locations were pooled. As far as is known, all the songs were those of male birds. Unless otherwise stated, the song timed for each species was the generally-recognized territory or primary song. All timing information, unless otherwise cited, was obtained by the writer.

Results of the Study

A summary of the results for 52 species is given in Table 1. The average speed of delivery ranged from 1.1 seconds for the Whip-poor-will to 21.2 for the Ovenbird. Each cadence value is not discussed individually, but various cadences are cited to demonstrate the principal findings.

The Bobwhite's call was timed in several states, with 46 individuals averaging 12.5 seconds between "bobs." Although there were no consistent differences due to location, the state averages were calculated as follows: Pennsylvania, 12.8; Maryland, 10.5; Delaware, 11.7; Virginia, 11.6; North Carolina, 13.6; South Carolina, 12.4; Georgia, 12.8. Ranging farther afield, the cadences of four Bobwhites timed in Haiti averaged approximately 13 seconds. This species has been a resident of Haiti for more than a century. Although I had no reason to expect a change in singing speed, the fact that they sang at the same rate as the mainland birds gives evidence of an inherent rhythm in song delivery.

The commonly-recognized difference between cadences of the Whip-poor-will and the slower-singing Chuck-will's-widow is brought out in their cadence values of 1.1 and 2.6 seconds, respectively. In early reference to singing rate, Matthews (1904) gave one call per second for the Whip-poor-will. The Chuck-will's-widow cadence in Table 1 ranged from 1.9 to 3.8 seconds and this is close to the figure reported by Harper (1938)—2.1 to 3.7 seconds. In addition, he noted a change in the singing rate with the temperature—a cadence of 3.7 seconds at 60°F and 2.7 seconds at 76°.

TABLE 1

Cadence of Song-Delivery of 52 Species of Birds

Species	*Number of individuals*	*Cadence in seconds*	*Standard deviation in seconds*
Bobwhite *(Colinus virginianus)*	46	12.5	1.7
Mourning Dove *(Zenaidura macroura)*	34	12.9	1.9
Chuck-will's-widow *(Caprimulgus carolinensis)*	15	2.6	0.7
Whip-poor-will *(C. vociferus)*	10	1.1	0.1
Eastern Phoebe *(Sayornis phoebe)*	9	2.3	0.5
Traill's Flycatcher *(Empidonax trailii)*	7	4.2	1.0
Eastern Wood Pewee *(Contopus virens)*, daytime	45	8.2	2.1
Eastern Wood Pewee, twilight	7 (of 45)	2.3	0.5
Horned Lark *(Eremophila alpestris)*	15	5.7	1.2
Tufted Titmouse *(Parus bicolor)*	45	4.1	1.2
House Wren *(Troglodytes aedon)*	32	6.0	1.0
Winter Wren *(T. troglodytes)*	6	11.6	0.4
Carolina Wren *(Thryothorus ludovicianus)*	51	5.7	1.0
Long-billed Marsh Wren *(Telmatodytes palustris)*	17	5.1	1.0
Wood Thrush *(Hylocichla mustelina)*	85	4.6	1.0
Hermit Thrush *(H. guttata)*	13	5.3	1.3
Swainson's Thrush *(H. ustulata)*	16	5.8	0.8
Veery *(H. fuscescens)*	11	6.4	1.7
White-eyed Vireo *(Vireo griseus)*	21	5.1	1.1
Yellow-throated Vireo *(V. flavifrons)*	26	3.0	0.6
Solitary Vireo *(V. solitarius)*	8	2.5	0.3
Red-eyed Vireo *(V. olivaceus)*	121	1.3	0.3
Warbling Vireo *(V. gilvus)*	13	9.4	1.1
Yellow Warbler *(Dendroica petechia)*	28	11.2	2.4
Black-throated Blue Warbler *(D. caerulescens)*	8	10.7	2.5
Black-throated Green Warbler *(D. virens)*	14	11.0	2.5
Blackpoll Warbler *(D. striata)*	11	13.7	2.3
Pine Warbler *(D. pinus)*	15	10.5	2.3
Prairie Warbler *(D. discolor)*	20	12.9	3.3

TABLE 1 (Cont.)

Cadence of Song-Delivery of 52 Species of Birds

Species	*Number of individuals*	*Cadence in seconds*	*Standard deviation in seconds*
Ovenbird *(Seiurus aurocapillus)*	30	21.2	4.0
Northern Waterthrush *(S. noveboracensis)*	7	14.2	2.2
Louisiana Waterthrush *(S. motacilla)*	11	13.8	4.4
Yellowthroat *(Geothlypis trichas)*	44	11.9	1.7
Hooded Warbler *(Wilsonia citrina)*	6	9.8	1.9
American Redstart *(Setophaga ruticilla)*	30	8.5	2.3
Eastern Meadowlark *(Sturnella magna)*	40	7.5	1.9
Cardinal *(Richmondena cardinalis)*	70	8.7	1.4
Rose-breasted Grosbeak *(Pheucticus ludovicianus)*	7	12.1	1.3
Blue Grosbeak *(Guiraca caerulea)*	28	11.4	1.6
Indigo Bunting *(Passerina cyanea)*	76	11.1	1.6
Painted Bunting *(P. ciris)*	13	8.9	2.1
Purple Finch *(Carpodacus purpureus)*	7	7.3	1.0
Rufous-sided Towee *(Pipilo erythrophthalmus)*	66	6.3	1.0
Grasshopper Sparrow *(Ammodramus savannarum)*	19	11.1	1.4
Henslow's Sparrow *(Passerherbulus henslowii)*	12	4.7	1.5
Vesper Sparrow *(Pooecetes gramineus)*	35	11.5	2.2
Bachman's Sparrow *(Aimophila aestivalis)*	14	9.3	1.6
Slate-colored Junco *(Junco hyemalis)*	9	5.2	0.5
Chipping Sparrow *(Spizella passerina)*	52	9.4	1.8
Field Sparrow *(S. pusilla)*	50	13.3	1.8
White-throated Sparrow *(Zonotrichia albicollis)*	18	8.7	1.6
Swamp Sparrow *(Melospiza georgiana)*	24	13.4	2.0
Song Sparrow *(M. melodia)*	127	11.8	1.2

Three flycatchers, the Eastern Phoebe, Traill's Flycatcher, and Eastern Wood Pewee, had cadence values of 2.3, 4.2, and 8.2 seconds, respectively. In the same relationship the coefficients of variability of the same species were 22.7, 23.8, and 25.6. The daytime songs of the Wood Pewee, reported in Table 1, had essentially the same cadence as those studied by Craig (1943) which ranged from about 7 to 10 seconds. The rapid rate of singing phrases every 2 or 3 seconds that he reported for the predawn song also coincides well with my second cadence value of 2.3 seconds. The song of the Phoebe not only showed the same cadence as the twilight song of the Wood Pewee but also the same standard deviation. Is there any ancestral significance here? Traill's Flycatchers, where local populations sang the "fitz-bew" song, had a cadence of 4.2 seconds. No "fee-bee-o" birds were heard locally, but one which was timed near Rickett's Glen, Pennsylvania, sang somewhat slower at a cadence of 5.8 seconds. Perhaps the tape recordings made by Stein (1958) will show a difference in cadence between the two populations.

The song of the Horned Lark, given only during the "stationary-wing" portion of the flight, had a cadence of 5.7 seconds. This cadence could have been determined by sight alone, by measuring the time from the first moment of stationary-wing position.

Of the four wrens, the House and Carolina were closest in cadence values at 6.0 and 5.7 seconds. The Long-billed Marsh Wren was slightly faster at 5.1 seconds and the Winter Wren the slowest at 11.6 seconds. The latter had a standard deviation of only 0.4 second or a coefficient of variability of 3.4 per cent. Possibly the uniformity of the six Winter Wrens, all timed at Slide Mountain, New York, may be due, in part, to close relationship of these individuals. Borror (1956), who timed Carolina Wrens in Ohio, Florida, and other states, found some differences in each location. The average cadence of all the birds he timed was 5.25 seconds, not greatly different from the 5.7 seconds average in Table 1.

Wood Thrush

Wood Thrush songs had a cadence of 4.6 seconds for 85 individuals timed; Hermit Thrush, 5.3 seconds; Swainson's Thrush, slightly slower, 5.8 seconds; the Veery, 2 seconds slower than the Wood Thrush, 6.5 seconds. Unfortunately, only one Bicknell's Gray-cheeked Thrush *(Hylocichla minima bicknelli)* was timed. Its cadence was 4.9 seconds. White (1893) reported the Olive-backed Thrush (=Swainson's Thrush) as singing "with extreme regularity," with a cadence of 6.3 seconds, not far from the 5.8 seconds from 16 individuals in Table 1 and well within the range of the standard deviation—0.8 second.

Kelso (1935) gave the Hermit Thrush song a cadence value of 5.3 seconds, exactly the same as the value in Table 1 from 13 individuals.

Five of the vireos which occur in eastern United States were timed with these resulting differences: the Red-eyed Vireo was the fastest with a cadence of 1.3 seconds and the Warbling Vireo slowest—9.4 seconds. Two other vireos, the Black-whiskered *(Vireo altiloquus)*, six birds, and Latimer's *(V. latimeri)*, eight birds, timed in Puerto Rico, fall in line with the mainland birds, showing cadences of 2.6 and 3.7 seconds, respectively. No opportunity has yet been found to time the Black-whiskered Vireo in Florida. When the cadences of all species of vireos in this country have been determined, it may prove useful to incorporate such information in standard field guides.

Most of the warblers timed had cadence values from 10 to 14 seconds, except the Ovenbird with 21.2 seconds. Similar values for the last were shown by Hann (1937)—23.5 seconds, and Nice (1931)—from 17 to 32 seconds. The Ovenbird sings with a regularity not very different from faster singing birds, and its coefficient of variability, 19.3 per cent from 30 individuals, was not much greater than the average for all species, 18.8 per cent.

For the warblers, the fastest cadence was that of the American Redstart—8.5 seconds. Its high deviation, 27 per cent, reflected a large difference between individuals timed. Possibly my records included the faster, early-morning song, described by Hartshorne (1956). I kept no record of the nature of the song phrases themselves—whether they were two different alternating phrases or one phrase repeated. Some of the birds I timed may have been migrants and others residents.

Meadowlarks averaged 7.5 seconds in cadence and their comparatively large standard deviation, 1.9 seconds with a 25 per cent coefficient of variability, reflected a considerable difference between individuals. Lanyon (1957), although he gave no cadence values for meadowlarks, noted that the Eastern Meadowlark *(Sturnella magna)* has more variety in its song performance than the Western Meadowlark *(S. neglecta)*. During the 14 years covered by my present work, two meadowlarks—found alone on two separate occasions—were heard singing the *neglecta* type of song. One, in New Jersey, sang at a cadence of 12.5 seconds; the other, in Pennsylvania, at a cadence of 13.1 seconds. Both were well outside the cadence typical of Eastern Meadowlarks. Neither bird was collected, but, since Lanyon has shown that the primary song is principally learned and since there was no resident population of Western Meadowlarks in the vicinity, it is likely that these two birds were of the western species. It would be of interest to know what difference occurs when the two species are sympatric. Comparison can be made by using Lanyon's tape recordings and by making new observations.

Although a marked uniformity of cadence was to be expected in songs of rapid delivery, such as those of the Whip-poor-will and Red-eyed Vireo, it was not anticipated in the songs of species which sing more slowly. Indigo Buntings averaged 11.1 seconds and several individuals of this species were quite uniform with one sequence showing 10, 10, 10, 9, 9, 9, 9, 9, 9, 9, 10, 10, 10, and 9 seconds between successive first notes. Painted Buntings, timed in South Carolina, were faster than the Indigo with an average cadence of 8.9 seconds.

Blue Grosbeaks averaged 11.4 seconds; Rose-breasted, 12.1 seconds. The Cardinal was faster — 8.7 seconds. Rufous-sided Towhees had an average cadence of 6.3 seconds. Some individuals were fairly even: one sang a series of phrases at intervals of 7, 5, 6, 5, 5, 6, 5, 7, 7 seconds; another showed intervals of 6, 6, 6, 5, 5, 6, 5, 7, 5, 6.

Cadences were timed in less than a third of the resident and transient sparrows. The Grasshopper, Vesper, Field, Swamp, and Song Sparrows were similar with cadences between 11 and 13 seconds; the Chipping Sparrow slightly faster at 9.4 seconds; the Bachman's and White-throated, 9.3 and 8.7 seconds, respectively; and the Henslow's was fastest at 5.2 seconds. One Field Sparrow began all but one of 13 consecutive phrases at 10-second intervals. Slate-colored Junco "trills" at a cadence of 5.2 seconds were heard in late May on their breeding grounds in the Catskills of southeastern New York.

The average cadence of the "grasshopper" song of 19 Grasshopper Sparrows was 11.1 seconds. In southwestern Puerto Rico, a resident Grasshopper

Sparrow sang only a little slower—12.1 seconds. In a study of the same song of this species, Smith (1959) reported 220 songs in one hour as the maximum speed of delivery. This amounts to a cadence of 16.4 seconds. Although he gives no information on the total time the bird was away from its singing perches (not singing), the actual cadence must have been faster.

In computing the actual rate of singing, the timing of individual song units removes the uncertainty which occurs when only the number of songs per hour is used. I suggest individual timing as a standard method for determining cadence.

Discussion

Although I have emphasized the cadence value for species, I found significant differences both among individuals of a species and among the song performances of an individual bird at various times. The cadence of Field Sparrows averaged 13.3 seconds, but one individual sang at a rate of 10.1 seconds. Song Sparrows averaged 11.8 seconds, but two individuals averaged 9.9 and 13.0 seconds, respectively. For the Song Sparrow, Nice (1943) timed a number of series which (averaged from her data which gave both song and silent interval lengths) were from about 6.5 to 11 or 12 seconds in cadence.

Variations in the cadence of an individual bird may be affected by numerous factors. Without attempting to name the factors causing the differences, I am giving here the variations in cadence of an individual Song Sparrow near my home in New Jersey. Between 4 April and 1 August 1952, I timed 37 performances. The bird's cadence ranged from 8.7 to 15.7 seconds; 78 per cent were from 10 to 13 seconds; the average was 11.5 seconds, close to the 11.8 seconds for the cadence of 127 Song Sparrows in Table 1.

Three species—the Mourning Dove, Tufted Titmouse, Purple Finch—are included in Table 1 but not discussed because I have no data on closely-related species for comparison. Only cursory mention is made here of other species although comparisons might be developed. It is my principal purpose in this paper to open up and encourage the study of cadence by giving methods and examples rather than drawing conclusions.

Although the slowest singer in Table 1 is the Ovenbird, the regularity of which was surprising, the American Bittern *(Botaurus lentiginosus)* was the "champion of leisurely singing." Ten performances (groups of "pumps") at intervals of 50, 50, 45, 60, 55, 59, 60, 60, 54 seconds made a cadence average of 54 seconds. The 5 to 7 pumps in each song were almost exactly at one-second intervals.

There is no all-inclusive rule as to how many songs or song units must be timed to determine the average cadence of a bird. Eleven songs should be enough for a bird singing at a 5-second rate; six songs for one singing at a 10-second rate. More examples were usually used, but as the series were examined, there seemed to be no advantage in long series. With few exceptions, when the singing was in a long, continuous series, the rate did not vary measurably. One exception was the Chuck-will's-widow which, during the breeding season, may greatly accelerate its song. However, as was pointed out by Thorpe (1961: 44): "It is a characteristic of the territorial singing of birds that it proceeds for long periods at very regular intervals, the utterances seeming relatively independent of external stimulation."

From the practical standpoint, timing first notes from 11 songs results in 10 intervals which are easy to average. Regardless of the number of songs timed, the important factors are: (1) using a portion of the performance when the bird is in *relatively continuous song* and (2) recording each *song unit interval* rather than counting the number of units in an hour.

During this study, with few exceptions, the length of the song units and the silent periods between the song units were not kept separately as was done by Hartshorne (1956, 1958). Thus I have no comment on his thesis of song complexity, speed of delivery, and "monotony threshold."

Although only some of the cadence values in Table 1 have been compared with published references to the same species, I do not imply that my data on the others are unique. Many cadence references were found but not included in this paper.

Because of the factors which influence cadence, some may question the assigning of a cadence value from an essentially random collection of timings. It might be better to select a time in the life cycle—i.e., the courtship period—in studying the cadence of a particular genus. However, we must wait until we have more cadence values taken specifically in relation to the life cycle, temperature, time of day, etc. before we can find out whether some are more "species specific" than others. The example, given above, of the Song Sparrow, timed from April through July, showed that over 75 per cent of its singing was within the range of the average cadence of 121 random birds.

There is no rigid rule for the number of individuals necessary to find the normal cadence for a species. Ten birds are certainly adequate: only five may give a value which will include most of those timed later. The cadence for the first ten, second ten, etc. of the 121 Red-eyed Vireo songs showed little difference in the average cadence of each group. Large numbers might be desirable in studying the cadence of a geographic population within a species. I do not feel that large numbers are necessary in determining the cadence of a species. Normal variations will occur and be expressed by the standard deviation.

The choice of species in Table 1 has no significance except that they all had songs delivered in separable units, easy to time. The Robin *(Turdus migratorius)*, Catbird *(Dumetella carolinensis)*, and Starling *(Sturnus vulgaris)* were omitted because their songs have less distinct breaks or units.

The species presented, except for the Bobwhite, Mourning Dove, and two caprimulgids, give a cross section of the Passeriformes and illustrate various features of cadence study.

Some may question the accuracy of timing with such simple equipment—a wrist watch with a sweep second hand, a pencil, and paper—when electronic equipment is now available. It is true that electronic equipment would give the individual intervals to a fraction of a second, but, if one times from the beginning of the initial song unit to that of the final song unit and divides by the number of units, the *average* would be the same.

Bobwhite

Individual unit timing is important for comparative study. Also the recording of the individual records on paper is more dependable than mental records. Time spent in the field is the same since the first and last songs must be noted. Additional accuracy may be obtained from songs recorded on sound tape. One disadvantage to this is that the songs may not be of relatively continuous singing and periods of silence would lengthen the average cadence. Unedited tape, accompanied by field notes concerning the bird's activities, could be useful. The challenge now is to obtain new data from the field or from tape recordings on species throughout the world.

In addition to its use in field guides, life history studies, and taxonomic work, cadences may aid in identifying individual birds. Even though two birds are exactly alike and their songs are not distinguishable, their cadence may be different enough to identify each.

It is hoped that this description of song cadence will encourage the collection of cadences for all species — or for individuals within those species whose songs are given in a rhythmic manner.

Summary

In this paper are presented the results of timing the rate of song delivery of more than 1,500 individual birds of 52 species, mostly in the order Passeriformes. Cadence of song delivery is defined as the average time from the first note of the song unit to the first note of the succeeding unit when the bird is in relatively continuous, uninterrupted song. For a given performance, this is determined by writing down the position of a sweep second hand of a watch, as each "first note" is heard. Values for a number of individuals of a species are averaged to obtain the cadence for the species. This number is presented along with its standard deviation. It is recommended that the individual song-unit timing be used rather than counting number of songs per hour. Tape recordings of bird songs are suggested for additional information on cadence.

Birds timed were from the Atlantic Coast States. Altogether from 6 to 127 individuals of each species were timed. Those studied had songs with readily separable units (phrases, groups, etc.).

Results confirmed, and supplied numerical evidence, that the species studied have inherent rates of song delivery. Within certain limits, these rates are followed by all individuals of each species.

With added knowledge of this interesting feature of a species' song performance, simply determined and expressable as a number, the following uses of cadence values are suggested: (1) Listing cadence in standard field guides, (2) correlation of cadence and environmental factors, (3) incorporation in life history studies, (4) investigation of cadence as a factor in testing the validity of current taxonomic relationship, and (5) a possible aid in identifying individual birds among a study group in which cadence differences have been confirmed.

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