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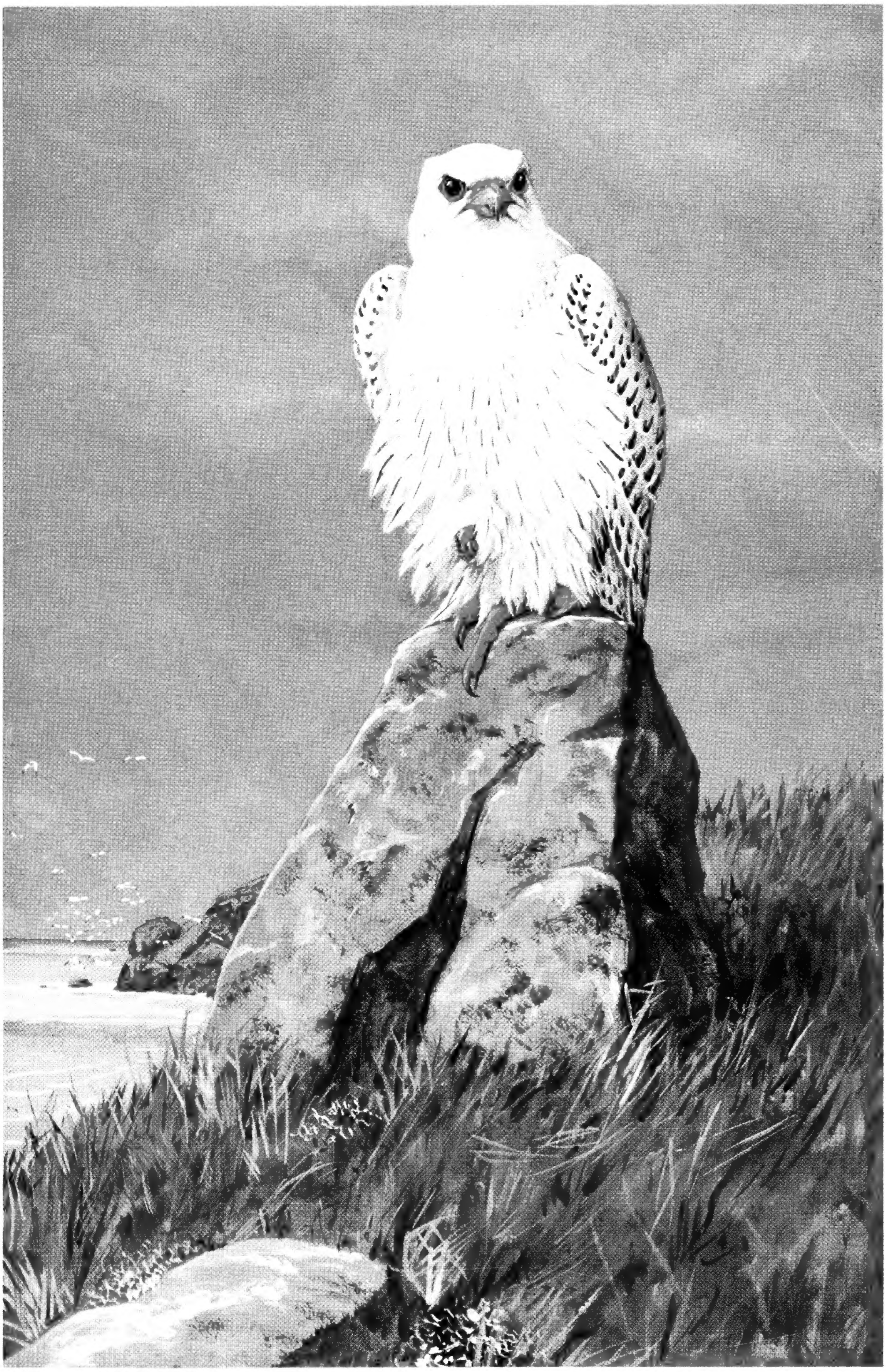

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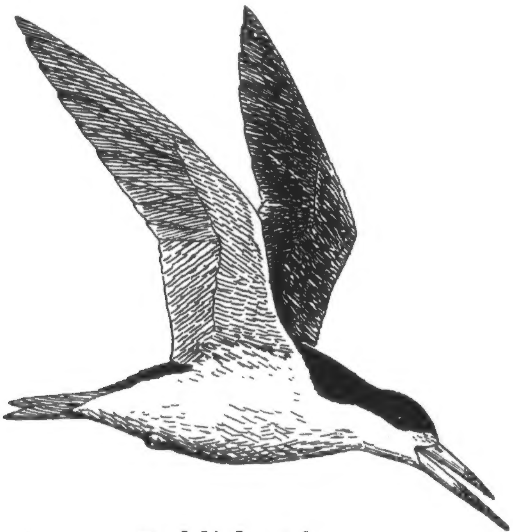

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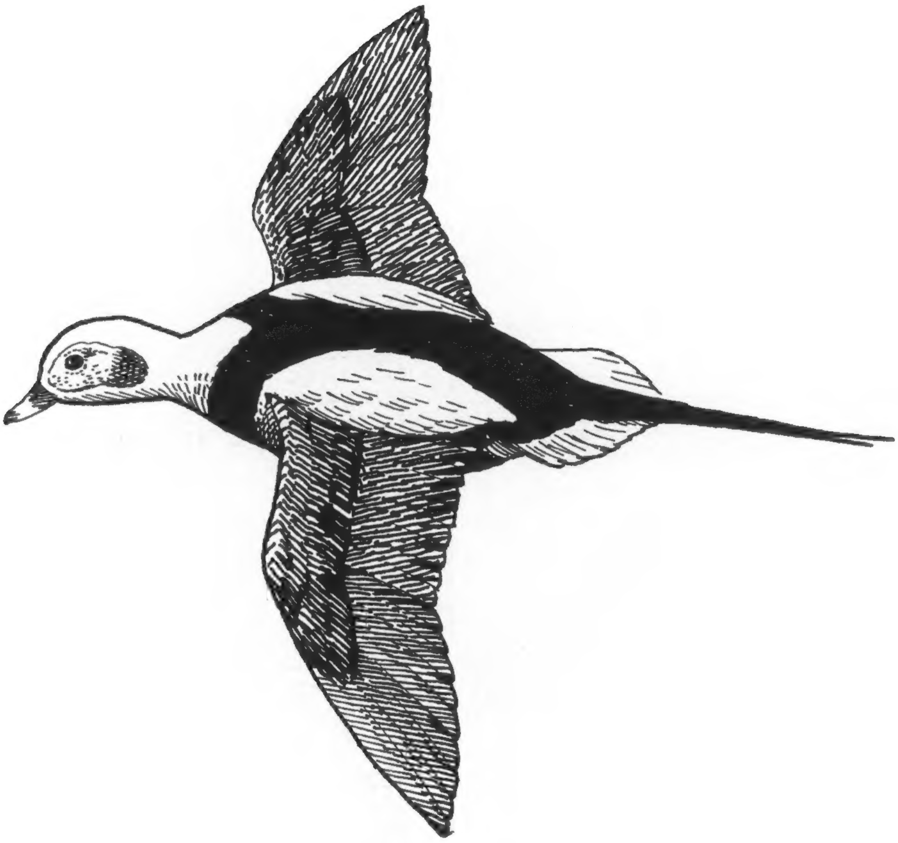

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Male Franklin's Grouse in courtship display. Based on a single frame of motion-picture film. Painting by John A. Crosby.

THE COURTSHIP AND TERRITORIAL BEHAVIOR OF FRANKLIN'S RACE OF THE SPRUCE GROUSE

S. D. MacDonald

Photographs by the author

The courtship displays of male grouse are, in most cases, spectacular performances, and the displays of each species differ. Visual effects combine with vocal and mechanical sounds, transforming the drab, cryptically colored male into a conspicuous creature of surprising beauty. Special arrangements of certain feather groups and special movements which throw into prominence the brightly or contrastingly colored areas make the displaying male appear unrelated to the original somber bird. In my observations of the courtship displays of the Spruce Grouse (*Canachites canadensis*) I was able to get details of an aerial display which was first noted by James Grant in the Trinity Valley of southeastern British Columbia and, to my knowledge, has not been previously published.

The Spruce Grouse occurs in coniferous woodland from about treeline in Canada and Alaska south to Oregon, western Montana, northwestern Wyoming, northern Minnesota, Michigan, northern New York, northern Vermont, northern New Hampshire, and Maine (Godfrey, 1967). In spite of its wide distribution, relatively few people have encountered the Spruce Grouse since it is confined to undisturbed forest areas and lacks vocalizations and conspicuous advertising displays, and even fewer have seen its courtship display in spring.

My observations on the spring displays of this Spruce Grouse were made during the months of May and the first two weeks of June in 1963-1967 at the R. B. Miller Biological Station in the Highwood Range of the Rocky Mountains, 21 miles west of Turner Valley, in southwestern Alberta, Canada. The population of Spruce Grouse in this part of the country belongs to the race *C. c. franklinii* which I will refer to henceforth in this paper as Franklin's Grouse.

Habitat

The habitat of Franklin's Grouse in the vicinity of the Biological Station is on the lower slopes of the foothills, at an elevation of about 5,400 feet. In this area (Figure 1) thick stands of lodgepole pine (*Pinus contorta*) of almost equal age have sprung up following a series of fires in the late 1930's. The dense growth of the pines is broken only by clumps of trembling aspen

Figure 1. The study area. In the background, immediately below the snowy slopes is the thick forest of lodgepole pine occupied by Franklin's Grouse. This area is on the lower east slopes of the Highwood Range of the Rocky Mountains in southwestern Alberta, Canada, and is part of the Bow River Forest Preserve. The forestry station buildings are visible in the left center of the picture, and the R. B. Miller Biological Station is less than one mile beyond them.

(*Populus tremuloides*), balsam poplar (*P. balsamifera*), grassy meadows, clumps of alder (*Alnus* sp.), and small islands of tall spruce (*Picea glauca*) which survived the fires. In the vast expanse of this forest the Franklin's Grouse appears to prefer specific areas. Pines, 20 to 30 feet in height with sufficient spacing to allow grouse to fly through them, seemed to be preferred to very dense stands, at least by displaying males.

First Encounters with Franklin's Grouse

My first encounter with a male Franklin's Grouse displaying before a female was on a mountain trail in British Columbia in July 1956. Startled and surprised by the sight of the contrasting black-and-white patterns and the large black tail-fan from which some of the rectrices were missing, I, like Thomas T. McCabe (*in* Bent, 1932), saw little of the display sequence before the female flew away and the male followed. Immediately after the birds vanished, I heard loud cracks like the breaking of twigs. Assuming that these cracks indicated the presence of a moose or bear nearby, I too left the area. Although I spent the rest of the summer in *franklinii* country, I never saw another displaying male.

I again encountered a courting pair of Franklin's Grouse in May 1963 in a stand of lodgepole pines a few miles from the R. B. Miller Biological Station. The male in striking display first caught my attention. With his tail partly spread and his crimson combs erect he moved slowly along a fallen, charred log. And, spectacular though he was, the black-and-white markings of his plumage blended remarkably with the sun-dappled maze of charred logs and the gray-brown trunks of the living pines. Soon the more cryptically colored female materialized from the mottled browns of the forest floor and slowly walked away. The male followed and they disappeared under the pines in the expanse of dead falls and tangled remains of the burned forest.

I returned to this spot the same day just after sunset and found the male feeding on the leaves of bunchberry (*Cornus canadensis*) at the side of a narrow trail through the pines. In attempting to get closer I alarmed him and he flew with a peculiar whirring flight to a pine branch about 12 feet above the trail, walked out near the tip of the branch, ate a few mouthfuls of needles, and then flew off, disappearing around a bend in the trail. Within seconds I heard two sharp cracks, like small branches breaking. Hurrying to a point where I could look along the trail, I found the male feeding on the ground. The above sequence was repeated except that this time I had a clear view of the bird as he flew down the trail at about eight feet above the ground. The flight was slow, fluttering, and also noisy. After flying about 100 feet, he seemed to pause momentarily in midair, drop vertically, and produce two sharp snaps with his wings before he landed. Within seconds I heard two more cracks in the distance and then two more even fainter. The double cracks of "breaking

Figure 2. Male Franklin's Grouse. Compare this photograph with the transformation in appearance which occurs during display. See Frontispiece and Figures 12 to 16.

twigs" were the previously undescribed advertising sounds of territorial male Franklin's Grouse.

Following these first encounters and experiences with Franklin's Grouse I undertook my study.

Methods of Study

The greatest difficulty in studying Franklin's Grouse was to find them. If they remained motionless, the remarkably cryptic patterns of their plumage rendered them almost invisible both on the ground and in the trees (Figure 2). Even when the male was in full display, it was difficult, if he kept still, to separate him from the charred, weathered logs on the forest floor.

Working with R. A. McLachlin and K. H. McCourt, who were conducting their own research on male and female Franklin's Grouse, we at first located territorial males by the advertising wing claps, a system which worked well when there was little or no wind. Most of the time we had to make a long systematic search of an area even though we had located a grouse there previously. We snared all birds found and marked them individually with colored leg-bands for future identification.

The daily systematic search for birds was so time consuming that we spent much effort in devising some means of calling the birds to us as did Stirling and Bendell (1966) with the Blue Grouse (*Dendragapus obscurus*). Finally I succeeded in recording the aggressive vocalizations of a female while she attacked the mounted skin of a female Franklin's Grouse which was put down so we could observe any responses. When played back, these vocalizations attracted both sexes. The males responded to this sound with a vigorous full display of plumage, as if the female were actually in sight, and frequently flew directly to the tape recorder. The vocalization was so stimulating to the males that they soon exhausted themselves in flight-displays. The females responded aggressively and revealed their presence by answering the call or searching for the source of the sound on foot.

Since this vocalization was effective in calling both males and females, its value for census purposes is obvious. There was a limiting factor however. The females responded to it only prior to the onset of incubation, and their vigorous reaction to any other conspecific female would seem to have the effect of spacing them throughout the suitable habitat. After the eggs hatch, females with young may be found in close proximity without any apparent evidence of aggression towards each other. McLachlin (oral commun.) succeeded in calling up a female as late as 20 June. She was followed by a courting male and, while observed, was responding only to the recorded female vocalization. The last date on which McLachlin could get a male to respond was on 29 June. This bird appeared to exhibit a low motivation and "walked up in a half-hearted strut." No birds responded during July or August; and no information is available on their aggressive behavior during the molt.

Having succeeded in attracting the male to us, we sometimes presented him with a specimen of a female, mounted in a crouching position to simulate the precopulatory attitude. When this decoy was in full view of a territorial male and the observers at least 30 feet away and motionless, he usually reacted by courting it and ignored us completely. By moving the female or by forcing the male to approach from another direction we could stimulate most males to repeat the courtship display at least twice.

We photographed the display sequences with a Bolex H-16 reflex camera and a Nikon F 35 mm camera with an electric drive and a 135 mm *f*3.5 lens, and recorded all vocalizations on a Uher 4000 Report-L tape recorder with a matched microphone without a reflector.

To induce a territorial male to give aggressive responses and threat vocalizations we tried mirrors. A single mirror was unsatisfactory because the male invariably circled it and, when he could no longer see his reflection, lost his desire to attack. However, two 15-by-16-inch mirrors, mounted back to back, brought high-intensity aggressive responses and threat vocalizations. We also used the female vocalization to call males to the assumed edge of their territories and induce them to interact over the boundaries.

Territoriality

We do not know yet whether the male Franklin's Grouse defends the whole of the home range that it occupies during the breeding season or only a certain area within it. Stoneberg (1967) reported that, for two consecutive years, four marked adult males in his Montana study area occupied home ranges which varied from 10 to 15 acres in size. Another male established a new home range which was three acres in size. McLachlin (1966) found that males two years old or older did not share their home range with any other males of like age, and that his marked birds also occupied the same home range year after year. Both noted, as I did, that males have preferred areas in their home ranges in which they seem to spend most of their time during the courtship period. My observations suggest that the male's home range is too large to have distinct boundaries, and that firm territorial lines are established only in areas of interaction with an adjacent male. Within his area each male seems to have several favored locations (Figure 3) from which he moves out in all directions to investigate any grouse-like sounds. I believe that the males establish territorial boundary lines after a very brief period of threat displays and seldom engage in actual fighting. A male, called by the playback of the recording of female vocalization into the area of another male, displayed vigorously if the resident was not in sight. After a few minutes, however, he apparently experienced a lowering of motivation, possibly because he could not locate the female. He then became agitated and soon flew back to one of his favored locations. There, where previously he had been silent, he began to advertise his position with flight-displays and wing-clapping.

Displays of Interacting Males

During the day, Franklin's Grouse fly back and forth from the ground to the trees to feed, to display, or to roost. Males are very perceptive of such wing-sounds and are quick to investigate them. These sounds are of low frequency and have little carrying power; thus audible wing-sounds always indicate the close proximity of another bird. Wing-sounds can be detected by humans up to a distance of about 150 feet on windless days. McLachlin (oral commun.) told me that males sometimes flew to the area in response to fluttering when he had snared a Franklin's Grouse for banding, but he was unable to determine the distance over which the male had responded.

The first reaction of a territorial male to a wing-sound is to raise his tail to about 45 degrees and partly spread it so that the white-tipped upper tail coverts contrast sharply against the black rectrices. This movement allows the long under tail coverts to spread downward in a "sunburst" pattern of black and white. Simultaneously, the neck plumage is raised and rearranged to present a solid black patch on each side of the neck, and the dorsal neck plumage is manipulated to form a gray cape. The male then begins to peck

Figure 3. Territorial males of Franklin's Grouse have several favored areas within their territory where they spend much of their time. Note the accumulation of droppings on the ground below a favorite roosting tree.

vigorously on any solid object within reach, or to pull twigs, leaves, or grasses which he immediately drops. While the grouse is pecking, the half-spread tail is usually held vertically or tipped forward over the back, and the under tail coverts are spread. The pecking is then interrupted by a few steps in the direction of the sound with the lateral rectrices on each side spread downward alternately as the foot on the same side begins to move forward. The combs, almost fully erect, turn blood red. Head-bobbing and neck-stretching grade into flight-intention movements as the male, with some deliberation, selects an overhead branch and flies vertically up to it (Figure 4). This flight is slow and noisy with exaggerated whirring sounds followed by the slaps of the primaries striking any twigs which happen to be in the way (Figure 5).

After alighting on the branch the male gives one, two, or all three of the following displays: (1) With an incipient rush of several inches along the branch he suddenly spreads both wings and tail in a spectacular display. He closes them and again spreads the tail fully and vertically and holds it open for about two seconds. He then resumes vigorous pecking. (2) A second and less common display resembles the drumming of the Ruffed Grouse (*Bonasa*

Figure 4. A male Franklin's Grouse begins the whirring flight to an overhead perch from which he will begin the wing-clap display.

Figure 5. A male Franklin's Grouse during the vertical whirring flight. The long, white-tipped breast and under tail coverts hang loosely and vibrate during this display.

Figure 6. The display position of a highly excited male Franklin's Grouse. The wing movements and the sound they produce are similar to the initial drumming movement of the Ruffed Grouse.

umbellus). Standing upright, the male (Figure 6) makes three or four wing-strokes like the initial movements of a drumming Ruffed Grouse, though shallower. Each stroke produces an audible drum-like thump. There appears to be no selection of an open spot for this drumming behavior since it may be given on a branch, a fallen log, or on the ground. Branches and twigs often limit the movements of one or both wings. The position differs from that of a drumming Ruffed Grouse in that the tail is held at an angle of about 45 degrees with the under tail coverts fully spread. Following one or more drumming sequences, the male begins flight-intention movements and flies off noisily in an advertising flight. (3) The third display is the wing-clap.

Wing-clap Display

The wing-clap display is the only loud and directional sound produced by male Franklin's Grouse and its main function is to advertise the exact position of the territorial male. During my observations the sequence of this display never varied. The male began the wing-clap flight from a branch or, occasionally, from a fallen log, never from the ground. However, McLachlin (oral commun.) observed a male which wing-clapped as it flew from the

Figure 7. Just before the advertising wing-clap is produced, the male Franklin's Grouse rises slightly in flight and pauses momentarily before he strikes the wings together over his back. Note how the white pattern in tail and wings is emphasized.

ground to a clearing. Another male was reported by D. R. Gray (oral commun.) to have wing-clapped as it alighted in a tree in which a female was perched. Launching from a branch, usually between 10 and 20 feet in height, the male flies, with shallow wing-strokes, through the trees. The wings make a soft fluttering sound and the upper tail coverts form a conspicuous white semicircle against the black, fully spread tail (Figure 7). The flight may be in a straight line if openings in the trees permit it, or it may be sinuous as the male moves toward any nearby clearing. On reaching the edge of the clearing the male rises slightly, his body and tail swing down below the horizontal, and with a very deep wing-stroke, he pauses in midair. Instantly the wings are brought sharply together over the back and the impact produces a sharp crack as the bird drops vertically to the ground (Figure 8). A second wing-clap always follows before landing. This sound seems to be produced by the manus and the shafts of the primaries as they are forceably struck together. My photographs show that the upper surfaces of the fully extended wings seem to meet over the bird's back at the moment the clap is heard, but the detail is not sufficient to show exactly how the sound is made. The secondaries appear too soft to be effective in this sort of mechanical production of sound, but the primaries with their stiff shafts, together with the firm manus, should be capable of producing the loud wing-clap when struck sharply together. Very active males tend to lose some of the lesser wing coverts by the end of May, leaving an irregularity in the smooth contour of the upper surface of the antebrachium and exposing the downy bases of the remaining coverts. I suspect that the loss of these feathers may be somehow related to wing-clapping activity.

Following the wing-clap the male walks forward, tail and under tail coverts erect (Figure 9), selects another branch overhead, and, within a few minutes, begins the display sequence again. On hearing the wing-clap of another bird, highly motivated males may fly directly from a branch to the area of the sound stimulus, wing-clap, and make further investigations of the source of the sound from the ground while in full display.

Aggressive Male Displays

If another male is present, the resident male is quick to recognize the rival, presumably by the presentation of black areas in the plumage. Recognition seems to be almost instantaneous, and both males indulge in vigorous pecking at the ground and branches. The blows of their bills make audible thumps which may serve to fortify the visual activity.

Both birds threaten from a distance and continue to move slowly about. The resident male sleeks his plumage, utters a series of guttural, staccato vocalizations, and flashes the white-tipped upper tail coverts. He raises his tail slightly above the horizontal and very quickly opens and closes the lateral rectrices. This rapid movement produces a flickering white pattern against the black rectrices, since the upper tail coverts can also move laterally with the rectrices. At this point, attack is imminent. The male runs toward his adversary with neck and tail extended and lowered and the wings held slightly away from the sides.

The trespassing male assumes the same sleeked position and begins running obliquely towards the path of the resident male. They gradually approach and either begin to parallel each other at a distance of 15 to 25 feet, or the resident male simply runs straight at the other male. When a direct approach is used, the trespassing male always flies off, usually pursued by the

Figure 8 *(above)*. As the male's wings are struck together, the impact produces a sharp crack like a dry branch being broken. A second similar wing-clap always follows the first. This drawing was made from a photograph and is accurate in detail except for the primaries which were blurred. Drawing by the author.

Figure 9 (*below*). On alighting, the tail is flipped up and closed, presenting a sudden display of the under tail coverts. Drawing by the author.

resident. In one instance the pursued male, very reluctant to leave, merely flew into a tree. The resident began the elaborate tail-swishing and tail-flick displays, flew, and wing-clapped. Finally, he flew into an adjacent tree, threatened attack as above, and flew at the other male, chasing him in full flight through the treetops. After the resident had driven a second male away, he returned to his original place and began vigorous sequences of display and wing-claps.

We were never able to entice one or the other of adjacent males to cross the boundary line established by their parallel display if the resident was in sight. Furthermore, this boundary line extended much farther than the distance covered by the males in their parallel display. I therefore believe that their territorial boundaries are really linear projections of a short line of interaction between adjacent males. The greatest barrier to each male exists at the line of encounter, and it gradually decreases along the projection of this relatively short distance. If this is indeed the case, Franklin's Grouse have territories which are vaguely delineated except at specific, favored spots. Research in progress at the R. B. Miller Biological Station is concerned with this aspect of their territorial behavior.

I never saw any actual fighting between males although, when confronted by his image in a mirror, a male, after prolonged threat, will attack and fight. In fighting his image (Figure 10), he seemed to aim his bill at the head, possibly at the fleshy combs, and to deliver blows from powerful wing-strokes to the neck and back of the opponent (Figure 11).

Courtship Behavior

When a territorial male locates a female in his home range, the initial response is the same as described under the displays of interacting males. The elevation of the plumage to emphasize white-and-black markings becomes extreme as the male begins to approach. The combs are erected and, in some males, may meet over the midline of the crown. The color of the combs is a deep vivid red, and the erect rows of tiny papillae give them a three-dimensional effect. Head-bobbing, accomplished by dipping the head downward, quickly becomes aggressive pecking and thumping of sticks and logs on the ground with the bill. While pecking at the ground, the male always faces the female and the lowered head is often tipped sidewise. This movement gives an oblique view of both combs, thus increasing the area of red and making it contrast sharply with the black and white of the tail and breast as well as the grayish dorsal plumage.

The male may begin courting the female immediately or he may continue pecking for five minutes or more. This depends on his level of motivation.

Tail-swishing Display

During the beginning of this display the male holds both head and tail erect with the under tail coverts so widely spread that each feather stands out separately. The movements of the feet are synchronized with the alternate spreading of the lateral rectrices on each side while the central portion of the tail remains stationary (Figure 12). As the feathers move, they produce a swishing sound which varies in loudness with the amplitude of downward movement. The gait is slow and measured and the feet are placed in a "pigeon-toed" plane. The combined effect of the tail-swishing display and pigeon-toed gait is an exaggerated swaying motion. Seen from the front or back the white-

Figure 10 (*above*). This photograph shows part of the props used to elicit displays of Franklin's Grouse. The double mirror is on the right, and the mounted female on the left. The male has just noticed his reflection in the mirror and has begun to make the threatening tail-flicking movements prior to attack. The wings are already moved outward exposing the wrists.

Figure 11 (*below*). This shows the characteristic fighting position of a male Franklin's Grouse. Low-pitched, gutteral vocalizations accompany this position.

tipped upper and lower tail coverts seem to flicker against the black background of the side-to-side movement of the rectrices.

As the male approaches a few steps nearer the female, the slow, swaying walk gradually becomes a quick, short-stepping run and the tail-swishing increases in tempo (see Frontispiece). At the same time he extends his neck slightly forward and away from the midline of the body and the female, while turning his head obliquely toward her. The wings, during this display sequence, are held slightly away from the sides and the brachium is lowered so that the primaries are parallel with the substrate. The alulae are prominently extended beyond the whitish leading edges of the primaries.

The approach becomes a short run in an arc toward the female. At the climax the swishing sounds increase in tempo and volume to a continuous hiss. Suddenly, the male stops with a slight bowing motion and snaps his tail to a full spread. This startling movement frequently separates the tips of the rectrices and produces a loud *whoosh*. The wings are simultaneously fully extended downward and outward and somewhat forward. The head is flipped slightly upward, producing a hiss, like exhaled air. If this display is on the ground, as it frequently is, the primaries cannot be fully extended because they are pushed against the substrate. In about a second the wings are withdrawn to a closed position leaving the alulae exposed, the tail-fan is closed, and the head is tipped slightly downward with the neck still extended. In this stiff position the tail is again snapped fully spread, held briefly, and closed (Figure 13). At the initial spread the fully fanned tail is tilted from side to side (oblique to the midline of the body), and also forward and back (Figure 14). Again, this movement emphasizes the contrasting black-and-white tail plumage. In some males the tail is momentarily tipped forward over the back, exposing the glistening white-tipped under tail coverts which then project above the black rectrices (Figures 15 and 16).

The short rushes of this display are repeated every few feet as the male moves in arcs in front of the female. Most of the displays are oriented toward her head, but some are to her side although the male's head always faces her. Some displays are occasionally directed away from the female. During this courtship behavior some males produce a soft, very low-pitched *hoot* which is generally audible to humans only when amplified by sound-recording equipment. Possibly there are several hoots. I have heard only one and could detect no visual indication of any vocalization being produced.

Squatting Display

The squatting display is similar to the "head-jerk display" of the Spruce Grouse as described by Lumsden (1961). I prefer to label it squatting display to separate it from head-bobbing movements described earlier. Lumsden thought the head-jerk display was a precopulatory display, and, although my observations support his opinion, an occasional male in the spring will omit it from the described sequence.

As the male approaches the female, the arcing rushes increase in frequency until he is within two feet of her. After watching intently for several seconds, he sinks to the ground in a squatting position. His head, with the neck plumage erect, is extended upward and the bill is parallel with the ground or tipped slightly upward. He holds his half-spread tail vertically with the under tail coverts fully spread and his wings slightly away from the body and lowered with the alulae prominent.

Figure 12 (*above*). Frames from a 16 mm motion-picture sequence of the tail-swishing display. Note that the movements of the right side of the tail and the right foot are synchronized, and that the brachium is lowered. Note also the change in the neck plumage.

Figure 13 (*below*). The final phase of the tail-swishing display. Note the position of the wings with the alulae extended. The side-to-side tilting of the tail is beginning, and this portion of the display will not be complete until the right foot is brought forward. The position of the tail indicates that this movement has begun.

Figure 14 (*above*). This is the final phase of the initial tail-fanning movement. It is terminated by a forward bow which brings the under tail coverts into view above the rectrices.

Figure 15 (*below*). The second tail fanning display is not so elaborate as the first, but is held a longer time. The sudden spreading of the rectrices separates them at the tip and produces a loud *whoosh*.

The male always orients himself so that he presents a side view to the female. Suddenly he begins to make quick tramping movements, as if settling on eggs, and jerks his head up and down quickly. At the height of the upward movement he tips his head sidewise as if to peer at something overhead. This head movement emphasizes the vivid combs. With each head motion the tail is jerked open and the wings brush the ground. Still squatting he quickly increases these movements to spasmodic bursts of activity accompanied by loud swishing of the rectrices. Periodically he stops and "freezes" in the squatting position for about 15 seconds. He may then continue the movements of the squatting display or get up and move around the female in a new series of tail-swishing displays. With each display the male stops nearer to the female. I have watched birds give as many as nine tail-swishing and four squatting displays in sequence in a period of half an hour. During the courtship approach and display sequences the male moves with great deliberation and caution in coming near the female. Late in the spring, these display sequences are shorter and the male no longer shows hesitancy in approaching. With the final squatting display the male gets up and walks with plumage still erect to the side of the female. With no further display he steps on her back, holds her nape feathers in his bill, and attempts copulation.

Copulation

Male Franklin's Grouse usually attempted copulation with the mounted specimen used to elicit displays (Figure 17). While holding her crown or nape feathers the male makes treading movements with his feet which are placed over the lower extremities of the female's scapulars. The wings, particularly the primaries, are extended and spread on each side of the female, and their tips press against the ground for balance. There is no flapping or fluttering to maintain balance. The neck is withdrawn and pulled downward so that the throat rests on the front of the breast. The dorsal plumage at the base of the neck is raised and in profile gives the neck a peculiar U-shaped contour. The male makes pushing movements with each foot alternately with the tarsi flat against the female's back as his tail and rump make side-to-side movements in an effort to establish cloacal contact. After several such attempts the male dismounts with no postcopulatory display. Frequently the male pecks gently at the female's combs (which were not apparent on the mounted specimen) or touches her back between the shoulders with his bill. At this point some males walk away from the female in full display and fly into a tree to feed or begin the whole courtship sequence again. Other males remain with the female, attempting copulations without any further displays.

Summary

The Spruce Grouse (*Canachites canadensis*), in spite of its wide distribution in the boreal forest of North America, is one of the least known of North American grouse species. For five years, during May, I studied the courtship displays of the race *C. c. franklinii,* which I refer to as Franklin's Grouse, on the eastern slope of the Rocky Mountains in Alberta, Canada.

Using the wing-clap of the territorial male to locate birds—and later the recorded vocalizations of female Franklin's Grouse—with mounted females for decoys, I was able to make detailed observations of courtship behavior. I have described the displays of adult males during courtship of the female and during interaction between rival males. All displays are based on the presenta-

Figure 16. Two additional views of the display shown in Figure 14. Note the arrangement of the neck plumage. The chin feathers are erect. Both views show the side-to-side tilting of the tail. This movement causes the white tips of the upper tail coverts to flicker against the black rectrices.

Figure 17. Two views of a male Franklin's Grouse mounting and attempting copulation with a stuffed decoy hen.

tion of black-and-white patterns in the plumage, and these markings function as signals in visual communication, yet without their associated movements they provide cryptic patterns against the light and dark of the forest floor. I have also discussed the establishment of territorial boundaries between adjacent males.

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Kestrels, *Falco tinnunculus*. Drawing by Eric A. R. Ennion.

ALARM SOUNDS AND RESPONSES OF BIRDS AND THEIR APPLICATION IN CONTROLLING PROBLEM SPECIES

Gordon W. Boudreau

The advent and improvement of the modern tape recorder has intensified the research in animal sounds in recent years. To many students of wildlife the battery-powered tape recorder has become as indispensable as binoculars, with the result that a considerable amount of data on wildlife sounds has accumulated.

Because of their effusive characteristics, birds have been more intensively studied in this respect than any other class of animals. Although most of these studies have been concerned with their territorial songs, always the easiest to record, a few investigators have recorded other vocalizations of birds.

Bio-acoustics is the science that treats of the sounds and the vocal and auditory mechanisms of animals. Laboratory and field investigations involve complex combinations of physiology, neurophysiology, animal psychology, behavior, ecology, and numerous other disciplines. Recently we have added electronics to this list. One must frequently rely on one or more of these disciplines to interpret correctly the responses of animals to various acoustic stimuli. And one must make final determinations of the significance of an animal sound in the field with free animals under natural conditions. If repeated exposures to a sound influence an animal's behavior consistently, then one may presume that his interpretation of the sound's significance is correct.

My work in bio-acoustics is on applied research in the various communication sounds of animals, particularly birds, which we may develop into acoustic stimuli to influence their behavior. Of special interest to me are the survival sounds—alarm, alert, and distress signals—that we may use as effective controls for certain species commonly regarded as "problem," or "nuisance," birds. This area of applied research, intensively studied in Europe (Busnel, 1963; Frings and Frings, 1967; Seubert, 1964), has received little attention here in North America.

A problem species is any species which, habitually or occasionally, adversely affects the economic status or physical well-being of man. Some people call these birds nuisance species and in certain situations they are only a nuisance. But where human lives, health, and economic status are involved, the term nuisance is hardly appropriate.

In this paper I shall discuss the alarm sounds of birds, the responses thereto, and some observations on bird behavior which I made while searching for sounds to disperse or repel problem species. The studies, conducted principally in Arizona, California, Colorado, Georgia, Florida, Hawaii, Texas, and Wisconsin, began in November 1958 and still continue. I also made occasional studies on Midway Island in the Hawaiian chain and in Mexico. Since 1958 I have recorded and cataloged the survival sounds of 145 species representing 40 families in 13 orders.

We can better understand the birds' responses to sounds if we know something of the nature of the sounds themselves and the conditions under which they are produced. Although several authors (Armstrong, 1963; Frings and Frings, 1964; Thorpe, 1961) have written extensively on bird sounds, they have invariably given more attention to songs than to survival sounds. In this paper I shall attempt to correct this deficiency insofar as my investigations will allow. For convenience we shall divide the sounds that alarm birds into two groups—natural sounds and anomalous noises. I shall also discuss a recent development—the use of synthesized versions of the natural alarm sounds of birds.

There appears to be some confusion in the literature regarding the terminology which describes the vocalizations of birds. Most authors designate any bird sound which is not a territorial song as a "call." Webster lists no less than 15 definitions for the word call, two of which are "utterances in a loud voice" and "summoning by calling." Neither of these aptly describes the threat bill-snapping of albatrosses and owls or the alert notes of sparrows. "Sky call," "morning call," and so on may describe the posture of the bird or the clock-time but are meaningless insofar as the significance of the sounds is concerned. "Alarm call" seems hardly appropriate, in view of the definition by Webster, since alarm calls are not always loud nor do they summon other birds. Often they repel them. To avoid confusion, I shall refer to audible emissions from birds as "sounds" and identify the nature or significance of each.

Natural Sounds

Natural sounds are those emanating from biological sources and include not only the communication sounds of animals but also sounds of botanical origin—e.g., rustling leaves, creaking trees—and meteorological sounds—wind, water, and rain.

Alarm Sounds

Since most bird species are subject to predation, they have developed more or less well-defined alarm sounds indicating the presence of a predator. Some of the larger species, particularly pelagic birds with few natural enemies, apparently have no alarm sounds and, if they experience alarm reactions at all, seem to rely on visual cues. The Laysan Albatross (*Diomedea immutabilis*) and the Black-footed Albatross (*D. nigripes*), nesting in colonies on Midway Island, emit no true alarm sound under any circumstances. The characteristic "bill clapper," emitted when their nest is approached, is more of a threat sound. Anyone who has approached too closely and had his leg nipped will confirm this. Often threat sounds are misinterpreted as being true alarm sounds.

Albatrosses are exceptions. Most gregarious species have alarm sounds that are well developed and of important significance. The development and use of alarm sounds appears to depend on the social organization of the species and its vulnerability to predation. Small gregarious species, subject to predation from both earth and sky, usually have well-defined alarm sounds which, by their nature, often identify the predator as avian or terrestrial.

True alarm sounds appear to be innate. Consequently, they are quite species-specific—i.e., the alarm sound is different in each species. Basically, they contribute to the survival of the species and characteristically they consist of certain parameters—frequency, repetition, modulation, and so forth—that the species recognizes. Associated species may temporarily respond to the alarm sound of another species — a target species, for instance — through visual conditioning to the response of the target species. However, after a time or a separation from the target species, the associated species will not continue to react. For example, when Brown-headed Cowbirds (*Molothrus ater*) associate with Red-winged Blackbirds (*Agelaius phoeniceus*), the cowbirds respond with the blackbirds to the Red-wing's alarm notes, at least for two or three days. Other flocks of cowbirds associated with House Sparrows (*Passer domesticus*) ignore the Red-wing's alarm sound. Western Bluebirds (*Sialia mexicana*), when associated with House Finches (*Carpodacus mexicanus*) in a vineyard, respond to the finches' alarm sound for about a week. After that, while the finches continue to respond to their alarm sound, the bluebirds ignore it. These examples indicate that visual cues are important factors in interspecific responses.

There is little doubt that all birds, being endowed with highly developed optic systems, rely on visual alarm stimulation. Many species respond equally well to either acoustic or visual alarm stimuli. In other species alarm sounds appear to merely alert the birds which respond only after they have seen the predator.

To be useful, an alarm sound must be readily distinguishable from the environmental noise in which the species resides, and it must contain identifying parameters which isolate it from the alarm sounds of other species in the same habitat. In general, the pitch of a bird's alarm sound relates to the size of the species and, as the size increases, the pitch becomes lower, due to a longer trachea and other physical characteristics. One can appreciate this by comparing the sounds produced by a piccolo with those from a tuba.

Some writers hypothesize that the high-pitched sounds of small species have ventriloquistic qualities, making their source difficult for predators to locate. This may be true for human hearing but most any avian or mammalian predator can easily locate the source of narrow beam, high-pitched alarm notes. Payne (1962) found that Barn Owls (*Tyto alba*) zero in on high-pitched mouse squeaks emanating from a loudspeaker hidden in darkness. My experience in the field reveals that hawks, owls, and crows locate the sources of well-hidden, high-pitched sounds in dense cover with ease. The location of sound sources by humans is complicated by reflecting surfaces, sound shadows, absorption, and other factors usually present in dense vegetation. Until one confirms the source visually, its location is in doubt and the sound appears to have a ventriloquistic quality. The location of sound sources, easy in bare open areas, becomes difficult in dense forests. Raptors, with their highly developed visual acuity combined with their sensitive aural perception, locate prey efficiently even though they are not always successful in capturing it. These considerations make the ventriloquistic hypothesis difficult to accept.

Many vociferous species will shun noisy environments simply because they cannot readily communicate with one another. Birds will avoid areas in a feed lot where a high-pitched hammer mill is operating, yet readily feed, roost, and loaf close to heavy vehicular traffic. High-pitched or high-intensity environmental noise masks their usual alarm sounds while lower-pitched traffic noise does not. Species with few natural enemies and poorly developed alarm sounds can tolerate abnormally high levels of ambient noise, but usually do so in more or less open areas where visibility is good.

The nature of birds' alarm sounds vary from a simple one-note utterance to the quite complex, depending on the species and the circumstances. They are often characterized by sharp onset times—in the region of 10 to 30 milliseconds (ms). In the alarm notes of 20 species the fundamental frequencies ranged from 900 to 6,000 Hertz (Hz=cycles per second), and most were amplitude modulated in the area of 75 to 350 Hz. The duration of the notes varies; usually it is quite short, 100 ms or less (Figure 1).

Field experiments using synthesized versions of some species' alarm sounds revealed that the above parameters, of which there may be infinite combinations, are important in conveying specific information to the birds. Apparently, each species, attuned to its own combination, discriminates against all others even though it may be conscious of them. This would account for the phenomenon of species specificity in bird alarm sounds. If the species did not discriminate and all species attempted to respond to the communication sounds of all others, chaos would prevail.

In some species emotional as well as physical distress will elicit distress sounds. For instance, a bird in the presence of a predator from which it cannot escape may emit a sound similar to that usually regarded as its distress sound even though the bird itself is physically unharmed. I obtained these sounds during October 1965 in a series of separate tests with Starlings (*Sturnus vulgaris*), Western Meadowlarks (*Sturnella neglecta*), Red-shafted Flickers (*Colaptes cafer*), Acorn Woodpeckers (*Melanerpes formicivorus*), and Western Bluebirds. In these experiments I released a well-fed Sharp-shinned Hawk (*Accipiter striatus*) into a large outdoor cage containing several of the study species. Although the hawk did not molest the birds—but rather sat on a perch about four feet above the floor of the cage and ignored them—the caged birds emitted their characteristic distress sounds immediately and continued to do so for 15 to 30 minutes as they fluttered about trying to maintain a maximum distance from the hawk. Eventually they quieted down, only to resume their squalling each time the hawk moved ever so slightly. When recordings of their sounds were compared aurally with recordings of their distress calls, the two were found to be very similar.

When they were within three feet of the hawk, the Starlings usually emitted their raucous, squalling, prolonged distress sound, the same squalling sound heard when they are being released from mist nets or handled roughly; elsewhere in the cage they gave their usual chucking or chipping alarm notes. This would indicate that the so-called Starling distress call is actually a modified alarm sound emitted when the bird is in imminent danger as well as in physical distress.

Incidentally, during these tests I observed that typical threat postures often accompanied the sounds and believe that portions of the sounds recorded had some threat significance, particularly in meadowlarks and flickers. During each test, prior to releasing the hawk into the cage, I introduced a Common Crow (*Corvus brachyrhynchos*). Usually, I heard very little sound and saw no alarm behavior by the other birds, indicating that the study species did not regard crows as enemies.

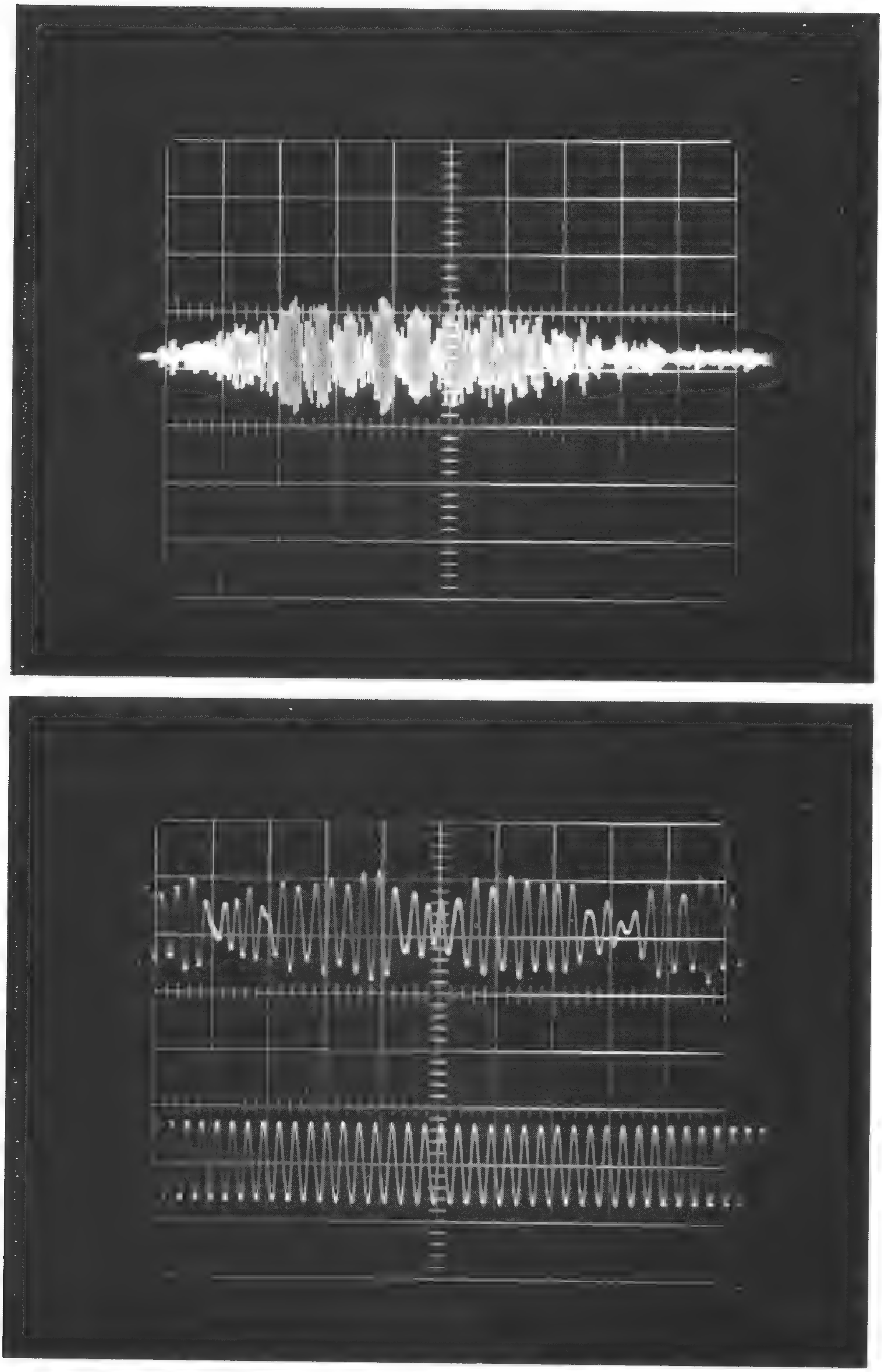

Figure 1. *Top:* A typical female House Sparrow alarm sound displayed on an oscilloscope. Each vertical line represents five milliseconds in time. The trace moves from left to right. Duration of this sound is slightly over 50 ms. Note the rapid onset time of 10 ms at the left end. *Bottom:* The upper trace displays the same sparrow alarm sound expanded five times. Each vertical line represents one ms in time. The dips caused by amplitude modulation are well displayed. The lower trace is an unmodulated pure tone signal of the same frequency which is 3,500 Hz.

Several years ago (Boudreau, 1963) I determined that the alarm sounds of the problem species I worked with were far more effective for control purposes than were their distress sounds. The one exception was the Starling which responded best to its distress sound. Now I am convinced that Starlings do conform to the patterns of the other species and that their so-called distress sound is one form of their alarm sound. I can now conclude that the alarm sounds of all my study species are much more effective as a control than their distress sounds.

One is often amazed at the similarity of the alarm notes of a species to some of its other vocalizations. Careful analysis generally reveals subtle differences in frequency or modulation. Because of this similarity, it is easy to misinterpret bird sounds. We have not yet developed techniques either in the laboratory or the field to monitor neural and physiological responses of birds to alarm stimuli although several investigators are engaged in this research. Hence, one must rely on the overt responses in the field to identify alarm stimuli correctly.

The territorial songs of birds often involve learning and result in the development of regional dialects (Thorpe, 1961). Although there is some evidence of regional dialects in birds' alarm calls, I have not yet compared my recordings, spectrographically, with others of the same species in distant areas. In the southwest, my principal study area, I could detect by ear no distinction in the alarm sounds of individuals of the same species. Robins (*Turdus migratorius*), both summer residents and migrants in Arizona, appeared to have similar alarm calls; California House Finches uttered similar alarm and distress sounds as did Arizona House Finches. Red-winged Blackbirds and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), wintering in Arizona, have alarm sounds very similar to resident blackbirds. Recordings, made of the alarm sounds of Arizona Starlings, were effective in controlling Starlings in California, Kansas, Illinois, Pennsylvania, New York, South Carolina, and other widely separated areas. Robin alarm sounds, recorded in Wisconsin, successfully controlled this species in Arizona. House Finch alarm sounds, recorded in northern California, were effective in southern California and Arizona. The alarm sound of a Glaucous-winged Gull (*Larus glaucescens*), obtained from an individual wintering in the San Francisco area, was very effective when used on other Glaucous-winged Gulls wintering there the following year. We can safely assume that the summer ranges of these gulls extended from Washington north to Alaska.

The above evidence strongly suggests that regional dialects in alarm sounds are not likely and that we can attribute any minor differences in tone to individual physiological or anatomical characteristics similar to other physical differences often noted within a species. More important than the tone quality is the modulation and repetition rate of the sound, both of which are critical factors in eliciting responses from birds of the same species. This is an area of bio-acoustics that needs additional study.

In addition to their greater effectiveness in controlling birds, alarm sounds are less obnoxious to the public than the raucous, squalling of the distress sounds. The cacophony of a Starling distress sound has limited its use and is largely responsible for its unpopularity as a bird repellent, especially in quiet residential neighborhoods where numerous Starling problems occur. When alarm sounds are used, people are in most cases unaware of any bird-control program. In fact, during a properly conducted program the average person cannot distinguish the alarm sounds from the birds' normal vocalizations.

Alert Notes

Many species use alert sounds which, like true alarm sounds, have both social and survival significance. Usually the alert sounds warn of impending danger at a distance—analogous to the Navy's, "Now hear this!"—and prepare the bird for sudden escape if necessary. Generally, on hearing the alert sound, the birds will cease their activity and assume attentive attitudes. Some of the more timid individuals may leave or seek cover but no sudden evacuation of the flock occurs and, if no attack is forthcoming, the birds quickly resume their activities. This is particularly true of highly refractory species such as cowbirds, gulls, and others. Alert sounds temporarily lower the birds' response thresholds to a point where they may be easily stimulated to escape.

Although birds will not respond consistently to alert sounds alone, they may respond to a combination of alert sounds and alarm sounds. One of the most effective sounds I ever developed consists of four alert notes closely followed by two alarm notes and definitely discouraged House Finches feeding in grape vineyards. During the past several years this sound has protected hundreds of acres of vineyards from damage by finches.

Distress Sounds

Since Frings (Frings and Jumber, 1954) described the responses of Starlings to their own distress sounds, many investigators have attempted to control Starlings by using these vocalizations. A distress sound, or distress call, implying physical distress or pain, is elicited from a bird by handling it roughly or confining it closely in the hand. Some species—Starlings and various woodpeckers—emit distress calls quite readily; others give none at all regardless of the circumstances. In general, young or immature birds emit distress sounds more readily than do adults. Nearly all immature House Sparrows voice distress sounds while only about four per cent of adults do.

Distress sounds are often more or less raucous, squalling vocalizations as in the sustained distress sounds of Starlings, flickers, and meadowlarks. Distress signals emitted by Horned Larks (*Eremophila alpestris*), some sparrows, Cedar Waxwings (*Bombycilla cedrorum*), and hummingbirds are only about one second or less in duration and have more of a squeaky quality. The distress sound of a Wedge-tailed Shearwater (*Puffinus pacificus*) closely resembles the crying of a young infant. The distress sounds, produced by birds after ingesting certain commercial chemicals, in no way resembled the natural distress sounds of the 18 species I tested and compared.

If a bird will give a distress signal at all, it will do so immediately after it is captured and often for a very short period. Thereafter it will remain mute. The chances of obtaining a distress sound from a bird caged for some time are remote.

I have noted that Mockingbirds (*Mimus polyglottos*) quickly learn the distress sounds of other species. Resident Mockingbirds will repeat distress calls, elicited from Starlings, Robins, and Loggerhead Shrikes (*Lanius ludovicianus*), for several days after hearing them. They will also repeat taped versions of the same sounds. I have not had the opportunity to test the effect of the Mockingbird's version on the target species. It would be interesting to know whether a Starling would respond to a mimicked version of its distress sound. I have never heard a Mockingbird mimic the alarm sound of another species.

Anomalous Noises

The anomalous noises encountered during my study were of human origin and included the sounds of guns, various detonators, traffic, aircraft, mills, farm equipment, and so forth. In many instances these noises were important factors in my control experiments.

Numerous frustrations await the field investigator as he attempts to record or evaluate specific bird sounds either near centers of population or in the remote wilderness. Few places in America today are completely devoid of noise from aircraft or sonic booms. Unexpected noise, particularly from aircraft, frequently interrupts the recording at critical moments or frightens the subject of a carefully staged experiment so that much time is lost waiting until all conditions are again favorable.

For centuries man has used noise-making devices to protect his crops from the depredations of birds and he still uses primitive devices in many areas (Büttiker, 1962), for until recently very few new devices have been introduced. Now, however, we have various types of automatic exploders, pyrotechniques, and electronic devices, all designed to frighten away the birds. Most of these are of dubious value for control purposes since they only elicit temporary startle responses.

Birds become inured to the intensity of sounds as well as the nature of sounds. At the end of the runways at the Luke Air Force Base in Arizona, immature Starlings fed in table-grape vineyards where, when jet aircraft passed over at altitudes of 200 feet, the sound pressure levels were in excess of 130 decibels (db—reference 0.0002 microbar) or roughly the equivalent of a sound made by a large pneumatic hammer at a distance of four feet (Peterson and Gross, 1960). A few of the Starlings left when a plane passed over, but most of the birds, having adjusted to the anomalous noise, merely settled deeper into the foliage. Researchers believed that those which flew were unseasoned birds, new arrivals in the vineyards that day. We have not yet established the highest sound pressure level that a bird can tolerate.

From time to time we see new devices for controlling birds, which produce, or are supposed to produce, sounds in the ultra-sonic range (20,000 Hz or higher). Several investigators agree with my findings that birds do not respond to ultra-sonic sounds. In fact most birds cannot hear them, and if they could, these high-pitched, narrow-beam sounds would mean little to them. In general the hearing range of birds roughly parallel that of humans.

Field Equipment for Reproducing Sounds

The equipment used to reproduce the sounds in field tests is fully transistorized, requiring only a 12-volt storage battery for operating without utility power. Solid-state equipment eliminates troublesome power supply problems and is more compact and reliable—always desirable features in the field.

I reproduced my test recordings on special cartridge-type tape players using endless loop tape which repeated the program and eliminated rewinding. I recorded two or four tracks and could instantly change the program by a selector switch. I prepared several cartridges with different arrangements of the sound and quickly interchanged them when comparing the birds' responses to the various arrangements. The tape speed of the players was 7.5 inches per second; the tape player output was fed into an amplifier with an output power of 35 watts, adequate for most field evaluation tests. I projected the sounds over, or through, the study areas by means of outdoor type loudspeakers (Figure 2).

Figure 2. Experimental sounds being evaluated in a vineyard. The operator remains in the vehicle and manually regulates the sound and aims the loudspeaker.

The sound-pressure level reaching a target depends on its distance from the sound source. Each time the distance is doubled the sound-pressure level is reduced by six decibels. Each time the output power is doubled the sound-pressure level is increased by only three decibels. Other factors determining the intensity of a sound at an objective are the direction and velocity of the wind, the presence or absence of sound-absorbing materials, and the type and intensity of ambient noise. Sound which carries well over water or bare fields is rapidly absorbed in a deciduous forest or a fruit orchard. In field experiments one must be sure of the sound reaching the target with sufficient intensity.

I rarely used automatic timers or actuating devices to control the duration and rhythm of the sound emissions. The manual operation of the equipment allows the operator to observe the response to each emission and, even though it requires full-time duty during daylight hours, it quickly discloses which sounds are ineffective and can be eliminated. Also, the constant surveillance makes possible an intensive study of the birds' behavior patterns and serves to develop information that is invaluable in analyzing results and programming new experimental sound. When I have determined the most effective sounds and established their correct duration and rhythm, I can then program them with automatic timers. Usually, much empirical testing is required before this objective is attained (Figure 3).

Figure 3. An automatic sound source in a vineyard. Sound projections are scheduled by an electronic programmer. The speaker rotates during the sound emissions and effectively covers an area 2,000 feet in diameter.

Responses of Birds to Sounds

There is considerable diversity in the responses of birds to acoustic stimuli. In this paper I shall consider that a target species responds to an alarm stimulus when the species is actually flushed, repelled, or dispersed. In the course of these experiments which were all made with free birds in the field I often observed other patterns of behavior that I shall describe later.

An important variable that influences birds' responses to stimuli is their response threshold or level, defined as the sensitivity of birds to various stimuli. The response level varies with the species, its social organization, environment, pertinent activity, season, clock-time, light intensity, and other factors including its age. To elicit a response from a bird the stimulus level must be higher than the prevailing response level. Birds respond more quickly when their response levels are low. For example, the response level of sparrows feeding dangerously in an open field some distance from cover is low and the birds would be quick to fly away. Contrariwise, Red-winged Blackbirds, snug and relatively safe in their roosts at night, have a high response level and are slow to fly—if they fly at all. We consider species with generally high response levels as "refractory."

Let us regard a bird's neural system as a complex arrangement of connecting electrical circuits controlled by an intricate switching mechanism. Although there are many circuits all interlocked, we shall consider, for simplicity, only three: sensory, inhibitory, and activating.

The inhibitory mechanism intercepts the neural pathway between the sensory and activating circuits and largely determines whether or not a bird will respond to a stimulus. The purpose of the inhibitory circuit is to prevent a needless expenditure of energy which most species can ill afford. In electronics the inhibitory circuit would be known as a "variable resistor." When a stimulus is received in the sensory circuit and its significance is important enough to overcome the inhibitory resistance, it proceeds into the activating circuit and the bird responds. If the stimulus cannot get by the inhibitory circuit, there is no response.

The inhibitory circuit can change levels. The first few times the sensory circuit receives a strange alarm stimulus, the inhibitory circuit drops to a low level as a precaution. If this sound has no significance to the bird, repeated exposure to the same stimulus allows the inhibiting resistance to rise higher and higher until the bird no longer wastes energy responding. This explains the rapid inurement of birds to noises such as traffic and gunfire.

The inhibitory mechanism, so important in determining the response level of birds, appears to be quite sensitive to environmental conditions and physiological requirements. Hungry birds have a higher resistance level than well-fed birds and are, consequently, more difficult to evict from feeding areas. Birds close to protective cover have a higher resistance level than those far from cover and thus do not respond as quickly to stimuli. Birds respond readily in the morning to stimuli they may ignore later in the day. While this concept of avian neurophysiology is rather crude, it conforms very closely with behavior observed in the field.

In general the response levels of diurnal species vary inversely with the light intensity—the more light, the lower the response level. Both Starlings and blackbirds arriving at a night roost begin to disregard acoustic alarm stimuli as darkness approaches. I was unable to move Red-winged Blackbirds from their roost in a Georgia swamp either in the morning or the evening when the light intensity was below 25 foot-candles, yet, using the same alarm sound later in the day, I evicted them from cornfields. One must constantly bear in mind, however, that behavior patterns vary with species. Murbach (1962) reports that Carrion Crows (*Corvus corone*) were successfully evicted from their roosts in Switzerland by projecting their distress sounds during the night. He adds, though, that snow on the ground and bright moonlight provided considerable illumination.

Response levels, which rise quickly as a bird attains a safe perch or cover, usually remain high as long as the bird is in a relatively safe place, and an increase in the intensity of the acoustic stimulus is necessary to move it. Species with inherent high response levels, occupying relatively safe places at low light intensities, represent the acme of temerity in birds. This combination of factors has frustrated more than one investigator.

During late April and throughout May 1966, Band-tailed Pigeons (*Columba fasciata*), which had invaded plum orchards to feed on green plums, were subjected to intensive harassment by gunfire and detonators. In June 1966, I tried broadcasting their own protest sounds—sounds not actually of distress or alarm—and found they were quite responsive. In the spring of 1967, due to a poor crop of plums, the growers did not harass the pigeons with gunfire and detonators and, in June, these birds did not respond to the same protest sound I had used so successfully in 1966. Except for the harassment in the spring of 1966, conditions for the two years were very similar. Obviously, in 1966 the preconditioning had affected my study. To test this possibility, I subjected a flock of 300 Band-tails that fed in a barley field of about 20 acres to the intense acoustic harassment of gunfire, shellcrackers, and pigeons' protest sounds. Initially, on 8 June, the birds refused to move even at ranges of only 25 yards. At the end of the first day, they responded occasionally to one or more of the sounds at ranges up to 75 yards but did not leave the field. By 1100 hours on 9 June, they began responding quite well to their protest sounds and, by the end of the day, they were responding at ranges of 175 to 200 yards and many left the area. Apparently, some conditioning was developing.

The birds were unmolested on 10 June. When I resumed the experiment on 11 June, the birds failed to respond. During the one-day respite from harassment, they had reverted to their pretreatment response level. The results indicated that two days of harassment was not enough to make the pigeons respond. In 1966, although they had apparently become used to the noises that had been harassing them for about 30 days, they responded well to their protest sounds. These experiments and my experiments with other species revealed that about four days of exposure to alarm sounds is necessary before depredating populations will respond consistently to their own sounds and be reduced to significant levels. In other words, the pigeon will become inured to anomalous sounds the more it hears them, but it will respond better to its own sounds the more it hears them. The studies with the Band-tailed Pigeons convince me that even the most refractory species can be conditioned to respond to certain acoustic stimuli. The trick is to discover the proper stimuli.

Possibly the inhibitory resistance of the central nervous system decreases after the fourth day, allowing the bird to respond. Or possibly the repeated exposure to biologically significant sounds develops a distinct neurosis. The fact that most species inure to anomalous sounds by the fourth day indicates that the inhibitory mechanism is functioning normally. This area of investigation needs additional basic research.

I made many of my experiments on birds which had established firm feeding habits in certain areas and were reluctant to deviate from their entrenched behavior patterns. I first studied each species to determine its normal behavior patterns and to record its most effective alarm sounds. I usually tested the species by using its own survival sounds recorded in the field; occasionally I used sounds recorded in the laboratory. The sounds from captive birds were generally not as effective as those made in the field and I attributed this both to the absence of natural background sounds and the presence of unnatural conditions which affected the caged birds' responses. Acoustic phenomena, such as long reverberation periods and standing waves that are sometimes present in enclosures (Tremaine, 1959), may adversely affect the quality of the laboratory recordings or introduce characteristics foreign to the birds' hearing. On the other hand, the normal background sounds in field recordings aided in eliciting responses from free birds. Birds accustomed to feeding or roosting near busy highways ignored the traffic noises in my recordings.

The duration and rhythm of sound emissions, necessary to elicit a response, varied with the species: for most small passerines and many others, a duration of five seconds was sufficient; for the more refractory species, 45 to 60 seconds. The rhythm, determined empirically for each species with adjustment for local conditions, ranged from an exposure of every 10 to 15 minutes in routine projections to every three minutes for refractory species in the early phase of a program. I found that the closer the feeding area was to suitable cover or perches the sooner the birds would return.

The purpose of any bird-control program is to reduce a population of depredating species from a feeding area or to clear birds from a roosting area. During the first two days of a control program, certain species are unusually persistent in returning to cleared areas after being evicted by their alarm sounds. On several occasions Starlings persisted in returning to feeding areas even in the face of intensive sound. They seemed to fly directly toward my speakers. After they had entered the feeding area — a vineyard — they responded normally to the next emission of sound (Boudreau, 1960). This site-tenacity usually appears on the first and second day of the program. If the investigator is equally persistent in projecting the alarm sounds, the population of the target species will decrease during the third day and continue to decrease thereafter until the lowest level is reached (Boudreau and Royall, 1963; see Figure 4).

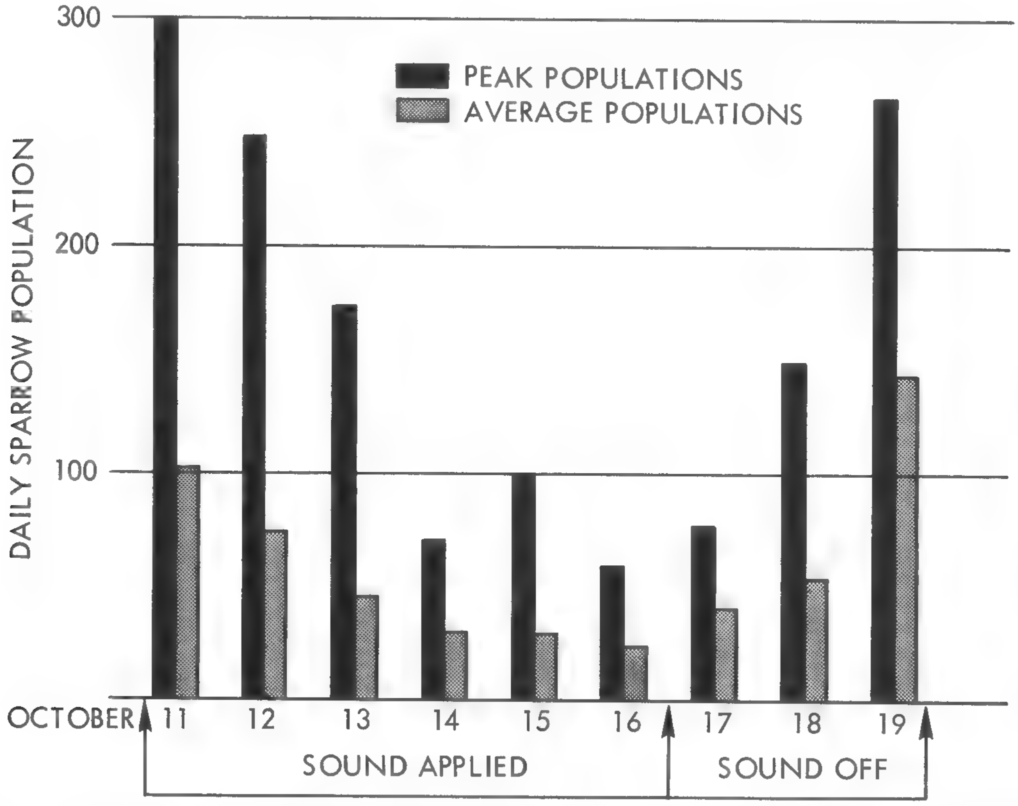

Figure 4. Reduction in population of inveterate House Sparrows, feeding in a millet field, in response to periodic projections of their alarm sound. Peak populations were noted in early morning and late afternoon. The population increased when the sound was removed.

The population of all the species tested dropped in three or four days, often as much as 80 per cent or more in four days, a useful criterion in evaluating the effectiveness of a control program.

Birds displayed the same persistence in returning to an established roost. Intermittent applications of pertinent alarm sounds during the early evening hours—before the light intensity lowers—often clears a roost in three or four nights. Such actions should be expected in birds whose behavior is largely mechanical, stereotyped, and instinctive (Welty, 1963).

Although I have noted delayed responses in some species, the birds generally respond to their alarm sounds immediately or nearly so. Horned Larks commonly delay 20 to 25 seconds after the sounds cease. Band-tailed Pigeons and gulls may delay from 7 to 10 seconds. Usually, delayed responses occur in the beginning of a control program, and as the birds condition to the sound stimulus, they react more quickly. Apparently, the delayed responses, identified with the more refractory species, are a function of the neural inhibitors.

Large flocks of birds respond more readily to their alarm sounds than do isolated individuals of the same species. The results are best when a flock numbers five or more. For example, three marked House Sparrows consistently ignored their alarm sounds when they were alone, yet responded readily when associated with three or more other House Sparrows. We might speculate that certain refractory individuals require a visual reinforcement—the flushing of a more timid bird—before they too can respond.

There is considerable evidence that a given flock of a species, particularly of the more refractory species, consists of several factions, each with a different response level to alarm stimuli. After prior conditioning, large segments in a flock of gulls or Band-tailed Pigeons regularly respond to the initial notes of their alarm sounds; the remainder leave in small groups at intervals of several seconds. Often a prolonged emission of one minute is required to clear an area of gulls, which flush as their response levels are lowered, with the boldest group leaving last. Obviously, individuals of a species are not stereotyped insofar as their response levels are concerned. The precise motivation behind this prolonged response pattern is not clear. It may be visual cuing or it may be that reflex responses and/or the interpretation of the significance of a sound is quicker in some individuals than in others. This behavior would constitute an interesting study for neurophysiologists and animal psychologists.

We have determined the level of the acoustic stimulus, required to elicit responses from birds under normal conditions, for only a few species. These levels vary with the species: Lesser Goldfinches (*Spinus psaltria*) respond to their alarm sounds at a sound-pressure level of three decibels above the ambient noise level. The human ear can detect changes in sound intensities of slightly less than three decibels. The Western Gull (*Larus occidentalis*), although it became attentive at lower intensities, responded only when the alarm stimulus reached 10 db over the ambient noise. Band-tailed Pigeons, feeding in a mowed barley field, failed to respond at sound levels of 30 db above ambient noise.

The size of the egg-clutch, regarded as an indication of a species' vulnerability to natural predation, is a rough guide to a species' tendency to respond to a sound stimulus. Predation is not an important factor in the survival of a species which lays only one egg; hence these birds have no well-developed alarm sounds or alarm responses. I have never yet elicited a valid alarm sound from any of the different albatrosses or doves and pigeons that I have studied. Members of both the Diomedeidae and Columbidae have exceptionally high response levels. In fact I have had to push an albatross to move it from its nest and I have actually driven a car over Band-tailed Pigeons picking up grit on a road. Shotguns and rifles, fired directly into a feeding flock of Band-tails, often fail to move them. The foregoing experiments with Band-tails showed that intensive high-level harassment will lower their response level and force them to react.

Startle Responses

A startle response is a sudden flushing of a bird on hearing any strange sound. Most, but not all, species try to escape when they hear a foreign sound for the first few times, illustrating how dependent birds are on hearing for survival. Usually, sounds with a sharp onset time—e.g., a shotgun blast—elicit escape behavior better than sounds with slow onset times—an approaching airplane. The sound with the gradual onset time allows the bird to adjust to the strange stimulus and, if it does not contain certain alarm parameters, the bird, except for becoming temporarily alert or attentive, ignores it.

Percussion sounds of all types have sharp onset times and produce initial responses, but with a little practice the birds adjust even to these and will no longer react. Nearly all species adjust to anomalous noises in time, some faster than others. I noted a rapid inurement to strange sounds in western House Finches, House Sparrows, various blackbirds, Brown-headed Cowbirds, Horned Larks, and various gulls. House Sparrows and House Finches in flocks began to adjust to gunfire and detonator noise after six consecutive exposures at four-minute intervals, and all had adjusted after about the fifteenth exposure. The time required to develop complete inurement in any species varies but is closely related to the time interval between each exposure to a certain noise and perhaps also to the bird's previous experience with that noise. Certain physiological drives—hunger, mating, and such—may induce temporary boldness in birds, causing them to adjust to strange sounds more rapidly than they normally would. Long intervals of silence between exposures delay inurement; short intervals encourage it.

Seasoned birds, having become adjusted to detonator explosions, seldom respond to shotgun fire consistently unless the weapon is aimed directly at them. In this case, the birds seem to be responding to the pellets striking near them rather than to the explosion itself. Shots fired into the air at the same range fail to move the birds. A .22 caliber rifle is often more effective than a shotgun for dispersing seasoned birds and many farmers use this method. Although the initial explosion of the rifle is not loud, the sound of the bullet traveling over the birds motivates a response, yet sooner or later the birds adjust to it. Rifle fire used sparingly obtains the best results.

The success of a program of killing or wounding birds by gunfire or any other method depends on the species involved. A wounded House Sparrow or Band-tailed Pigeon fluttering on the ground arouses no response from the rest of the flock feeding nearby. Drugged sparrows, shrieking in the throes of convulsions, are ignored by other sparrows. In many species—e.g., blackbirds—the sight of a bird in physical distress arouses curiosity and others of the species gather round the stricken bird—a situation hardly desirable in a bird-control program.

In assessing the value of any acoustic stimulus one must disregard startle responses. The time required for birds to adjust to a repetition of strange sounds varies with species and conditions and may range from less than one hour to five days. If one obtains consistent responses to a given sound after four days, he should be encouraged to continue the test for a longer period.

Interspecific Responses

Because only rarely is a single species involved in a bird problem, interspecific responses warrant more discussion. As the search continues for a panacea applicable to all bird problems, the prospects of finding such a solution appear dim indeed. Nevertheless we must explore even minor leads and a critical investigation of interspecific responses may provide some clues.

In fruit orchards, vineyards, and airports ten or more species may be the offenders. Even though one or two gregarious species usually predominate, we cannot neglect the associated species. One California vineyard provided an excellent laboratory in which to study interspecific responses. California Quail (*Lophortyx californicus*), Scrub Jays (*Aphelocoma coerulescens*), Robins, Western Bluebirds, Western Tanagers (*Piranga ludoviciana*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), Brown Towhees (*P. fuscus*), and House Finches were all feeding on grapes. Oregon Juncos (*Junco oreganus*) and Lesser Goldfinches were present in small flocks but I was not sure they were eating the grapes.

Since House Finches were most important numerically, I used only their alarm sounds as stimuli. Initially, although there was little similarity in the alarm sounds of the various species, all the species present responded. I disregarded this behavior. I first noted a failure to respond in the Robins, then the tanagers, quail, jays, towhees, and goldfinches in that order. The juncos and bluebirds responded sporadically for several days but only when the House Finches were present. The response of the target species must have motivated the responses of the associated species.

Other experiments suggest that a similarity in alarm sounds may be important in eliciting responses from different species, particularly members of the same family. I tested the alarm sound of a Glaucous-winged Gull on flocks of gulls, both mixed and segregated, feeding in refuse dumps. All the gulls—Western Gulls, Herring Gulls (*Larus argentatus*), Glaucous-winged Gulls, California Gulls (*L. californicus*), and Ring-billed Gulls (*L. delawarensis*)—responded consistently. Since I have not recorded valid alarm sounds of all the gulls mentioned, I am unable to compare them, but I suspect that a detailed analysis of each—by recently developed techniques—will show critical parameters common to all. Seubert (1964) mentions that Giban, in France, believes that the distress sound of either a Jackdaw (*Corvus monedula*), Rook (*C. frugilegus*), or Carrion Crow would be effective in preventing crop depredations by the other two species. Careful analyses of icterid alarm sounds may reveal some interesting similarities and explain the interspecific responses so common in blackbirds.

Our present knowledge of interspecific responses to the alarm sound of one species indicates that visual cues are responsible in some cases, a similarity of acoustic alarm parameters in others, and probably both in many instances.

Attraction to Strange Sounds

An interesting phenomenon often observed in the field is the temporary attraction of animals to strange sounds, termed "positive phonotaxis" by European investigators (Dumortier, 1963). Not all researchers agree on this term; some suggest that "phonoresponse" is more appropriate. I shall use phonotaxis—*positive* phonotaxis for the temporary attraction of an animal to a strange sound source and *negative* phonotaxis for the retreat of an animal from a strange sound source.

Positive phonotaxis is often used to attract fish, birds, or mammals. It is best displayed in birds by the response of certain species to their own or another species' distress sounds—e.g., blackbirds—and it is well developed in species—crows and jays—which engage in mobbing behavior. It is not well developed in many non-gregarious species. I have never observed positive phonotaxis in any of the doves and pigeons.

Hordes of cowbirds hovered six feet above my head when I projected Starling distress sounds in a feed lot for cattle. A male Bullock's Oriole (*Icterus bullockii*), protesting his removal from a mist net, attracted other orioles of both sexes. Mockingbirds quickly investigate strange sounds. Crude imitations of rabbit distress sounds will lure hawks, owls, and mammalian predators within rifle or camera range. In fact, "varmint calling" is a popular activity in many parts of the West. Fortunately most of the varmint callers are poor shots or have exchanged their guns for cameras. Horses, cattle, and often deer are attracted to the initial emissions of strange sounds. The young of these animals respond more readily than the adults; the milch strains of cattle much more readily than beef breeds. Field ornithologists use "hand-kissing" to attract small passerines. Usually, by the third or fourth consecutive exposure to these sounds the animals begin to ignore them.

Many animals, particularly birds, are attracted to the source of their specific communication sounds which are biologically significant, such as territorial, feeding, and assembly sounds. The responses to these significant sounds differ from those cited above in that they may occur repeatedly. Territorial songs consistently attract males, and even females, of numerous species, particularly during the breeding season.

I once demonstrated for a television station in San Francisco the influence of communication sounds on bird behavior. By projecting a gull alarm sound briefly I cleared a garbage dump of about 10,000 gulls of mixed species. They moved to a dump about a mile away. After about a ten-minute interval, by projecting their feeding sound toward the distant dump, I recalled most of them. When they had arrived back and were circling overhead, I again projected the alarm call and cleared the dump a second time.

The information the sound conveys—a predator to mob, the presence of a mate or a rival, food to eat, or any number of other things—determines whether or not phonotaxis occurs. In some instances there may be similarities in the communication vocalizations of the animal and the parameters of the sound. Though we know little about the parameters of animal sounds, we cannot discount the possibilities that such similarities exist. In mammals, curiosity is often the only explanation for some positive phonotaxis; agonistic tendencies account for others.

Positive phonotaxis caused me some embarrassment—and the observers great amusement—several times during my early studies when I tried to demonstrate the effectiveness of the distress sounds I was then using to repel birds. The birds flew toward the sound rather than away from it! My composure was regained, however, when the birds left the area after the third projection of the sound. I have seldom observed positive phonotaxis in response to a bird's valid alarm sound.

Bird Sound Analyses and Syntheses

Until now our analytical equipment has consisted mainly of oscilloscopes and spectrographs, both of which, though revealing, leave much to be desired insofar as detailed analyses of sounds are concerned. A very recent development is a technique by which we may precisely analyze animal sounds and identify their critical components and characteristics. It has been my privilege to work with Dr. John L. Stewart of Santa Rita Technology, Inc., Menlo Park, California, who has designed and built instruments that have greatly facilitated these analyses. His analog ear (Stewart, 1966)—an electronic analog of the human cochlea—is invaluable in the analyses of human speech and, with some modification, has been successfully adapted for use with bird sounds. Another exciting step in analyzing and identifying bird sounds is the contour spectrograph or voice-print, the acoustic counterpart of the fingerprint which, hopefully, may enable us to identify not only the sound of a species but possibly the individual bird emitting the sound.

I have mentioned the characteristics of a few bird alarm sounds as revealed by our analyses. Since we have recorded the alarm vocalizations of relatively few species, we have not yet determined the ultimate high and low limits of the pertinent frequencies or other parameters. The data we have accumulated, up to July 1967, indicate that a considerable diversity exists in fundamental and modulation frequencies, onset rate, repetition rate, and chirp duration, and that certain combinations of these parameters are species-typical. Once we recognize these characteristics, we can synthesize them electronically. Synthesized bird-alarm sounds contain only the critical parameters identified with each species and have no resemblance to the actual alarm sounds. Most of the synthetic sounds resemble a buzzer.

My first experience with synthetic alarm sounds was with House Sparrows feeding in a baited area. I first tested these birds with their natural alarm sounds. They responded to 94 per cent of the emissions. When I projected the synthesized versions of their natural alarm sounds, they responded, during the several days of consecutive exposures, to 83 per cent of the emissions. These results were very encouraging. There was no interspecific response to either the natural or synthetic sounds; the Mourning Doves (*Zenaidura macroura*) and Brown Towhees, both feeding on the bait, ignored them all.

In a brief test using the synthesized alarm sound of a Starling on flocks of Starlings, Brewer's Blackbirds (*Euphagus cyanocephalus*), Tricolored Blackbirds (*Agelaius tricolor*), and feral pigeons, only the target species responded the first day. By the end of the third day all the others were responding, apparently having been conditioned to the response of the Starlings. Killdeer (*Charadrius vociferus*), numerous in the vicinity, ignored the sounds throughout the test.

In a study of Red-winged Blackbirds flying to and from their winter roosts over an air base, their natural alarm sounds, so successful on blackbirds feeding on the ground, produced little or no variation in their flight pattern, indicating that the response threshold rises once the birds are in an escape mode—in this case, flight. I did notice that the birds reacted to T-38 jets and that they made spectacular attempts to evade T-37 jets. We isolated the compressor noise from the T-37 jet and projected this sound to the airborne blackbirds. At levels above 73 db they detoured widely around the sound source. Then we broadcast a synthesized version of this same sound and caused even greater deviations in the flight pattern. The T-37 sound, natural or synthetic, had no effect on the other species in the vicinity—Loggerhead Shrikes, Robins, Brown-headed Cowbirds, and Eastern Meadowlarks (*Sturnella magna*).

We do not know the precise neurophysiological and psychological reactions to the T-37 sounds in the blackbirds. This must await the development of more precise monitoring methods. One can speculate that the T-37 sounds affect certain portions of the bird's cochlea and result in annoyance or even pain. There is also the possibility that the sound of the T-37 masked or jammed the normal flight sounds of the birds, and they were trying to reach areas where the sound intensity was tolerable.

The superiority of the synthetic T-37 sounds over the natural version indicates that we may expect "supernormal" responses from birds to pure and concentrated sound stimuli similar to the reported responses of various insects to chemicals. The synthesized versions of the T-37 noise and the natural alarm sounds were "pure stimuli" consisting only of pertinent frequency and modulation combinations and devoid of harmonics and extraneous noises.

It is too early and we have too little data for conclusions, but the concept of synthetic acoustic stimuli and responses thereto open a vast and fascinating field.

Discussion

In field investigations one constantly observes the variance of birds' behavior patterns in their responses to different stimuli. We may trace much of this variance to adaptive radiation and discover the causes of other behavior by studying the pertinent species. Yet, certain aspects of bird behavior and the underlying motivations defy interpretation. Eventually, as we continue laboratory and field research, we may understand these enigmas.

The increasing hazard of birds to aircraft provided the impetus for undertaking bird behavior studies after we realized that existing knowledge could contribute very little toward a solution of the problems. At present, bird-aircraft problems are being created faster than we are developing solutions for them. We can reduce populations in or near airports and reduce the possibility of bird-aircraft collisions. We must now find a method to repel *all* species from the entire flight path of all aircraft, including the new supersonic airliners. Conceivably, acoustic devices mounted on the aircraft may be effective provided that (1) jets fly at sub-sonic speeds through altitudes used by birds and (2) we can find a universal acoustic stimulus. The latter provision is visionary in view of the species-specificity of the natural alarm sounds but we might discover and develop synthetic sounds with universally effective parameters. Our brief experiments in the use of synthetic sounds have already provided fascinating clues which we should explore further.

In this problem of bird control we must consider only non-lethal methods for no informed person would agree to the massive extermination proposed by the ecologically ignorant. Among other alternatives is the possibility of using electromagnetic waves. So far we know little of the effect of these waves on birds (Nelson and Seubert, 1966). The solution for bird-aircraft problems will test the ingenuity of biologists and engineers alike.

Summary

Extensive field research in bird-control programs reveals that considerable diversity exists in the nature of the alarm sounds of birds and their responses thereto. Some species have no alarm sounds; most gregarious species do. Birds respond much better to their alarm sounds than they do to their distress vocalizations. Response threshold levels vary with conditions and may change from low to high in a few seconds. At high threshold levels birds are reluctant to respond to any stimuli. Regional dialects in birds' alarm sounds have not yet been detected. Birds quickly become inured to anomalous noises which are therefore of dubious value for control purposes. Interspecific responses to alarm stimuli, often noted, appear to result from visual conditioning of associated species to the responses of the target species. Proper use of alarm sounds results in the reduction of the population by 80 per cent or more within four days. Positive phonotaxis, the attraction of an animal to a strange sound, is observed in response to distress signals but rarely to alarm sounds. Initial tests with synthetic alarm sounds indicate that supernormal responses may be expected.

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THE SINGING ASSEMBLIES OF LITTLE HERMITS

D. W. Snow

In forest hummingbirds of the genus *Phaethornis* a well known but nonetheless puzzling feature of behavior is the singing assemblies of males. Brewster and Chapman (1895) described the singing assemblies in the Green Hermit (*P. guy*), Davis (1934) in the Reddish Hermit (*P. ruber*), and Nicholson (1931) and Davis (1934) in the Long-tailed Hermit (*P. superciliosus*), while Skutch (1951) and Arp (1957) gave detailed accounts of this behavior in the Little Hermit (*P. longuemareus*). This paper, based on observations that Mrs. Snow and I made on Little Hermits in the Northern Range of Trinidad from 1956 to 1963, mainly in 1959-1961, is concerned primarily with the song of this very small hummingbird.

I do not claim in this paper to clarify the function of the assemblies any more than have the authors of earlier papers. The behavior has puzzled all observers, partly because of the extremely rapid movements of the birds and partly because the sexes are hardly distinguishable in the field. Birds collected at the assemblies have on examination all turned out to be males. Thus the assumption, which I believe correct, is that the singing assemblies are "leks," comprised of males, which the females visit for mating. A somewhat parallel behavior occurs in manakins (Pipridae)—see, for example, the recent review of the subject by Sick (1967).

The Little Hermit is extremely small, even for a hummingbird. Its weight averages just over three grams. Like other members of its genus it is rather dull-colored — brownish above and buff below, with a dark eye-stripe and blackish throat. The long central tail-feathers are tipped with white. The long, decurved bill is dark except for the basal part of the lower mandible and the gape which are yellow (Plate I).

Little Hermits are more abundant than any other hummingbird throughout much of the Trinidad forest. They spend most of their time inside the forest or along the edges, within a few feet of the ground, sucking nectar from the flowers of a large variety of herbs, shrubs, trees, vines, and epiphytes, as well as taking insect food. In spite of their abundance they are so inconspicuous and their movements are so quick that one rarely has an opportunity to watch one for long, except at the leks or singing grounds. In common with other hummingbirds in Trinidad, they breed from December to June—that is, from about a month before the dry season begins until about a month after it ends (Snow and Snow, 1964). The nest, suspended in the fashion typical of hermits from the tip of a leaf or fern frond, usually is very difficult to see. In spite of the birds' abundance we found only eight occupied nests in the course of over four years' field work. It seems very probable, though critical observations are lacking, that only the female is associated with the nest (Skutch, 1951).

The Singing Grounds

My first experience with a singing assembly of Little Hermits was on 25 February 1956, at about 2,300 feet up on a ridge of the Northern Range of Trinidad. In a part of the forest where the undergrowth was rather thick and tangled, I found myself surrounded by the sound of many squeaky, chittering songs which seemed to rise from the ground all around me. With a little patience I discovered that these songs came from a group of Little Hermits, each of which was perched in the undergrowth about a foot above the ground and about ten yards or so from its nearest neighbors. The whole assemblage occupied an area of perhaps 100 by 30 yards. In spite of the poor light, the twiggy undergrowth, and the minute size of the birds the singers betrayed themselves in the end by a continuous up and down wagging of their white-tipped tails.

Later, I found that in hilly country the singing grounds of the Little Hermit are usually on a ridge, similar to the one where I had my first experience, and that in parts of the Northern Range where the birds are very common, the singing assemblies may be almost continuous for considerable distances. Indeed, one may walk for hundreds of yards along the main ridge without being out of earshot of the songs of these little birds. Flat country suits them too. I found singing assemblies in an absolutely level, swampy forest near the eastern side of the island. And in every situation, no matter where it is, a certain amount of twiggy undergrowth is necessary to provide perches and cover for the singing birds. Arp (1957) suggested, from his observations, that singing grounds have to be on south-facing slopes, since song and display apparently depend on a certain level of illumination. Though I did not study this point, the main singing grounds which I observed were in fact on slopes which faced predominantly south.

The singing grounds are traditional, and there is every reason to believe that they persist indefinitely as long as the forest is suitable. One assemblage, on a steep ridge behind our house in the Arima Valley, was occupied in 1957, the year I first climbed the ridge. It was still occupied in 1963; and at least from 1959, when we began our detailed observations, onwards, the same perches were occupied year after year. I never had any evidence of a singing assembly changing its site.

The Daily and Seasonal Pattern of Activity

As I have mentioned already, the Little Hermits in the Northern Range of Trinidad breed from December to June. During the period of post-breeding molt — from July to September — they cease singing and displaying. The singing grounds are deserted. The birds begin to re-occupy the grounds in November, and by the end of the month or by early December most of the old birds are back at their perches. There they maintain their activity, with no marked fluctuations, until the following June. Activity declines in July, when most of the adults come into molt, and has practically ceased by the end of the month.

On several occasions I saw new, unestablished birds appear at the singing assemblies about April, and I assumed that these were young birds of the previous breeding season. A few other newcomers appeared in June and July, right at the end of the season. Their songs were rather undeveloped and I therefore surmised that they were young, possibly six months old, from the early nestings of that season.

Plate I. A Little Hermit feeding at the flower of an introduced tree, the Pride of Burma (*Amherstia nobilis*), in the Arima Valley, Trinidad. Photograph by B. Brower Hall.

Throughout the singing season, each individual is on its perch for the greater part of the day. Our hour-long watches at a number of song perches between 0700 and 0900 showed that at this time of day the birds were present from 67 to 92 per cent of the time.

We maintained a continuous watch on the perch of one individual from the time it arrived in the morning at 0641 until it left in the late afternoon at 1717. The bird left its perch 48 times that day. Twenty-two of its absences lasted under two minutes, and only five of them lasted over eight minutes. The bird sat on its perch a total of 444 minutes, or 70 per cent of the time, and the length of periods when it was on its perch averaged about nine minutes.

The birds sing more or less without a break all the time they are on their perches, at the rate of about 30 songs per minute. The maximum recorded was 32 per minute. Thus the singing is divided into a number of song-bouts, corresponding to the periods when the bird is present. Typically, at the beginning of a song-bout the songs are uttered in rapid succession, and towards the end of the bout the frequency falls off a little and the songs may be incomplete. The bird becomes restless; it may stretch and gape; and eventually, often after a short aerial display, it flies off.

The output of song is remarkable. The particular bird which we watched all day sang for approximately 400 of the 444 minutes it was on the perch. Our large number of counts revealed that the songs were uttered at an average rate of one every two seconds, a total of about 12,000 songs in a day. And we had no reason to suppose that this individual was any more persistent than the other singers.

Song Variation

The song is a brief, high-pitched, chittering phrase, usually lasting from 1 to 1.5 seconds, with a fundamental frequency mainly between 5,000 and 9,000 cycles per second (Figures 1 and 2). To my ear a typical utterance sounds something like *ee-wee tiddly weet,* and this three-part rendering, though far from perfect, brings out some of the main characteristics of the song-type prevalent in Little Hermits in the Arima Valley of Trinidad. These characteristics are as follows: In Part 1, one or two introductory notes (the *ee-wee*), longer than any other notes of the song, showing in spectrograms as a U-shaped section followed by a downward slur. In Part 2, a complex central phrase (the *tiddly*), rather variable but, when well developed as in Males K and P in Figure 1, showing a succession of extremely rapid changes of pitch. In Part 3, a terminal, lower-pitched note (the *weet*), occasionally repeated, rising and falling sharply in pitch and with distinct harmonics which are lacking in all the other notes.

There is a good deal of individual variation in song within this general pattern. Though Part 1 may consist of just one rather than two notes, it is apparently never omitted altogether. Part 2 is very variable but is apparently never omitted. Part 3 may be omitted altogether. Each individual, however, has a fixed song which is variable only to the extent that, when the motivation for singing is low, some elements, especially the terminal *weet,* may be dropped out.

The most striking thing about the different song-types is that birds with neighboring perches tend to have similar songs. Thus within a singing assembly there are typically a number of groups of birds each of which has a song-type recognizably different from the songs of the other groups. Figure 3 is a sketch map of the singing assembly where I made most of my detailed observa-

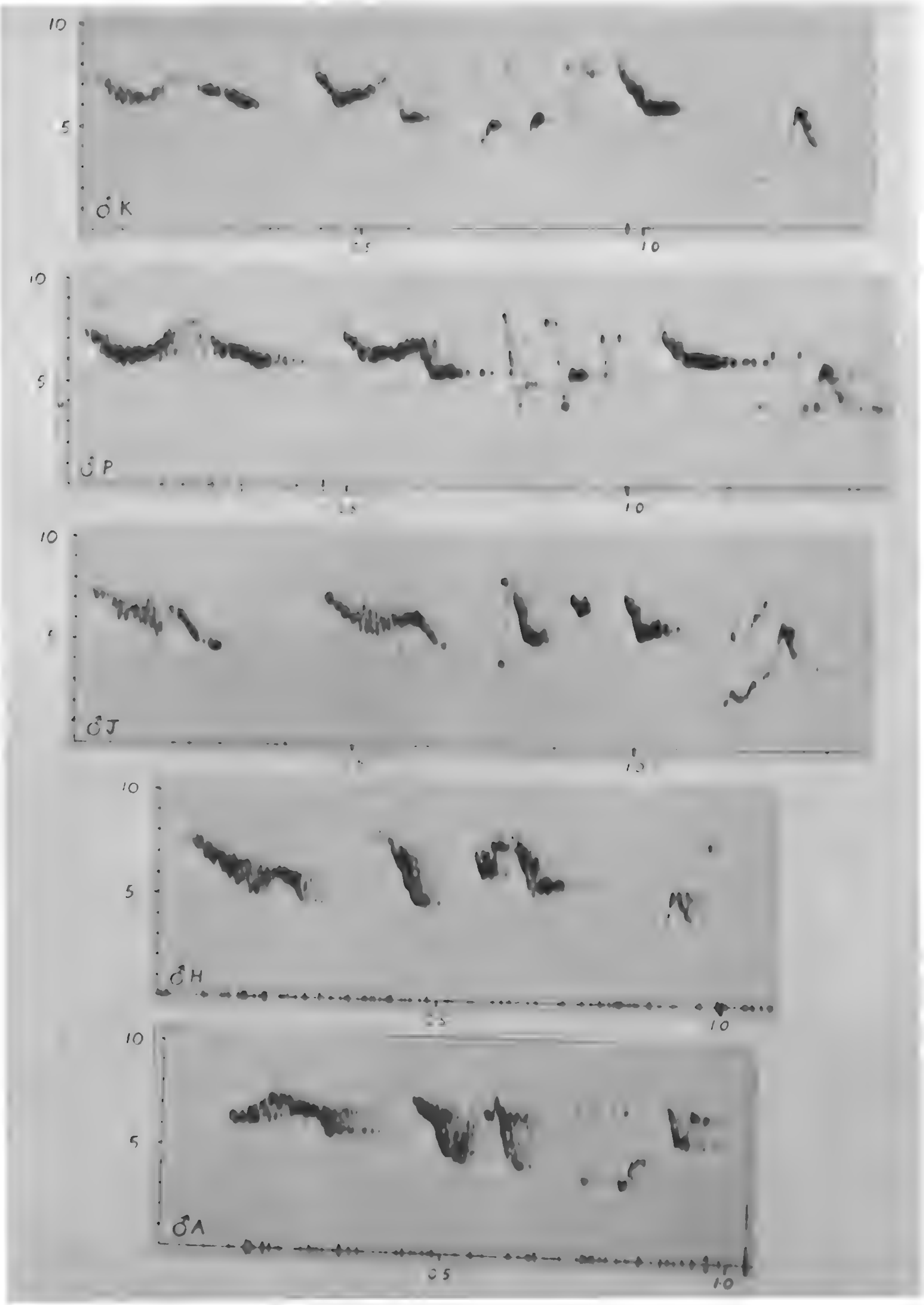

Figure 1. Spectrograms of the songs of five Little Hermits from the singing ground mapped in Figure 3. Vertical scale—kilocycles per second; horizontal scale, seconds. Note that Males K and P closely resemble each other as do Males G, H, and I. Male J, possibly a young bird, is different from both groups, yet most like Males G, H, and I.

tions, and Figure 1 shows spectrograms of the songs of five birds from this assembly. The very close resemblance between the songs of Males K and P, from the same group, is apparent. Male J, possibly a young bird recently settled, occupied a position between this group and the group of Males G, H, and I. It seems that the form of the notes in both the first and second parts of the song of Male J approximates that of the latter group. Figure 2 illustrates the songs of four individuals in another singing assembly, and again the extraordinary similarity of the songs of Males a and b, which had neighboring perches, contrasts with the songs of two Males, c and d, from other parts of the singing ground.

Figure 3 demonstrates that birds with similar songs had perches mainly from 20 to 30 feet apart. Some outlying members of the groups were as close to members of different song groups as they were to members of their own, but to a large extent the song groups followed the spatial groupings of the song perches, which probably depended on the distribution of suitable perches and cover. This figure shows the distribution of song-types as they were early in 1960 when the singing assembly was in full activity. This distribution persisted virtually unchanged until July 1961, the end of the singing season. When I revisited the singing grounds in January 1963, three years after the map was made, nearly all the song-types which I was able to check were the same. I recorded some minor alterations however. On a new song perch, first occupied in November 1960, the occupant, Male L, in the beginning sang a song similar to that of Males K, O, etc.; later, in February 1961, the song at this perch was the same type as that of Males G, H, and I. Was there a different bird on Perch L? The songs at Perches E, F, and some of the outlying positions were less stable than the rest, and these perches were perhaps occupied by a succession of different birds. Song Perch Q was first occupied in June 1961 and the song at that time was rather simple; but in January 1963 the bird at this perch was singing a song identical to that of Males K, O, etc. Almost certainly the bird I recorded in June 1961 was a young one establishing itself.

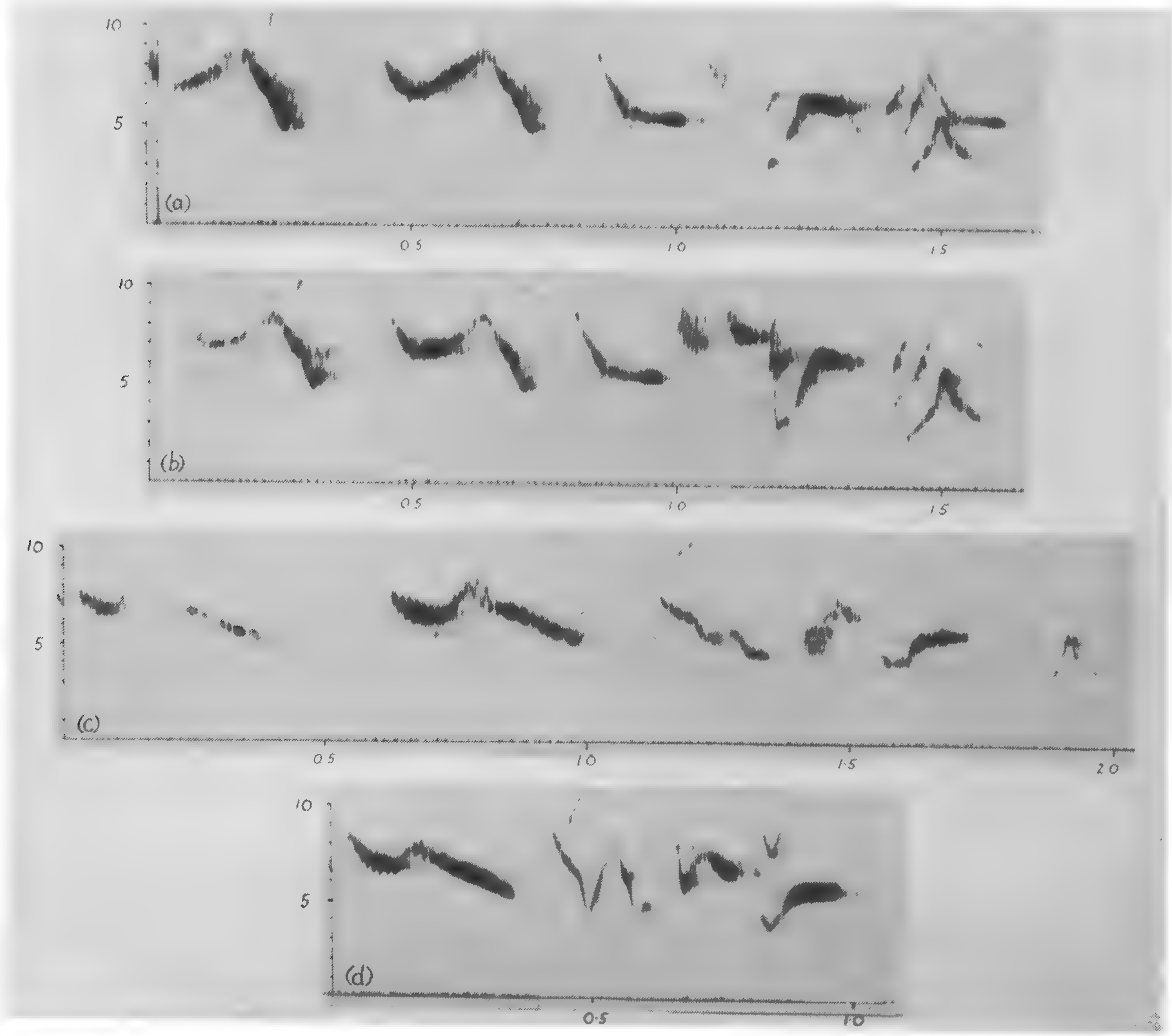

Figure 2. Spectrograms of the songs of four Little Hermits from a singing ground about three miles from that shown in Figure 3. Birds a and b occupied neighboring song perches; birds c and d were from other parts of the singing ground.

The persistence of the singing behavior of the individual birds was strikingly illustrated by Male K (Figure 1). He sang a song typical of his group, but tended to omit the terminal *weet* much more often than the other birds in that group, more and more frequently towards the end of a song-bout and also more and more frequently as the day wore on. A large number of counts throughout the day on 18 February 1960 showed that the incidence of the terminal *weet* declined fairly steadily from 80 per cent between 0600 and 0700 to 22 per cent between 1600 and 1700, while only 4 per cent of the few songs heard after 1700 included it. Three years later, in January 1963, the same song-type was being sung from this same perch. In contrast to the other birds in the group, which were singing full songs, the terminal *weet* was being omitted with about the same frequency as it had been three years before: in a bout of song at 0715, 87 per cent of the songs included the terminal *weet*.

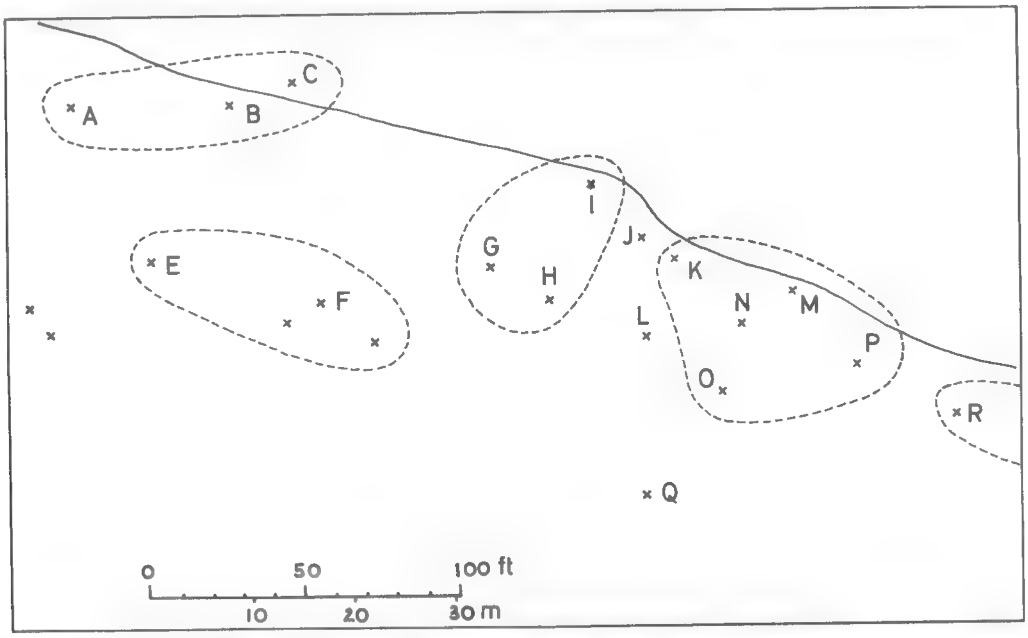

Figure 3. Distribution of song perches of Little Hermits in the central part of the singing ground where the recordings in Figure 1 were made, showing groups of birds singing recognizably different songs. The diagonal line indicates the crest of a steep-sided ridge with the song perches distributed mostly a little way down the south-facing slope. Letters mark song perches permanently occupied during the period of study. There were 28 in all. Crosses without letters indicate perches not consistently occupied.

From these and similar observations, there can hardly be any doubt that individual Little Hermits, when they acquire perches at a singing ground, develop a song similar to those of their nearest neighbors, and that, once acquired, this song persists unchanged. The distribution of suitable cover for song perches and the relatively long life of the adults are probably sufficient to account for the stability of the song groups at the singing ground over the years. The situation is to some extent parallel to that found in the Chaffinch (*Fringilla coelebs*) and other passerine species which have local song dialects (Thorpe, 1958), but on a much smaller scale, the dialects being confined to areas measured in hundreds of square yards rather than in hundreds of square miles.

Other Displays

Periodically, Little Hermits perform aerial displays above or in the vicinity of their song perches. These do not last very long, and some parts of them, being exceedingly rapid, are difficult to observe accurately. Since the sexes are for practical purposes indistinguishable and the birds were not individually marked, I cannot elucidate the significance of the displays. Thus, I confine the following account to a brief description of the main movements supplemented by the observations of Skutch (1951) and Arp (1957).

The displays occur most frequently at the end of a singing bout. Characteristically, as the bird nears the end of a song-bout, it utters a few rather squeaky, hurried songs; then it may stretch on its perch and gape upwards. Finally, it rises from its perch, hovers, and may either fly straight off, presumably to feed, may move away slowly with its body upright, examining the undergrowth as it goes, or it may execute some striking aerial displays before departing. In the most usual display it holds the body horizontally with the neck stretched upwards, the tail pointing up, and the feet usually hanging down. The breast feathers may be fluffed out. In this boat-like posture the bird may move slowly for a few inches, then turn rapidly and move back the other way, and so on. This is often followed by one or more very rapid flicks downward towards the perch, each flick being accompanied by a soft *tock* after which the bird usually flies off. Whether the *tock* is vocal or mechanical, I cannot say.

In encounters which seem to be primarily aggressive, especially between males establishing themselves at a singing ground, chasing is frequent. Singing is intense, and a note very like the terminal *weet* may be uttered in flight. A perched bird, if approached aggressively by another, usually responds by intensifying its tail-wagging movements, fanning its tail, and gaping. Arp (1957) describes a low trilling uttered by both birds in such encounters, but I did not record this. Arp's account suggests that he was observing a singing assembly which was in a comparatively unsettled state, since his birds, when they stopped singing, regularly flew towards another bird, apparently aggressively. This was not usual in the singing assemblies where I made most of my observations. The boat-like flight and "tocking" do not seem to occur in aggressive encounters.

In encounters that appear to be primarily sexual, the display usually begins with one bird hovering in boat-like flight just over the other, which is perched. (I make no attempt here to say which bird is male or which bird is the "owner" of the perch.) The hovering bird may then make very rapid downward flicks, with a *tock* accompanying each flick, over the perched bird. Alternately, the two birds may change places in rapid succession. Or the perched bird may fly up and both birds move upwards, first one and then the other making little upward darts, as though they were attached by invisible threads. Skutch (1951) and Arp (1957) both describe variants of these maneuvers, the usual outcome of which is that, after some very confusing and rapid movements, both birds fly off.

Several times I observed birds, at the end of a song-bout, fly a little way from the perch and execute the downward flick, with *tock,* over a dead leaf. Arp also recorded this and mentioned that the leaf, or a piece of moss, was always the same one for each individual bird and tended to move in the slightest breeze. He also mentioned that a passing butterfly or a falling leaf might stimulate the display, suggesting that these observations not only show the importance of movement in stimulating display, but also help to explain the constant wagging of the white-tipped tail.

Skutch described two display sequences, apparently sexual, which took place away from a singing assembly. In one of these, in addition to the usual boat-like hovering posture with slow flights back and forth, the upper bird occasionally shot rapidly back and forth over a distance of a foot or two above the perched bird, making a loud buzzing noise with the wings.

We need many more observations and field experiments before the significance of these activities is clear, but I offer the following preliminary suggestions and hypotheses. Although no one has recorded copulation in the Little Hermit, it probably takes place on the display perch. This would be in agreement with what occurs in other "lek birds." Indeed, the singing assembly would be largely inexplicable if this were not the case.

The male must, therefore, first attract the female to his perch. Song achieves this, aided by the tail movements and perhaps, when the female is at close quarters, also by the gape. As Arp (1957) noted, the tail movements are intensified when another bird approaches a perched bird; and, in the undergrowth, the yellow gape may be more conspicuous than any part of the plumage. The female presumably approaches and hovers above the male. The male must then induce her to alight. This is probably the functional significance of the rapid change of place, which is sometimes seen between two birds at a perch, and is now sufficiently ritualized to occur at other times also—perhaps between two birds of the same sex.

The downward flick and *tock* of a hovering bird towards a perched bird is probably a precopulatory movement. When directed at a dead leaf or similar object, it may be redirected activity. The fact that such substitute objects are liable to shake in the breeze suggests that rapid tail-wagging by the female may be an important element in her soliciting behavior.

Finally, it seems significant that in each song-bout there is a gradual change from uninterrupted singing to more intermittent singing, accompanied by an increasing tendency to aerial displays as the bout draws to an end. It would seem that aggressive motivation is uppermost at the beginning and sexual motivation uppermost at the end of the bout.

There is ample scope for further field work on this species, which could lead to a more complete understanding of its complex social organization. Individual marking of birds, high-speed photography, and experiments using models will all be essential to such an investigation, as well as a more complete analysis of the song and other calls than is possible at this stage.

Summary

Singing assemblies of males are known in several species of hummingbirds of the genus *Phaethornis,* among them the Little Hermit (*P. longuemareus*). In the Northern Range of Trinidad, where this species is common, the assemblies are typically situated high up on the forested ridges. The singing grounds are traditional and within them the same song perches are occupied year after year.

The singing assemblies are active from November or early December to July when the post-breeding molt occurs. Throughout the active period, each male is at its perch for a high proportion of the daylight hours. One bird, for example, was present for 70 per cent of the entire time. While the bird is on its perch, it sings on the average of once every two seconds, or a total of about 12,000 songs per day.

The song, a high-pitched phrase lasting about one second, varies a good deal. Birds with neighboring perches tend to have similar song-types, and at one singing ground the distribution of the song-types persisted largely unchanged over a period of three years. This suggests that males, when they first acquire a song perch, develop a song similar to that of their nearest neighbors.

Several aerial displays are described and provisional suggestions made as to their probable significance. Much more detailed observation, and also

experimentation, will be necessary to clarify the relationships between the sexes and between the individual males at the singing assemblies.

Acknowledgments

I am grateful to Mr. C. A. Sutherland for making the sound spectrograms used in this paper and to Dr. R. C. Stein for helpful advice. The originals of these and other recordings are in the Cornell Library of Natural Sounds. B. Brower Hall very kindly allowed the use of his fine color photograph of a Little Hermit feeding (Plate I). I acknowledge with pleasure the help of my wife, especially in maintaining the continuous watch at one song perch throughout the daylight hours. The work was done while I was in receipt of NSF Grant G 4385.

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Common Loon, *Gavia immer*. Drawing by Walter J. Breckenridge.

OBSERVATIONS ON THE BEHAVIOR OF KITTLITZ'S SANDPLOVERS AT THE NEW YORK ZOOLOGICAL PARK

WILLIAM G. CONWAY AND JOSEPH BELL

Photographs by the authors

When we startle a bird on its ground nest, we expect it to jump up and run, stand and threaten, or fight. We take it for granted that certain ground-nesting species will perform a distraction display and call loudly. But when we startle a small plover, which is incubating its eggs in a sand-scrape, and it jumps up, kicks sand over its eggs so systematically that they disappear in six seconds, and then runs, we are impressed. Since 3 January 1965, we at the New York Zoological Park (the Bronx Zoo) have continued to be impressed by just such behavior in the Kittlitz's Sandplover (*Charadrius pecuarius*) as we startled one after the other on their nests and watched them jump up, hide their eggs with sand, and then run (see Figure 1).

Many birds customarily cover their eggs when leaving the nest. Some grebes pull aquatic vegetation over the eggs; some ducks, geese, and gallinaceous birds cover their eggs with down, feathers, or other nesting material. All these birds routinely use their bills. When surprised, however, they often leave without covering their eggs. The Kittlitz's Sandplover covers its eggs when startled, using its feet, and at the Zoo, only when startled by humans.

The Kittlitz's Sandplover is a small shorebird that nests throughout most of Africa, east and south of the Sahara and in Madagascar. Harris (1901), Hall (1958, 1959, 1960), Pitman (1965), and others, after studying this species in the field, reported on the curious habit it has of covering its eggs by kicking sand over them when surprised on its nest. Well aware of their findings we watched with great interest as pairs of sandplovers in our Aquatic Birds Building began digging nest-scrapes in the soft sand on the floor of their enclosures.

The enclosures, which the sandplovers share with several other species of birds, measure eight by six meters. They have a controlled temperature of from 20° to 30° C and are illuminated by daylight through the glass roof plus some necessary floodlighting for the unusually dark evenings in midwinter. Being open-fronted for exhibition purposes, the enclosures are ideal for photography except during the shortest days of winter—the time when the sandplovers often choose to nest. However, the chance to observe the birds from a distance of only 15 feet and the high speed of the new films compensate for the light problems.

Figure 1 (*above*). The Kittlitz's Sandplover at the New York Zoological Park, caught in the very unplover-like act of kicking sand over its eggs. This curious behavior occurs when the bird is startled while incubating its eggs in its cup-like nest in the sand.

Figure 2 (*below*). The nest and eggs of the Kittlitz's Sandplover at the New York Zoological Park. In Africa and Madagascar, where this small shorebird occurs, the nest is usually in open sandy areas never far from the shores of rivers and lakes. The two cryptically colored eggs, the normal clutch, rest in an unlined scrape in the sand. As in most shorebirds, the eggs are large in proportion to the bird's body. The weights of five eggs, less than two days after laying, were 6.9, 6.8, 6.5, 6.4, and 5.3 grams.

We are fortunate that the sandplovers breed in these group exhibits because we have been able to study the breeding behavior of a number of pairs from the time they begin digging their nest-scrapes until the young are independent. We have also been able to watch the behavior between two or more breeding pairs of sandplovers and the interaction of the sandplovers and the other species of birds in the exhibit.

Egg-laying and Incubation

From January 1965 through January 1968 at least six pairs of Kittlitz's Sandplovers nested and renested in the exhibits. During 1965 and 1966 we counted 38 eggs from which a total of 17 chicks hatched. The number would have been much larger if we had not given some birds and eggs to other research workers and if we had had room enough to keep the breeding pairs well separated. We made observations on the incubation and egg-covering behavior of 10 nestings. Nine of the clutches had two eggs; one had one egg. According to Hall (1958) two eggs is the normal clutch (Figure 2).

The intervals between the laying of the first and second eggs in the nine two-egg clutches varied as follows: two, two-day intervals; five, three-day intervals; and two, four-day intervals. Considering the efficiency of the sandplover in concealing its eggs, we cannot overlook the possibility that the four-day intervals reflect an error by the observer.

We observed 14 incubation periods from the day the first egg was laid until the day the last egg hatched. Usually the birds did not start incubating consistently until the second egg of the clutch was laid. In all of the nests with two fertile eggs both hatched on the same day, sometimes several hours apart. In eight nests the periods from laying to hatching of the first eggs were: two periods of 26 days, three of 27, two of 28, and one of 30. In six nests the periods for the second eggs were: two of 23 days, two of 24, one of 26, and one of 27. The 30- and 27-day periods were for nests where the pair left both eggs unattended for several days before starting to incubate. One egg, taken from an unincubated clutch and placed in a forced-air incubator at a temperature of 99.5° F, hatched after 24 days. This period, along with the times reported above, is compatible with the incubation periods considered most valid by Hall (1959) from his field data—24.5±.5 and 25.5±1.5 days.

Figure 3. A pair of Kittlitz's Sandplovers digging nest-scrapes in the sand. When pairing starts the two birds dig several nest-scrapes side by side. They squat down and kick back vigorously with the feet, then turn and kick in another direction. By turning and kicking again and again, they form a neat cup-like hollow with a low rim.

Figure 4 (*above*). A Kittlitz's Sandplover, startled on the nest, jumps up and starts covering its eggs with sand. The eggs are still visible. The bird straddles the nest in a partly crouching position and kicks inward strongly, first with one foot and then the other very quickly.

Figure 5 (*below*). The eggs still show slightly; the bird has moved clockwise just a bit. As it kicks, it moves around the nest.

Figure 6 (*above*). The eggs have disappeared; only part of the rim remains to show the location of the nest. Egg-covering happens very quickly, often in less than six seconds.

Figure 7 (*below*). As soon as the eggs are covered, the sandplover, still in a crouching position, will make a quick run from the nest.

Figure 8 (*above*). The nest of a Kittlitz's Sandplover so well concealed that the rim hardly shows. When the disturbance has passed, the sandplover usually runs about in the vicinity of the nest for a while before returning. It may flip small pebbles and bits of shell in the direction of the nest, something it also does when making the nest-scrape.

Figure 9 (*below*). Here the sandplover is probing the sand around its buried eggs. When the bird returns to the nest, after being disturbed, it first flicks away the larger pebbles from the mound of sand. Then it leans over and probes deeply with its bill in the sand above the eggs.

Figure 10 (*above*). Kittlitz's Sandplover uncovering its eggs. After the flicking of pebbles and the probing with the bill, the bird fluffs out its breast feathers, as if to incubate, and lowers itself over the mound of sand.

Figure 11 (*below*). After lowering itself on the sand-covered nest, the bird kicks vigorously, sending a shower of sand out behind it. It then stands, turns perhaps as much as half a circle, squats again, and kicks some more.

Figure 12 (*above*). The nest is deeper now. The bird is still standing, squatting, and kicking the sand behind it.

Figure 13 (*below*). The bird now has most of the sand cleared from the nest. It will soon settle down to a period of quiet incubation. The egg-covering and uncovering behavior will vanish as soon as the eggs hatch.

Behavior at the Nest

Like most small plovers, the Kittlitz's Sandplover deposits its eggs in a small scrape which it makes by squatting down in the sand as if to incubate and kicking the sand out behind it with its feet, then turning and kicking, and turning and kicking until it has hollowed out a small cup. Our Zoo birds do not line the scrape; rather they surround it with a few large pebbles or bits of shell, forming a sort of rim. And using its bill the bird may flip small pebbles, bits of shell, and even hardened whitish excreta directly into the nest-cup. During pairing the male and female may simultaneously dig several nest-scrapes side by side (Figure 3). Copulation usually occurs close to the one particular scrape where the female eventually deposits the eggs. And here, as incubation starts, we see a most unplover-like behavior—nest-covering, or egg-covering, which in our Zoo birds is a behavior elicited only by human disturbance.

When the incubating bird is startled by a person, keeper or observer, it jumps to its feet and, straddling the eggs in a half-crouching position with its legs far apart, it begins an extremely rapid, yet systematic, kicking (see Figures 4, 5, 6, and 7). The feet kick inward alternately, shuffling the sand over the eggs as the bird moves, usually in a clockwise direction around the nest. This happens very quickly. On two timed occasions, both eggs were completely covered in six seconds. Hall (1958) records instances of three seconds. The birds often bury their eggs with sand so well that the rim of the nest is the only clue to the location.

As soon as the nest is covered, the bird makes a quick, crouching run away from the nest. Only once have we seen a distraction display when a bird was surprised while incubating. On that occasion the keeper surprised a bird so very suddenly that it jumped off the nest and ran without taking time to cover the eggs. Then it hesitated and performed a distraction display with spread and drooping wings like the display of a Killdeer (*Charadrius vociferus*), but without the elaborate wing-fluttering and tail-spreading of that plover. Harris (1901) noted more elaborate distraction displays in some of the Kittlitz's Sandplovers he studied in the field.

The sandplovers often left the first egg of a clutch unconcealed and unguarded. The nest-concealment behavior seemed to begin with the onset of incubation and to disappear shortly after the chicks hatched. For a few hours after the first egg of a clutch hatched a pair of sandplovers could be induced to shuffle sand over the remaining egg and the newly hatched chick. After the second egg hatched and the chicks were dried, a pair could rarely be induced to cover them with sand. After the hatching of the chicks the adults more readily employed distraction displays, a fact also noticed by Harris (1901) in his original description of the behavior of the Kittlitz's Sandplover.

When the disturbing stimulus, usually a keeper, departs, the bird does not always return directly to the covered nest (Figure 8). Instead, it may run about near the site, flicking with its bill small pebbles and bits of shell towards the nest-site—the same flicking that is evident in the original digging of the scrape. These flicks are moderately accurate with some of the materials falling within the nest-rim even though tossed a distance of nearly two feet.

Upon returning to the concealed nest, the sandplover usually bends down and probes the sand with its bill (Figure 9). The importance of bill-probing is difficult to ascertain. Presumably bill-probing helps locate the eggs, especially when they appear to be deeply covered. But the birds do not seem to find it necessary to search, and the probing merely appears to confirm the position of

Figure 14 (*above*). A Kittlitz's Sandplover extending its wing in an attempt to brood its chicks. The chicks leave the nest shortly after they are hatched and dried and the adults brood them wherever they happen to be in the enclosure. Newly hatched sandplovers are tiny. One chick tipped the scales to 4.7 grams, and another to 4.3.

Figure 15 (*below*). Trying to brood three chicks. This bird and its mate brooded the two chicks of their own and an incubator chick during some part of each day for 29 days.

the eggs already located by visual cues. After probing, the returning bird proceeds to uncover its eggs (Figures 10, 11, 12, and 13). First it flicks the larger pebbles and sand particles from the nest-site with its bill. Then it fluffs out its breast feathers in anticipation of brooding and squats down on the sand over the eggs. With its breast resting over the eggs it begins kicking away the sand from behind them. Next, it stands and turns, perhaps in a half circle, probes, squats, and kicks the sand from the eggs in another direction. Sitting and kicking strongly—as if preparing a nest-scrape—the bird eventually digs out the eggs. The movements it uses in uncovering its eggs are similar and probably derived from the movements used in digging the original nest-scrape.

These observations are at variance with those of Hall (1958) who, in describing the bird's return to the nest, relates that "it would typically stand, momentarily, at the edge of the nest, then appeared to turn around on the spot with a few very quick shuffling movements of the legs as it settled onto the eggs — these movements presumably serving to uncover the eggs for brooding."

Both the male and female sandplovers incubate the eggs and cover them with sand when disturbed. They do not, however, kick sand over the eggs while changing places in the normal course of nest-relief. Hall (1959) described nest concealment by the non-incubating member of a pair when a disturbance frightened the incubating bird from the nest just as the two birds were about to change places. We have observed this also. In addition, we have noted that it is not too uncommon for a sandplover in the Zoo, upon being suddenly startled from the nest, to run away at first and then run back, cover the eggs, and run away again.

Figure 16. A Kittlitz's Sandplover brooding one big chick. The sandplovers sometimes brooded a chick for a long period. One pair brooded a single chick off and on for 42 days. When the chicks are so large that the adult must stand up to brood it, we have a curious picture—a sandplover with four legs.

Care of the Young

As soon as the young hatch, one of the adults carries the egg shells to the far side of the exhibit.

Within a few hours after they hatch, the chicks wander, or are led, from the nest and brooded in various areas in the exhibit (Figures 14, 15, and 16). We saw one adult pull a newly hatched chick from the nest-rim and brood it, and another parent use its bill to extricate a chick from the grass clump where it had become entangled.

We did not see the chicks eat during the first 24 hours, nor did we see the adults feed them or even try to feed them. However, during the second day, the chicks randomly pick at small objects on the exhibit flooring and accompany their parents to the food dishes where they eventually learn to feed. Within three days most of the chicks discover the food dishes or the bits of food spilled around them.

Both adults brood the chicks throughout the day with a frequency that seems to have little to do with the temperature of the enclosure. Most of the time the parent birds initiate the brooding. The chicks definitely respond to the calls of the adults and, on hearing certain calls, run to be brooded.

Brooding continues for quite some time—until the chicks are quite large. One pair brooded a single chick some part of each day for 42 days (Figure 16). Another pair brooded their two chicks together with a third, an incubator chick, for 29 days (Figure 15). After that the three chicks made short flights and appeared to be quite independent. On one occasion a pair began to renest while they were still brooding chicks. In this case the female stopped brooding and incubated the eggs alone for several days.

On hot days the sandplovers brood standing up (Figure 16). And as the chicks grow large, they are *forced* to brood them standing up. This is an odd sight—an adult trying to brood one chick looks like a sandplover with four legs; or when brooding two chicks, like a sandplover with six legs.

Although both male and female incubate the eggs and brood the chicks, the male takes over most of the incubation toward the latter part of that period and later performs most of the brooding—at least during the daylight hours. Since the lights frightened all the birds in the group, we made very few observations at night.

Territory and Aggression

Because six to 12 sandplovers were crowded into a relatively small area in the exhibit, constant chasing and other agonistic encounters were the rule rather than the exception. The abnormal restrictions of exhibit cages do not permit breeding sandplovers to establish satisfactorily large territories or to escape easily from the aggression of other sandplovers. Both male and female sandplovers try to defend an area around the nest from other sandplovers. And, for our Zoo birds, the area to be defended by one pair seems to include most of the exhibit cage. Fighting can be serious in this species because it has had, in its life in the wild, little need to develop ritualized agonistic behaviors. Despite the fact that, in the field, nests of Kittlitz's Sandplovers may be as close as nine yards to each other without any sign of aggressiveness between the owners, at no time were two pairs with concurrent nests in an exhibit cage able to bring off successful hatches.

The males exhibited far more effort in territorial defense than did the females. Neither of them paid much attention to the other species in the

Figure 17. An Oriental Pratincole approaches the nest of a pair of Kittlitz's Sandplovers. The nest is behind the log. Usually the sandplovers ignore the other species in the enclosure. This pratincole has come just too close to their nest. Instead of covering the eggs and fleeing as they do in the case of a disturbance by a human, the birds stay by the nest. Their behavior seems to be halfway between aggression and distraction.

group—Wood Sandpipers (*Tringa glareola*), Little Stints (*Erolia minuta*), Puna Plovers (*Charadrius alticola*), Egyptian Plovers, (*Pluvianus aegyptius*), White-winged Black Terns (*Chlidonias leucoptera*), and Oriental Pratincoles (*Glareola pratincola maldivarum*)—unless one of these birds approached the nest very closely.

We did not observe the nest-covering behavior on the few occasions when a larger, more aggressive species, such as an Oriental Pratincole, came near the nest (Figure 17). At such times the sandplover either attacked the intruder directly or employed a behavior that was half attack and half distraction display.

When the chicks hatch, the territory defended is wherever in the exhibit the adult and chicks may be. In fact, one adult, usually the male, often abandons the chicks for considerable periods while he relentlessly chases other sandplovers from their vicinity.

Discussion

The advantages of egg-covering in the Kittlitz's Sandplover seem clear. Concealed eggs are not only less subject to predation than exposed eggs, they also stay warmer in cool weather and cooler in hot weather. One might suppose that the egg-covering behavior would be highly developed in many species that nest in the open; but this is not the case.

Egg-covering behavior in such birds is rare. Even among the whole suborder Charadrii there are few species that cover their nests when leaving them. The Egyptian Plover, it is said, incubates its eggs only at night and buries them by day in the sand where the sun keeps them warm (Butler, 1931). The Patagonian Seed Snipe (*Thinocorus rumicivorus*) reportedly buries its eggs in dry earth when it leaves the nest (Gilliard, 1958). To the best of our knowledge, the only species with an egg-covering behavior at all like the one we have described in the Kittlitz's Sandplover is the White-fronted Sandplover (*Charadrius marginatus*). In this species the behavior, while similar, is apparently less consistent and less well developed (Hall, 1960; Liversidge, 1965).

Although the protection of the clutch from the hot sun may be the stimulus for the egg-covering behavior of the Kittlitz's Sandplover, the concealment of eggs from predators seems a more likely stimulus for the evolution of egg-covering, a behavior that appears to occur in a conflict situation between the drive to escape and the drive to incubate. The suggestion by Hall (1960) that the related behavior of the White-fronted Sandplover "may represent a series of intention-settling movements and intention-leaving movements" is the most plausible explanation for the egg-covering behavior yet proposed.

Summary

With lateral movements of the feet, the incubating Kittlitz's Sandplovers (*Charadrius pecuarius*) at the New York Zoological Park kicked sand onto the nest, covering the eggs in as little as six seconds. When uncovering the eggs one parent sat on the covered nest after probing into the sand with its bill and scraped sand off the eggs with backward kicks of the legs. The young were highly precocial, leaving the nest within several hours. The parents did not feed the chicks, but continued to defend and brood them after leaving the nest.

Acknowledgments

We wish to record our gratitude to the New York Zoological Park's Manager of Birds, Mr. Andrew Winnegar; to Assistant Manager, Mr. Eric Edler; and to keeper Mr. Walter Nielsen for helpful observations and notes. Especial thanks are due senior keepers, Mr. C. James Bardsley and Mr. Robert Edington, who maintained the study birds and made daily observations on them.

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NEW YORK ZOOLOGICAL SOCIETY, BRONX PARK, NEW YORK CITY

EXPERIMENTS ON THE HOMING ABILITY OF PURPLE MARTINS[1]

WILLIAM E. SOUTHERN

In the summer of 1958 I conducted my first homing experiments on birds, using Purple Martins (*Progne subis*) from a colony on the campus of the University of Michigan Biological Station in Cheboygan County, Michigan. To review the results (Southern, 1959) briefly: Between 25 June and 18 July I trapped 16 Purple Martins, 14 females and two males, from a colony of 60 pairs occupying four houses on the southeast shore of Douglas Lake. Five of the females had eggs in the nest, one female had eggs and small young; eight birds had young. I marked each bird with colored "airplane dope" for individual recognition and shipped it by car or plane to a predetermined release point. The release points varied both in distance and direction from the colony. All 16 birds flying different distances, from different directions, and under different weather conditions returned to their colony and to their nests.

The data resulting from this first trial yielded two facts for particular attention: (1) All the birds returned and (2) one female traveling by night covered 234 miles in 8.6 hours, an average speed of 27.2 miles per hour. The extraction of these findings from the body of the data, which was, after all, based on a very small sample, and the interpretation of them as being representative of the ability of Purple Martins to return to their homes led to conclusions that were premature and tended to overrate the homing ability of the species.

During my absence from the Station, Douglas A. Lancaster continued the study of the martins in 1959 and Larry L. Wolf in 1960. Both of these gentlemen have consented to the use of their data in this paper. No studies were conducted in 1961 because unseasonably cold weather in the late spring apparently caused a high mortality among the martins and too few remained. I resumed my work in 1962.

Study Area and Techniques

Lancaster (1959) and Wolf (1960) used Purple Martins from the same colony that I worked on in 1958. There were 48 pairs in 1959 and 32 pairs in 1960. Because only 27 individuals were present in 1962, I trapped only a few birds there and obtained the others from a colony of approximately 80 pairs, about 10 miles from the Station—at Bowersoc's Landing in Indian River, Cheboygan County.

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[1] Contribution from The University of Michigan Biological Station

Male Purple Martin. Drawing by Charles L. Ripper.

We snared the Purple Martins with nylon nooses (Southern, 1959) or trapped them in houses equipped with special doors, color-marked them with airplane dope for individual recognition, and applied Fish and Wildlife Service bands or color bands or both. We placed each individual in a cigar box and delivered it at once to a bearer—the pilot or crew member of an airplane or the driver of a car—who took it to a predetermined site and released it. He then recorded on a mimeographed form the time of day, prevailing weather conditions, general flight behavior, and any other information he considered important. He returned the form to us by mail.

The technique described above was successful in respect to gathering data on time and weather conditions. Since it was difficult in some cases to interpret the observations on behavior made by untrained individuals, we have relatively little dependable information on the actions of the birds upon their release. To the best of our knowledge the period during which the birds were confined in the box—from two to 15 hours—had little, if any, detrimental effect on the birds. We failed to receive reports on two birds sent by air and neither returned to the colony. Since we have no assurance that either survived the trip or was ever released, we have omitted the data on these two from our computations.

Experimental Results

Between 24 June and 20 July of the three summers we used 92 Purple Martins in homing trials—25 in 1959, 27 in 1960, and 40 in 1962. In some of the computations in this paper I have also included data from the 16 birds in the 1958 trials. Of the 108 martins, 96 were adults or subadults and 12 were juveniles. We varied the release sites in direction and distance in an effort to determine whether either factor influenced homing speed and success. We sent 55 individuals to one particular site—Detroit in Wayne County—to note the influence of weather. Detroit was a convenient release point because North-central Airlines conducted several flights daily to this city from their Pellston airport in Emmet County, only six miles from the Station, and meteorological data were available for both Detroit and Pellston as well as for several localities en route.

Success Rates Relative to Direction of Release Site

We released 94 adult and subadult Purple Martins at sites situated in eight compass directions from the colony. Seventy-five, or 79.8 per cent, of the birds returned. Table 1 shows that the success rate for each of the eight groups ranged from 66.7 per cent for those coming from north and northwest to 100 per cent from the northeast, east, south, southwest, and west. Of 12 juveniles—birds-of-the-year—released in four directions from the colony at distances up to 234 miles, only two, or 16.7 per cent, returned. Both of these individuals were released in sight of the colony.

The largest sample of birds released in one direction was 55 birds at Detroit in the southeast category. We had a 74.5 per cent return. From these experiments there was no obvious indication that the direction of the release had any effect, good or bad, on the homing success. And although an evaluation of this factor does not make any clearer the orientation method used by the martins, it does show that, whatever the method, it is probably equally efficient regardless of the direction from the home base.

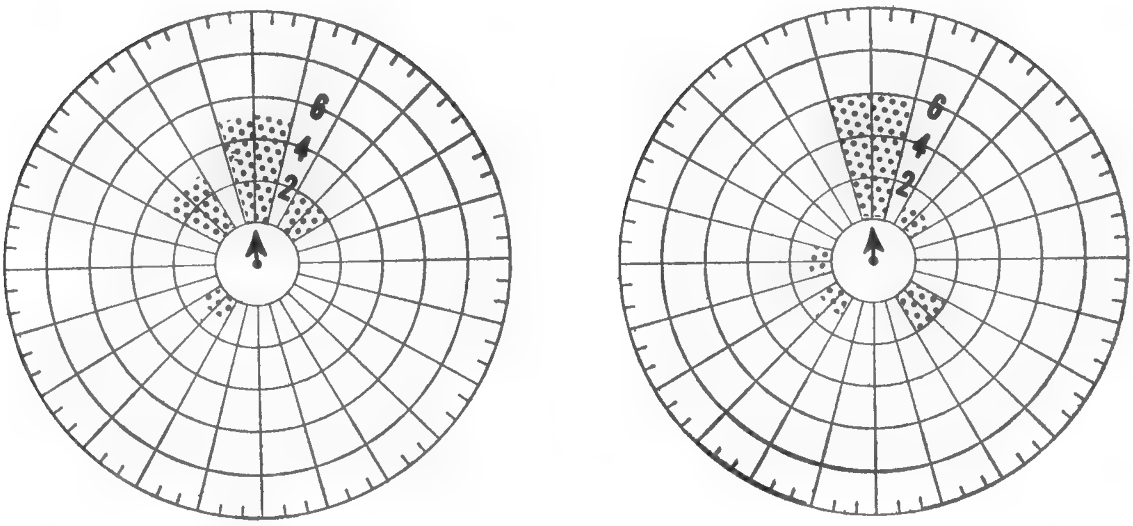
The difficulty encountered in trying to recapture a successful homer prevented us from having many repeat trials. We did manage to trap one male three times. Released in Detroit on each occasion, he made his second trip 0.67 hour faster than his first and his third 2.33 hours slower, showing a significant lack of improvement as a result of experience with the route or conditioning to the rigors of the experiment.

Success Rates Relative to the Distance of Release Site

In an effort to determine whether or not increased distance resulted in poorer homing efficiency, we established five distance categories and released martins at sites ranging up to 594 miles from the colony. The success rates for 94 adults averaged 79.8 per cent, and, as might be expected, decreased as the distance increased (see Table 2). At ranges less than 25 miles the average success rate for six birds in our study was 100 per cent. Nicholls (1963), using 34 birds in similar trials, had an 88.2 per cent return. At 26 to 150 miles, we had a 94.1 per cent return on 15 birds; Nicholls, an 81.8 per cent return on 11 trials. The percentages of returns decreased as follows: 151-250 miles, 76.7 per cent; 251-300 miles, 66.7 per cent; 351-594 miles, 60 per cent. The initial headings for birds released at these same distances (see Figure 1) show similar tendencies. The figures in Table 2 suggest that an increase in distance adversely affects the mechanism used by Purple Martins for orientation during the breeding cycle, irrespective of the direction of the release sites from the colony. As a result the birds do not return promptly. We must also consider the fact that some martins may experience, among other behavioral modifications, a reduction in homing tendency which lowers the likelihood of their returning to the colony at all during the current breeding season.

A. 1–25 miles

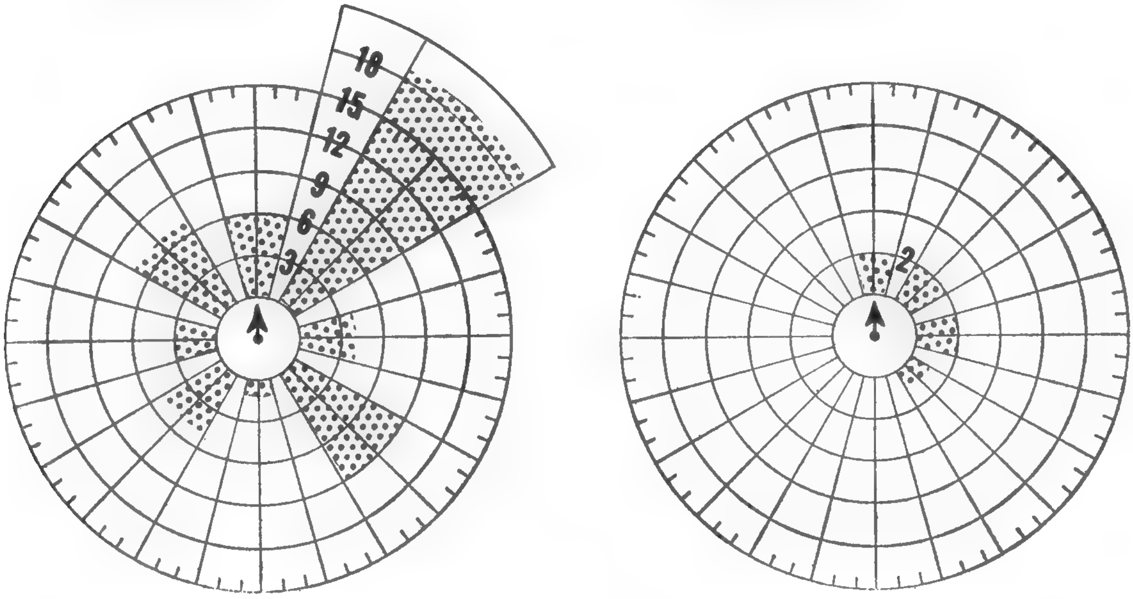
B. 26–150 miles



↑ = home direction

C. 151–200 miles

D. 251–350 miles



E. 351–450 miles

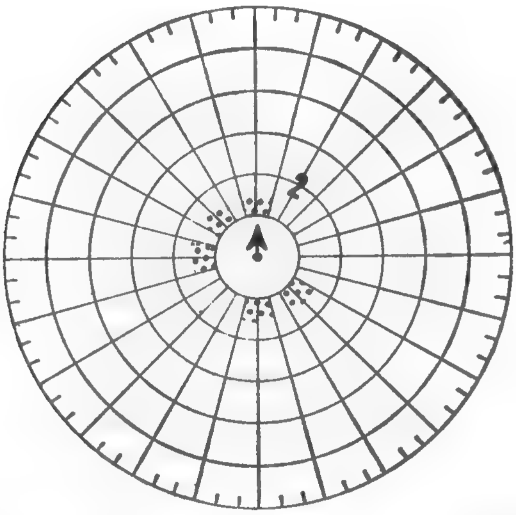


Figure 1. Departure headings relative to distance of release sites from the home colony of Purple Martins. Numbers refer to individuals released and show preference for that particular heading.

We released 12 juveniles, five within 25 miles of the colony and seven between 151 and 250 miles away. Only two, both released within sight of the colony area at distances from 0.5 and 2.4 miles, returned. Possibly these two found their way by following learned landmarks, by responding to other martins in the area, or by accidentally heading in the right direction. The other 10 failed to return. There is, however, no reason to expect that young martins should possess a tendency to come back immediately to the home colony.

Success Rates in Relation to Age, Sex, and Reproductive Cycle

We recognized four groups of Purple Martins on the basis of plumage characteristics—adult males, adult females, immature males (one-year-olds), and juveniles—and consider the first three groups in this section.

Of the 56 females used in the homing trials (see Table 3) 44, or 78.6 per cent, returned from distances ranging from 1.75 to 415 miles. Unfortunately we were able to test only six adult males. There seemed to be fewer males than females in the colonies and since the males seldom entered the nests during the early stages of the nesting cycle, it was difficult to snare them. All six of the adult males returned from distances ranging between 32.5 and 426 miles. Of the six immature males, released at distances of from 68 to 385 miles, four, or 66.7 per cent, came back.

The sample of males, both adult and immature, was so small that it was impossible to compare their performance with that of the females. It appears, however, that members of both sexes and age groups have similar tendencies to return to the colony and that each group uses similar orientation methods. The disproportionate amounts of flight experience between the one-year-old males and those older may account for the difference in performance. Similar differences could exist between the first year and older females. It was impossible to distinguish between the two age groups of females on the basis of plumage characteristics.

A positive correlation existed between the homing-success rate and the stage of the bird's nesting cycle (see Table 4). Thirteen female Purple Martins, released at distances up to 295 miles when they still had eggs in the nest, returned. By comparison, Nicholls (1963) had an 83.9 per cent return for 31 martins released during the egg stage at distances of from 1.5 to 110 miles. We released 13 individuals from nests containing small young—up to nine days of age—at distances ranging from 19.5 to 594 miles. Ten, or 77 per cent, returned. We released 41 from nests containing large young—over nine days of age—at distances ranging from 249 to 385 miles. Thirty, or 73.2 per cent, returned. Nicholls (*op. cit.*) released 10 martins, which had young, at distances ranging up to 141 miles from the colony and all of the birds returned to their nests. He did not report the age of the young. The fact that his trials were over distances from which we normally had a higher return rate than the 77 and 73.2 per cent shown above leads me to consider the possibility of a correlation between homing success and the stage of the nesting cycle. While the differences in percentage of returns are not drastic, they do show a definite reduction in the number of returns as the nesting season progresses.

The females in particular appear to possess stronger tendencies to return during incubation and when the young are small, the two periods during which they perform most, or all, of the nesting duties. There was also an increase in the time required to return as the nesting cycle advanced.

TABLE 1

Success Rates of Return of Purple Martins Released at Various Directions from the Colony

	Compass direction							
	N	*NE*	*E*	*SE*	*S*	*SW*	*W*	*NW*
Number released	3	6	1	55	3	13	1	12
Number returned	2	6	1	41	3	13	1	8
Per cent returned	66.7	100	100	74.5	100	100	100	66.7

Total released: 94. Total returned: 75. Per cent returned: 79.8

TABLE 2

Success Rates of Return of Purple Martins Relative to Distance of Release Sites from Colony

	Distance (miles)				
	1-25	*26-150*	*151-250*	*251-300*	*351-594*
Number released	6	17	60	6	5
Number returned	6	16	46	4	3
Per cent returned	100	94.1	76.7	66.7	60

Total released: 94. Returned: 75. Per cent returned: 79.8

TABLE 3

Success Rates of Return of Purple Martins Relative to Sex and Age

	Sex and age			
	Adult male	*Immature male*	*Adult female*	*Juvenile*
Number released	6	6	56	11
Number returned	6	4	44	2
Per cent returned	100	66.7	78.6	18.2

TABLE 4

Success Rates of Return of Purple Martins Relative to Nest Contents and the Stage of the Breeding Cycle

	Nest contents		
	Eggs	*Small young*	*Large young*
Number released	13	13	41
Number returned	13	10	30
Per cent returned	100	77	73.2

TABLE 5

Success Rates of Return of Purple Martins Relative to Circling Behavior

	Behavior	
	Circled	*Did not circle*
Number of birds	52	12
Number returned	38	10
Per cent returned	73.1	83.3

Number of birds tested: 64. Per cent circled: 81.3

TABLE 6

Homing Speeds of Thirty-six Purple Martins Released at Detroit, Michigan

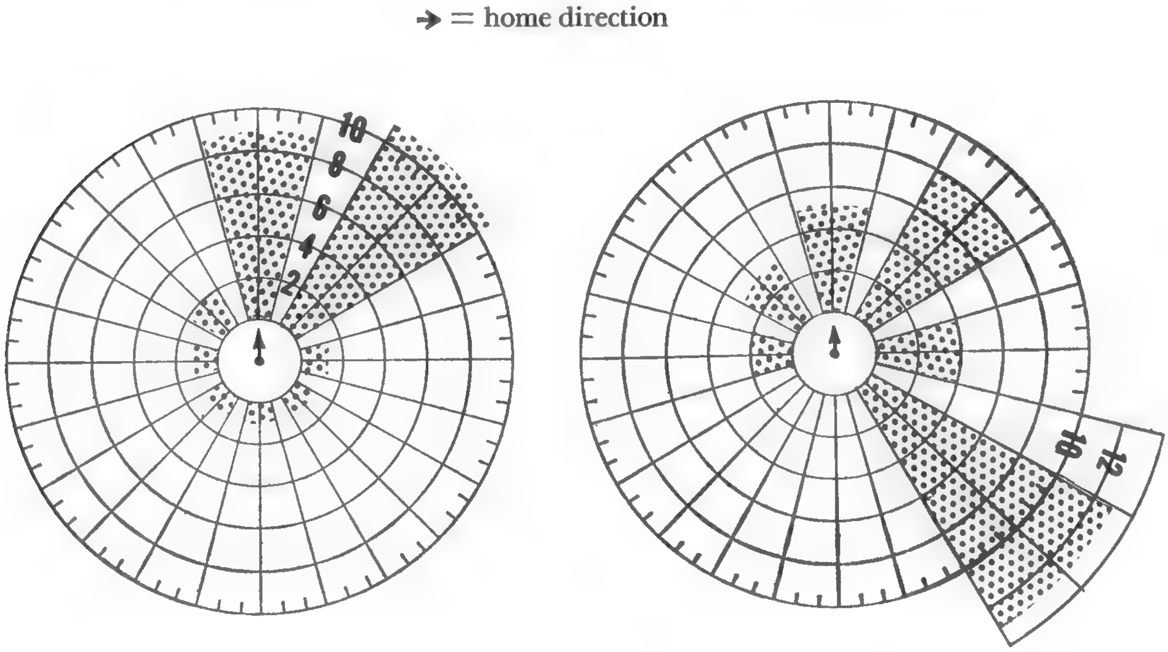
	Sky cover		
	Clear	*Partly cloudy*	*Complete overcast*
Number released	12	16	8
Speed range (mph)	1.23–9.19	2.76–13.83	3.77–22.63
Average speed (mph)	5.86	7.39	9.02

Cumulative average: 7.24 mph

Importance of Behavior upon Release

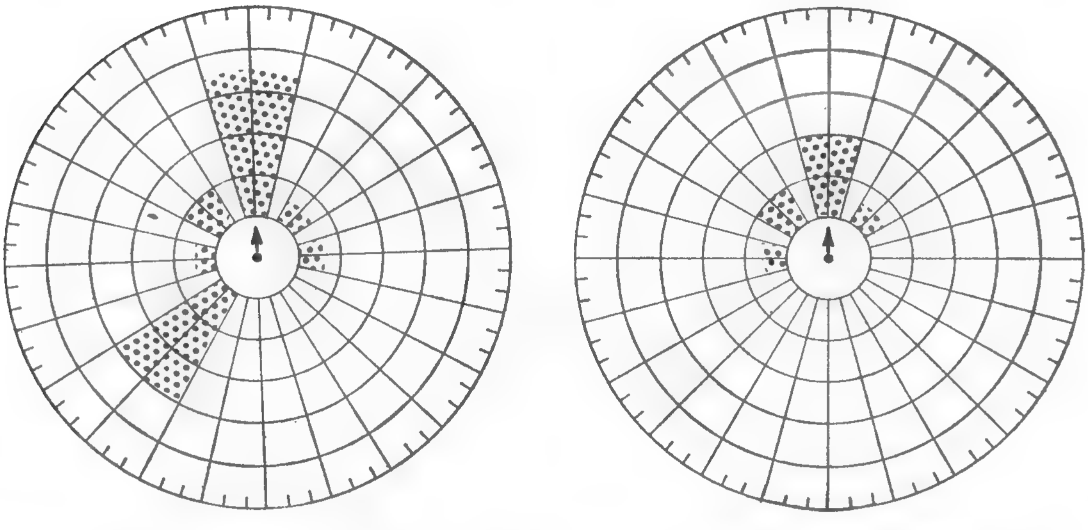
Although some consider behavior-upon-release homologous to orientation attempts, the actual significance of the bird's activities leading up to its selection of a direction for departure is unknown. The various flight patterns—straight, zig-zag, circling, spiraling, and so on—may be only a type of displacement behavior occurring prior to the selection of a direction for departure, or they may constitute a period of searching — appetitive behavior — during which the bird perceives environmental clues and becomes orientated.

If the bird perceives environmental clues, we would expect that a majority of departures would be in a homeward direction. Such should certainly be the case if the bird uses celestial, magnetic, or other widespread clues, present at all release sites. On the other hand, if the bird uses more localized types of clues such as familiar topographical features that are not present at all release sites, it would make somewhat random departure headings and alter its course later upon encountering suitable clues.



Clear sky

Partly cloudy sky



Completely overcast sky

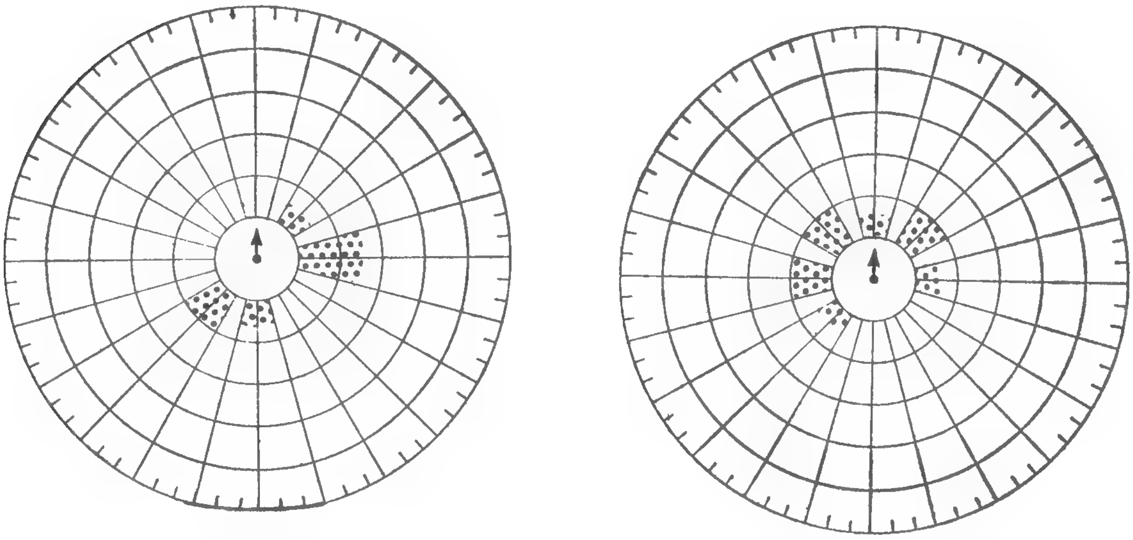
Juveniles under all skies

Figure 2. Departure directions of Purple Martins released under various sky conditions at all release sites.

We have descriptions of the type of flight following release for 64 individuals: A few birds—16.7 per cent—went in rather straight or zig-zag flights; the majority—83.3 per cent—circled at least once or twice before departing. The circles were in a clockwise or counterclockwise direction or both and varied in diameter from wide circles to spirals. Usually the birds reached an elevation of at least 300 feet before the departure which generally occurred within one to three minutes after release.

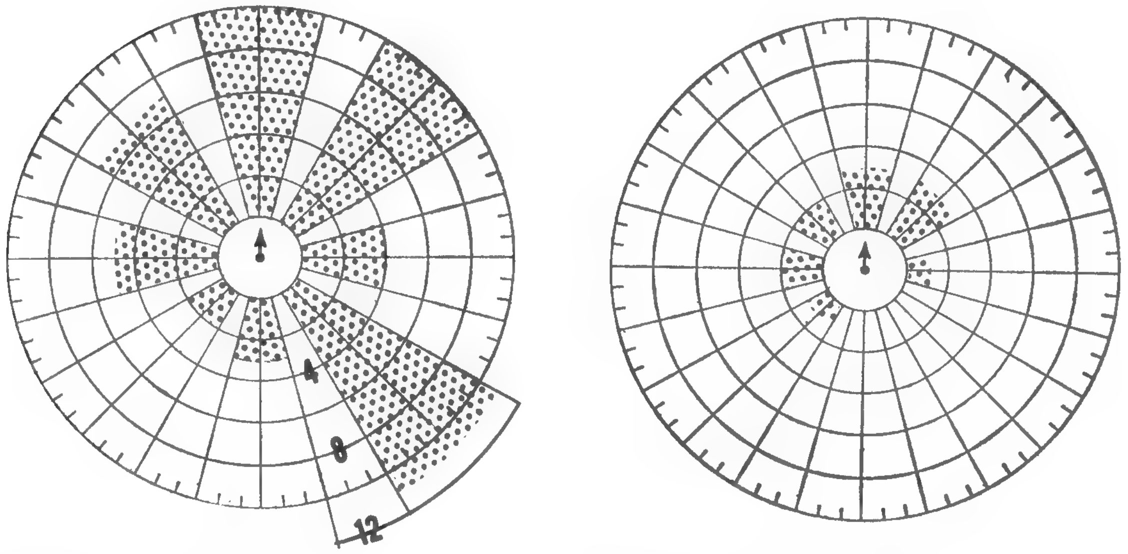
Of the 52 martins that circled, 38 returned to the colony; of the 12 that did not circle, 10 returned (see Table 5). This indicates to me that circling was not necessarily a part of their orientation behavior and that the birds not flying in circles were equally capable of returning. It is possible though that the birds that did not circle on release may have done so later on in the flight. The circling may have enabled the birds to remain in a given area while searching for, or interpreting, environmental clues on which to base their departure headings.

→ = direction of wind



1–25 miles from colony

26–150 miles from colony



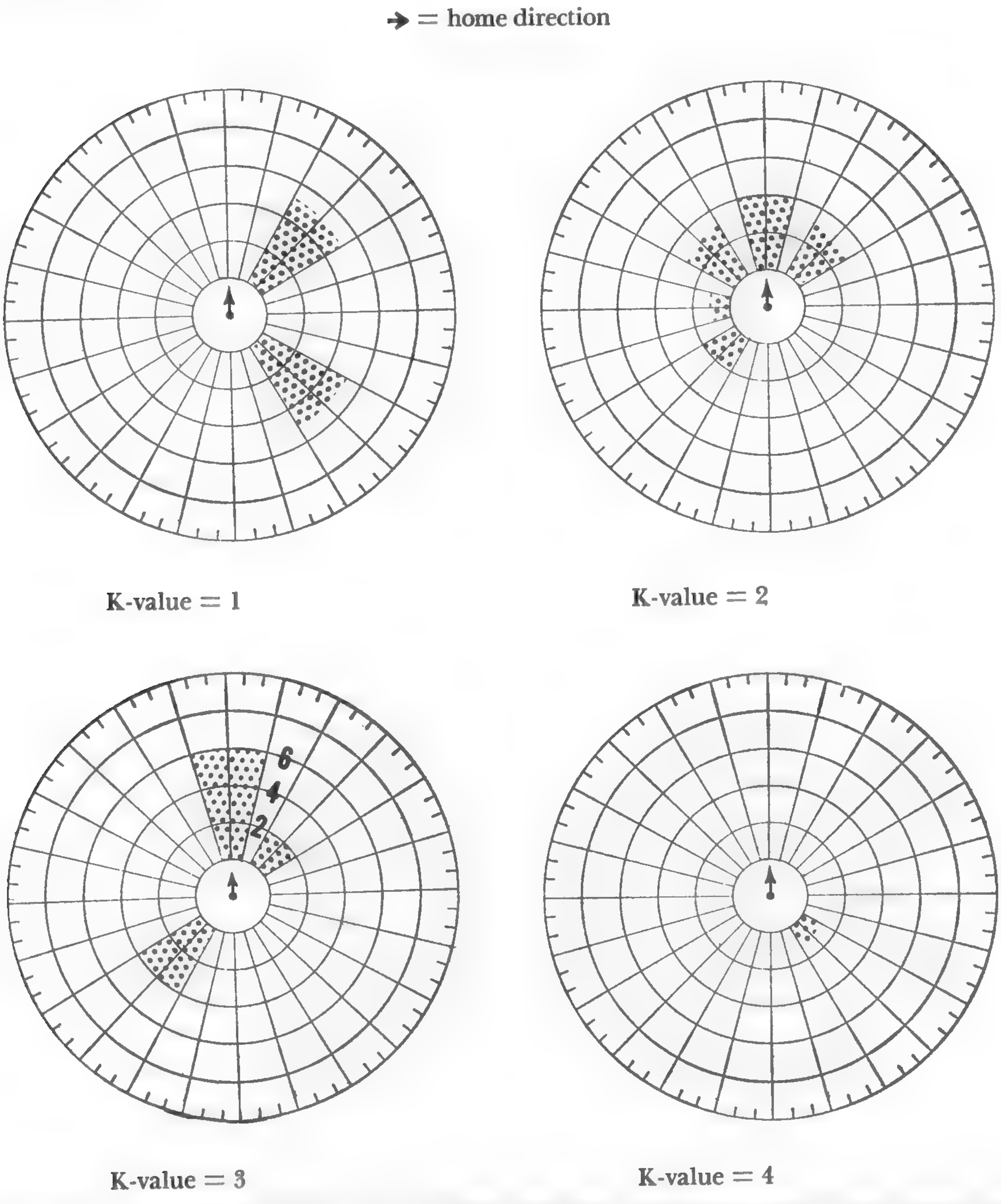
151–250 miles from colony

251–450 miles from colony

Figure 3. Departure directions of Purple Martins relative to wind bearings at release sites located at various distances from home.

The initial behavior after release was similar during clear and overcast conditions, suggesting that the circling was not directly associated with solar clues. Figure 2 shows the departure headings in relation to the sky conditions at the release sites. More martins generally headed homeward under clear skies than when the skies were overcast or cloudy. While this might suggest that the sun provides clues for homeward orientation, we note that the success rates for birds returning home under clear skies were not significantly higher than the rates for those released under overcast skies, nor were their average speeds greater. Although the birds may possibly use the sun as an orientational clue, it seems unlikely that it is associated with a form of true navigation.

We could not determine whether martins released under an overcast sky experienced similar conditions during the entire flight because we had no way of tracking the birds. This was my main reason for discontinuing my work with Purple Martins. It seemed unlikely that we could ever solve the orientation problem on the basis of behavior observed only at the release sites and in the colony. Therefore, I turned my attention to gulls and radio-tracking techniques.



K-value = 1

K-value = 2

K-value = 3

K-value = 4

Figure 4. Departure directions of Purple Martins during magnetic disturbances (storms) ranging between 1 and 4K in intensity.

Homing Success Relative to Wind Direction and Magnetic Storms

In Figure 3 I have plotted the departure headings in relation to the wind direction for Purple Martins released at each of the four distance categories and found no correlation between wind direction and preferred headings. Also, the velocity of the wind, between 0 and 28 miles per hour, had no apparent effect on their flight behavior. Ring-billed and Herring Gulls, on the other hand, showed preferred headings whenever the wind was blowing (Southern, 1967).

Since the Purple Martins released over the iron fields of the northwestern portion of Michigan's Upper Peninsula and near Duluth, Minnesota, both areas of magnetic disturbances, exhibited poor success rates in homing, I compared the departure headings of the 1962 releases with the fluctuations of the earth's magnetic field at that time. These measurements, obtained at the Fredericksburg Observatory in Virginia by the Coast and Geodetic Survey, represent world-wide fluctuations. "Magnetic storm" activity is expressed in K-values ranging from 1 to 14 with factors of 0-1 representing minor storms, 2-4 light storms, 5-8 moderate storms, and 9-14 severe storms.

No severe or even moderate magnetic storm activity occurred during the releases in 1962. It is impossible to predict what effect they might have had. Mild fluctuations had no apparent detrimental effect upon the initial orientation of the birds (see Figure 4). I could not determine whether the magnetic fluctuations served as a clue in orientation while the birds were en route, or if, possibly, they influenced the orientation of the juveniles as appeared to be the case with gulls (Southern, 1967).

Homing Speeds

The average homing speeds, expressed in miles per hour, were computed on the basis of the maximum return time, that is, from the time of release until the bird was first observed in the colony. These figures may or may not indicate the true homing speed because, with all the confusion and interaction that normally occurs around a martin colony, it was difficult to note the exact moment of a bird's arrival. Often a bird, upon returning from a "trip," appeared only briefly at the nest-site and then vanished for several hours before turning up again. Then too, birds arriving at night could not possibly be recorded until the following morning.

Very few of our experimental birds homed at average speeds approaching that of which the martin is believed capable. Schnell (1965) recorded by Doppler radar the flight speeds of 169 martins flying near the colony on a windless day and obtained a mean of 21.7 mph with a range of from 5 to 41 mph. The relatively slow speeds of our experimental birds (Tables 6 and 7) suggest that either the martins encountered difficulties in orientation or that they hesitated returning to the colony because of experiences associated with the trial.

The average homing speed for 36 individuals released at Detroit, 249 miles SSE of the colony, was 7.24 mph with a range of from 1.23 to 22.63 mph. Table 6 shows the average speeds for individuals released during clear, partly cloudy, and overcast conditions as: clear, 5.86 mph; partly cloudy, 7.39 mph; and overcast, 9.02 mph. The slowest speed was for a bird experiencing clear skies during its flight, and the fastest, as well as the highest average, was for a bird released during overcast conditions. It seems, therefore, that the availability of solar clues, or lack thereof, is not directly responsible for the variations in flight speeds.

TABLE 7

Homing Speeds of Purple Martins in Relation to Distance of Release Sites from Home

	Distance in miles				
	1–15	*16–100*	*101–200*	*201–300*	*301–500*
Number released	5	12	8	9	3
Speed range (mph)	6.7–22.0	0.59–19.25	0.71–27.37	0.63–27.31	2.37–9.88
Average speed (mph)	10.9	6.08	9.81	7.71	5.54

The speeds for individual birds in other distance categories (see Table 7) showed no consistent trend that indicated any correlation between the speeds and the distance traveled. At distances between 1 and 15 miles the homing speeds ranged from 6.7 to 22.0 mph with an average of 10.9 mph; between 16 and 100 miles the range was 0.59 to 19.25 mph, average 6.08 mph; from 101 to 200 miles the range was 0.71 to 27.37 mph, average 9.81 for eight birds. A female, released 109 miles north of the colony, achieved a speed of 27.37 mph, the fastest recorded during the study. Two other birds in this distance category had relatively high speeds—12.5 and 15.42 mph. The homing speeds of nine martins released 201 to 300 miles from the colony, at locations other than Detroit, ranged from 0.63 to 27.31 mph, average 7.71 mph. The fastest flight for this group was for the female, mentioned previously (Southern, 1959), that flew by night from Ann Arbor, Michigan, a distance of 234 miles. The final distance category, 301 to 500 miles, had speeds from 2.37 to 9.88 mph with an average of 5.54 mph.

The enormous variation that existed between individual speeds within each distance category prevented me from drawing any definite conclusions regarding the actual effect of distance on homing speed. I believe, however, that particular individuals are not handicapped by increased distances and that the few rapid flights may have been caused by chance headings which later resulted in sightings of familiar or "usable" clues.

Discussion

On the basis of these data one cannot possibly speculate to any great extent on the orientation method used by Purple Martins. Even so, our findings do provide a clearer picture of the homing ability of the species than was possible from my initial inquiry (Southern, 1959).

The average rate of homing success, 79.8 per cent, for 94 adult and subadult Purple Martins used in this study and the 86.7 per cent success reported by Nicholls (1963) for 21 individuals in 45 trials suggest that these birds are persistent homers and that, given time, a sizable percentage will return to their colony from a variety of directions and over fairly long distances. Let us remember, however, that we worked with experienced birds, individuals that had endured the rigors of at least one round-trip migration and long-range orientation. The less capable birds had probably already been removed from the population. This being true, the wide range of abilities, based on success rates, homing speeds, and general behavior, must be the result either of individual differences in orientational ability (there being poor, average, and good homers), or of differences in motivation. Although Purple Martins appear to be more tolerant of disturbances than some of the other species used in homing trials, the experience of being trapped may have made some individuals reluctant to return to the colony. We should determine the validity of the homing trials before we apply it further in our analysis of orientation behavior.

Most certainly Purple Martins are capable homers and possess a mode of orientation which permits them to home equally well from almost any compass direction and from distances of over 500 miles. The sun, when visible, may serve as an orientational clue, but may not be essential nor necessarily used as a basis for true navigation. The relatively slow average return speeds for most martins indicate that they may not always proceed in straight-line flights. Possibly they follow a meandering route, searching for familiar geographical landmarks. Variations in climatic conditions or in time of release, day or night, have no apparent detrimental effect on the success rates or homing speeds. Trials with juveniles indicate that they are able to return to the colony only when released close enough to see it while circling. Young Purple Martins did not home from greater distances. This may have been due to their inexperience with geographical landmarks or to a lack of motivation.

Summary

To test the homing ability of Purple Martins (*Progne subis*), Douglas A. Lancaster, Larry L. Wolf, and the author used 92 birds from two colonies in northern Michigan. The data from these trials, made in 1959, 1960, and 1962, were added to the data from the author's tests on 16 birds in 1958. Individuals were released at eight compass directions and at distances up to 594 miles from the colony. Fifty-five martins were released at one site, at different times, in an attempt to determine the influence of weather; 74.5 per cent returned.

The success rates for groups released at different directions from the colony ranged from 66.7 to 100 per cent with an average of 79.8 per cent. The rates declined as the distances increased. Similar tendencies were shown in initial departure headings.

Of 12 juveniles, released at distances up to 250 miles from the colony, only two, both released within sight of the colony, returned.

Of 56 adult females tested, 44, or 78.6 per cent, returned from distances between 1.75 and 415 miles. Of six adult males tested, all, or 100 per cent, returned from distances up to 426 miles. Of six subadult males tested, four, or 66.6 per cent, returned from distances up to 385 miles. Both sexes showed similar tendencies for returning. A definite correlation was noted between the stage of nesting and homing success, with more birds returning during the egg and small young stages than later in the season.

The initial flight behavior upon release did not indicate the homing performance to follow. Some of the recorded behaviors may serve as a displacement function. There was no correlation between wind bearings or velocity and preferred headings. Nor was there any correlation between the homing results and magnetic disturbances in 1962.

Flight speeds ranged up to 27.37 miles per hour and the average homing speeds decreased as the distance of the release sites from the colony increased. The average for 36 individuals, released 249 miles SSE of the colony, was 7.24 mph.

Homing performances varied greatly between individuals and no evidence was found to support the occurrence of true navigation and the use of solar

clues in a bicoordinate method. There was equally little evidence to support the use of other types of clues for orientation. Most of the circumstantial evidence tended to support the use of geographical landmarks.

As a result of these experiments the author feels that the use of homing trials is not a satisfactory means of determining the method used by birds for orientation and that a new approach must be developed before we can advance our knowledge of the technique of avian orientation.

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Purple Martins, Drawing by Charles L. Ripper.

SOME NOTES ON THE CHICK-CARRYING BEHAVIOR IN THE AFRICAN JACANA

JOHN B. D. HOPCRAFT

Photographs by the author

Kenya's numerous environments provide habitats for a rich avifauna of over 1,000 species. In the floor of the Great Rift Valley that passes through Kenya are scores of relatively small and predominantly alkaline lakes that have no natural outlets. Lake Naivasha, some 50 miles northeast of Nairobi, is a notable exception, being fresh. The lake is approximately 7 by 15 miles with a belt of papyrus growing around the western and northwestern edge. Most of this papyrus is floating and varies from 100 yards to a mile in width. Lacking a natural outlet, the lake undergoes great fluctuations in level. In 1961, following a dry period of years, heavy rains raised the lake some 18 feet and created lagoons of water along the western side between the papyrus and the shore line. These lagoons, now mostly covered with water lilies that are protected from the waves of the lake by the papyrus barrier, offer an ideal habitat for a number of water birds, particularly rails, sandpipers, plovers, and lily-trotters.

The lily-trotters, or jacanas (Jacanidae), can be found in the Old and New World tropics in marshy areas where water lilies abound. Some species of these distinctive birds have brightly colored frontal shields; all species have greatly elongated toes and claws that facilitate walking on broad-leaved water plants, thus the name lily-trotter. The African Jacana (*Actophilornis africanus*) is the larger and more common of the two species found in Kenya. Its ten-inch-long body is covered with a chestnut-brown plumage. The white sides of the head, throat, and upper breast contrast sharply with the black crown and hind neck and eye-stripe. The sexes are similar, but the female is usually somewhat larger. The bill and frontal shield are a conspicuous powder blue. This combination of colors makes the bird hard to see when it crouches or stands still, blending very well into the surrounding habitat.

African Jacanas usually move in pairs, walking and foraging on the lily pads, often turning over lily leaves in search of snails and arthropods. They normally lift their feet high as they walk, and they can run over the lilies at considerable speed. They sometimes fly low over patches of open water, using their rounded wings in short and seemingly labored flight with long legs trailing at about a forty-five-degree angle. Their flight is accompanied by a characteristic call note. On flights of longer distances they stretch their legs straight out behind them. Jacanas normally keep a safe distance from human intruders, walking and running over the lily pads. They seek the cover of the

Figure 1 (*above*). An African Jacana carrying young under its wings. The legs of the chicks can be seen dangling down on either side of the parent's body.

Figure 2 (*below*). With chicks under its wings, the parent jacana walks away from the camera.

papyrus only at night when they roost. Although capable of swimming, the African Jacana does not normally do so. And if a bird accidentally falls into the water, it scrambles out again as soon as possible.

The African Jacana in Kenya normally breeds in May during the latter part of the long rainy season. It constructs a simple nest, usually a flat, sodden platform of floating vegetation, set among the lilies out in the open with no protective reed cover. The female usually lays four glossy eggs that are marked with irregular dark brown to black scribbling on a uniformly lighter brown background. The female alone incubates and cares for the young although the male may visit the nest vicinity regularly (Cunningham-van Someren and Robinson, 1962).

The chicks are not highly precocial. The downy covering is sparse, and "the eyes remain closed for several hours" after hatching (Cunningham-van Someren and Robinson, 1962). They are weak during their first 24 hours and can move about only with difficulty. But they develop rapidly and at three days of age can run agilely over the pads behind the female. During the early stages of the young jacana's life, the parent, especially watchful against possible predators, leads the chicks away and conceals them in a patch of floating grass if there is any apparent danger. When the danger becomes imminent, the parent may give a sharp alarm call, to which the chicks respond by crouching on the lily pads and "freezing" while the parent bird walks, runs, or flies a short distance. If the danger persists, the parent may return to the vicinity of the chicks and, with a marked alarm call, perform diversionary behavior, such as wing-fluttering or feigning injury with "broken-wing" or "broken-leg" displays.

Most of these behavior patterns are common to a large group of shorebirds, especially the ground-nesting species. There is, however, a distinctive behavior which appears only during the vulnerable period of the chick's life and which I observed on five separate occasions. It is best described as it occurred on the morning of 7 June 1967.

Figure 3. The parent jacana pauses to check on the chicks under its wings.

At sun-up, approximately 6:50, I saw the jacana with its three chicks, which were now five days old, on the lily pads about 100 feet from shore. In my small boat I rowed out towards them, fairly rapidly, keeping a close watch on them all the while. When the parent bird gave the alarm call, I noted the place where the chicks "froze" and was at the spot in less than a minute, found the chicks, and approached to within three feet of them. They did not move. The parent bird, decidedly agitated, made repeated low flights over me, rendering a piercing, screeching cry. It landed some 20 feet away and performed a "broken-wing" display. I slowly backed the boat off to about 10 feet from the chicks and, with my camera in hand, lowered myself slowly in the boat and waited, motionless. The parent came nearer and nearer in a series of semicircular approaches, stopping periodically to watch me. Finally reaching the chicks, it crouched down and made a low churring noise. The chicks immediately ran under the parent's wings, as if to be brooded. The parent adjusted its wings slightly, gave a single piercing call, stood up, and, holding its wings firmly to its sides, walked away carrying chicks under both wings (Figures 1 and 2). Their long legs and feet were plainly visible, dangling down on either side of the parent's body. After walking about 12 feet, the parent stopped and turned to watch me for a few seconds. Then it bent its head under each wing to check on the chicks and walked on (Figure 3). About 60 feet from me, it stopped and put the chicks down. Although in this sequence the bird carried only two chicks, I have observed a jacana carrying three young at one time, two under one wing and one under the other.

Chick-carrying in any fashion is an unusual behavior in birds. The behavior is observed in some anseriforms (see the article on parental-carrying in waterfowl by Paul A. Johnsgard and Janet Kear in this issue of *The Living Bird*). Among the jacanas it has been reported in the African Jacana and the Lotus-bird (*Irediparra gallinacea*) of Australia. The first record seems to date from 1934 when Potter and Cobcroft both reported the observations of Cobcroft who saw a parent Lotus-bird carrying one chick under each wing. Cobcroft (1934) also reported this behavior in greater detail. For the African Jacana, Pitman (1960) provides circumstantial evidence for under-the-wing carrying by the parent. And, more recently, Cunningham-van Someren and Robinson (1962) documented it in this species.

D'Ombrain (*in* Potter, 1934) observed that each "shoulder-joint" had a small bare area that appeared to have been caused by rubbing. This patch was, he thought, "due to the down having been rubbed off the prominent shoulders as a result of the pressure exerted by the parent's wings when carrying the young as described."

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NAKURU, KENYA, EAST AFRICA

A REVIEW OF PARENTAL CARRYING OF YOUNG BY WATERFOWL

Paul A. Johnsgard and Janet Kear

The occasional stories of female ducks carrying young while flying from elevated nest-sites, though ignored for the most part, still persist. Recently, the astonishing observations of Cade and Maclean (1967) on the sandgrouse *Pterocles namaqua* transporting water to its young in its feathers and the excellent photographs by Truslow (1967) of the Pileated Woodpecker (*Dryocopus pileatus*) carrying its eggs from a ruined nest, two behaviors previously regarded by ornithologists as improbable or highly unlikely, have led us to examine once again the reports of parental carrying in ducks.

Most authorities on waterfowl—for example, Phillips (1922:220; 1924:64) and Kortright (1942:227, 265)—have not taken these accounts seriously. And why should they? Photographic evidence convinces us that downy young of several species, including the Wood Duck (*Aix sponsa*), Common Goldeneye (*Bucephala clangula*), and Common Shelduck (*Tadorna tadorna*), normally jump from the nesting hole. In these species observers have repeatedly noted that when the female stands at the base of the nesting tree and calls, the young scramble up the sides of the nesting cavity and jump out in quick succession. Audubon himself subscribed to the idea that this method of egress was normal in Wood Ducks although he also believed that, if the nest was a great distance from water, the female carried the young in her bill.

We have many other accounts of the young jumping from the nesting hole. A. S. Hawkins and F. C. Bellrose (*in* Kortright, 1942) provided one of young Wood Ducks and both Brewster (1900) and Macartney (1918) described the same behavior in the Common Goldeneye. Rittinghaus (1956) reported and photographed the aerial descent of downy Common Shelducks, and Robinson (1940) and Bjärvall (1967) described almost identical behavior in Mallards (*Anas platyrhynchos*), which do not regularly nest in trees. Likewise Yocom (1952) and Craighead and Stockstad (1958) told of newly hatched Canada Geese (*Branta canadensis*) jumping from aerial nests.

Thus this type of departure from elevated nests has been observed among species representing five tribes of Anatidae (Delacour, 1954-1964), including all those with typical tree-nesting forms. In her recent studies on the behavior of newly hatched nidifugous birds, Kear (1967) demonstrated that ducklings of the tree-nesting species lack what is otherwise an almost universal characteristic — a tendency to avoid sharp drops. She suggested that this relatively dangerous behavior evolved because of the necessity of jumping to the ground soon after hatching.

Figure 1. Female Shoveler removing eggshell from the nest. This drawing, by Robert Gillmor, is based on a published photograph by Lyle Sowls.

In view of this evidence we must regard the accounts of female ducks carrying their young while flying either as hoaxes, inaccurate observations, or a representation of distinctly atypical behavior. To consider such young-carrying as pure fabrication is nullified by too many people of diverse backgrounds reporting on it in reputable journals. It seems, therefore, that another look at the accounts of parental carrying, or how young birds might otherwise leave nests in trees, is in order.

Parental Carrying in Birds Other than Waterfowl

It is at once apparent that, of all the tree-nesting avian groups, nearly every account of carrying young concerns only a few orders, most members of which are ground-nesting and leave the nest immediately after hatching. E. A. Armstrong (*in* Thomson, 1964) and Nice (1962) reported that three species of rails (*Rallus*) have been seen carrying young, and between them they indicated that similar behavior has been reported in a gallinule (*Gallinula*), a sandpiper (*Actitus*), both genera of woodcock (*Scolopax* and *Philohela*) and, curiously, a cuckoo (*Centropus*). Labitte (1960) mentioned several reports of parental carrying by various European birds, especially hawks and owls. E. W. Farmer (*in* Bent, 1932:349) observed parental carrying by a chachalaca (*Ortalis*). Cunningham-van Someren and Robinson (1962) reported parental carrying by the African Jacana (*Actophilornis africanus*) and this issue of *The Living Bird* has a paper on the same subject by John B. Hopcraft. Finally, Schäfer (1959) provided an account of parental carrying by European Woodcock (*Scolopax rusticola*) and von Frisch (1966) has described and photographed parental carrying by a Montagu's Harrier (*Circus pygargus*).

Parental Carrying in Waterfowl

It appears, therefore, that definite records substantiate the carrying of young for representatives of five or more orders exclusive of the Anatidae. However, one important difference between all of these birds and waterfowl is that waterfowl are almost totally unable to pick up anything and carry it about. According to Harrison (1967), waterfowl do not carry nesting material but pass it backwards over the shoulder. Our own observations indicate that they do not transport food in order to deal with it in a more secure or convenient place, do not normally remove eggshells from nests at hatching time, and do not bring food to their young. (We shall explain later that some species do carry eggs and eggshells.) In a few species where the adults help the young obtain food, the young come to the parent's side, either voluntarily or when called. The parents never go to them. Even in the Red-crested Pochard (*Netta rufina*), in which the male performs courtship-feeding, the female approaches the male and takes the material from his bill. But, despite this well-established disinclination to carry objects, a surprising number of accounts of flying adults carrying young do appear in literature, and such accounts involve species that represent most of the recognized tribes.

Apparently the only report of parental carrying by whistling ducks is for *Dendrocygna javanica* (Hume and Marshall, 1879-1881). Hume recalled two instances in which he personally observed adults carrying young in their claws. Yocom (1952) cited a second-hand account of Canada Geese removing young one at a time in the bill from a high nest-site, and Pedersen (1934) told of seeing two Barnacle Geese (*Branta leucopsis*) flying down from a high cliff in Greenland, each carrying in its bill an object later identified as a downy young. Madsen (1925) reported that a Barnacle Goose, after being disturbed on its nest, flew 35 meters down a Greenland cliff with one young on its back. Johnson (1965) stated that a sheep rancher in Chile had observed Black-necked Swans (*Cygnus melanocoryphus*) carrying young on their backs while in flight, and that the natives mentioned seeing Ashy-headed Sheldgeese (*Chloephaga poliocephala*) carrying goslings in the bill from tree nests. Ludlow (1950:44) quoted Colonel Stackley to the effect that Ruddy Shelducks (*Tadorna ferruginea*) carry their young to water by "tucking them in between the neck and the shoulder" and volplaning down to the shore. Several observers, quoted in Phillips' work (1922-1926), reported parental carrying by Common Shelducks. One of these, Lumsden (1898), saw a female Common Shelduck drop from its bill an object which proved to be a recently hatched duckling, and another, Payne-Gallwey (1882), reported seeing a Common Shelduck carrying ducklings on its back. Roberts (1957), as well as Clancey (1967), indicated that carrying of the young may occur among Egyptian Geese (*Alopochen aegyptiacus*) and Comb Ducks (*Sarkidiornis melanotos*).

Forbush (1922, 1925), having contacted a number of observers who claimed knowledge of the means by which another perching duck, the Wood Duck, might bring its young from the nest, thoroughly discussed the matter. He stated (1925:229) that three persons saw young carried on the female's back. In all other cases, if the parents transported the young at all, they carried them in the bill. Phillips (1925) indicates that there were 13 cases of this. Kingsford (1917) also reported carrying in the bill. Forbush added that on several occasions when the young were evidently not held in the bill, more than one clung to the female simultaneously. On the other hand, Dr. Gilbert Gottlieb (pers. commun.) told us that he was unable to induce parental carrying experimentally among Wood Ducks by any means.

Recently, Mr. Douglas Wagstrom of rural Ottertail County, Minnesota, informed me (PAJ) that in 1966 he observed apparent parental carrying by a female Wood Duck that nested about 18 feet up in an elm tree, 40 feet from the bedroom window of his farmhouse. Early one morning the female repeatedly flew from the nest entrance straight to the edge of the closely mowed lawn some 80 feet away where she dropped suddenly to the ground and stopped. After the last flight he saw a brood of ducklings, all clustered together, follow her into the tall marsh grass adjacent to the lawn. The light was not strong enough for Mr. Wagstrom to determine how the young were carried but he was positive that they did not jump from the nest-hole and run across the lawn. In 1967, Wood Ducks occupied the same nest-site, and, from 29 June, I made daily visits to the nest at sunrise in hopes of observing the departure. Although I missed the exodus by a few hours on the morning of 5 July, the Wagstroms saw it. The young definitely jumped out of the nest while the female stood at the base of the tree. If we assume that the same female Wood Duck nested there both years, this would suggest a surprising variability of behavior.

Regarding the dabbling ducks, most of which normally nest on the ground, we have only a few cases of possible parental carrying. In Australia the Black Duck (*Anas superciliosa*) often nests in elevated sites (Frith, 1967), and Miles (1950) provided a first-hand account of the female carrying the young to the ground on her back. However, Chapman (1951) gave an equally detailed description of the same species in New Zealand bringing the young from a treetop nest in her bill.

Several species of sea ducks typically nest in tree cavities or elevated sites. Various accounts of parental carrying can be found for both species of goldeneyes, such as Bailey's (1918) for the Common Goldeneye. Dr. Frank McKinney (pers. commun.) informed us that Alaskan fishermen told him of seeing Pacific Eiders (*Somateria mollissima v-nigra*) carrying young on their backs, and Bent (1923) cited some accounts of female Hooded Mergansers (*Mergus cucullatus*) and Common Mergansers (*M. merganser*) carrying young in the bill.

The only stiff-tailed duck for which we have any information concerning adults possibly flying with young is the Musk Duck (*Biziura lobata*). Mr. H. A. Robinson (pers. commun.) told me (PAJ) that Australian fishermen have reported seeing Musk Ducks taking flight with young on the back.

Possible Means of Carrying Young

Thus, observers have repeatedly described two diverse means of parents carrying young—on the back or in the bill.

Although the second method seems especially improbable, the observations of Sowls (1955) and others on damaged eggs or eggshells being carried from the nest (see Figure 1) demonstrate a clear capacity for removing objects in the bill—regardless of the statements by Nethersole-Thompson (1942). Sowls reviewed earlier reports of Mallards and Mexican Ducks (*Anas diazi*) carrying whole eggs or cracked eggs; and, in addition, he induced eggshell carrying in incubating Shovelers (*Anas clypeata*) and Pintails (*Anas acuta*) by planting eggshells among the clutch. Hochbaum (1959:92) writes of a Shoveler carrying an egg in flight. McKinney's description (1967) of captive female Shovelers carrying eggs or eggshells on three occasions strengthens these observations. There are also older published accounts of removal of addled eggs by Muscovies (*Cairina moschata*) and Common Mergansers. Similarly,

Figure 2. An unusually large family of Mute Swans. Notice how the wings of both adults (female in foreground) are slightly raised, providing a convenient "cockpit" for the young. Photograph from the files of the Wildfowl Trust; photographer unknown.

Figure 3. Female Mute Swan with two young aboard. Photograph courtesy of the *Reading* (England) *Evening Post.*

E. Merikallio (*in* Hildén, 1964) reported that female Common Eiders (*Somateria mollissima*) may remove eggs broken during incubation, and D. J. Brand (*in* Siegfried, 1965) reported that female South African Shovelers (*Anas smithi*) may carry away the empty shells as the eggs hatch. Clancey (1967) indicated that similar eggshell removal may also occur in Yellow-billed Ducks (*A. undulata*) and Weller (1959) has seen the same behavior in Redheads (*Aythya americana*). The only observation of egg-carrying by birds at the Wildfowl Trust was made by Dr. G. V. T. Matthews (pers. commun.) in April 1968 when a full-winged female Wood Duck swam across the pond in front of his window, carrying in her bill an apparently addled egg. She traveled some 45 yards before dropping it. Thus we cannot entirely discount the carrying of young in the bill.

The other method of carrying young—of flying with them on the back—is also difficult to accept. Nonetheless, we know that swimming adults do sometimes carry the young on the back. This behavior is marked in the three temperate-breeding swans, the Mute Swan (*Cygnus olor*), Black Swan (*C. atratus*), and Black-necked Swan, all of which may carry their young on their backs while swimming during their first two weeks of life or even longer (see Figures 2, 3, 4, 5, and 6). This activity in the temperate-breeding swans partly replaces brooding which in the northern, mostly arctic-breeding species, *C. cygnus* (including *buccinator*) and *C. columbianus* (including *bewickii*), takes place entirely on land. Although brooding on land seems to be restricted to the females of all swans, both sexes of the three temperate-breeding species carry cygnets on their backs. The male Mute and Black Swans do so only occasionally, but the male Black-necked Swan often swims about with three or four cygnets on its back at one time.

Figure 4 (*above*). Black-necked Swan at the Wildfowl Trust with one young cygnet visible on its back. The adult shown is probably a female. Photograph by Russ Kinne.

Figure 5 (*below*). Male Black-necked Swan at the Wildfowl Trust with three young on its back. One is barely visible under the bird's right wing, a second is looking over the adult's left shoulder, and a third is behind the second, with its head hidden under the wing or scapular feathers of the adult. Photograph by Paul A. Johnsgard.

Figure 6. Male Black Swan at the Wildfowl Trust, brooding one newly hatched cygnet on its back while others stand beside it on the nest. Unlike other species, male Black Swans regularly assist in incubation. Photograph by Paul A. Johnsgard.

In these species the cygnets initiate the carrying by climbing on at a point between the folded wing and the tail (Figure 7). The parents do not assist them except perhaps by remaining motionless until they are aboard; thus, the carrying depends mainly on the young themselves. Not only do the arctic-breeding swans never carry cygnets, but also, if we give the cygnets of arctic-breeding species to temperate-breeding adults to rear, the temperate-breeders do not carry them (JK, unpublished data). We have not yet attempted the rearing of temperate-zone cygnets with adults of the arctic forms at the Wildfowl Trust. We note, however, that the arctic species, all of which are migratory, do have longer wings that fold closely over the back, presenting a smooth lateral outline that might make climbing difficult. And we also note behavorial differences in the cygnets of the two groups. The cygnets of the temperate-zone forms exhibit a strong climbing tendency that the arctic species do not possess, at least to the same extent. For example, a small hand-reared Mute Swan is restless when sitting in a human lap and must reach the shoulder before settling down (Figure 8); a small hand-reared Trumpeter Swan is not.

Figure 7. Black-necked Swan cygnets climbing onto an adult. This method of "boarding" is typical of all the swans that carry their young; the parent provides no assistance. Drawing by Robert Gillmor.

At least two ducks also regularly carry their young, the Musk Duck (Serventy and Whittell, 1948; Lowe, 1966) and Salvadori's Duck, *Anas waigiuensis* (Delacour, 1954-1964). The Musk Duck is a large, short-winged Australian stiff-tail and in this case, since the male Musk Duck assumes no parental role after copulation, the female alone carries. The clutch size is small, two eggs being the commonest number (Frith, 1967), and the brood is often reduced to a single offspring (Lowe, 1966) which rides around on its mother's back, even apparently diving with her by holding on to her neck feathers with its bill (Serventy and Whittell, 1948). The behavior has not been investigated in detail in the Musk Duck, nor in the Salvadori's Duck where again it is apparently only the mother that carries. Observers have also noted carrying during swimming in the Common Goldeneye (Bailey, 1918), Black-bellied Tree Duck, *Dendrocygna autumnalis* (Bolen *et al.*, 1964), two sheldgeese, *Chloephaga poliocephala* and *C. melanoptera* (A. W. Johnson, pers. commun.), two mergansers, *Mergus serrator* (Cory, 1878) and *M. merganser* (Baird *et al.*, 1882:115), and the Wood Duck (Allen, 1961:192). At the Wildfowl Trust we have seen the young of nearly all these species sitting or standing on the backs of foster-parent hens (Figure 9).

Figure 8. A hand-reared Mute Swan cygnet climbing up to the shoulder of Dr. Kear. Photograph taken at the Wildfowl Trust by Jan Rietz.

Discussion

The advantages of adults carrying young while swimming seem so obvious that we wonder why most waterfowl species do not do so. Presumably the adult must be relatively large and the brood small enough for all to be accommodated, and the adult must not need to fly much. It seems significant that at least four of the species which carry their young while swimming have relatively short wings. As in the grebes (Podicipedidae), the ducks carrying young would spend a great deal of time afloat and, therefore, obtain much of their food on or below the water surface. The evolution of the trait of carrying the young while swimming was possibly influenced by predation and in this respect certain differences in the life histories of swans may be relevant: The arctic species, which do not carry their young, hatch when the summer night is short or even non-existent; the temperate-zone cygnets, on the other hand, daily experience some hours of darkness when they are particularly vulnerable and need protection from predators. Further, the arctic cygnets grow very rapidly and perhaps they become too large too quickly for easy carrying.

From a consideration of parental carrying while swimming, two points emerge: First, in at least all the species which are well studied the young initiate the carrying; and second, in one species that dives the duckling reportedly clings so tightly to the neck and back feathers that even when the adult submerges, the young is able to remain attached. Dr. Kear, when handling newly hatched ducklings of about 100 species of waterfowl, has noticed how many of them, perching ducks in particular, cling to fingers and clothing. When startled they occasionally bite and hang on tightly for some seconds. Forbush (1922:15) reported somewhat similar behavior for newly hatched Wood Ducks which clung to the backs of foster-parent hens during their first few days of life. Thus, in certain species at least, the two behavioral prerequisites for taking flight with the young on the back are fulfilled, namely, the ability to climb onto and take a firm hold of the parent. The adult's behavior—swimming, diving, or taking flight—is relatively unimportant, but being able to fly with the young would surely have great survival value. For instance, it

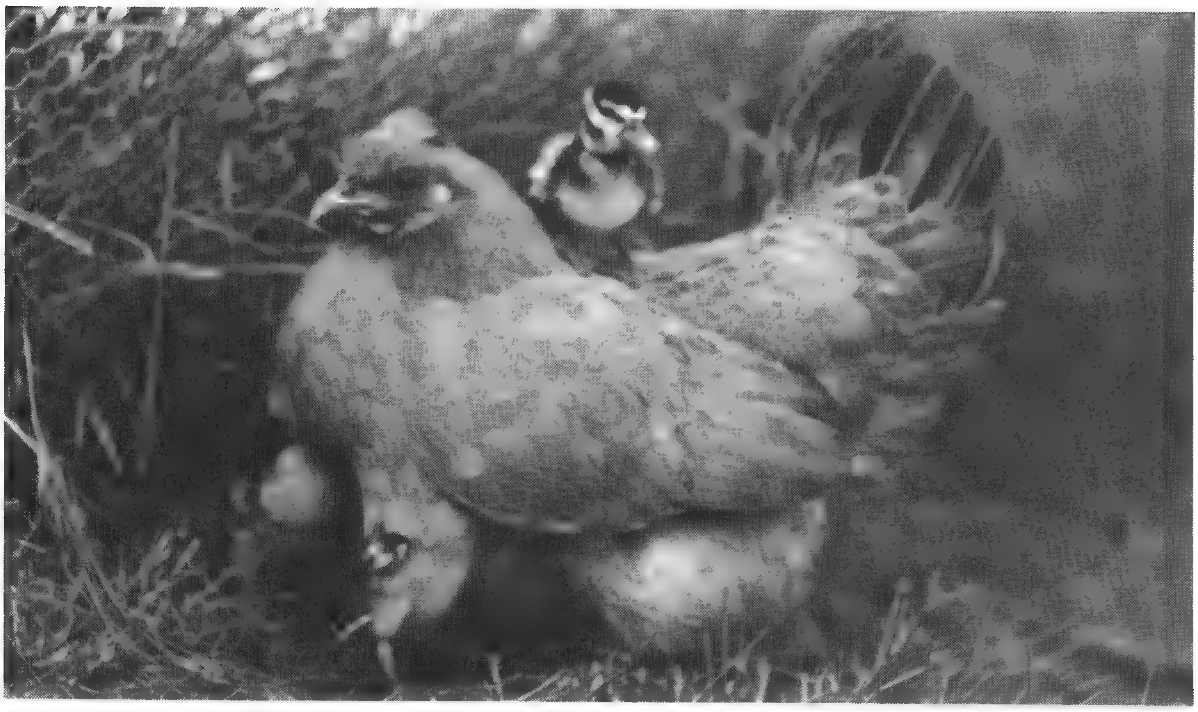

Figure 9. Downy Black-bellied Tree Duck standing on the back of a bantam hen at the Wildfowl Trust. Photograph by Philippa Scott.

seems reasonable that for the highly aquatic Musk Duck such a method of transporting the young might be more feasible than walking with them when the breeding ponds dry up.

We feel that authorities on waterfowl have discounted too hastily the possibility of parents transporting young. Although jumping from the nest at the mother's signal is the normal procedure for hole-nesting waterfowl, the evidence suggests that parental carrying among the feathers might occur on rare occasions or in special circumstances and, where it occurs, depends mainly on the behavior of the young themselves. And, in the light of recent observations on waterfowl carrying eggshells from the nest, we cannot dismiss too casually the fact that some waterfowl may at times carry the young in the bill.

Summary

A review of literature reveals that published accounts of parental carrying among waterfowl are numerous and of diverse origins. Parental carrying on the back while swimming has been reliably seen in three species of swans, two sheldgeese, and at least seven species of ducks. Parental carrying of young in flight has also been reported for at least 16 species representing seven of the generally recognized waterfowl tribes. The majority of such accounts have involved carrying the young in the bill, a possibility that is somewhat substantiated by reliable observations of egg or eggshell carrying by females of several species. In addition, at least those species that regularly carry the young on the back while swimming may be preadapted to similar carrying of them while in flight. It is suggested that occasional parental carrying by either or both techniques is sufficiently probable as to warrant additional consideration and attention.

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BEHAVIOR OF HAND-RAISED KIRTLAND'S WARBLERS

ANDREW J. BERGER

Most of the wood warblers (Parulidae) of North America range widely either across the continent or in its eastern or western segments. Only a few such as the Kirtland's Warbler (*Dendroica kirtlandii*) live in relatively restricted areas. Not surprisingly, the Kirtland's Warbler (Plate I) is on the list of rare and endangered species of North American birds. Censuses conducted in 1951 and 1961 revealed that the total breeding population of the species was about 1,000 birds (Mayfield, 1953, 1962), all on the sandy jack pine (*Pinus banksiana*) plains in the upper part of Michigan's lower peninsula. Here birds find conditions suitable for nesting when the jack pines are from three to about 25 feet high. It is only in trees of this size that the pattern of thickets and open spaces and the ground cover appear to provide the necessary ecological requirements for breeding.

Early Records of Nesting and Raising Captive Birds

It was not until 1903 that E. H. Frothingham and T. G. Gale (Holden, 1964) discovered the nesting grounds of Kirtland's Warbler. Norman A. Wood found the first nest on 8 July 1903, and the second nest the following day (Wood, 1904; Holden, 1960). Additional nests were found in the following years, but the first important life history study was written by Leopold (1924).

In his unpublished field journal, Norman A. Wood recorded that he took the nestling Kirtland's Warblers from his first nest on 11 July 1903 and kept them "alive by feeding them House flies until the 13th, when I found them dead, and I made them up into skins." Wood (1904) collected his second nest on 14 July 1903, stating: "I brought the 5 young back alive, although I had to Chloroform and preserve them the next day."

Josselyn Van Tyne first visited the nesting grounds of Kirtland's Warbler in 1930 and continued his studies on this species until his untimely death in 1957 (Mayfield, 1960; Berger and Radabaugh, 1968).

Van Tyne had tried at least three times (1939, 1948, 1955) to hand-raise nestling Kirtland's Warblers, but without success. I know of no records on his experiences with the young warblers. When Van Tyne and I were on his study area near Mack Lake in Oscoda County, Michigan, during the first week of July 1956, he asked me to try raising a nestling Kirtland's Warbler. On 23 July 1956, I collected one of four nestlings from a nest I had found with four eggs on 3 July. It died five weeks later on 31 August, presumably from asphyxiation, perhaps complicated by fright (Berger, 1965).

Figure 1. A Kirtland's Warbler shortly after leaving its nest. Drawn direct from life, 24 July 1948, by George Miksch Sutton.

I collected another warbler in 1957, only a few hours after it had left the nest; six nestlings from two nests in 1958; and, in 1963, two more nestlings—the last of a brood of four in a nest that had clearly been subject to predation. This paper is based on my experiences with all of these birds.

Figure 1 depicts a young Kirtland's Warbler shortly after leaving the nest.

Feeding

The feeding posture of the fledgling Kirtland's Warbler is typical of many passerine species—the bird crouches, flutters its wings, and gives food-begging calls.

For several days after they left the nest the hungry young birds hopped about on the aviary floor, begging loudly but refusing to come to me for food. Two birds first came to me at the age of 12 days when I knelt down and offered food in forceps. By the time they were 14 or 15 days old all the young warblers were flying to me to be fed, often alighting on my hand, head, or shoulders in response to a whistle. Table 1 outlines their gradual development to independence. Some items defy charting. By the time the birds were 14 or 15 days of age they were pecking at the ground, watching ants, and sometimes picking them up and then discarding them, or trying to. (One bird, 16 days old, went around almost all day with the mandibles of a large, dead black ant securely clamped to the tip of its tongue. After several tries I finally removed it.) By the time they were 21 days old they were discriminating between insects that they ate and ants that they did not care for.

Sometimes they were afraid of moving insects. One bird refused to pick up a fluttering cabbage butterfly, but readily took it from the forceps and ate it. Another bird, about 21 days old, suddenly coming upon a mayfly on its back with legs kicking, jumped nearly a foot in the air, then recovered, and snapped up the mayfly. At 21 days old, all of the birds could pick up and manipulate small insects; about this same time they first approached the food dish holding a mixture of raspberries, Pablum, hard-boiled egg, and grated carrot. I first

Plate I. Male Kirtland's Warbler feeding a young bird just out of the nest.
Painting by George Miksch Sutton.

noticed a bird (1958) chase and catch an insect in the air at the age of 32 to 33 days. They were all successfully "hawking" insects from the air by the time they were about 35 days old, and, about that same period, they ceased giving food-begging calls in response to my whistle.

TABLE 1

Feeding Behavior of Young Kirtland's Warblers

Description of behavior	*Days of age*			
	1956 *1 bird*	*1957* *1 bird*	*1958* *5 birds*	*1963* *2 birds*
Flew to forceps offering food	12			
Sometimes hopped to forceps offering food in response to whistle				12
Flew to man to be fed, alighting on hand, head, or shoulder	13–14	13–14	13–14	13–14
First attempt to pick up food; pecked unsuccessfully at ant	13			
Discriminating between ants and other insects	21			
First successful attempt to pick up food—small green larva	15			
First turned head to follow moving insect; saw shadow of moving insect and pecked at piece of wood near it	10			
Followed flying insect visually; head movements slow	13			
Followed flying insect visually; head movements rapid	19			
Showed fear of fluttering cabbage butterfly; of mayfly	17:21			
Caught butterflies and insects easily	28			
First went to food dish	20		1 19–20 4 23–24	
Picking up and manipulating small insects — grasshopper, damselfly	20	22		
Difficulty wiping bill — ate grasshopper, spider web, and grass	21			
Chased small moth but did not catch it			21–22	
Caught small moths and insects easily			24–25	
Had tug-of-war with siblings over moth			23–24	
Essentially independent but still accept food from forceps	26	26	27–28	26–28
Unsuccessful attempt to capture insect in air	33			
First successful capture of insect in air			32–33	
All successful "hawkers"	35	35	35	35
No longer responded to whistle by giving food-begging calls			35–36	

Defecating

When voiding, the nestling elevates its cloacal region, usually turns from a quarter to a full circle before passing the fecal sac, and then often returns to its original position in the nest. Such movements by one nestling cause the nest-mates to shift about considerably.

During their early stages my young birds voided a fecal sac after every feeding. As they grew older and the feeding-defecation reflex became less automatic, they voided only after every second or third feeding.

At the age of 10 days two of the birds (1963) voided not only after feedings but between feedings as well, and they did not always turn around to void. They simply elevated the cloacal region and backed up a short distance.

The first warbler (1956) voided three fecal sacs between 11:00 PM and 6:35 AM when it was eight days old and five sacs between 11:00 PM and 7:00 AM when it was 14 days old.

Figure 2. The captive 1956 Kirtland's Warbler preening its wing feathers when approximately 11 days old. Photographed by the late Josselyn Van Tyne.

Preening

Two Kirtland's Warblers (1963) stretched the same wing and leg simultaneously, stretched both wings over the back, and sometimes flapped them at about six days of age. Two days later the smaller bird preened its breast and scapular feathers and the larger bird preened its short primary flight feathers, still mostly sheathed (Figure 2).

Table 2 shows the rapid advance in preening and flight of one bird (1956). All of the warblers were able to fly well at the age of 14 or 15 days.

TABLE 2

Preening and Flight Behaviors of Young Kirtland's Warblers

Description of behavior	*Days of age*	
	1956 *1 bird*	*1963* *2 birds*
Stretched wing and leg on same side simultaneously; stretched both wings over back and flapped them		6
Preened breast and scapular feathers and short primary feathers		8
Preened ventral feather tracts	8	
Preened, stretched wings, scratched head, stretched high by rising on both legs	8	
Hopped and flew about the breezeway about every two hours; slept or sat quietly in between, stretched, preened	11	
Able to fly from floor to 12-inch perch with ease	11	
Flew 9 feet, losing only one foot elevation. Unable to recognize perch	11	
Flew 10 feet gaining elevation	12	
Flew well	14	

Head-scratching

Recently I (1966c) called attention to the ontogenetic pattern of development of head-scratching in passerine birds. A nestling bird may be able to scratch its head over the wing (indirect head-scratching) because the bird sitting in the nest does not have to stand on one leg. After leaving the nest the young bird has the drive to scratch its head indirectly before being physically capable of doing so. The bird draws one leg forward with the "intention" of scratching and abruptly retracts it in order to regain its balance on the perch. About 24 hours after these first attempts neuromuscular coordination is established and the bird is able to scratch its head either directly (under the wing) or indirectly.

I have watched many adult Kirtland's Warblers in the field and have never seen them scratch their heads any other way than indirectly—over the wing. One of my captive birds once scratched its head directly at the age of about 14 months. Otherwise, I saw nothing but indirect head-scratching in all the captive birds (see Table 3).

Anting

As of 1957 there were no records of Kirtland's Warblers anting (Mayfield, 1960:66). The one record in my captive flock was for an adult (1958), on 20 May 1959. While turning its tail 90 degrees from the normal position, first to the right and then to the left, the bird picked up an ant or ants in its bill and rubbed them on the under surface of the base of the tail near the vent. It did this four times and then ate a mealworm pupa (see Table 3).

TABLE 3

Miscellaneous Behaviors of Young Kirtland's Warblers

Description of behavior	*Days of age*			
	1956 *1 bird*	*1957* *1 bird*	*1958* *5 birds*	*1963* *2 birds*
Head-scratching:				
Head-scratching in the nest	8			
Head-scratching on perch unsuccessful at first; successful one hour later	10			
Head-scratching in nest as red ant crawled on neck				8
Head-scratching on perch successful				13
Anting:				
Anted four times			11 months	
Tail-bobbing:				
First tail-bobbing	17		11–12	14
Sleeping and roosting:				
Turned head backwards on left side				8
Head turned backwards over right or left shoulder	10			
Extension of toe while sleeping on perch	15		19–20	
Sometimes perched on one foot for 20 or 30 seconds			23–24	
Hopped or fluttered to highest perch it could reach	11			
Rested on tarsi on ground or windowsill			16–17	
Slept at night on high perch			26–28	
Slept beside Blue-winged warbler		28		
Slept on high perch with Traill's and Yellow-bellied Flycatchers		32		
Slept 5 or 6 inches apart			4–8 months	
Tendency to sleep on isolated perches			9 months	

Tail-bobbing

Van Tyne (1953:422-423) pointed out that "wagging" is an inappropriate name for the conspicuous tail movements of adult Kirtland's Warblers when he wrote: "Actually, the tail is jerked downward and then—more slowly—returns." Mayfield (1960), describing the warbler's tail movements in the same way, noted that he first observed tail-bobbing by wild Kirtland's Warblers "at the age of about 18 days." I first noticed tail-bobbing earlier in my captive birds (see Table 3).

Sleeping and Roosting

Any very young nestling passerine bird sleeps with its head and neck resting on the bottom of the nest or on top of one of its nest-mates. As the bird grows, it tends to rest its head on the rim of the nest. Further neuromuscular development is necessary before it assumes the adult sleeping posture of turning the head backwards over the shoulder and placing the bill in the scapular feathers (Figures 3 and 4).

When one of my young warblers (1963) was eight days old, it turned its head backward on the left side as though it were trying to put its bill in or under the scapulars although these feathers were not yet long enough to conceal the bird's bill (Table 3). The bird closed its eyes and its bill rested on the surface of the feathers. Very soon, as the bird slept, the head slowly turned so that the bill rested at right angles to the body, and, within a few minutes, the head gradually turned forward until the bill pointed straight ahead. This sequence of events led me to believe that the instinct for sleeping with the head turned backwards and the bill buried in the scapulars was at work, but that the muscle development and coordination enabling the bird to maintain this sleeping posture were not yet fully developed.

Another warbler (1956) slept with its head turned backward over the right or left shoulder when ten days old, and, for the next ten days, it slept much of the time either on the floor or perched in low branches, often under cover of a clump of leaves.

A number of descriptions of the mechanism that enables a bird to hold its grasp on a perch while sleeping suggest that the tendons of muscles that cross the back of the "heel" joint are stretched so much that the toes are "locked" around the branch. I have noted that sleeping Kirtland's Warblers do not maintain a vise-like grip on the branch. Rather, at relatively short intervals of from 10 to 30 seconds, the sleeping bird lifts one foot off the perch, rapidly extends and flexes the toes, and then grasps the perch again. The bird may thus relax the muscles of the legs alternately or may raise the same foot several times in succession. Occasionally a bird will raise one foot and then the other within two or three seconds.

I first noted this toe extension of a sleeping bird in one warbler (1956) 15 days old. I watched the same behavior pattern when the bird was 19 days old and heard a characteristic sound each time the sleeping bird flexed its toes to grasp the branch again.

Several of the warblers (1958) exhibited this toe-extension pattern when they were 19 to 20 days old, and, by the time they were 23 to 24 days old, they sometimes slept perched on one foot for brief periods—20 to 30 seconds. When on one foot they usually extended and flexed the hallux every few seconds with little or no observable movement of the anterior three toes. Once one of the birds, perched on both feet with its head turned backwards and bill tucked into the left scapular feathers, released its grasp with the left foot to flex the toes, missed the branch, slipped, and woke up. It immediately tucked its head into the scapular feathers and went back to sleep.

When my Kirtland's Warblers first left the nest, they often tried to hop or flutter to the highest perch they could see, but many times it was well beyond their reach. This behavior, apparently different from that of wild Kirtland's Warblers, may have been because the aviary floor was bare—without thick ground cover. As the birds gained flying skills, they usually perched in low branches or on the floor during the inactive periods. I noted a change in the behavior of the 1958 warblers at the age of 16 and 17 days: Although they

Figure 3 (*above*). Sleeping posture of a hand-raised Kirtland's Warbler when approximately 11 days old. From a color transparency taken by the author on 23 July 1963.

Figure 4 (*below*). The same sleeping warbler as shown in Figure 3 but viewed from above. Note that the bill is not concealed by the scapular feathers.

flew around the aviary skillfully, they spent most of the time sitting on their tarsi either on the ground or window sill and seemed to have lost the motivation to ascend to higher perches.

There were other birds in the aviary in 1957—two Blue-winged Warblers (*Vermivora pinus*), a Traill's Flycatcher (*Empidonax traillii*), and a Yellow-bellied Flycatcher (*E. flaviventris*). When 28 days old the Kirtland's Warbler slept perched beside a Blue-winged Warbler of approximately the same age. When 32 days old the warbler went to sleep on a high perch, three inches from the two flycatchers. Within 45 minutes the two flycatchers moved up to the warbler and the three slept in contact with each other.

During the fall and winter of 1958, two or three warblers often slept within five or six inches of each other in a potted shrub. By the first week in March 1959 they sometimes tended to select isolated sleeping perches.

The first light in the outdoor flight cages was from an ordinary desk lamp which I lighted at 7:15 PM on 16 August 1957. Although it was not yet dark, the Kirtland's Warbler and the two Blue-winged Warblers had already settled on their perches and did not leave. The two flycatchers, however, were still capturing moths attracted by the light when I turned it off at 10:15 PM. During the months that followed the Blue-winged Warblers went to roost first, the Kirtland's Warbler about 15 minutes later, and the flycatchers last.

During the summer of 1958, when I used floodlights every night, one or more of the Kirtland's Warblers often foraged for short periods each evening, catching insects on the ground, on the wire of the cage, and in the air.

Bathing and Drinking

Standing water is rare in the pine barrens, the breeding habitat of the Kirtland's Warbler. Although I assume that the birds may bathe in puddles when they occur, I know of no records of them bathing in puddles in the wild. Captive birds readily bathe in standing water. The older birds, however, do not prefer this method.

Table 4 gives a summary of the bathing habits of the captive birds. When I watered the plants in the outdoor aviary, all of the birds invariably flew through the fine spray or perched on branches under the spray, bathed, and then flew to dry perches to preen and dry. The Kirtland's Warblers bathed less than the Blue-winged Warblers and the flycatchers.

In general the older birds bathed in rain or spray, by walking through the wet grass, or by flying to wet leaves where they would crouch, press the breast feathers against the surface of the leaves and engage in typical bathing motions. In the winter they often performed bathing motions at the mere sight or sound of water dripping from the plants on a shelf. I seldom saw them drink water.

Sunbathing

The first evidence of sunbathing occurred in a bird about 10 days old. It simply raised its head and opened its bill slightly while perched in the sun. Later the sunbathing became more elaborate (see Table 4). At times they simply sat on their tarsi facing the sun. At other times they perched with their backs toward the sun.

Chasing Display

Except for the Mockingbird (*Mimus polyglottos*), most of the birds that I raised lived in harmony with a minimal amount of interspecific antagonism (Berger, 1966a, 1966b).

TABLE 4

Bathing by Young Kirtland's Warblers

Description of behavior	*Days of age*				
	General	*1956 1 bird*	*1957 1 bird*	*1958 5 birds*	*1963 2 birds*
Bathing in water:					
Bathed when put in water, did not preen or shake feathers		16			
First voluntary bathing	19–20				
Perched on pan of water. Hopped out when put in		11			
Hopped through water but did not bathe or drink					15 16 17
Hopped through water, did not bathe or drink but 20 minutes later preened and shook wings as though it had. Later in day, bathed, preened, and shook wings		19			
Got so wet bathing it could not fly; repeated in afternoon		22			
Wet by rain, preened, and shook wings		26			
Flew to ground under spray, went through motions as if in puddle, preened, and dried on perch					67
Drank water from pan			32	21–28	18
Drank drops from branch			over 1 year	7 months	
Sunbathing:					
Raised head and opened bill slightly in sun		10			
Sat on tarsi, stretched neck forward, opened bill slightly, and leaned away from sun			13		
Elevated head with crown feathers erect, bill half open, tail lowered, wings drooped		17			
Perched with head and tail raised, bill slightly open, wings drooped but not spread. Crouched on limb and opened bill		19			
Leaned away from sun, spread tail, extended wings, and pointed half-open bill upward				20–22	

TABLE 5

Chasing Displays of Young Kirtland's Warblers

Description of behavior	*1957*	*1958*
Threatened a Yellow-bellied Flycatcher with open bill when it moved too close on branch	31	
Threatened Traill's Flycatcher with open bill when awakened at night. Then fell asleep	32	
Five 1958 birds introduced to cage with 1957 female. No overt response		30
Young warblers chased adult female		36–37
Flew swiftly around cage in "play flights" and chasing		38–39
Still chasing, very tame and curious—flew to man, pecked at shoes, hopped in front of or behind		75

The Kirtland's Warbler (1957) threatened the Yellow-bellied Flycatcher once by turning its open bill toward the flycatcher (Table 5). It also threatened the young Traill's Flycatcher once when the flycatcher flew to the perch where the warbler was sleeping. I introduced the adult female (1957) to the 1958 birds when they were 29 to 30 days old. When she hopped to within six inches of a youngster taking a sunbath, the young bird responded by drawing back slightly and opening its bill a little wider. Otherwise, within a period of two minutes, the adult female and the four young registered no overt response as they passed within one foot of each other.

They all did a lot of chasing as soon as they could fly well — 38 to 39 days old—in and out of the shrubbery or from the south cage through the entryway to the north cage. At 75 days of age they still chased and they also were very tame and curious, flying to me as I entered the cage, pecking at my shoes, hopping in back and in front of me.

Agonistic Displays

I banded the 1958 birds with colors—pink, blue, orange, yellow, and black. The summary below refers to the individuals by their colors and gives examples of their displays and dominance one over the other and over the adult female (1957) which shared the cage.

Seventy-one to Seventy-two Days Old

Blue, a male, gave a hoarse song and displayed to Pink, also a male, by spreading wings and tail and "waddling" away several times. Pink flew and Blue followed. Twice they flew into the air facing each other. Thereafter, they foraged separately.

Five Months of Age

On 25 November 1958, Pink was dominant over Blue, Black, and Yellow and in turn chased them from the food dish. Pink was dominant for several weeks.

Six Months of Age

In December, chasing increased and by the end of the month was the dominant behavior. Pink chased Yellow and in a few minutes Yellow chased Pink. Blue chased Orange and the adult female (1957). Although both the adult and the young sometimes intimidated another bird by crouching and turning the half-open bill toward the intruder, throughout most of the day they hopped and perched near one another without any sign of hostility. Two or three often slept within a few inches of each other in the shrubbery.

On 28 December 1958, Blue spent much time chasing Orange. Once Blue flew to a branch near Orange, crouched slightly, opened its bill, and spread and lowered its wings. An instant later Blue chased Orange. Later, both flew to a mealworm larva; Orange picked it up and flew; Blue did not follow.

Seven Months of Age

In January 1959, Blue flew toward Pink, perched on a branch. Pink crouched and opened its bill; Blue veered off. Pink intimidated others by walking slowly and fanning tail, exposing white on outer tail feathers.

On 13 January 1959, Pink sick, lost coordination, distance-judgment, and flying ability. Improved slowly and was dominant over the other birds by 21 January.

On 21 January 1959, adult chased Blue repeatedly, once making snapping sound with bill at start of chase. Later, Blue fanned tail from perch as adult flew to pile of bran with mealworms and extracted one. Blue and Orange flew close to female. Female dashed toward Blue which flew off, fanned tail, and darted toward Orange. Blue and Orange flew to perch. Female ate beetle.

On 25 January 1959, Blue chased female most of day. She fanned her tail showing white feathers.

Eight Months of Age

From 21 to 28 February 1959, chasing decreased. By March 1, birds paid little attention to each other and roosted on separate perches.

Ten Months of Age

On 1 April 1959, birds put in outdoor flight cages. No chasing, no antagonism.

On 21 April 1959, chasing resumed.

Call Notes and Song

From the age of 11 days one warbler (1956) always gave its food-call, a *chip,* when it was hungry and I appeared. Although it continued to chip, it paid no attention to the songs of Chipping Sparrows (*Spizella passerina*) and House Sparrows (*Passer domesticus*) nesting outside the aviary. At the age of 34 to 35 days some of the warblers (1958) were giving two adult call notes, a harsh chip and a softer location note, often heard between members of mated pairs on the breeding ground. The first song I heard when the bird (1958) was 41 days old sounded more like the notes of the Purple Finch (*Carpodacus purpureus*), Warbling Vireo (*Vireo gilvus*), or House Wren (*Troglodytes aedon*) than anything I had ever heard from a male Kirtland's Warbler on the breeding grounds. There was also a whisper song during the following weeks.

The first song attempts continued until about mid-September. I next heard the whisper song on 20 January 1959, and, although Pink and Blue both uttered whisper songs during February and early March, there was nothing persistent and none of the songs resembled in any way the song of the adult male on the breeding grounds. Table 6 outlines my notes on song.

I cannot say from the meager evidence that the young Kirtland's Warbler learns its territorial song from singing males during its nestling and fledgling life, but the evidence I have seems to cast doubt on the possibility that the song is entirely innate.

At no time during 1959 was there any indication of nest-building behavior. It is impossible to say whether this was a dietary matter, inappropriate vegetation, the absence of adult territorial song, or other factors.

TABLE 6

Call Notes and Song of Young Kirtland's Warblers

Description	*Days of age*				
	General	*1956 1 bird*	*1957 1 bird*	*1958 5 birds*	*1963 2 birds*
Often gave food-begging *chip* but paid no attention to call notes of Chipping Sparrow and House Sparrow outside aviary		21			
Rapid *chip* notes at end of short flight	12				
Two adult call notes—a harsh *chip* and a softer note				34–35	
Pink gave first song — low hoarse warble unlike any heard from male on breeding ground. Sang frequently following weeks				40–41	
Pink or other warblers sang whisper song for 5 minutes				77	
Blue gave hoarse indefinite song several times				70	
20 January 1959, whisper songs				7 months	
2 February 1959, Blue sang soft warbled whisper song with bill closed.				8 months	
10 March 1959, birds rarely sang				9 months	
11 and 16 May, Blue sang full-voiced song unlike any song of Kirtland's Warbler male on breeding ground				11 months	
Mid-July, one warbler sang off and on for about a week				13 months	
19 August 1959, Cardinal (*Richmondena cardinalis*) sang at 5:05; warbler sang for few seconds				14 months	
21–22 August, Blue sang loudly for several minutes each day, staccato-like notes reminiscent of the song of male Kirtland's but still bore little resemblance to it				14 months	

Migratory Restlessness

On the night of 25 August 1957 the young warbler, 69 days old, gave call notes. On 27 August 1957 it called at 12:47 PM, 1:05 AM, and 1:13 AM. During the latter part of August 1958 all the warblers became active at night and gave their "chip" call notes at all hours.

The night of 7-8 September 1957 was clear with a full moon and air temperature at 11:45 PM of 55°F. Migratory warblers moved through the woods surrounding our house and the Kirtland's Warbler and the two Blue-winged Warblers became active, giving call notes and flying around in the outdoor cages.

Summary

In this paper I have discussed my experiences in raising wild Kirtland's Warblers (*Dendroica kirtlandii*) from the nestling and fledgling stages to beyond their first year. I have outlined the development of their behavior in feeding, preening, head-scratching, bathing and drinking, chasing, agonistic displays, call notes, and migratory restlessness.

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SURVIVAL OF RUFFED GROUSE IN A BOREAL FOREST[1]

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For the past 11 years, from April 1956 through November 1966, we have studied the demography of Ruffed Grouse (*Bonasa umbellus*) living on or near the Cloquet Forest Research Center about 20 miles west of Duluth, Minnesota. King (1937) used this same area in the early 1930's for his intensive investigations of this species.

We designed our study of the Ruffed Grouse primarily to measure the impact of modern methods of forestry management on a population of this species in an area where no concessions have been made to its welfare. The survival rates of individual birds, computed statistically, provided a basis for understanding this relationship.

We used several parameters. For the males: (1) The historical status of occupied activity centers and drumming logs; (2) the influence of predominate forest types; (3) the protection of the refuge; and (4) the color phase—whether red or gray—of the individual grouse. Because of insufficient data we could examine the survival of the females only in relation to males with comparable data, and the survival of juvenile males over their first winter from the time they were banded as chicks until they used drumming logs in the spring.

Prior Studies

The elusive nature of the Ruffed Grouse accounts for the paucity of information on the survival of individual birds. Previous studies depended on changes in estimated population densities, based on flushing counts, or upon an analysis of seasonal changes in sex and age ratios or both, with widely differing results.

King (1937), using the "King census method," believed that overwinter (October to April) losses in the population were about 17 per cent and that juvenile losses—probably before the young left the brood in the fall—were 75 per cent.

Morse (1939), using the King method in the Cloquet Valley about 40 miles northeast of the Cloquet Research Forest, showed a 57 per cent overwinter loss in 1935-1936 and a 69 per cent loss in 1936-1937.

Fisher (1939), using the King method in the Pigeon River country in Michigan, found overwinter losses (15, his Figure 3) from 93 per cent (September 1933 to May 1934) to 66 per cent (September 1935 to May 1936). Also (17, 18) he noted a 43 to 46 per cent drop between September and November each year and believed that the hunter kill accounted for less than 14 per cent.

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Bezdek (1944:88), studying seasonal changes in age ratios of Ruffed Grouse, brought from Alberta, Canada, and Wisconsin and released in Ohio, concluded: "not over 20 per cent of the individuals might be expected to live through two winters, or to exceed the age of 22 months!"

Bump *et al.* (1947) and Edminster (1947) reported separately on repeatedly censused grouse coverts in the same New York areas. According to Bump *et al.* (1947:318), data from the flushing rates in specific areas as the season progressed showed an annual mortality varying from 14.3 per cent on Connecticut Hill in 1930-1931 to 78.1 per cent in the Adirondacks in 1934-1935, with an average overwinter loss (September-April) of 41.6 per cent on Connecticut Hill and 52.6 per cent in the Adirondacks from 1931 through 1941. Bump considered a grouse to be an adult on 1 September after hatching.

Frank (1947), estimating grouse survival based on a study of drumming logs in Connecticut and comparing spring drumming counts with fall data gathered by the King method, computed a 93.9 per cent overwinter loss among young birds in 1944-1945 and 96.2 per cent in 1945-1946. Since he did not work with marked grouse, we suspect he did not realize that one male bird after another might use the same drumming site. Our studies have shown conclusively that the same "stage" on a log is often used repeatedly by successive birds (Gullion, 1967a). Frank stated that his population of drumming male grouse consisted of 30 to 40 per cent one-year-old birds, 30 to 40 per cent over six years old, and 20 to 40 per cent from two to five years old.

Hardy (1950:21), using Frank's methods in Kentucky, estimated that the drumming male population consisted of: "10 males at least 3 years old, 6 males at least 2 years old, 1 male at least 1 year old." He recorded the loss of two out of 18 birds (11 per cent) from spring 1949 to spring 1950.

Palmer (1956:341) in Michigan, using survival data based upon banded grouse for the first time, the "Hayne modification" of the King method (Hayne, 1949), and from a survey of drumming males, reported a fall to spring survival of from 22 to 34 per cent on unhunted areas and from 23 to 45 per cent on hunted areas from 1950 to 1955, and a generally larger spring breeding population on the hunted areas than on the unhunted.

Dorney and Kabat (1960:36) calculated fall and winter losses in Wisconsin as between 76 and 88 per cent from 1950 to 1958: "based on February-March flush counts and fall age ratios."

Later Palmer and Bennett (1963:637), reporting on Palmer (1956) and additional data from Michigan, concluded that: "On both study areas [hunted and unhunted], annual turnover was about 70 per cent. At the Rifle River Area from 1951 through 1956, hunters removed an average of 30 per cent of the preseason population."

The Locale

The University of Minnesota acquired 2,215 acres of the Cloquet Forest Research Center in 1909. This area, now increased to 3,365 acres and under the jurisdiction of the Minnesota School of Forestry, is the locale for research in and teaching of the latest concepts of forest management (Anonymous, 1960). Except for one experimental Ruffed Grouse hunt on 1,600 acres in 1961 (Gullion, 1962a), the Cloquet Forest has been a refuge for small game since 1924. Allison and Brown (1946), Magnus (1949), Marshall (1958), Burcalow and Marshall (1958), Anonymous (1960), Gullion, King, and Marshall (1962), and Marshall and Gullion (1963) have discussed various aspects of this forest and the game management programs in effect here.

The extent of the grouse habitats, off the forest but included in this study, was expanded several times until they now total about 4,300 acres. These lands have diverse ownerships and forest management histories which largely are neither as intensive nor as well documented as on the Cloquet Research Forest.

Ruffed Grouse in winter. Drawing by William Zimmerman.

Climate

The Cloquet Forest, in one of the coldest parts of the midwestern and Great Lakes region, has a mean annual temperature of 38.6° F (Schantz-Hansen and Jensen, 1956) with readings frequently of −30° F and occasionally below −40° F. Sixty per cent of the mean annual precipitation of 28.4 inches falls during the growing season; snow, averaging 58 inches annually, usually covers the ground from December to mid-April. Light frosts can occur in any month; killing frosts (below 28° F) from mid-September to the first week in June.

The Forest Habitats

The Research Forest, from 1,228 to 1,293 feet above sea level, consists of about one-third lowland bog and two-thirds sandy uplands.

Lowland.—The lowland bogs support forests varying from dense stands of black spruce *(Picea mariana),* balsam fir *(Abies balsamea),* and white cedar *(Thuja occidentalis)* with sphagnum "ground" cover, to open muskeg where scattered, dwarfed black spruce and tamarack (*Larix laricina*) are the only trees in a taiga of Labrador-tea (*Ledum groenlandicum*), leather-leaf (*Chamaedaphne calyculata*), bog laurel (*Kalmia polifolia*), and bog cranberry (*Vaccinium Oxycoccos*).

Other forested bogs include stands of black ash (*Fraxinus nigra*), with scattered yellow birch *(Betula lutea),* usually with an understory of moderately dense brush, mostly of mountain maple (*Acer spicatum*).

In riparian associations balsam-poplar *(Populus balsamifera)* grows commonly, and, on better quality alluvial soils, speckled alder *(Alnus rugosa)* often forms an extensive coppice. Where the alder is not too dense, willows *(Salix* spp.), highbush cranberry *(Viburnum trilobum*), and red-osier dogwood (*Cornus stolonifera*) develop small, brushy thickets. About the margins of muskegs, in tamarack stands, and other open, boggy situations the bog birch *(Betula pumila)* is often a dense shrub.

Various ferns, including *Botrychium* spp., *Osmunda Claytoniana,* and *Dryopteris cristata,* grow under forest canopies, and herbaceous, food-producing plants such as bunchberry *(Cornus canadensis)* and goldthread *(Coptis groenlandica)* are abundant, along with bluebead-lily *(Clintonia borealis),* stemless lady's-slipper *(Cypripedium acaule),* and various ground-pines (*Lycopodium* spp.). Under the alder coppice and in open meadows rank growths of bunch-grasses and tuft-forming sedges (*Carex* spp.) dominate.

Uplands.—The uplands consist largely of a sandy outwash, shed some 12,000 years ago by the melting of an ice block remaining from the last glacial advance. One prominent esker (finger of sand and gravel) penetrates deep into the basin left by this ice block. All but about 80 acres of the majestic red and white pines (*Pinus resinosa* and *P. strobus*) that once covered the upland were cut prior to 1910. In 1959 the upland forest included about 1,100 acres of pine, much of it second-growth red, white, and jack (*P. Banksiana*), with small plantations of Scots pine (*P. sylvestris*).

The remainder of the upland vegetation consists of about 836 acres of hardwoods, mixed hardwood-coniferous forest, and brushland, and 52 acres of non-forested lands (Anonymous, 1960). The most abundant hardwoods include both trembling and large-toothed aspen (*Populus tremuloides* and *P. grandidentata*), paper birch (*Betula papyrifera*), and red maple (*Acer rubrum*), with a few red oaks (*Quercus rubra*), basswood (*Tilia americana*), sugar maple (*Acer saccharum*), and elm (*Ulmus americana*).

Wherever the forest canopy permits, beaked hazel (*Corylus cornuta*) is the dominant shrub cover. As Hsiung (1951) pointed out, the tallest, most rank (but not densest) development of hazel is usually associated with the low light intensities under closed-canopy pine stands. However, in very tight canopied red pine and upland spruce-balsam sites the shrub undergrowth is virtually non-existent.

The berry-producing alternate-leaved (or pagoda) dogwood (*Cornus alternifolia*) sometimes forms quite dense brush under aspen-birch stands. Throughout the forest other common fruit-producing shrubs and trees include mountain ash (*Sorbus americana*), thornapple (*Crataegus* sp.), Juneberry (*Amelanchier* spp.), choke- and pin-cherry (*Prunus virginiana* and *P. pensylvanica*), raspberry (*Rubus strigosus*), and roses (*Rosa* spp.), in addition to the red-osier dogwood and highbush cranberry.

Common low shrubs include two blueberries (*Vaccinium angustifolium* and *V. myrtilloides*) and bush-honeysuckle (*Diervilla Lonicera*). Bracken fern (*Pteridium aquilinum*) and wild sarsaparilla (*Aralia nudicaulis*) often form a dense canopy two to three feet above the forest floor from mid-June until flattened by heavy snow in late fall.

The ground cover includes a number of cosmopolitan forest herbs — big-leaved aster (*Aster macrophyllus*), checkered-teaberry (*Gaultheria procumbens*), bunchberry, twin-flower (*Linnaea borealis*), bearberry (*Arctostaphylos Uva-ursi*), starflower (*Trientalis borealis*), false lily-of-the-valley (*Maianthemum canadense*), trailing arbutus (*Epigaea repens*), strawberries (*Fragaria virginiana* and *F. vesca*), liverleaf (*Hepatica americana*), various shinleaves (*Pyrola* spp.), and several others.

This description of the Cloquet Forest applies equally well to the surrounding areas included in this study, except that outside the Research Forest the pine stands are very limited.

Scattered throughout the lowlands in the study area are isolated islands with upland vegetation, forming what Pierce (1954) terms an "archipelago" pattern.

On some 730 acres of the Research Forest all the mature aspen—40 to 50 years old—has been cut during the past 11 years, leaving only conifers and other hardwoods. The harvesting of the aspen, which resulted in an apparent decline in the carrying capacity of the area for Ruffed Grouse, fortunately coincided with our study and was crucial in developing our viewpoints. We have data which indicate rather convincingly a close relationship between the abundance of mature clones of male aspen and the distribution of grouse in this area (Gullion, 1966a, and unpublished).

Methods and Techniques

We trapped and marked 978 Ruffed Grouse by various methods (Gullion, 1961; Gullion, Eng, and Kupa, 1962; Gullion, 1965a, 1966b) and entered the data acquired on marginally-notched cards to facilitate information retrieval (Gullion, 1962b; 1963:96-113; 1964a:116-126).

We used every method of sex and age determination of grouse found in recent literature (including Hale *et al.*, 1954; Dorney and Holzer, 1957; Palmer, 1959; Dorney, 1966), plus a few innovations of our own—length of middle toe, number of transverse bars on central rectrices, and a comparison of the length of the ninth primary with the length of the central pair of rectrices (Gullion, 1964a). We found that even with all these external criteria we could not be absolutely sure of the sex of about 0.5 per cent of our birds. We did feel reasonably safe, however, in assuming that if a bird drummed on

TABLE 1

Success in Identifying Drumming Male Ruffed Grouse, Cloquet Forest Wildlife Project, 1956-1966

Year	*Acreage intensively covered**	*Acreage on the refuge*	*Number of occupied activity centers†*	*Drumming males trapped or identified*	
				Number	*Per cent*
1956	748	538	24	20	83
1957	1,713	1,462	39	31	79
1958	2,072	1,773	53	50	94
1959	2,885	2,228	92	77	84
1960	2,826	2,239	87	73	84
1961	3,507	2,389	113	103	91
1962	3,819	2,389	113	96	85
1963	4,301	2,389	97	71	73
1964	1,082	1,032	58	34	59
1965	5,250	2,389	69	54	78
1966	5,856	2,389	83	66	80

*Includes only the forested lands on the 7,600-acre study area which may be considered year-long Ruffed Grouse habitat. These figures may differ from those used elsewhere.

†Some activity centers may have been outside of the area intensively covered, including logs where we made no effort to capture the attending grouse.

a log in the spring, it was a male despite the fact that its feathers failed to meet all the criteria of maleness.

Significance of Data

We used the Fisher *t*-test for finding the significance of the differences between means, and chi-square tests for the significance of other related values (Snedecor, 1956).

Since in many instances we dealt with data on about 90 per cent of the male grouse population on a large area (Table 1), the ecological significance of these differences may vary somewhat from their statistical significance. Small sample size, stratified at several levels, plus the almost certain probability that individual grouse respond differently to factors affecting their livelihood, means some of our data occasionally deviate widely from expected values.

There is another, often more important level of significance when studying an animal population, which we call *demographic significance*. This refers to whether or not differences in survival rates (which may be statistically significant) are reflected in the population dynamics of the species. In the following sections we will often demonstrate statistically significant differences in longevity between different grouse populations, but these differences are often insignificant to the population as a whole.

Figure 1. A female Ruffed Grouse marked with a back-tag. Although these tags aided in our identification of grouse running through the forest, or standing on a drumming log, they evidently were responsible for significantly accelerated losses among the grouse marked with them.

A third level of significance, which cannot be ignored altogether, is the management or economic significance of these data. Often the lack of statistical or demographic significance in our data becomes highly important economically.

Problems in Handling Survival Data

Not all of the Ruffed Grouse marked provided useful survival data. Research procedures affected the survival of some birds making it necessary to exclude some data at times and include them at others.

Effects of Back-tagging

For example, after back-tagging, the chance of survival of gray-phase males was less than red-phase males (Figure 1; see also Gullion, Eng, and Kupa, 1962). Gray-phase males with back tags lived for a mean of 9.4 months after tagging while those with color bands lived for a mean of 17.2 months after banding (df.$=164$; $t=3.332$; $p<0.001$). Fifteen back-tagged, red-phase males lived an average of 12.2 months as compared to a mean of 11.9 months for 68 color-banded red birds. Therefore we omitted the back-tagged, gray-phase males in computing most of the survival rates, feeling that the back-tagging had definitely lowered their chance of survival.

Other Problems

The different fates of the 446 marked males (Table 2), known to have used drumming logs at some time during the study, require different treatment. We have excluded from further consideration the 62 grouse, lost through trapping injuries and radiotelemetry studies, killed by hunters during the special hunt or in traps by predators, or having insufficient follow-up records, and will refer to them as "research affected grouse."

We have handled the records of the 54 male grouse, still alive on 1 December 1966, differently, depending on the parameters being considered. Since these grouse have not lived out their full life-span, the inclusion of their longevity figures would supposedly shorten the mean survival rates. However, this was not always true.

A Uniform Basis for Survival Computations

The base period of time for computing survival varied. We considered the *life-span* or *total survival* from the time of hatching, normally the first two weeks of June (Kupa, 1966:25), and *survival based on drumming activity* from the first April that we knew the bird was an established drummer even though we were sure in many cases that the males had used their logs the previous autumn. Since we may have missed other male grouse that were established on logs in the fall and failed to survive their first winter, we considered the April date a fair and uniform base.

TABLE 2

Number of Drumming Male Ruffed Grouse Included in This Study, and Factors Affecting the Usefulness of Their Data

Type of datum	*Legal status of location* *On-refuge*	 *Border**	 *Off-refuge*	*Totals*
Assumed dead from natural causes	172	25	61	258
Known kills:				
Normal predator	30	1	8	39
Hunter reported†	5	9	14	28
Special research hunt	6	–	–	6
Hit by cars	4	0	1	5
Trapping‡	16	1	8	25
Radiotelemetry§	8	1	1	10
No records‖	7	1	13	21
Still alive (12/1/66)	19	2	33	54
Back-tagged♯	(45)	(6)	(7)	(58)
Totals	267	40	139	446

*Includes all male grouse established on the refuge but within 4 chains (264 feet) of the border. These birds are considered as accessible to hunters as those living off the refuge.

†Hunter kills during the normal fall hunting seasons.

‡Includes grouse known or suspected of dying from injuries incurred during trapping or subsequent handling, and those killed in traps by predators.

§Eight more, included elsewhere, carried radios without apparent undesirable effects.

‖"No records" includes birds living in areas where there was an inadequate follow-up to permit an estimate of period of loss.

♯Included among the birds listed above.

Figure 2 (*above*). A lily-pad trap in place in winter, baited with dyed, shelled corn and ready to be covered with the balsam fir boughs, seen to the right of the trap. This is a non-selective method of trapping and is our primary means of capturing Ruffed Grouse hens and juvenile birds.

Figure 3 (*below*). A mirror trap. If a male Ruffed Grouse were at his usual stage, in the lower left corner, he would see his image in the mirror at the back of this trap, and, believing it to be an interloping male on his log, would enter the trap to attack his "rival." This is a selective form of trapping.

When we first encountered a grouse as an adult, we assumed that it had hatched a year prior to the nesting season immediately preceding. Thus, adults, taken for the first time in October, were assumed to be at least 16 months old and those taken for the first time on drumming logs in April were probably at least 22 months old. We realize that some of the 50 birds, taken as adults for the first time as we expanded our study area, could have been six or eight years old. However, a review of these 50 birds shows a longer survival than for the others—where we knew the age—so we find no valid reason for excluding their records from most parameters.

Four Levels of Demographic Information

(1) The least useful and reliable from a survival point of view were the data obtained by the use of the lily-pad traps (Figure 2—Liscinsky and Bailey, 1955; Gullion, 1965a, 1966b), a *non-selective* method by which most of the hens and all of the juveniles were captured for initial banding.

(2) The second level, back-tags and four-color combinations of aluminum bands, gave us an opportunity to observe birds and obtain records without retrapping.

(3) The third level, mirror-traps (Figure 3), modified from the design of Tanner and Bowers (1948) and used for the *selective* trapping of male grouse

Figure 4. An accumulation of fecal droppings beside a drumming log can provide us with much useful information concerning the current and past history of the log and its occupant. Here is an accumulation of 422 droppings representing approximately 105 hours of attendance at this site in the spring of 1962, prior to 24 April. The darker droppings to the left are part of many hundreds remaining from earlier seasons, and the interlayering of droppings and needle litter let us back-date the use of this site for at least two years.

established on drumming logs, were most successful for only about three weeks in spring. The mirror-traps allowed us to handle many males we could not capture by other means (Table 1).

We computed the mean life-span for 31 male grouse, trapped originally in lily-pad traps, as 11.5 months. Later, when each of these 31 was selectively retrapped on a drumming log, the additional data obtained increased the mean life-span to 24.9 months. In the same way we computed the mean life-span for 26 birds, originally taken in mirror-traps as 38.6 months, and later from non-selective lily-pad trapping as 22.0 months.

(4) The fourth level—the sign left on or near drumming logs by attendant males (Figure 4)—was the best method of obtaining information and the basis of this paper so far as possible.

The accumulation of droppings, on or beside a log (Frank, 1947; Bump *et al.,* 1947:280), varied from as few as half a dozen to 1,116 at one log in 1961. Continued observation and counts of droppings beside the logs permitted us to maintain a fairly accurate record of the status of each individual male using a drumming log.

Also, in the summer the molting grouse often leave a sequence of remiges and rectrices beside the logs. We discovered that the central rectrices are about as distinctive for identifying grouse as fingerprints are for identifying humans. When we found a molted rectrix beside a log, we compared it with rectrices taken when the grouse were banded and, if it matched, we were nearly as confident in identifying the grouse as if we had handled the banded bird.

The usefulness of sign for determining longevity of individual male grouse is demonstrated in the records of 241 birds. Based on trapping or band-code identification at the drumming log, these 241 male grouse had a mean life-span of 23.1 months, but based on sign associated with their use of drumming logs we computed their mean life-span at 28.3 months (df.=480; $t=4.099$; $p<0.001$).

Strong Attachment of Male Grouse to One Area

Survival data, based on the use of specific logs by individuals, provide a more reliable basis for determining survival than any other method currently available, provided we know the behavior of the drumming grouse and the history of the logs they were using. We feel confident that we maintained contact with most male grouse drumming on the study area for as long as they lived.

Our study, as well as studies by Palmer (1956), Eng (1959), and Dorney and Kabat (1960), suggested that the male manifests a high degree of faithfulness to a certain drumming log and that a prolonged absence from the log indicates that the bird is dead. However, continuing studies reveal that, in spite of this fidelity, about 36 per cent of our 168 established males living at least 12 months or longer, moved to another log sometime during their drumming careers. Most of these site-transfers averaged about 300 feet (Gullion, 1967a:91; Gullion and Eng, unpublished), usually within the same activity center; but at least 20 birds moved to another activity center.

Dating Losses

The accuracy in estimating the time of death for birds lost from our population varied from the exact minute for hunter-killed birds to a vague "during the summer" or "between December and late March" for some birds killed by predators or unknown causes. We tried, where possible, to date a loss in one of four periods: spring drumming season — April and May; summer — June through September; autumn — October and November; or winter — December through March. If we could not establish the time of death in one of these periods, we did not include the record in our analysis.

Evaluation of Forest as Grouse Habitat

Abandoning the conventional methods of forest typing, we have described the forest (Table 3) on the basis of features favorable to the survival of grouse, features which are detrimental, and features which are neutral—unimportant

TABLE 3

Examples of Forest Habitats Considered in This Study

*Field code**	*Forest habitat description*
	No hardwoods present
0−1	Scattered, isolated, high-tree pines, usually over heavy brush undergrowth.
0−3	Closed-canopy, high-tree pine stand, open to moderate brush undergrowth (Figure 19).
0−8	Scattered clusters of low- to high-tree spruce-balsam-cedar-tamarack, usually no brush within clusters but often dense brush between them.
0−13	Upland brush, mostly hazel, without any conifers or other significant forest canopy.
	Hardwoods present, without aspen
1+2	Hardwood canopy with scattered clusters, or clumps of high-tree pines, over moderate to dense brush.
1+4	Hardwood canopy over dense stand or plantation of shrub or low-tree pines, usually with no undergrowth.
1+11	Hardwood canopy between scattered clumps of mixed-age and mixed-species of conifers (including pines, spruce, balsam fir, and tamarack).
1+14	Lowland hardwoods over swamp brush (alder, mountain maple, bog birch).
	Hardwood stand with aspen present but not prevalent
2+2	Mixed hardwoods with scattered clumps of high-tree pines, over dense brush.
2+10	Mixed hardwoods with scattered, isolated conifers of mixed-age and mixed-species, usually over dense brushy undergrowth.
	Aspen most abundant hardwood present
3−0	Dense stand of aspen saplings.
3+1	Mature aspen dominates hardwood stand with scattered, high-tree pines, with usually dense, brushy undergrowth.
3+6	Aspen or balsam-poplar with moderate canopy of tamarack, usually with little undergrowth.
3+12	Aspen prevalent hardwood in a closed-canopy stand of mixed-age, mixed-species of conifers, with scattered to dense undergrowth.

*First number refers to density of aspen; second number, the density of conifers or only brush.

to the security of the birds. These classifications, based on the tree cover in sight from the log or logs used by each male grouse are, of course, general in nature.

Aspen is perhaps the most important feature encouraging a grouse to use a certain activity center in the Cloquet area. In Table 3 the first number indicates the prevalence of the aspen in a given forest area, and the second number indicates whether there are conifers or only brush. We have classified the coniferous species in groups—pines, spruce-balsam-cedar, or mixed pines and spruce-balsam. Tamarack is separate. We also classified the conifers according to the density of the stand and the height (Smith, 1958)—"shrub-tree," "low-tree," and "high-tree."

Survival of Male Ruffed Grouse

Parameter 1: The Historical Status of the Drumming Site

We have discussed elsewhere (Gullion, King, and Marshall, 1962; Gullion, 1967a) the varying patterns or traditions of use of the sites selected for drumming and as activity centers by male Ruffed Grouse. Briefly, an activity center is "a central area of intensive activity in the proximity of one or more drumming logs used by a single male grouse . . . [bounded by] . . . a flexible periphery to a defended area . . ." (Gullion, 1967a:89). Our term "activity center" seems to be more or less synonymous with the "territory" of Bump *et al.* (1947:257), Dorney *et al.* (1958), Dorney and Kabat (1960), Hale and Dorney (1963:253), and Sumanik (1966), and with the "Primary Areas" of Fowle (1953:49). We have meager evidence that the females use activity centers in the same way as males, but we do not have the data to explore this further (see Kupa, 1966:36).

We define a transient log in a transient activity center as a log used by one male in his lifetime; a perennial log in a perennial activity center as a log used by a succession of male grouse in a center with a history of repeated occupancy by different grouse; and a transient log in a perennial center as a log used by a single bird in his lifetime in an activity center with a long tradition of use.

We should also make clear some terms related to drumming: In the literature *drumming site* often refers to the *drumming log* or *logs* used by male grouse as well as the immediate environs (Chambers and Sharp, 1958; Eng, 1959; Palmer, 1963; Sumanik, 1966; Gullion, 1967a). Sometimes the term "site" is synonymous with "drumming log"; sometimes it approaches our term *activity center*. Earlier (Gullion, King, and Marshall, 1962) our "drumming site" meant the specific spot on the log where the grouse drummed and Meslow (1966) adopted this. More recently, because of the confusion, we have preferred the term *drumming stage* to drumming site (Gullion, 1967a). Sumanik (1966) calls this location a "drumming platform."

Two factors govern the male's choice of a drumming log and an activity center: (1) An adequate number of mature (40- to 50-year-old) aspen within sight of or near the drumming log; and (2) a tradition of occupancy as a drumming location. The tradition is so important that the grouse will stand considerable change in the vegetation of the area before deserting it. Hickey's (1942) term "ecological magnet" seems appropriate here. One radical change that will cause a grouse to abandon a log or activity center is the removal of all the mature aspen from the area. This is true even though the rest of the forest remains the same.

Grouse Survival.—The prior occupancy of a drumming log has more influence upon the survival of its occupant than the prior use of the activity

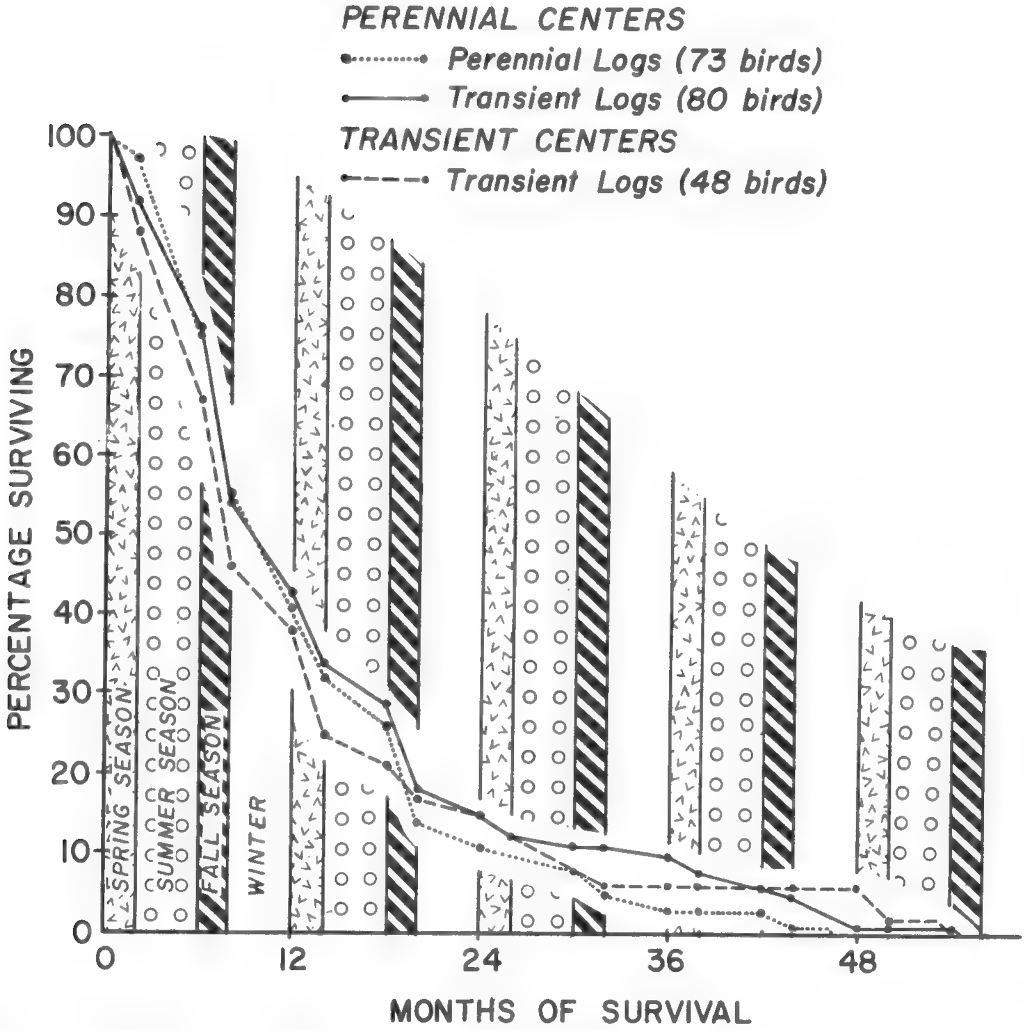


Figure 5. Comparative survival of drumming male Ruffed Grouse according to the historical status of the sites selected. These data exclude most back-tagged grouse, all of those that shifted activity centers, and most of the birds affected by our research activities. Differences in survival are not significant until 36 months when the differences between transient and perennial logs in perennial centers have a chi-square value of 5.14, at 1 df.

center. Figure 5 shows survival rates for grouse choosing each of the three categories of drumming logs. The grouse selecting a transient log in a perennial center has a likelihood of living four months longer than the grouse occupying a perennial log in a perennial center and an insignificant 0.2-month advantage over a bird choosing a transient log in a transient center (Table 4).

In considering the color phase of the individual birds in relation to the logs we find that, among grouse choosing a perennial log, the color phase does not matter — both the red and gray are shorter lived. But among birds choosing transient logs, the gray-phase grouse have a distinct advantage over the red-phase (these differences approach significance: df.$=140$; $t=1.991$; $p<0.100$).

Why?—Our data suggest that survival of the drumming grouse is not related so much to the quality of the site chosen as it is to the hunting behavior of the raptors, the major predators upon grouse in the Cloquet Forest.

We have found that few losses from predation occur on drumming logs. In our several thousand contacts with grouse on logs, we have recorded only five instances of probable predator-grouse struggles on or in the immediate vicinity of drumming logs, and we know that two of these grouse survived. This is in contrast to the statement by Bump *et al.* (1947:276) that "many birds are killed each year on their drumming logs."

Figure 6 (*above*). A transient drumming log in a perennial center. This log was the primary log, from 1962 to 1966, of the longest lived male Ruffed Grouse known to date from the Cloquet project. Note the fairly dense hazel brush beside the log and the flared roots of the wind-thrown spruce at the left. These two features are common characteristics of the most successfully and repeatedly used drumming logs.

Figure 7 (*below*). A hardwood forest, with no coniferous trees present—31 drumming Ruffed Grouse occupying activity centers in this forest type have lived an average of 19.3 months after becoming established on their drumming logs. This is a 2 + 13 forest habitat type.

Figure 8 (*above*). A stand of aspen over a cluster of low-tree spruce. The 15 drumming male grouse using this type of situation as their activity centers have survived for a mean of 17.0 months after becoming associated with a drumming log. This is a 3 + 5 forest habitat type.

Figure 9 (*below*). A cluster of high-tree red pines dominating an activity center where four male grouse have lived an average of only 7.5 months after commencing use of the perennial drumming log. This is a 3 + 2 forest habitat type.

We found (Gullion, 1964b:58), as did Meslow (1966:36), that most male Ruffed Grouse select a drumming log in a situation that is essentially "predator-proof" (Figure 6). Even so, an accelerated predation occurs within the activity centers and in reference to the drumming logs which have perennial use. We suspect that predators, learning the whereabouts of the perennial drumming logs, frequently wait in ambush when the grouse is using it. Around these ecological magnets it makes little difference whether a grouse is red or gray.

Although birds using logs with histories of prior use have poorer survival than the birds using "new" logs, the losses do not occur on the logs, but rather in their proximity in the activity center. It appears that the predators learn to ambush the male grouse while they are moving en route to or away from the perennially used drumming logs.

TABLE 4

Male Ruffed Grouse Survival Related to the Historical Status of the Occupied Drumming Site

Site	*Gray phase*		*Red phase*		*Totals*	
	Number	*Months survived*	*Number*	*Months survived*	*Number*	*Months survived*
Perennial Centers						
Perennial log	57	12.1	41	12.3	98	12.2*
Transient log	93	18.1	49	13.2	142	16.4*
Transient Center and log	56	18.0	27	12.5	83	16.2*

*Statistical significance: differences between transient and perennial logs in perennial center – df. = 223, $t = 2.272$, $p < 0.025$; between perennial log and center and transient log and center – df. = 179, $t = 2.281$, $p < 0.025$.

On the other hand, when a grouse selects a new log in a perennial activity center, or a new activity center and log, the raptors have to "scout out" the situation and find a position from which they can ambush the occupant. While scouting, the raptors must frequently blunder and alert the grouse to their presence. The few males that lived to a fairly old age all occupied transient logs. One died in the spring of 1966 at an age of 94 months, over seven years (Gullion, 1967b). Still, red-phase males do not enjoy much additional longevity when they select a transient log (Table 4).

The longevity data for several grouse that changed logs during their tenures as drummers support the idea that the raptors must learn how to take male grouse in certain situations. Eighteen grouse that shifted from one transient log to another within a perennial center increased their mean longevity to 30.4 months. By moving only a few hundred feet from one log to another they nearly doubled their life expectancy.

Another group of seven grouse, that had survived for a mean of over 7.5 months on their transient logs, shifted to perennial logs and lived only 13 months more.

Our study suggests that the habitats in the transient centers are of basically poorer quality than those in the perennial ones. This may explain why one area is a perennial center and the other transient. Although the initial occupant of a transient log in a transient center may survive as long as a bird

TABLE 5

Survival of Male Ruffed Grouse in Relation to Forest Habitat

Habitat type	*Number of grouse*	*Mean survival (months)*
Hardwoods and brush with scattered high-tree pines	21	17.1
Hardwoods and brush among scattered stands or clumps of high-tree pines (Figure 9)	27	13.9
Scattered hardwoods, some brush in closed-canopy high-tree pines (Figure 19)	41	12.6*
Hardwoods with an understory of shrub- or low-tree pines, balsam fir or spruce	10	16.5
Hardwoods and brush with scattered low-tree spruce and balsam fir, upland and lowland (Figure 8)	15	17.0
Hardwoods and brush among clumps or scattered stands of spruce and balsam fir	48	15.5
Closed-canopy spruce-fir with scattered hardwoods and little or no undergrowth	20	17.2
Hardwoods and brush with scattered conifers of mixed-ages and species	19	17.2
Hardwoods and brush in openings between clumps or scattered stands of mixed-age and mixed-species of conifers	48	17.8
Closed-canopy mixed-age and species of conifers with scattered hardwoods, usually little if any underbrush	6	15.8
Hardwoods and brush, no conifers present (Figure 7)	31	19.3*

*Differences between these means are statistically significant: df. = 70, $t = 2.354$, $p < 0.025$. Differences between other pairs of means are all less or not significant.

TABLE 6

Effect of Forest Type Edges on Male Ruffed Grouse Survival

Forest habitat type	*In solid stand*		*Edge situation*	
	Number of grouse	*Months survived*	*Number of grouse*	*Months survived*
1. Hardwood-brush, no conifers	25	19.0	10	13.5
2. Hardwood-brush, with scattered conifers	53	17.7	3	15.3
3. Hardwood-brush, with clumps or scattered stands of conifers	116	16.5	14	18.1
4. Closed-canopy conifers, with scattered hardwoods, and varying brush densities	28	16.2	41	12.5

Differences between solid stand and edge situations, excluding Group 3, are highly significant: df. = 158, $t = 2.308$, $p < 0.025$.

TABLE 7

Survival of Male Ruffed Grouse by Color Phase in Relation to General Forest Habitat*

Forest habitat group	*Gray phase*		*Red phase*	
	Number of grouse	*Months survived*	*Number of grouse*	*Months survived*
Hardwood-brush, no conifers	21	21.0	15	15.3
Hardwood-brush, scattered conifers	32	20.4	27	13.4
Hardwood-brush between clumps or stands of conifers	82	17.4	40	14.5
Closed-canopy conifers with scattered hardwoods	42	15.0	31	13.0

*None of the differences within habitat types or groups are statistically significant.

on a transient log in a perennial center, once the raptors have solved the riddle of how to catch grouse in the transient center, his successor, if he has one, has a short future—even shorter than the birds replacing earlier occupants on perennial logs. Six grouse, which attempted to establish a perennial occupancy on the primary log in a transient center, survived on an average of only 9.5 months and were not replaced. On the other hand, there is no difference in the survival of replacement grouse moving onto previously unused transient logs in the perennial centers.

Although the 35 male grouse which first appeared on drumming logs as adults had a shorter survival (12.3 months) afterwards than the 213 immatures that became established as drummers (13.9 months), these differences are not statistically significant.

In spite of a statistically significant difference in mean longevity when comparing the survival of grouse in the three categories (Figure 5), the season by season decline does not become very different until 36 months after the birds began using the logs (2=5.14; 1 df.). By that time all three populations represent such a small part (less than 20 per cent) of the breeding population that these differences can hardly be considered significant from a demographic viewpoint. The presence, or absence, of all three combined would have little effect on annual production when compared to other factors affecting annual recruitment.

Parameter 2: Effects of Forest Habitat on Grouse Survival

Since there is considerable diversity in the forest habitat on the Cloquet study area, an evaluation of male grouse survival in the different habitats is worth our examination (Tables 5, 6, and 7). These survival rates represent longevity of 286 male grouse after the first spring season of occupancy in a drumming activity center.

In the preceding section we noted that most predation occurs, not at the drumming log, but elsewhere in the activity center. Therefore, in addition to its historical status, the quality or character of the forest cover on the whole 10-to-30-acre activity center determines the life-span of the grouse, rather than

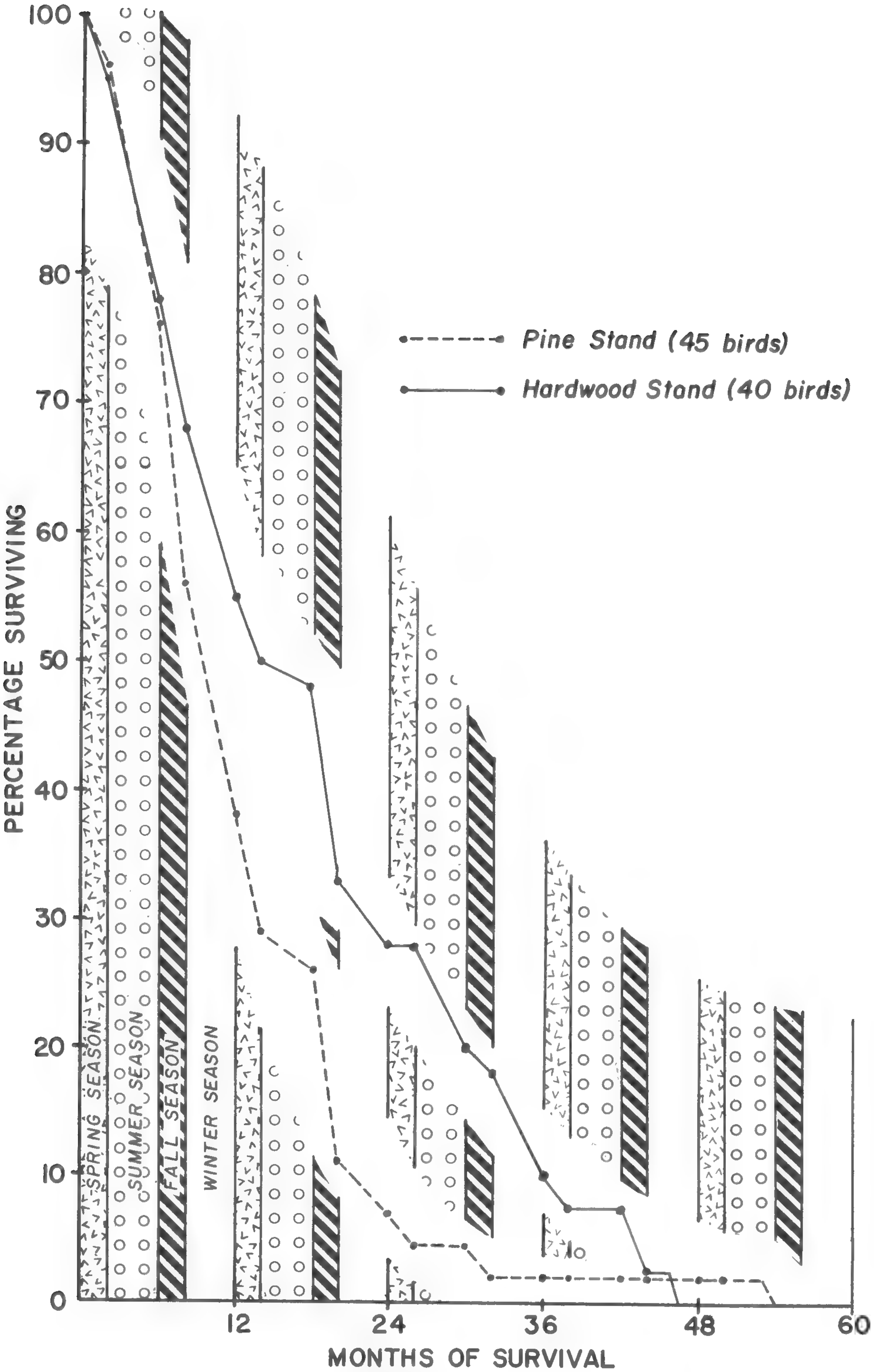


Figure 10. The rates of survival of male Ruffed Grouse living in pine stands (as seen in Figure 19) as compared to those choosing all-hardwood areas (as shown in Figure 7). These data include grouse living both on and off the refuge and both age classes, but exclude back-tagged grouse and other birds affected by our research activities. Differences are significant at 14 and 26 months ($X^2 = 4.35$; $X^2 = 8.34$, respectively at 1 df.).

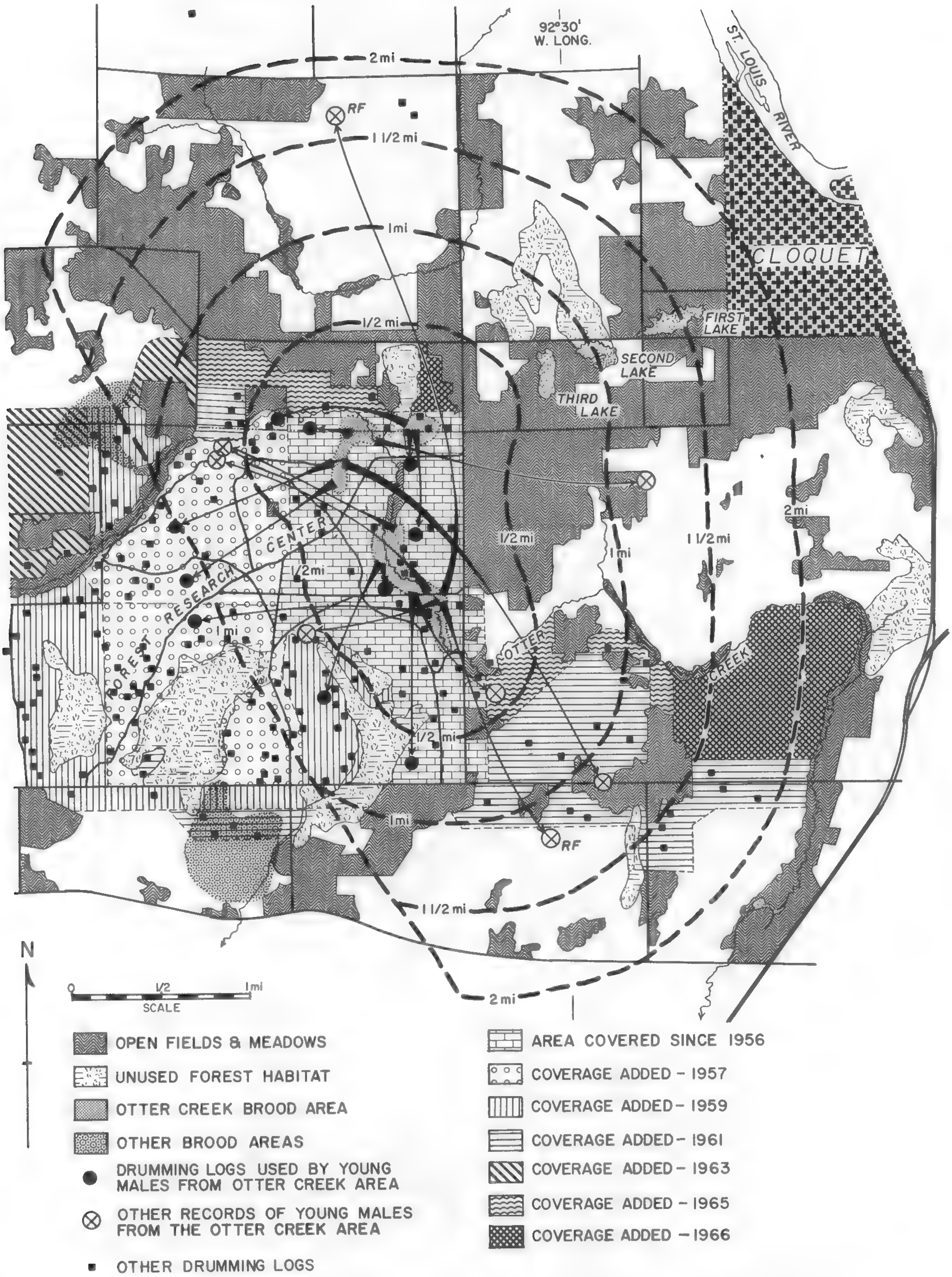


Figure 11. The eastern portion of the Cloquet study area, including most of the Forest Research Center. This shows patterns of dispersal of young grouse from the Otter Creek brood production area and the extent of intensive coverage for drumming log activity each season. The white, unpatterned parts are believed to be good grouse habitats which we have not thoroughly searched for drumming logs. The heavy dashed lines represent radial intervals of 0.5 mile from the Otter Creek brood area. The records marked "RF" represent the end of dispersal movements of young males carrying radio transmitters and tracked in the fall of 1964 by G. A. Godfrey. "Other drumming logs" represents sites where the attending males have been identified; there were other active logs within this area whose occupants were not identified, but these sites are not shown in this figure (see Table 1).

the cover immediately adjacent to, or above, the drumming log (as reported by Eng, 1959; Palmer, 1963; Meslow, 1966; Sumanik, 1966).

Radiotelemetric data (Marshall and Kupa, 1963; Marshall, 1965; Brander, 1965; Schladweiler, 1965; R. W. Barrett, unpublished), as well as our trapping and observational data, clearly show that activity centers are not circular with the drumming log in the middle, but may be elliptical or triangular with the drumming log well off center. Therefore, some errors in judgment may occur as we attempt to classify the dominant features of the forest cover on the several activity centers.

By relating the survival of individual grouse to the type of overhead forest cover, we imply that raptor predation played a major role in the losses of adult Ruffed Grouse. An examination of predator kills supports this view. We examined 279 predator kills and determined the predator species in 243 cases. Of these 243, 208, or 86 per cent, were due to raptor predation. Elsewhere (Eng and Gullion, 1962), we described the depredations of one pair of Goshawks *(Accipter gentilis)*. The above figures do not include the 94 grouse whose remains have been recovered near the nest of these Goshawks since 1958.

Grouse Survival.—Tables 5, 6, and 7 summarize the salient relationships between Ruffed Grouse survival and the character of the forest habitat. We make five generalized statements on the basis of these data: (1) Grouse survive best in hardwood forests devoid of evergreen conifers (Figure 7). (2) Spruce and balsam fir in a forest situation does not significantly shorten grouse survival (Figure 8). (3) Grouse survival decreases as the frequency of "high-tree" pines increases in a forest stand. (4) Survival is longer in activity centers dominated by a uniform forest type, not bisected by a forest "edge" situation. The exception is in the "hardwood-scattered clumps of conifers" situation where an "edge" exists on the periphery of each clump of conifers and the grouse with part of their activity centers outside of such a habitat type have longer survival than those living wholly within this type (Figure 9). (5) Red-phase males survived best in the all-hardwood habitats, but their survival is not much poorer in centers dominated by conifer cover, whereas the survival of gray-phase males decreases significantly as the density of the conifers increases.

Significance. — The significance of these data from a demographic and management standpoint is more difficult to assess than the statistical significance. In one statistically significant example from Table 5, a comparison shows that grouse living in the closed-canopy pine stand (at 12. 6 months mean survival) die sooner than those in the all-hardwood stand (at 19.3 months mean survival). Demographically these differing rates of survival appear to be significant, too, because in the pines only 29 grouse out of the original 100 survived from their first breeding season to the second, while in the hardwoods 50 birds out of 100 survived to breed the second year (Figure 10).

But whatever the implications of demographic significance, or lack of it, these data suggest that, in the Cloquet Forest anyway, extensive and expensive management efforts directed towards establishing conifer stands in hardwood forests, or towards increasing the prevalence of "edge" situations, is probably not justifiable — not if its main purpose is to improve the habitat for Ruffed Grouse.

Parameter 3: The Protection Afforded by a Refuge

The importance of the refuge has long concerned sportsmen and wildlife managers. Bump *et al.* (1947:392), after a three-year comparison of Ruffed

Grouse abundance on a hunted area in New York with one not hunted, noted: "The conclusion seems inevitable that refuges are of little value in maintaining populations of ruffed grouse when hunting pressure is not excessive. Fluctuations continue regardless of the protected or unprotected status of the coverts."

Palmer (1956) and more recently Palmer and Bennett (1963) provide data suggesting that grouse survive about as well, and sometimes better, from year to year on an area where they are heavily hunted as on a refuge where they are protected.

Since the Cloquet Forest Research Center has long been a refuge, we have useful data concerning the longevity of 188 grouse living on and 117 living off the refuge.

The Ruffed Grouse living off the refuge are subjected to quite intensive hunting pressure during the fall. About 125,000 people live within a 25-mile radius of the study area, and at least 72 families live within or immediately adjacent to it. These lands are laced with access roads (Figure 11) and many forest trails as well. So this is not an isolated, inaccessible population of Ruffed Grouse.

Figure 12 compares the survival of two populations of 100 grouse each on a year to year basis. At the end of the first 12 months the difference was six grouse. Fifty of those living on the refuge were lost, and 56 of those available to hunters died. After two years this difference still remained: 22 out of 100 were alive on the refuge and 16 were alive off the refuge. The off-refuge population became "extinct" sometime after the fourth year or after the fifth breeding season. On the refuge one grouse out of the original 100 lived to the fifth year and beyond.

In a season by season analysis of population shrinkage, the results emphasize that the differences in survival after the first hunting season (Figure 13) are: (1) greatest between the grouse living in the border zone and the "refuge of inaccessibility" ($X^2=6.72$; 1 df.); (2) least and insignificant between the grouse living on the legal refuge and the border zone ($X^2=2.31$; 1 df.); and (3) significantly different ($X^2=5.39$; 1 df.) at the end of the first hunting season between grouse living on the legal refuge and those available to hunters.

However, by the next breeding season, when they would be demographically important, these differences between the on- and off-refuge populations are not significant ($X^2=0.87$; 1 df.). For a reason we do not understand, the grouse population living in the remote "refuge of inaccessibility" becomes extinct long before the other two populations.

Figure 13 illustrates another aspect of grouse survival — that male grouse, continually subjected to hunting pressure, learn to live with this harassment and are not as easily taken. The leveling of the curve representing the border zone population after the second hunting season reflects this response. Losses from this population thereafter appear to be largely due to natural attrition and closely parallel the losses from the population living under full refuge protection.

Statistical analysis of the survival data shown in Table 8 reveals that the only significant differences in survival after appearance on a drumming log are related to the color phase of the grouse, not the refuge status of the birds' activity centers. Among the immature males, the gray-phase birds live significantly longer than the red-phased, both on and off the refuge; but on-refuge gray birds do not live significantly longer than off-refuge gray-phased, and the same is true of the red-phase males. None of the differences in adult survival is statistically significant.

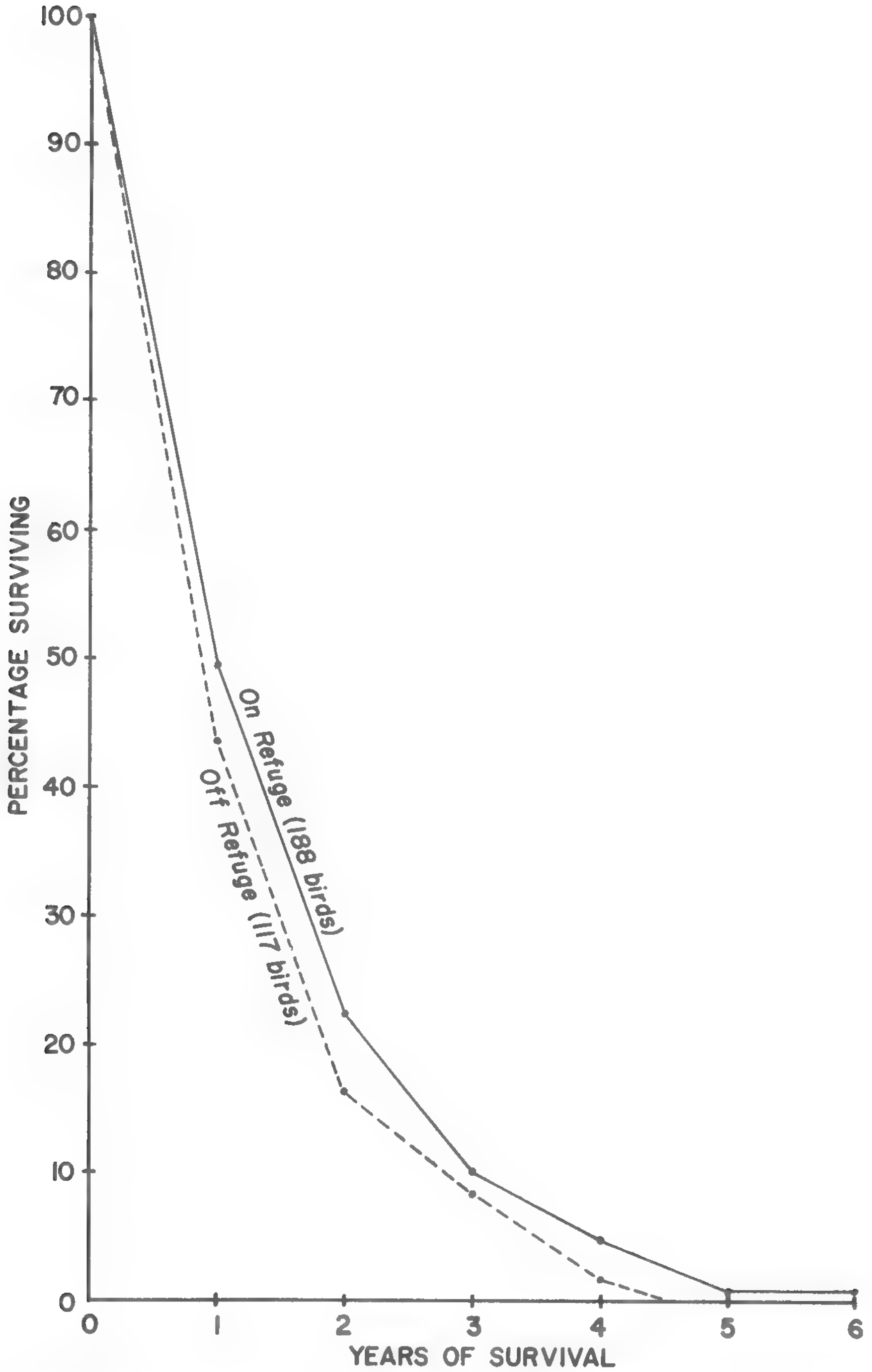


Figure 12. A comparison of the rate of population shrinkage among male Ruffed Grouse living on a refuge (and more than 4 chains—264 feet—inside its borders) and those living in the border zone of the refuge as well as off the refuge. All back-tagged grouse are excluded, but the gross data shown later in Figures 15 and 16 are included.

These data, while providing what seems to be conclusive evidence that hunting does not significantly alter longevity in a population of adult grouse, do not tell us anything about the relative rates of survival among those immature grouse confronted by heavy hunting pressure when only about three months old. This remains an important subject for further investigation.

Parameter 4: Survival Related to Color Phase

Throughout the preceding paragraphs that examine the several factors affecting male Ruffed Grouse longevity, we have pointed to a fairly consistent difference in the survival rates of the red and gray phases. These two phases (portrayed *in* Wetmore, 1937:234, and on the frontispiece in Bump *et al.*,

1947) refer to the dominant color of the bird's tail or rectrices. A Ruffed Grouse may also have either reddish or grayish contour plumage and black or chocolate sub-terminal tail bands and ruffs (tail band and ruff are always the same color). There are also various intergrades between the combinations. But for the purpose of this study we refer to the predominate tail color and class the intermediates with the gray-phase.

Our data show that 185 gray-phase male grouse with color-bands survived a mean of 16.6 months, significantly longer than 92 red-phase males with color-bands which survived the mean of 11.4 months (df.=275; $t=3.191$; $p<0.005$). Figure 14 graphically demonstrates the more rapid loss of red-phase grouse from the population, as compared to the gray birds. By the end of the first fall season, eight months after banding, the difference between the number of surviving birds of the two color phases is already significant ($X^2=5.33$; 1 df.).

Survival among Ruffed Grouse Hens

In contrast to the sedentary nature of the adult male Ruffed Grouse, the adult females do not associate so closely with one locality on a year-long basis (Brander, 1965, 1967; Barrett, unpublished), and we have not been able to compile survival records for hens with as much confidence as for drumming males. However, we believe that we can develop a valid estimate of hen survival by comparing male and female data based on records obtained after capture in lily-pad traps.

Since the immature grouse handled in the fall show a sex ratio slightly in favor of the males (195 males: 188 females equals 104 males per 100 females),

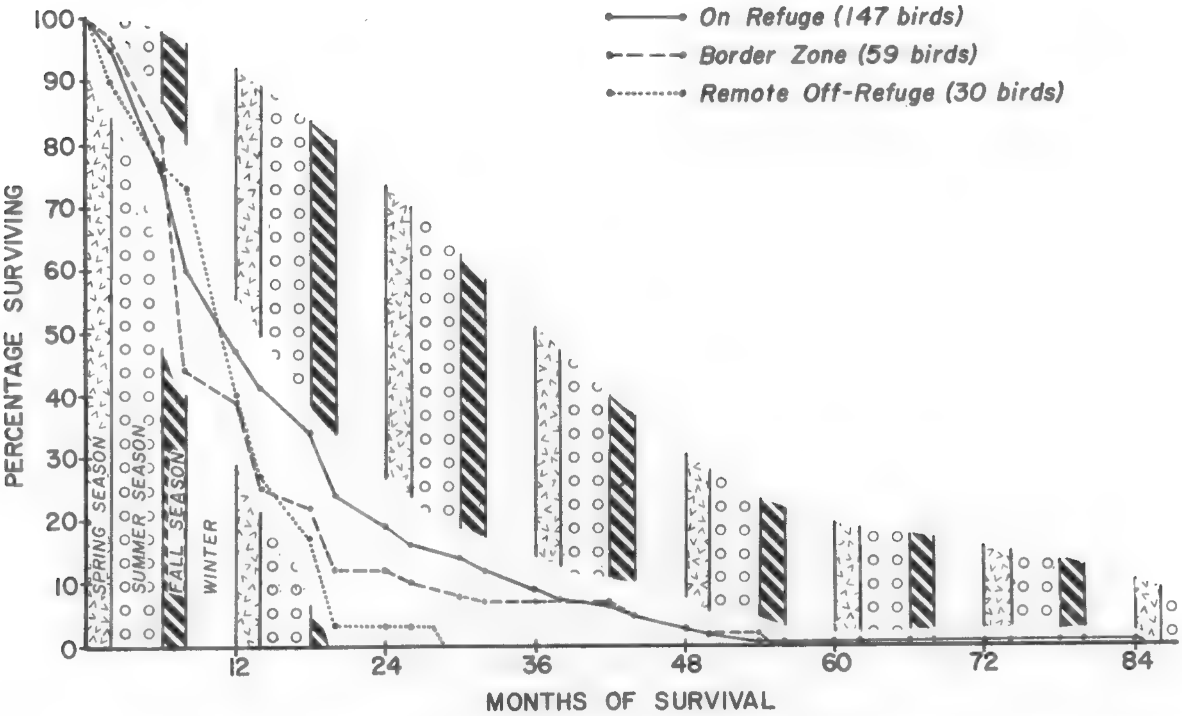


Figure 13. The season by season survival of drumming male Ruffed Grouse in relation to the refuge status of their chosen activity centers. The "on refuge" group all lived more than 4 chains within the border of the Cloquet Forest Refuge; those in the "border zone" lived in this 4-chain-wide zone inside the refuge borders, as well as within the same distance of hunter access roads, trails, and field borders off the refuge. The "remote off-refuge" includes grouse living more than 4 chains from easy hunter access off the refuge.

TABLE 8

Comparison of Mean Survival Rates of Male Ruffed Grouse According to the Legal or Accessibility Status of the Drumming Activity Centers

Class of grouse	*On-refuge*		*Border zone**		*Remote off-refuge†*	
	Number	*Months survived*	*Number*	*Months survived*	*Number*	*Months survived*
Immature males						
Gray phase	79	16.4‡	31	12.6§	12	12.3§
Red phase	38	9.1‡	17	8.7§	6	2.7§
Adult males						
Gray phase	28	20.8	21	17.8	11	17.1
Red phase	21	17.6	5	17.0	3	21.7

*Includes all grouse on the 4-chain-wide border fringe of the refuge as well as all birds living off the refuge within 4 chains (264 feet) of easy hunter access.

†Includes the male grouse living off the refuge and more than 4 chains from easy hunter access.

‡Differences in means between color phases are highly significant: df.=115, $t=2.917$, $p<0.005$.

§Combined differences in means, between color phases, are highly significant: df.=64, $t=2.279$, $p<0.050$.

and our later contacts with adult grouse (excluding contacts associated with drumming logs and nests) show a ratio favoring the hens (59 males: 67 females equals 88 males per 100 females), there does not appear to be any reason for believing that any sex-related bias to year-long rates of loss discriminates against the hens.

We can only assume that the differences in male survival rates which relate to refuge protection, color phase, and forest habitat apply equally well to the hens. The question of whether or not there are perennial nesting activity centers, equivalent to the drumming activity centers of the males, is something which we cannot adequately document now. However, there is some suggestion that this is the case (Kupa, 1966:36), and, if so, we could expect the same type of differential survival related to perennial use of a specific locality that we have shown for the males. As nearly as we can determine, hens are distributed throughout the various types of forest habitat in about the same frequency as the males. We should therefore expect the frequency of predation to be the same.

The female Ruffed Grouse apparently equals the male in survival rates (Table 9). Comparing the mean longevity for both red- and gray-phase immature hens against comparable immature males, the mean life-span of 8.56 months for 75 young hens is not very different from the mean figure of 8.63 months for 92 young males.

According to these data, we have little reason to suspect that the total survival of Ruffed Grouse hens differs significantly from the survival rates for the drumming males which are based upon the males' prolonged association with drumming logs. Even though their behavior and mobility differ somewhat, it appears that we can safely equate patterns of hen survival with that of males of similar color phase and choice of habitats.

TABLE 9

Comparative Mean Survival of Male and Female Ruffed Grouse Based on Lily-pad Trapping Records

Basis	Color-banded						Back-tagged			
	Females			*Males*			*Females*		*Males*	
	Immatures		*Adults**	*Immatures*		*Adults**	*Immatures**	*Adults**	*Immatures**	*Adults**
	Gray	*Red*		*Gray*	*Red*					
Significant subsequent	(21) ‡	(30)	(17)	(49)	(28)	(16)	(29)	(12)	(28)	(10)
records†	8.8	10.9	25.1	*9.2*§	9.5	*27.2*	9.8	20.8	7.0	17.8
Short-term trapping	(10)	(14)	(4)	(10)	(5)	(4)	(6)	0	(4)	0
repeats	6.5	4.7	17.5	5.2	*5.2*	*17.8*	4.2	—	*4.3*	—
TOTALS and	(31)	(44)	(21)	(59)	(33)	(20)	(35)	—	(32)	—
MEANS	8.0	8.9	23.7	*8.5*	8.9	*25.3*	8.8	—	6.6	—
Dead bird recoveries	(9)	(1)	(10)	(10)	(10)	(3)	(10)	0	(12)	(6)
	6.8	—	11.1	*11.0*	17.2	*33.3*	9.9	—	7.8	20.7

*Includes both color phases.

†Banded grouse recaptured or observed more than 0.25 mile from the site of original capture, or repeating at the same trap-site more than one month after original capture. The "short-term trapping repeats" are recaptures at the same or other traps within 0.25-mile radius less than one month after original capture.

‡Sample size is enclosed in parentheses.

§Categories in which males outlived females are shown in italics.

Overwinter Survival of Immature Male Ruffed Grouse

Another aspect of Ruffed Grouse survival which we can examine is the overwinter survival of the young males from the time they become independent to the next breeding season. Offhand it appears that we could determine this overwinter survival simply by banding a substantial number of young males each fall and then locating the survivors on drumming logs the following spring. Unfortunately, two problems complicate these computations: First, not all young male grouse become associated with a drumming log each spring and the percentage of birds that failed to do so seemed to vary from year to year (Gullion, 1966c:726); second, as the brood breaks up in the fall the young grouse often move far afield and out of our study area (Godfrey, 1967; Gullion and Eng, unpublished).

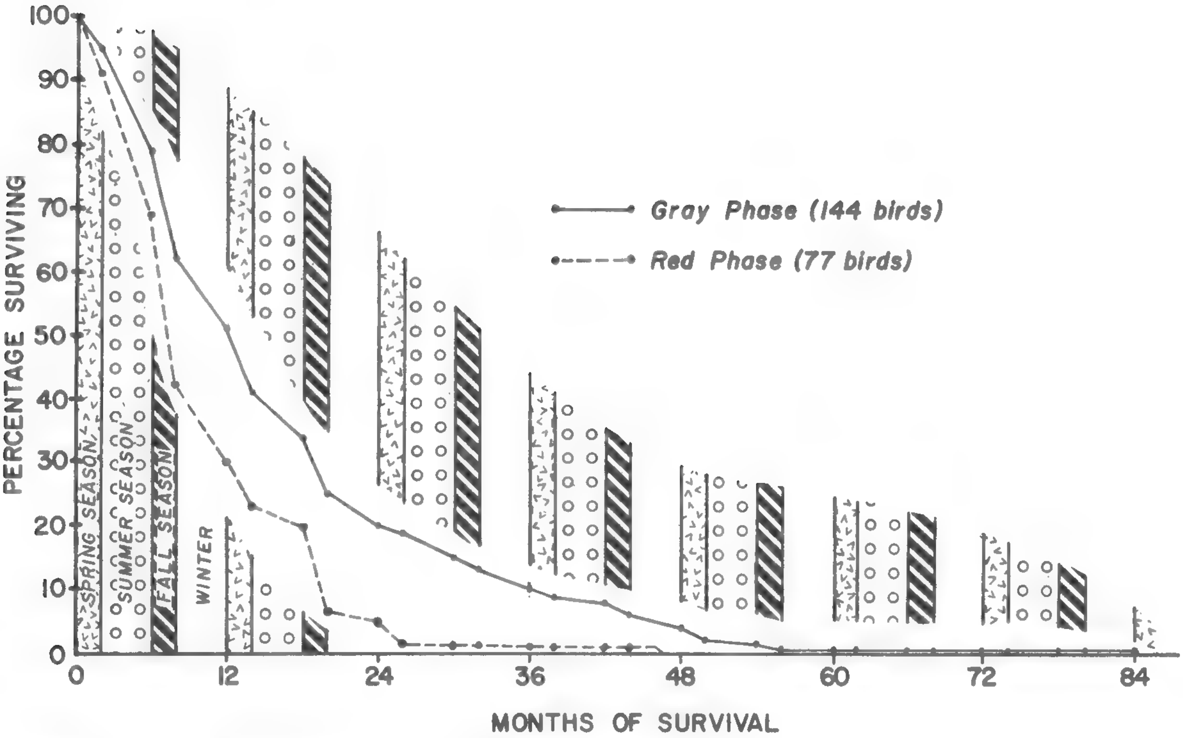


Figure 14. The comparable rates of survival by color phase of the individual male Ruffed Grouse. These data include both on- and off-refuge residents, but exclude all birds possibly affected by research activities, including back-tagging. Differences at the end of the first and second fall seasons are significant: $X^2 = 5.33$; $X^2 = 8.48$; respectively at 1 df.

Despite these two problems (and a recent warning about using these data — Gullion, 1967a:99) it seems worthwhile to compute a minimal overwinter survival figure from the information we have collected over 11 years.

Most of our banding of grouse broods and dispersing immatures has been in the Otter Creek area (described by Kupa, 1966:55-57). We banded 52 young males on this brood area prior to the fall of 1966, and their dispersal has not been random, but evidently more extensive to the north, east, and southeast. This we believe is the result of competitive pressure by other young males from other brood production areas southwest and west of the Otter Creek area. This asymmetrical pattern of dispersal probably placed many banded young grouse in forest habitats outside our study area, and we failed to make contact with them in the spring. Figure 11 shows the extent of this problem, analyzed in Table 10.

Based on banding and radiotelemetric findings we used a 1.5-mile radius as the limit for significant dispersal to the north, east, and southeast, and one mile to the west and southwest. Figure 11 shows the extent of the area, which has been intensively investigated, and the locations where males, originating from broods in the Otter Creek area, were found either in winter after their dispersal was supposedly completed or in spring on drumming logs.

In contrast to the complications in estimating survival of juvenile males, banded on their brood ranges in August and September, a fairly direct estimate of survival can be made for the 112 immature males banded in October, November, and early December. By this time most of these young males were on, or close to, the activity center they would occupy the next spring (Eng, 1959; Godfrey, 1967). Table 11 summarizes these data, and includes the estimates from Table 10, to provide a total of the overwinter survival of immature male Ruffed Grouse banded during this study.

These overwinter survival estimates of about 45 per cent, as given in Table 11, are minimal. They represent young grouse which we *know* survived overwinter. We may have missed additional birds each spring, either the non-drummers (several of which are included) or the silent males, those using logs but overlooked in the annual drumming log survey (Gullion, 1966c, 1967a).

TABLE 10

Percentage of Dispersal Area Checked for Spring Drumming in Relation to the Banding of Juvenile Male Ruffed Grouse in the Otter Creek Brood Area

Spring season	*Acreage checked*[1]	*Percentage checked*[2]	*Juveniles banded*[3]	*Located on drumming logs*	*Estimate of immatures in unchecked area*	*Estimated percentage of survival*
1957	1,508	34.7	2[4]	1	?	—
1958	1,508	34.7	10[4]	1	2	30
1959	1,683	38.7	10	3	5	80
1960	1,683	38.7	6	1	2	50
1961	2,371	54.6	5	1	1	40
1965[5]	2,513	57.8	10[6]	0	0	0
1966	2,842	65.4	9	2+1[7]	1	44
TOTALS			52	10	12	45[8]

[1] Estimated acreage of habitable range in the Otter Creek dispersal area is 6,266 acres, of which 4,345 acres are within a 1.5-mile radius of the brood production area (see Figure 11).

[2] Percentage checked based on the 4,345 acres within the area which accounts for 85 per cent of the young male grouse dispersing from this brood area.

[3] Juvenile males banded in late August and September of the preceding summer and not recaptured after the end of September (this figure includes one-half of the unsexed juveniles banded during this period).

[4] All back-tagged.

[5] No summer banding in 1961 through 1963.

[6] Five carried miniature radio transmitters (RF marked).

[7] +1 indicates the number known to be alive but not associated with a drumming log.

[8] Based on data for the years 1960, 1961, and 1966 when the survival was not influenced by back-tagging or radiotelemetry work.

TABLE 11

Overwinter Survival of Immature Male Ruffed Grouse Banded in the Fall, Based on Drumming Log Contacts

Season banded	*Number banded or handled*[1]	*Number recovered next spring*	*Percentage survival*	*Combined estimated survival*[2]
1956	11[3]	1	9	23
1957	15[3]	1	7	12
1958	10	6+1[4]	70	75
1959	22	6+3	41	43
1960	13	6	46	44
1961	10	3+1	40	40
1964[5]	21	9	43	29
1965	10	3+1	40	47
TOTALS	112	41	44[6]	45[7]

[1] May include young grouse banded earlier, but still known to be present on the study area during this period—October to early December.

[2] Including estimated survival rates from Table 10.

[3] All birds were back-tagged.

[4] +1 indicates one more young bird which survived and which did not become established on a drumming log the next spring.

[5] No data for 1962 or 1963.

[6] Excludes data for the years 1956 through 1958 when grouse were back-tagged.

[7] Excludes the same data excluded from the totals in Table 10.

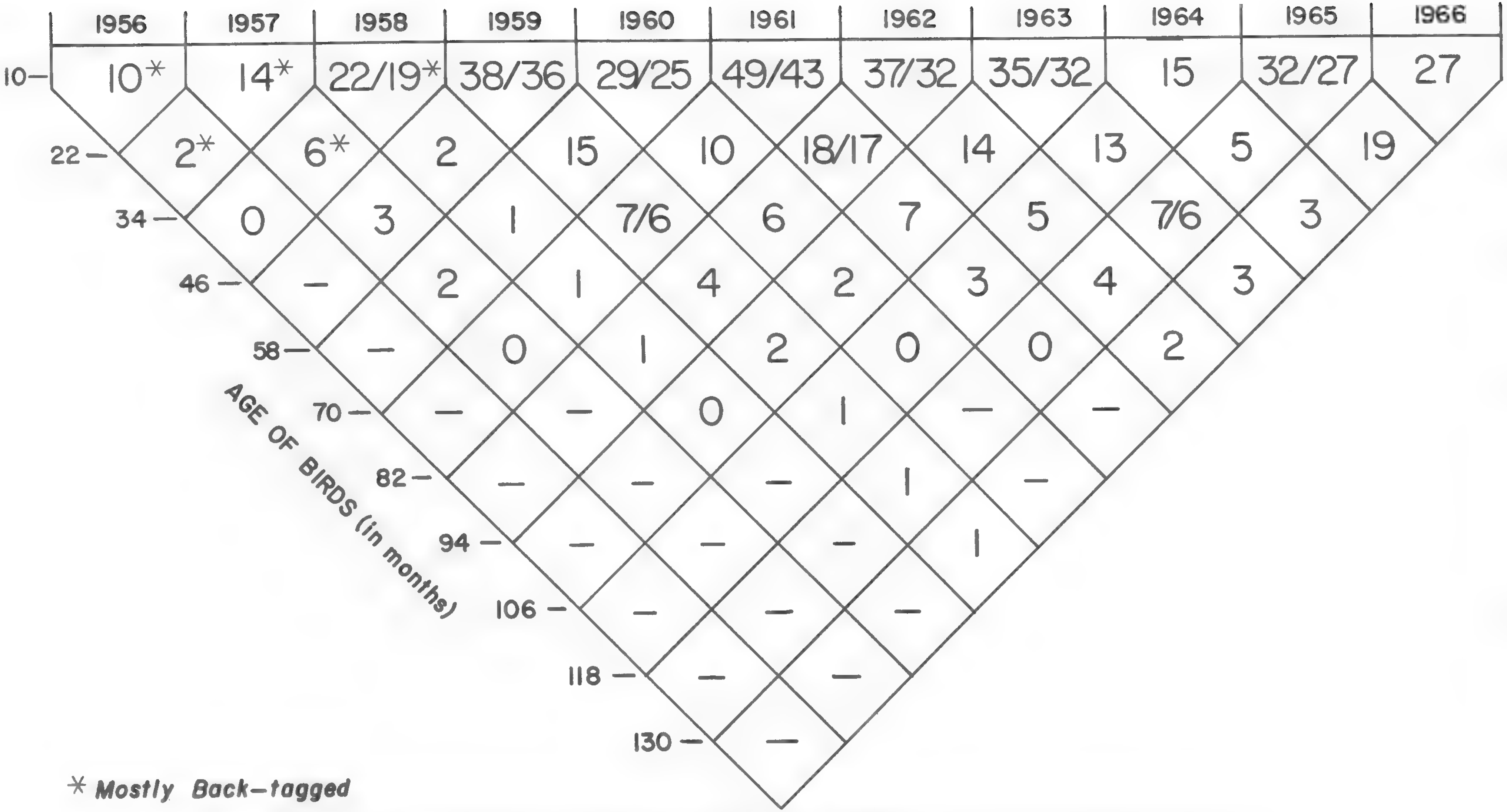
Total Life-span

Figures 15 and 16 are population triangles showing our gross banding and longevity data for immature and adult male grouse during 11 seasons. Figure 17 illustrates the rates of losses from each cohort of banded grouse, with some adjustments for accidental bird losses.

Table 12 further explores comparable survival data in a manner not presented before. Here, again, a fairly constant survival rate of about 47 per cent is evident among established drumming males during the 12 months from one breeding season to the next. The exceptions are (1) the years when the grouse were back-tagged; (2) the 1963-1964 season when the population dropped to its lowest level; and (3) 1965-1966 when recovery was under way and survival was the highest of any year in the past decade.

Once these grouse have reached adulthood, their rate of survival during a 12-month period is about equal to their survival during the first six months after they have dispersed from their brood ranges.

From all of the data presented in this paper we can construct a composite life-table, showing survival rates for male Ruffed Grouse in the Cloquet area from the time the birds are about 15 weeks old (Table 13). This computation estimates that 450 of the original 1,000 birds will live to their first breeding season, and that there will be 185 birds still alive by the second, 78 by the third, 41 by the fourth, 13 by the fifth, and only 3 by the sixth season.



	10	22	34	46	58	70	82	94	106	118	130
1956	10*	2*	0	—	—	—	—	—	—	—	—
1957	14*	6*	3	2	0	—	—	—	—	—	
1958	22/19*	2	1	1	1	0	—	—	—		
1959	38/36	15	7/6	4	2	1	1	1			
1960	29/25	10	6	2	0	—	—				
1961	49/43	18/17	7	3	0	—					
1962	37/32	14	5	4	2						
1963	35/32	13	7/6	3							
1964	15	5	3								
1965	32/27	19									
1966	27										

Mostly Back-tagged

Figure 15. Gross survival data for all banded immature male Ruffed Grouse known to have been associated with drumming logs on the Cloquet study area. The symbols such as "22/19" in 1958 mean that 22 birds were known to be using drumming logs, but for one or more of the reasons discussed in the text and listed in Table 2, only 19 can be considered for further survival analysis.

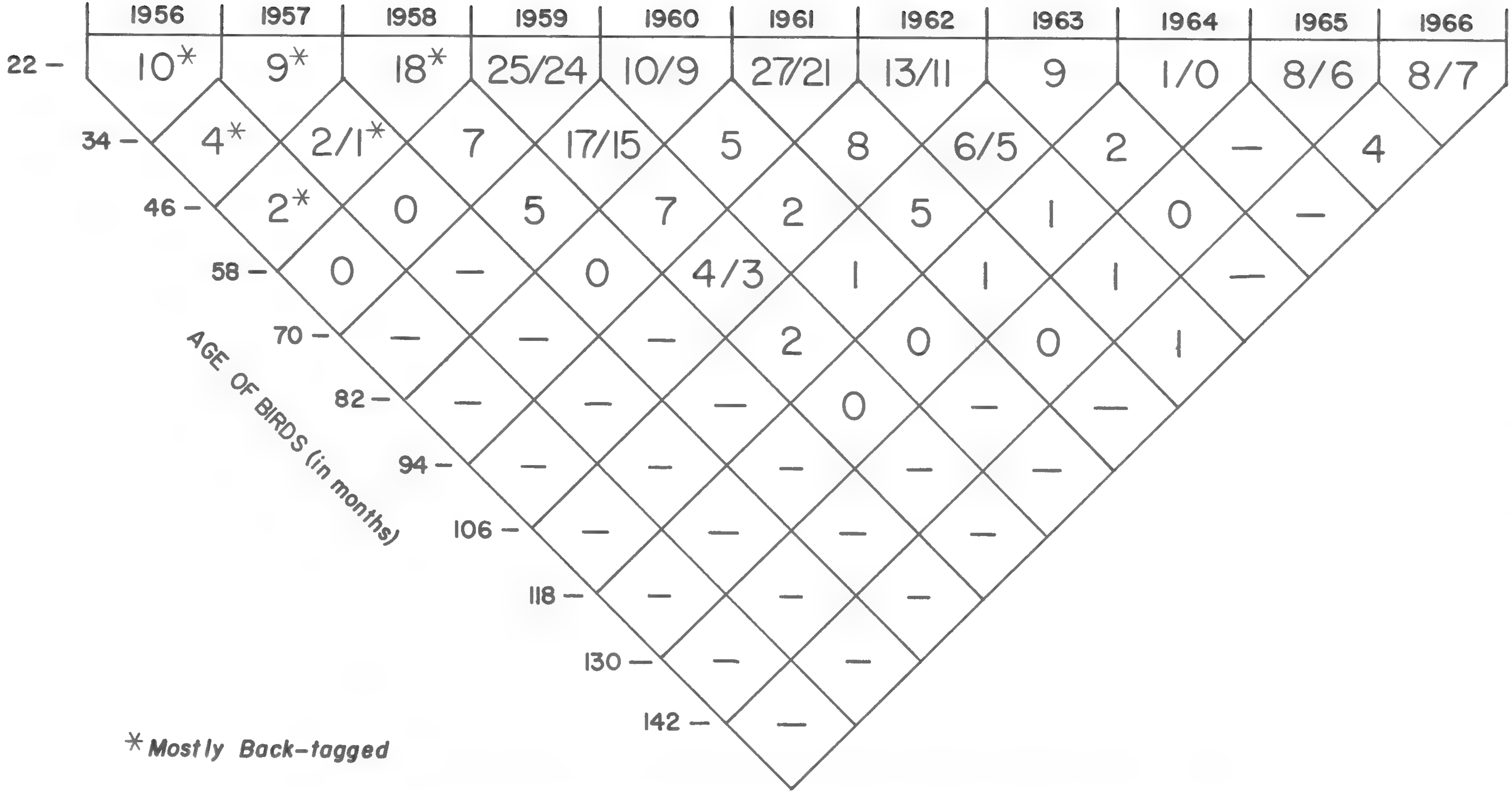


Figure 16. The same gross data for banded adult male Ruffed Grouse as shown in Figure 15 for immatures, and with the same adjustments.

Discussion

The story of Ruffed Grouse survival in a boreal forest as developed from our Cloquet study provides an opportunity to re-examine some concepts of the habitat, some aspects of the population dynamics, and some other interesting problems.

Differential Mortality of Back-tagged Grouse

We can do little more than speculate concerning the reason for the differential mortality between color phases of back-tagged grouse. One possible explanation could be that the gray-phase birds "feel safer" due to better protective coloration in this coniferous-forest environment and are therefore less wary. The back-tagging made the gray birds just as conspicuous as their red-phase brethren, but, because they were inherently less wary, they were taken by predators more readily than the red-phase birds. The red birds, out of phase with their habitat anyway, were inherently more wary. Thus the addition of the conspicuous back-tags did not appreciably alter their chance of survival.

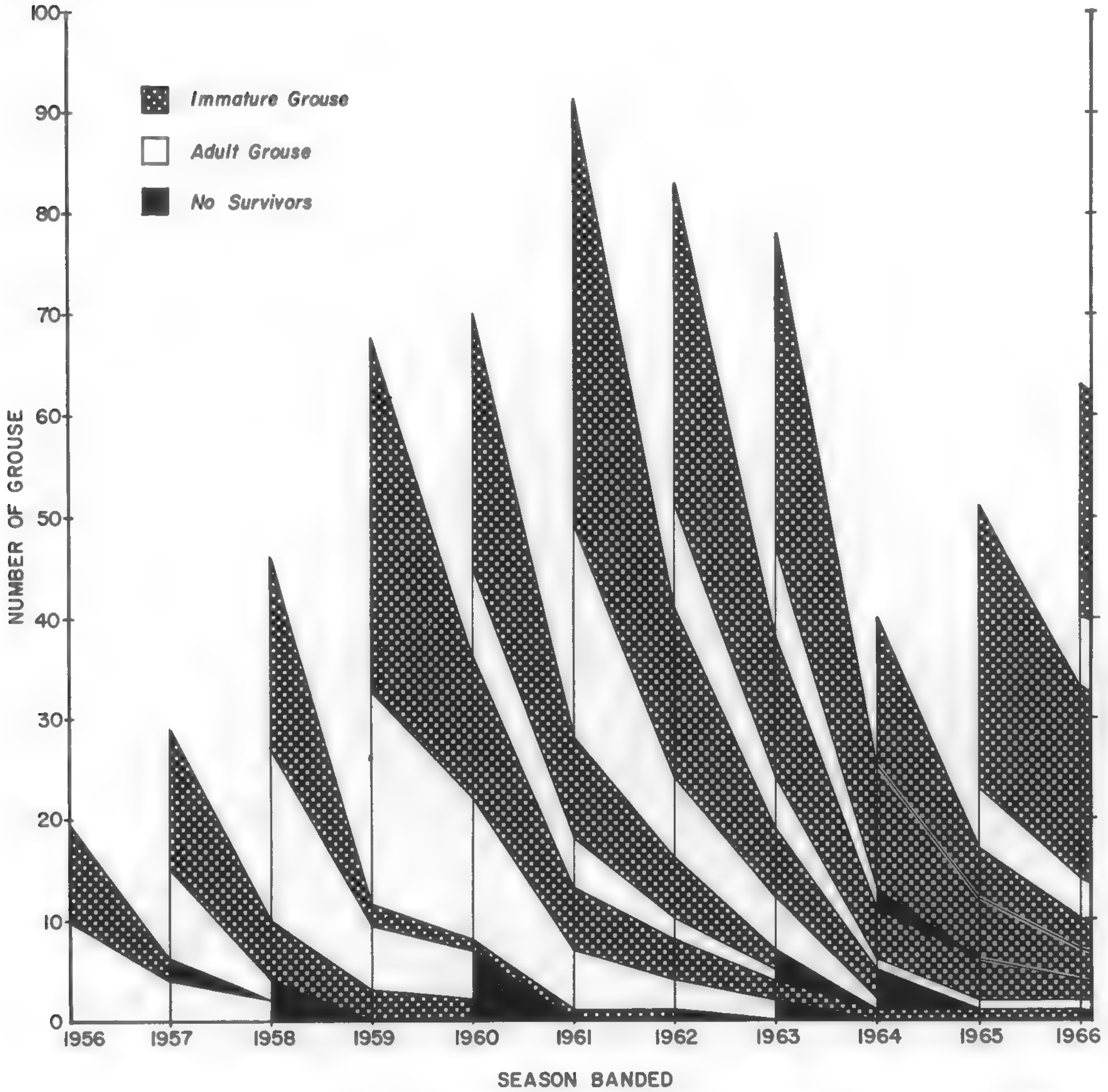


Figure 17. A graphic portrayal of the year to year shrinkage in various cohorts of banded male Ruffed Grouse. These data are based on grouse whose survival was not knowingly affected by research activities, except that they do include back-tagged grouse in 1956 to 1958. Note that no adults were included in the 1964 cohort.

TABLE 12

Season-to-Season Survival among Established Drumming Male Ruffed Grouse[1]

Season	*Number of established males*	*Number alive 12 months later*	*Percentage survival*
1956	20[2]	6	30.0
1957	29[2]	10	34.5
1958	46[2]	12	26.1
1959	72	40	55.6
1960	72	30	41.7
1961	93	43	46.3
1962	84	39	46.5
1963	79	26	32.9
1964	41	18	43.9
1965	51	33	64.7

[1] Includes all back-tagged and age classes, both color phases, and both on- and off-refuge grouse, but excludes all birds whose survival was known or suspected to have been affected adversely by our research (Table 2).

[2] Most were back-tagged.

Coniferous Forest as Ruffed Grouse Habitat

Inasmuch as our survival data in relation to type of forest cover are somewhat in conflict with the often expressed belief that conifer cover is an essential part of Ruffed Grouse habitat (*cf.* Bump *et al.,* 1947:157-159; Edminster, 1947:68-70; Trippensee, 1948:285; Smith, 1958; Brander, 1965), some discussion seems imperative.

Our experiences with Ruffed Grouse on the Cloquet study area have placed us in a rather unconventional position with regard to what constitutes good Ruffed Grouse cover. In our opinion, cover which normally provides concealment for the grouse is not nearly as important as a type of cover which

TABLE 13

A Composite Life-table for Male Ruffed Grouse on the Cloquet Study Area

	Alive in subsequent breeding seasons					
Initial immature fall population	*First (11)**	*Second (23)*	*Third (35)*	*Fourth (47)*	*Fifth (59)*	*Sixth (71)*
1,000	450	185	78	41	13	3
Percentage surviving each year	45.0	41.1	42.1	52.6	31.7	23.0

*Breeding season is May of each year. Figures in parentheses are ages in months, considering June as the month of hatching for most Ruffed Grouse in the Cloquet area.

Figure 18 (*above*). Ruffed Grouse hen on a nest in a typically open situation at the base of a mature trembling aspen. Although the ground cover was open around this nest, the surrounding forest canopy included many jack pines and she was killed by a raptor near her nest a few days later.

Figure 19 (*below*). A typical closed-canopy, high-tree jack pine stand, showing the effect of self-pruning below the forest crown. Compare with Figure 20. Drumming male grouse occupying this type of forest habitat have had a mean longevity of 12.6 months after appearing on their activity centers. This is a 0–3 forest habitat type.

permits the birds to maintain continuous and effective surveillance over their surroundings (contradicting a recent statement — Gullion, 1965b). Anything which diminishes the "openness" of their forest habitat decreases grouse survival in winter. This includes not only overhead cover but also brush piles, very brushy undergrowth, and accumulated litter on the forest floor — windfalls, large branches, and so forth. Ruffed Grouse evidently succeed best where they can depend upon both cryptic coloration and an advance warning of the presence of a predator nearby. These factors are rather clearly shown (Figure 18) in the sites selected for drumming by the male grouse (Gullion, 1964b) and for nesting by the hens (Kupa, 1966:47). However, as the grouse move from these select sites, they come under the influence of other types of habitat in their activity centers, some of which do not permit adequate warning of the presence of predators. The more frequent the contact with the less desirable habitats, the shorter the bird's life-span. Adult grouse, living in all-hardwood stands where they seldom have contact with conifers, can expect to live about seven months, or nearly one-third, longer than the grouse living where they are continually under a pine-forest canopy (Figure 19).

Figure 20. A plantation of shrub-tree red pines. In this type of cover Ruffed Grouse may find ample security during the winter, if there is sufficient food nearby. But by the time this stand is 20 to 25 years old it has lost its value as grouse cover and then becomes an "ecological trap." Compare with Figure 19. This is a 0–4 forest habitat type.

Of 133 grouse remains, found where the kill was made and where raptors were indicated, 118 (89 per cent) were in places where a background of conifer foliage could have screened the silhouette of a raptor. However, we question whether we found evidence of grouse kills as readily in other forest types as in conifer types.

In a sense, what we are doing is rating the forest habitats in terms of their suitability as raptor cover. Ground-level food resources in most Cloquet forest habitats appear equally satisfactory for adult grouse, but some forest habitats provide much better cover for the raptors, locally the primary predators upon Ruffed Grouse.

Certainly the drumming male grouse, which advertises his presence at four-minute intervals with a sound which we can often hear for one-quarter mile, is not as safe when hidden as when he is occupying a station where neither a mammalian predator nor a raptor can approach close enough to make a successful attack without alerting him.

Ruffed Grouse seem to recognize these qualities in the forest cover. Further evaluation of Brander's (1965) radiotelemetry work with wintering grouse showed that individual birds made detours in hardwood stands to avoid entering or approaching too closely a finger of high-tree pines which extended into the study area. Also using radiotelemetric methods, R. W. Barrett (unpublished) found evidence that hens with broods deliberately avoided dense stands of conifers. Godfrey (1967), using the same technique, discovered that young grouse dispersing in the fall avoided the pine stands. We find that, unless they are moving to a better food resource, all male grouse, shifting from one drumming log to another, go to a log having less dense coniferous cover than the one they abandoned.

We believe this difference in forest habitat quality is related to the conspicuousness of the avian predators in the different types of forest cover in fall, winter, and spring, when most predation upon adult grouse occurs. When the leaves are gone, a Goshawk, Great Horned Owl (*Bubo virginianus*), or Barred Owl (*Strix varia)* is very conspicuous in an aspen, birch, maple, or tamarack, but the same raptor perched in or under the crown of a pine, fir, or spruce is well concealed. We suspect that raptors prey most successfully upon Ruffed Grouse when they drop silently from ambush upon an unwary bird on the ground below. Generally in pine forests, once the trees are more than 15 to 25 years old (Figure 20), the lower branches have died and self-pruning has begun, resulting in the "high-tree" character defined by Smith (1958; see also King, 1937:530). From a high tree a raptor can drop upon its prey without warning. On the other hand, this self-pruning is not prevalent in balsam fir or spruce in this area, and even old fir and spruce retain the "low-tree" character, with living or dead branches hanging low to the ground. Here a raptor has trouble getting to prey on the ground without hitting branches en route and giving its intended victim a warning. Granted that it may only be a split-second notice, the differences in survival in the different forest habitats suggest that this fraction of a second, when compounded many times, can be important.

It is the growth form or physical characteristics of the trees rather than the species of trees that affect grouse survival in a forest habitat. Thus the growth form of pines as they mature makes them "ecological traps" for grouse. Spruce and balsam fir are less dangerous and hardwoods provide the best forest cover of all in this northern Minnesota countryside.

Since we are basing our evaluation of what constitutes the best forest habitat on the individual longevity, or success, of the birds occupying these various habitats rather than upon a "frequency of occurrence," we analyzed our data differently than most investigators. However, our findings agree with those of Magnus (1949), and Marshall and Winsness (1953) for this area. Dorney (1959:21), in downgrading the value of coniferous cover in nearby

Wisconsin grouse habitats, concluded that "areas devoid of conifers can sustain both excellent wintering and breeding populations of ruffed grouse."

The Color Phase and Protective Coloration

Of special interest here at Cloquet is the superior survival of the red-phase grouse, back-tagged in 1956 through 1958, over their successors, color-banded later. This situation and the knowledge that the "still-living" red-phase males (as of December 1966) have already exceeded the mean survival time for the birds which lived and died in the 1959 to 1963 period, provide another clue to the influence of weather, especially deep snow, in providing overwinter protection. As discussed recently (Gullion, 1966c), the winters of 1958-1959, 1960-1961, 1962-1963, and 1963-1964 lacked snow for burrowing. Evidently under these conditions mortality among red-phase grouse is more rapid than among the gray birds. But with the better snow conditions, prior to 1958, the red-phase birds with back-tags outlived their succeeding phenotypes. Grouse entering the population picture in 1964 likewise enjoyed very favorable snow conditions during their first winter and most of these birds were still alive at the end of 1966.

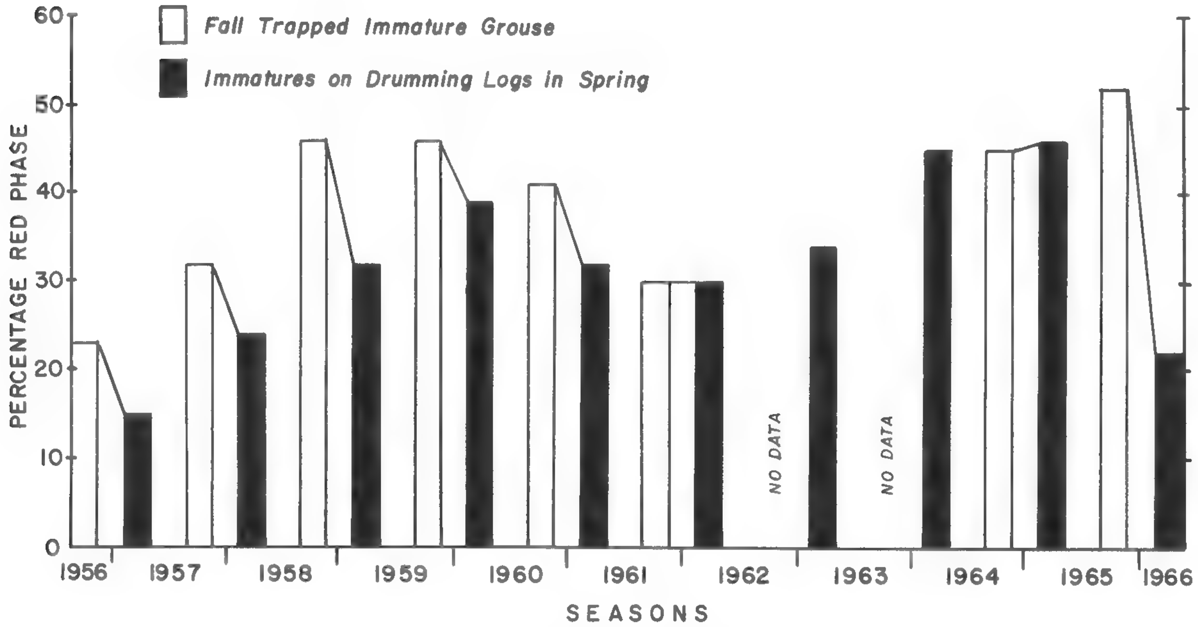


Figure 21. Shows the fall to spring changes in the percentage of red-phase grouse among the immature male Ruffed Grouse. These data include all back-tagged birds in 1956 to 1958, but not any other birds probably affected by our research activities.

An examination of Figure 21 provides further insight into this phenomenon of winter survival and color phase. Comparing the percentage of red-phase males in the juvenile population each fall with their percentage among the immature drumming males the following spring, the data suggest that, during the years when snow cover was deficient, the red-phase grouse sustained proportionately heavier loss than the gray-phase birds. During two winters since 1958, namely, those of 1961-1962 and 1964-1965, when snow conditions were especially favorable for burrow-roosting, the red-phase birds fared as well as the grays.

We have no information on the quality of snow prior to the winter of 1958-1959, but the accumulation in 1956-1957 was on a par with 1961-1962, and the 1957-1958 accumulation was about the same as in 1959-1960. Fall data concerning color-phase ratios are not available for the winter of 1962-1963, a season especially hard on the grouse at Cloquet. Although unexpected, the 1965-1966 change in color-phase ratios agrees somewhat better with the snow quality for the 1965-1966 season than does some of our other population data. Thus, change in color-phase ratios may provide a better measure of the severity of winter snow conditions for grouse than some of our other indices.

Geographic Variations in Coloration. — An examination of 3,320 sets of Ruffed Grouse wings and tails, sent by hunters to the Minnesota Division of Game and Fish from 1961 to 1964, show that, as the dominant forest types

TABLE 14

Prevalent Forest Types by Counties in Minnesota, and Percentages of Hunter-killed Ruffed Grouse Which Were Red-phase[1]

County	*Sample size*	*Percentage red-phased*	*County*	*Sample size*	*Percentage red-phased*
		Forests predominately aspen-birch[2]			
Kittson	125	44.8	Pennington and Red Lake	10	40.0
Roseau	118	43.2	Cook	171	43.3
Marshall	129	42.6			
		Forests aspen-birch and mixed spruce-fir and pines			
Lake of the Woods	200	40.5	Cass	307	45.0
Koochiching	184	44.0	St. Louis	302	45.4
Beltrami	138	48.6	Lake	143	51.0
Itasca	373	50.7	Carlton[3]	115	52.2
		Forests of aspen-birch and pines			
Hubbard	40	30.0	Crow-wing	35	40.0
Wadena	14	29.0			
		Forests of aspen-birch, pines and much northern hardwods			
Clearwater	47	36.2	Aitkin	190	47.9
Becker	62	45.2	Pine	191	48.7
		Forests predominately northern hardwoods			
Polk	17	52.9	Kanabec	109	55.0
Morrison	44	61.4	Anoka	26	53.8
Mille Lacs	179	52.5	All others[4]	51	54.9

[1] Sample size for period 1961 to 1964 totaled 3,320.

[2] From Cunningham *et al.*, 1958: map inside back cover.

[3] Site of Cloquet study area is in Carlton County.

[4] Including: Benton, Chisago, Douglas, Isanti, Mahnomen, Norman, Otter-tail, Sherburne, Stearns, and Todd Counties.

change from coniferous and aspen-birch in the north to the hardwoods towards the south and as snow becomes less of a "permanent" element in the winter ecology, the prevalence of red-phase over gray-phase increases (Table 14). This supports an earlier observation by Todd (1940) who correctly noted that among Minnesota specimens of Ruffed Grouse the "gray phase will be found in greater numbers in the northern part of the state, and the rufous phase in the southern."

Even in Carlton County, the locale of our study area, the hunter-kill sample for the four-year period shows red-phase grouse predominating over grays, in contrast to the color ratio on the 7,200-acre portion we studied. But agreeing with this is the fact that many of the forests in Carlton County were devastated by a fire in October 1918, and, as late as 1950, only 2.5 per cent of the forests consisted of pine stands (about 25 per cent of these are on the unburned Cloquet Forest Research Center), and 9.7 per cent of lowland conifers — mostly cedar, tamarack, spruce, and fir. The remaining forested land in the county includes aspen (39.7 per cent), other hardwoods (14.3 per cent), and various categories of brush and non-productive forest lands (Sandberg *et al.,* 1950).

Some Continent-wide Relationships. — In view of the fairly marked differences in the survival of the two color phases here at Cloquet, it seems worthwhile to explore briefly the continent-wide relationships between the color tones or phases and generalized forest types.

Aldrich and Friedmann (1943:88) recognized an ecological significance to the variation in color tones among the various races of Ruffed Grouse: "Although the life-form of dominant vegetation seems to be the chief agent limiting the distribution of the species as a whole, racial coloration seems to be correlated to a large extent with atmospheric moisture."

Ridgway and Friedmann (1946:155), in their key to the forms of *Bonasa umbellus* (Linnaeus), indicate that the grouse from the predominantly hardwood forested regions in the east and south tend towards lighter brown coloration *(B. u. umbellus, B. u. mediana* [not recognized as valid in the 1957 AOU Check-list], *B. u. monticola).* On the Pacific Coast, the brownish coloration prevails, but with the darker suffusion characteristic of most races of birds living on the humid western slopes of the Cascades and Coast Ranges *(B. u. castanea, B. u. brunnescens, B. u. sabini).*

On the other hand, farther north, as snow and conifers become more important in the grouse habitat, the racial coloration tends to be more grayish *(B. u. yukonensis, B. u. incana, B. u. umbelloides).* The race *B. u. togata,* ranging through the Great Lakes-St. Lawrence River region, is brown mixed with gray, and it lives where coniferous forest and hardwood stands are extensively intermixed (Aldrich's "Northern hardwood-conifer," 1963). This intermediate coloration also marks the races *B. u. phaia* and *B. u. affinis* [not recognized as valid in the 1957 AOU Check-list] which inhabit the drier, western, intermountain ranges and the western slopes of the Rockies, where extensive strips of riparian hardwoods dominate stream bottoms between ridges which are often forested with conifers and aspen groves. According to the distribution map in Aldrich (1963:535) our Cloquet study area is in the zone of intergrade between *B. u. togata* and *B. u. mediana.*

Pynnönen (1954:9) notes a similar trend in the coloration of the Hazel Grouse *(Tetrastes bonasia),* a close relative of our bird. He reports that Hazel Grouse living in the more northern latitudes of Eurasia tend to be grayish, while those living farther south in hardwood forests tend to be more red-brown.

Regional Prevalence of Color Phases. — Insofar as color phases within racial populations are concerned, data from the various regions are scarce in the literature. But evidently the red phase is the predominant form in eastern hardwood areas. In comparing *B. u. mediana* with the nominate race *(B. u. umbellus)*, Ridgway and Friedmann (1946:162) say, "On the whole this race is more often gray-tailed than brown-tailed, while the reverse is true in the nominate form" (but our Minnesota hunter-killed samples do not support this statement). Edminster (1947) indicates that grouse from the New York region were almost exclusively red-phase when he says, "The ground color of the eighteen tail feathers (rectrices) is a clear rufous brown . . . ." He mentions nothing about gray-phase birds, but acknowledges the occurrence of two color phases elsewhere.

Aldrich and Friedmann (1943) note that even the gray-phase birds of *B. u. monticola* are "apparently never so pure gray [as the nominate form], but always with at least a slight tinge of rufous." Chapman *et al.* (1952) note that "Ohio birds are normally . . . with reddish-brown tail" and comment about the occurrence of a gray phase in grouse populations elsewhere.

Bezdek (1944) provides useful data from farther west, based on grouse captured in central Wisconsin and central Alberta and released in Ohio. In a sample of 144 grouse from the vicinity of Babcock, Wisconsin (a mixed hardwood-conifer region where *B. u. togata* and *B. u. mediana* intergrade), the birds were nearly evenly divided between red- (39 per cent), intermediate- (39 per cent), and gray-phase (44 per cent). His sample of 736 grouse from near Lacombe, Alberta, within the range of *B. u. umbelloides* (and evidently in the "closed boreal [coniferous] forest" of Aldrich, 1963) were 58 per cent gray-phase, 19 per cent intermediate, and 31 per cent red. Bent (1932:173) notes that *B. u. umbelloides* "has a red phase which apparently occurs about as often as the gray phase occurs in the eastern birds."

The prairie-edge Ruffed Grouse *(B. u. incana)* lives in aspen parklands and groves and tends to be grayish even in its red phase. Aldrich and Friedmann (1943:100) say that a "red phased" grouse in this population is, "A very ashy bird, similar not to the brown but to the gray phase of *B. u. umbellus,*" and the gray birds are, "smoke gray with no buffy tone."

The most grayish of all Ruffed Grouse is *B. u. yukonensis,* a bird of the boreal, spruce forested regions of the Yukon River drainage. However, as Weeden (1965:20) notes, "In interior Alaska, ruffed grouse are found in stands of timber containing large amounts of aspen." In recent correspondence Weeden points out, "white birch and white spruce, together, comprise less than 10 percent of the trees in the stands to which I refer." Grinnell (1916), originally describing this race, wrote, "Three out of the eleven specimens at hand have pale rusty tails; but even in this 'red' phase the race is distinguishable from the corresponding phase in the other subspecies by paler tone of coloration" (yet a specimen sent us by Weeden which was taken near College, Alaska, on 5 March 1967 is as reddish as most of the red-phase grouse at Cloquet). Weeden *(in litt.)* reports on two recently collected (1966) groups from interior Alaska, in which only three of 37 grouse of one group tended towards the reddish coloration, while in an earlier selection of 23 grouse, collected from 1959 through 1965, six were red birds.

Once out of the zone of winter snows, and into the humid coastal parts of the west coast, reddish tones again predominate. Taverner (1934:155), for example, notes that *B. u. sabini* "is a very red bird with little or no gray anywhere" and, "The extreme grey phase is scarcely greyer than some of the red birds of other subspecies." Both Aldrich and Friedmann (1943:95) and

Ridgway and Friedmann (1946:169) point out that a gray-phase form of *B. u. castaneus,* from the Olympic Peninsula, Washington, did not occur among the 20 birds in the museum collections they examined. Although both the red and gray phases are known to occur among the Ruffed Grouse *(B. u. brunnescens)* on Vancouver Island, J. F. Bendell in recent correspondence, reported 55 (75 per cent) red-phase grouse among 73 specimens from Vancouver Island.

The Question of Differential Survival. — At this juncture it is easier to document a differential survival related to color phase among the Ruffed Grouse populations at Cloquet than it is to explain the mechanism or mechanisms responsible. There may be more than one factor playing a role, and the relative importance of each factor may vary from year to year as environments change.

As a generalization, the prevalence of red-phase grouse in the population increases as the continental climate grades from the Arctic south. This suggests that the difference in mortality may be related to the severity of the winter; or more specifically, that there may be a color-linked susceptibility to cold or other climatic conditions, which selects against the red-phase grouse.

This viewpoint partially supports the hypothesis of Chitty and his coworkers (see e.g., Chitty, 1960; Chitty and Phipps, 1966). We have demonstrated significant differences in the predominance of one color phase over the other between expanding and declining Ruffed Grouse populations and have shown that these changes can be related to density-independent, physical factors.

Earlier we believed that this differential survival represented periodically increased vulnerability to predation among red-phase birds (primarily as a result of insufficient burrowing-snow), and we still cannot discount this idea entirely. As noted earlier, gray birds usually constitute a larger fraction of the population where conifers and aspen-birch forests predominate. These are also the colder environments. Possibly the gray-phase grouse are less conspicuous than the red birds on the grayish leaf-and-needle litter of the boreal forests. On the other hand, where the ground litter is composed of the reddish leaves of oak, maple, basswood, and other northern hardwood species (the "Maple-basswood region" of Shelford, 1963:19), the red-phase grouse become predominant. However, red-phase grouse also prevail on the Pacific Coast, where they live in forests of Douglas-fir, cedar, spruce, and other conifers.

We have suggested that the red-phase grouse may be more conspicuous to raptors hunting overhead than are the gray-phase birds. Thus the red birds suffer substantially higher mortality in the conifer-forested habitats where raptor predation is most effective. In the hardwood forests, where raptors have poorer hunting cover and mammalian predation is heavier, the color phase of the grouse matters less.

However, we can find little support for this viewpoint in our Cloquet data. As Table 7 shows, the survival among red-phase grouse is only 18 per cent better in hardwoods than it is in all-conifer situations, whereas among the gray-phase birds survival in hardwoods is 40 per cent better than in conifers.

Ecological Significance of Color-phase Ratios. — We believe our data strongly suggest that the habitats in which red-phase Ruffed Grouse predominate and remain fairly static from year to year are probably better suited to this species. This is not to predict that the densest populations will be found in areas where red-phase birds predominate, because there are other influences such as quality of food resources and adequacy of cover which may affect densities in regions of better climate. But it does seem very likely that the habitats in which red-phase Ruffed Grouse predominate have the more stable year-to-year population densities. Leopold (1931:149) expressed the idea, "that the center of the north central region was the optimum range of the ruffed grouse," and this observation would agree with the increasing prevalence of red-phase grouse from north to south in Minnesota.

Admittedly, we do not understand the mechanisms which govern the selective loss of red-phase grouse at Cloquet, but in any event, as climate becomes less severe the red-phase birds increase in the population. Certainly our Cloquet example has shown that during winters when the red birds can burrow in the snow to avoid the cold they overwinter more successfully than during winters when this protection is not available. We cannot believe that

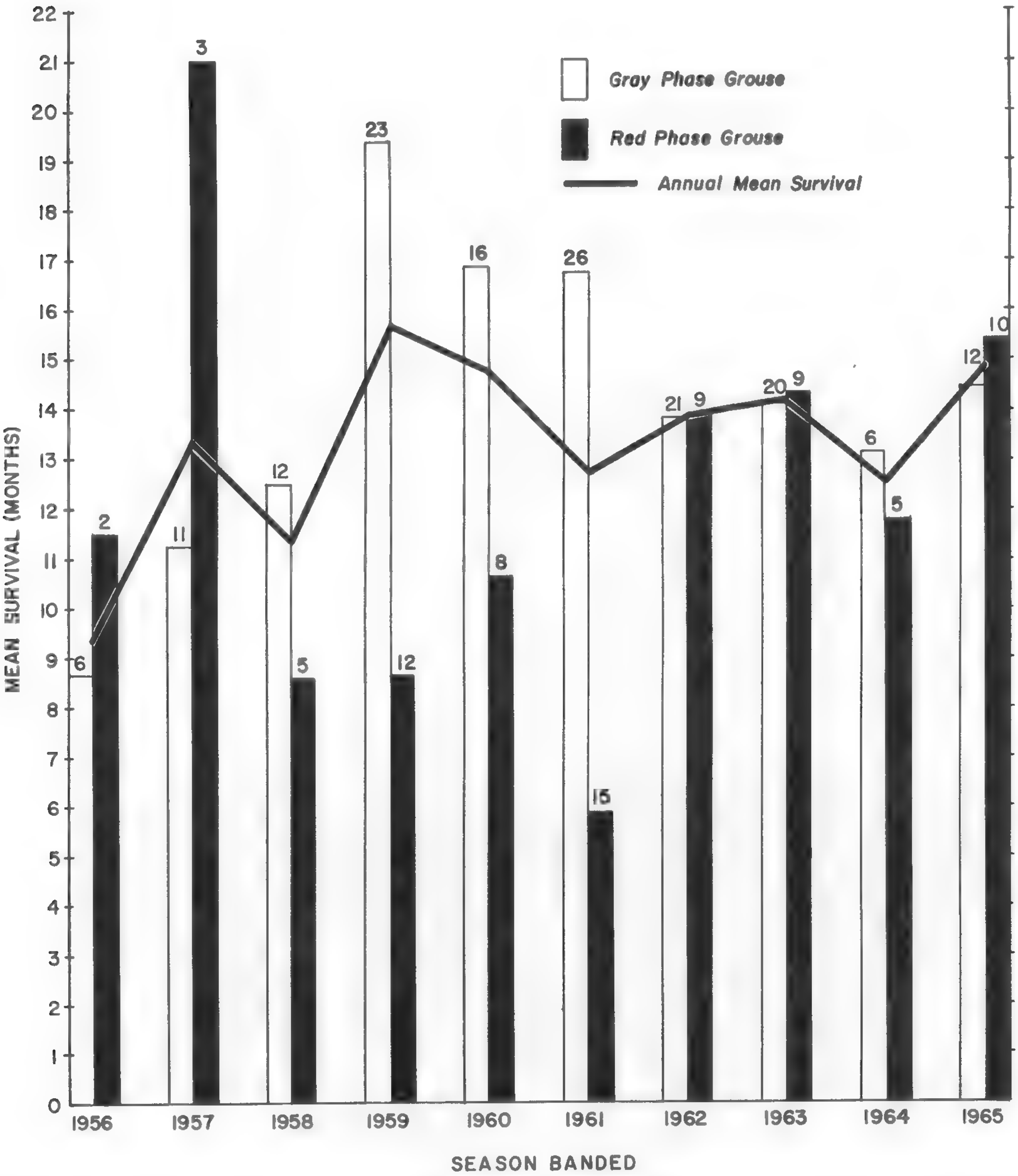


Figure 22. The comparative longevities, by cohorts, of immature male Ruffed Grouse associated with drumming logs. These data include back-tagged birds in 1956 to 1958, but exclude all other research-affected individuals. The numbers at the top of the bars represent the number of grouse included in each sample.

a red bird roosting in a tree or on the surface of the snow, because of inadequate burrowing-snow, would be any more vulnerable to predation than a gray bird in the same situation.

Data covering a span of one decade are not conclusive but, as Figure 21 shows, an increasing abundance of Ruffed Grouse in the Cloquet area (to a peak in 1960-1961) followed a sequence of years when red-phase birds became increasingly prevalent in the population (1956 to 1959), and the depth of the recent depression (1963-1964) followed a sequence of years (at least 1960 and 1961) when the proportion of red-phase grouse decreased in the population. While not included in the data presented here, the Cloquet grouse population reached a fairly high level of abundance in the fall of 1967, following at least four years of an increase of red birds in the population.

Therefore it appears possible that trends among Ruffed Grouse populations in the Cloquet area can be forecast a year or two ahead with some accuracy simply by noting the changes in color-phase ratios among the young grouse sampled in the fall.

Survival through Periods of Periodic Depressions

King (1937:532) stated that "only those birds born four, five, and six years before the 'crash' have sufficient stamina and reserve strength to carry them over the decline. It is this group of older birds that makes up the group of survivors and furnishes the breeding stock responsible for the next cyclic recovery." Trippensee (1948:274) repeats this statement, citing King's work.

Our Cloquet data provide some opportunity to examine this hypothesis, but do not warrant much statistical treatment. Figures 15, 16, 17, and 22 suggest little to support King's hypothesis. During our study period, 1961 was the year of the peak population and 1964 was the bottom of the decline. Yet these figures suggest that grouse, which began breeding during the periods of depression, survived as long as those which began breeding when the population was highest. In fact, Figure 17 shows that the two shortest-lived cohorts we studied were those entering the ranks of breeding grouse in the peak years of 1961 and 1962.

Overwintering Success of Young Males

Referring back to Tables 10 and 11, the low survival of the young males in 1956-1957 and 1957-1958 probably reflects the effect of back-tagging the young male grouse in the fall. On the other hand, the very high overwinter survival in 1958-1959 probably provides some insight into the role that competition plays in grouse survival. In the area where these young males were banded in the fall of 1958, every male established on a drumming log the preceding spring was marked with a back-tag. Only two of these 23 adult males survived the winter of 1958-1959, leaving 21 vacant activity centers, six of which were occupied by banded young males. Subsequently, overwinter survival of established drummers was considerably higher (Table 12), and the young males were less successful in competing against the older, established males for suitable activity centers.

The constancy of this survival rate among the young males is rather surprising. It does not deviate as much as would be expected, considering the great variations in winter weather and snow conditions during these several years.

The winter of 1958-1959 was especially cold with little snow (Gullion, 1966c:719), but survival among this small sample was very good. On the other hand, survival among young grouse over the winters of 1964-1965 and 1965-1966 was disappointing when compared to what we believed to be very favorable wintering conditions (and indicated by a higher survival among adults for 1965-1966; see Table 12). Perhaps some density-dependent factor, such as competition for a sharply reduced food supply resulting from the aspen cutting, limited the survival of the young grouse in this area in these latter winters.

The seasons, which might have provided data necessary for a clearer understanding of these relationships, were 1962 and 1963 when we did not engage in fall trapping.

The "Crash-decline"

Our data concerning Ruffed Grouse survival in the Cloquet area do not lend much support to the idea of a "crash-decline" or "die-off," which is often described as accompanying the so-called "cyclic" decline of this species (Erickson *et al.*, 1949; Grange, 1949:168; Keith, 1963:80; Allin, 1964). At least during the past decade, it appears that there has been little measurable change in the normal rate of attrition from the Cloquet adult grouse population. In fact, the rate seems remarkably constant, more so than we expect, recalling how grouse were "everywhere" in 1961 and even 1962, but so scarce in the Cloquet area by the winter of 1963-1964 that it was necessary to curtail one phase of the radiotelemetry project because we could not trap enough birds.

We agree with Miller (1942) and Bump *et al.* (1947:573) in believing that, during the years of decline, reproductive failure in the spring resulted in the production of too few grouse to replace those lost through normal decimation. This lack of replacement stock resulted from either a high proportion of hens failing to nest, and/or from a high frequency of nesting failures, and/or from chicks having inferior stamina. These are all manifestations of the adverse winter conditions which, as we have already demonstrated, depress the male's vigor and physiological condition, insofar as these are indicated by reduced drumming activity and lowered body weights (Gullion, 1966c, 1967c).

Certainly, nothing in our data suggests a widespread epizootic condition (*cf.* Erickson *et al.*, 1949; Allin, 1964), nor have banding returns suggested any mass movements of grouse off our area.

We believe that the often-reported "sudden disappearance" of grouse in a "crash-decline" is little more than a change in behavior which marks the "growing up" of young Ruffed Grouse. Hunter harvest figures from this region show that young Ruffed Grouse are taken out of proportion to their abundance in the population (Dorney and Kabat, 1960; Ruos, 1962; Gullion, 1962a:45, 48). Most of our impressions of grouse abundance are based on flushing contacts, and we believe, using the analogy as shown by hunter kill data, that young grouse are more readily flushed — hence counted — than are the adults.

The so-called "crash-declines" therefore reflect the cumulative effect of: (1) A real decline in grouse numbers, which is normally only moderate in degree; and (2) a change in the age structure of the population, with a higher proportion of adult grouse which are less inclined to flush when an observer passes nearby. The apparent grouse decline then includes an estimate based upon a real loss of perhaps 50 per cent of the population per annum, compounded by a factor of perhaps two or three, or greater, which represents the increased difficulty of finding adult Ruffed Grouse, as compared to the unwary young birds.

Our experience with drumming males provides ample evidence that these birds do change in their wariness. It is often easy to approach fairly close to unbanded young males on their drumming logs. But once these birds have been trapped and handled, the wariness of most of them increases so sharply that we usually cannot again approach within sight of birds we could walk around a week or two earlier. The traumatic experience of being trapped and handled evidently induces this increased wariness. We dealt with a few males that we were never able to catch in a mirror-trap and they remained easy to approach throughout the drumming season. But after we finally captured them they proved to be exceedingly elusive in succeeding years.

Conclusions

Among the several factors affecting the life-span of an individual Ruffed Grouse in the boreal forests of northern Minnesota, the color phase, inherited from its parents, appears to be the most crucial. Next in importance is the character of the forest habitat selected by the bird for its lifelong residence. For the male Ruffed Grouse occupying drumming logs, the history of prior occupancy of its site appears to be third in importance. Least important, certainly insofar as adult male grouse are concerned, is whether or not their activity centers are legally protected from annual hunting.

Summary

During an 11-year study of the demography of Ruffed Grouse *(Bonasa umbellus)* in a northern Minnesota boreal forest we have examined the longevity of male grouse in relation to: (1) the historical status of drumming sites; (2) the influence of predominant forest types; (3) the protection afforded by a refuge; and (4) the color phases of the species. We also examined some aspects of adult female and immature male grouse survival.

Using conventional techniques, we trapped and banded more than 900 grouse. Although various reservations limit the amount of data which could be used in this study, approximately 384 of the 446 banded male grouse, known to have been associated with drumming logs, provided usable data.

Four levels of obtaining demographic information are described, ranging from the least useful — non-selective trapping and banding with lily-pad traps — to the most useful — sign at the drumming logs occupied by banded male grouse.

For rating the forest cover as habitat for these grouse we have described a different scheme, based upon an evaluation of the features in the forest which favor grouse and those which detract from their longevity. We consider the presence of mature male aspen trees as a most important beneficial feature.

Male grouse survival in relation to the history of occupied drumming sites indicates that the record of prior use of the drumming log is more important than the history of the activity center. Male grouse, using transient logs not used by a predecessor, live an average of four months longer than those grouse replacing earlier drummers on perennial logs.

The character of the forest habitat dominating the activity center of a male grouse appears to be as important as the cover immediately adjacent to the drumming log. In this reference to the forest habitat, we can make five generalized statements: (1) Male grouse survive best in hardwood stands devoid of evergreen conifers; (2) the presence of spruce and balsam fir does not significantly detract from grouse longevity; (3) grouse survival declines as the density of mature pines increases; (4) male grouse in forest "edge" situations do not live as long as those in uniform forest types; and (5) red-phase grouse have poor chance of survival in all Cloquet forest habitats, but their differences of survival in the different types of habitats are not as great as they are for the gray phase.

Adult male Ruffed Grouse living on a refuge closed to hunting do not have a significant survival advantage over the birds living where they are subjected to annual hunting.

Red-phase grouse on the Cloquet study area are at a distinct disadvantage compared with the gray-phase birds, as far as survival in the coniferous and aspen-birch forests are concerned and where snow is an important part of the winter ecology. As other hardwoods become predominant in Minnesota forests to the southward, the red-phase grouse become a larger (and presumably more successful) part of the grouse population. Also, some continent-wide relationships between color tones and generalized forest types suggest that the Cloquet situation is more or less representative, on a small scale, of large regional trends in grouse coloration.

An analysis of data concerning the survival of female Ruffed Grouse indicates that the longevity of the hens can probably be equated with that of the males of similar color phase, occupying similar forest habitat with prior use histories.

Based on an involved analysis, necessitated by their fall dispersal behavior, we estimated that about 45 per cent of young male grouse survived each winter over a five-year period.

Beginning with 1,000 15-week-old grouse in early fall, we estimate that about 450 will survive to breed the following spring. By the second breeding season there will be 185 left; by the third, 78; by the fourth, 41; by the fifth 13; and by the sixth, only 3.

A brief examination of year-by-year survival of male Ruffed Grouse provides no support for the idea that some age groups, or cohorts, carry the population through seasons of "cyclic" lows.

Similarly, we can find no evidence which suggests that the Ruffed Grouse here have suffered a "crash-decline" or "die-off" during the past 11 years, even though grouse populations in 1964 were much below those of 1961-1962.

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The senior author took all the photographs and prepared all the other figures in this paper. Nomenclature of plants mentioned in this paper follows Lakela (1965).

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Carolina Wren, *Thryothorus ludovicianus*. Drawing by Charles L. Ripper.

THE BREEDING BIOLOGY OF THE PARASITIC BLACK-HEADED DUCK[1]

MILTON W. WELLER

In his classic work on the ducks of the world, John C. Phillips (1925:93) wrote of the Black-headed Duck (*Heteronetta atricapilla*): "Less is known of this species than of any other South American Duck, excepting perhaps the Brazilian Merganser." The careful work of Partridge (1956) on the latter species left the Black-headed Duck as one of the great bird mysteries of South America. The species has been of special interest because of its uncertain taxonomic position and because of its apparent parasitic behavior; no nest of the species has been reported. The fact that it is a shy bird during the breeding season has complicated its study. Since 1925, South American naturalists gradually have accumulated information on the hosts and distribution of the species but much of its breeding biology has been unknown. This paper is the result of 11 months of study of the species in eastern Argentina. Additional work during the courtship and laying season probably may modify some of the conclusions.

History of the Species

Salvadori (1895) and Phillips (1925) reviewed the synonymy of the species and Sclater and Salvin (1876) and Hellmayr and Conover (1948) summarized additional notes of interest. The Black-headed Duck is widely distributed in the marshes of the Pampas and Chaco regions of South America (Phillips, 1925). There are breeding records from most of its range in Argentina, Chile, and Paraguay, but only specimens of full-winged young and adults from Uruguay, extreme southern Brazil, and central Bolivia.

Phillips (1925) reviewed the information on the parasitic habits of the Black-headed Duck but the scarcity of his work and the additional interpretation of other notes merits summarizing. Rodriquez (1918) identified duck eggs, found in the nests of various water birds near Juancho, Province of Buenos Aires, Argentina, as those of the Rosybill, *Netta peposaca* (scientific names and classification follow Delacour, 1954-1964); and Daguerre (1920), basing his identification on a female collected with an egg in the oviduct, later attributed them to the Black-headed Duck. Holland (1892), Grant (1911), and Gibson (1920) also noted extensive parasitism but assumed it to be that of Rosybills. Friedmann (1932) presented a stimulating discussion of possible mechanisms of the operation of brood parasitism in ducks and of the

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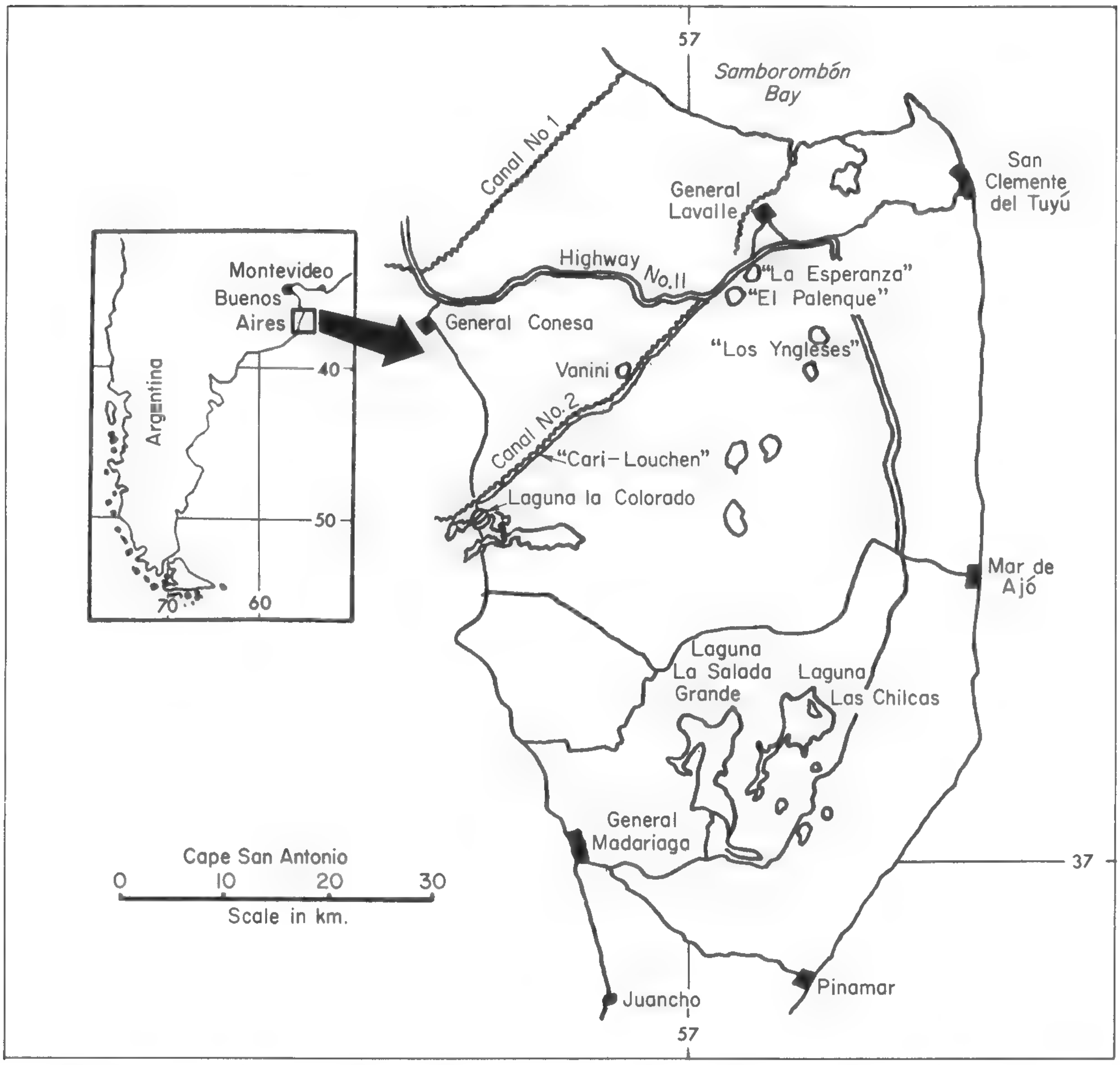


Figure 1. Location of the study area of the Black-headed Duck in eastern Buenos Aires Province, Argentina.

origin of the habit. Goodall, Johnson, and Philippi (1951) found eggs in nests of coots in Chile and attributed them to *Heteronetta*. These workers in Chile and others in Argentina placed eggs under hens and hatched the ducklings which proved impossible to rear. Peña (1962) has since reared the species by releasing them in a natural pond.

Study Areas and Methods

Because of the numerous observations of the Black-headed Duck in the Cape San Antonio area of eastern Argentina (Rodriquez, 1918; Gibson, 1920; Wetmore, 1926) and because of recent reports by interested residents on the abundance of the species, I established my study area (see Figure 1) near General Lavalle, Province of Buenos Aires, a low grassland situation described elsewhere (Weller, 1967b). Specific research areas were Estancia "El Palenque," five miles southwest of General Lavalle on Highway 11 and the Vanini Estancia, 12 miles southwest of General Lavalle along drainage Canal Number 2. El Palenque contained a series of densely vegetated, fresh-water marshes (Figure 2) totaling nearly 1,000 acres, contiguous with the extensive marshes of the adjacent Estancia "Los Yngleses" where Ernesto Gibson and Alexander Wetmore observed this species. The Vanini Estancia was approximately 1,000 acres, but I worked in one unit of about 250 acres, a marsh ideal for birds because of the many isolated pools in the emergent vegetation.

To obtain data on the laying habits of the species and the incidence and success of its parasitism, we made an intensive search from late August through December 1964 for nests of all the larger birds nesting in the marsh. Although we rechecked these nests when we encountered them on later searches, the marshes were so extensive that it was impossible to mark all nests so that we could find them easily and yet not make them conspicuous to the chief predators, Chimangos, *Milvago chimango,* and Caracaras, *Polyborus plancus* (locally known as Caranchos). We observed as many nests as possible, but we obtained our data on hatching success only from nests we could recheck after the eggs had hatched.

To determine the approximate stage in the incubation of the parasitic eggs in relation to those of the host species, we floated or candled most eggs (Weller, 1956).

Results

General Habits

Black-headed Ducks (Figure 3) have the general size and body proportions of a teal (*Anas* spp.) but are far less terrestrial, only rarely coming to land to sleep. They walk poorly, but occasionally stand in shallow water to preen. During much of the year they frequent isolated pools in dense marshes or open lakes where they get out of water only by clambering on bent tules as a submerged roost-site. They have an extremely large oil gland and very shiny plumage.

Figure 2. Prime habitat of the Black-headed Duck includes the *Azolla*-covered pools in extensive marshes of tules (*Scirpus californicus*) near General Lavalle, Buenos Aires Province, Argentina.

Figure 3. The Black-headed Duck (here a captive yearling male) has the general size and body proportions of teal (*Anas* spp.) but it is far less terrestrial.

Black-headed Ducks ride relatively low in the water and, like Ruddy Ducks *(Oxyura jamaicensis),* may have their tail on the water or uplifted at a 30-degree angle (Figures 4 and 5A). In general, they are more like divers than like dabblers in profile, being high above the water in the upper back area rather than the tail. Black-headed Ducks move through dense floating vegetation rapidly and easily in a sneak-like "scooting" position (Figure 5B).

Although not prone to flight, especially during the day, Black-headed Ducks are excellent flyers. They rise quickly, sometimes striking the water with their wings as do many dabbling ducks, at an angle of approximately 45 degrees in the absence of wind. They fly very fast and can be identified by their small, rapidly moving wings, elongate body, and low-head position (Figure 6). Birds often took flight without any preliminary actions, but most individuals, when alarmed by intruders, became alert, holding their heads and tail higher. Nervous birds sometimes head-pumped, gave head-flicks (terminology from McKinney, 1965), head-shakes, or the both-wings-stretch, but these movements did not seem sufficiently regular to be considered part of the preflight behavior.

An apparent escape reaction, possibly preflight behavior or perhaps prediving or even displacement-aggressive behavior, was an extreme wing-up, tail-up posture (Figure 5C). I saw this on three occasions, twice in response to potential predators, and once to the noise of the camera. Once, when a Caracara sailed over, several Black-headed Ducks gave the wing-up, tail-up posture as they moved into deeper water away from the potential predator. In another case, a juvenile, surprised by a landing Brown-hooded Gull *(Larus ridibundus),* gave this posture and moved away quickly until it recognized the gull as harmless. The adults nearby ignored the gull.

Black-headed Ducks proved to be excellent divers, this being a common method of feeding during the summer months. They dive easily and skillfully and do not use their wings as Wetmore (1926) thought they might. They jump fairly high before submerging and are much more skilled divers than are most dabbling ducks (Figure 5D). We saw them diving regularly with coots and Argentine Ruddy Ducks (*Oxyura vittata*). Several Black-headed Ducks dived continuously for 45 to 55 minutes. Dives averaged 11.4 seconds (range 3 to 14) for 76 dives of full-grown juveniles or adults in water of two-and-one-half to three feet deep. Adult Argentine Ruddy Ducks, in the same area, stayed under much longer, averaging 24 seconds (range 21 to 26) for eight dives. Between dives Black-headed Ducks tended to ride low in the water with the lower neck and upper back sometimes under water and the crown feathers depressed. When diving continuously Black-headed Ducks had a diving interval — surface rest — of 7 seconds (range 2 to 12) for 29 intervals.

Escape reactions observed in this study usually involved flying rather than diving. Wetmore (1926) reported that several pairs dived at the firing of a gun, an event noted only once in the collecting of numerous specimens during the present study. In this case the bird surfaced after its dive and took flight with only the slightest pause on the surface.

As noted by Gibson (1920), Wetmore (1926), and others, Black-headed Ducks are difficult to observe. They have been called "shy," but this shyness varies, depending on the season and their experiences with man. Although they were definitely wary at laying time, they were inconspicuous at other times mainly because of their habitat preference which has produced a false impression of rareness.

All comfort movements reported by McKinney (1965) were seen during this study and I noted no major differences between this species and other anatids.

In interspecific relationships all species of grebes, coots, and ducks, except the Versicolor Teal *(Anas versicolor)*, clearly dominated the Black-headed Duck. We occasionally saw Cinnamon Teal *(Anas cyanoptera)* with Black-headed Ducks and noted no aggressiveness. However, Peter Scott (1954) re-

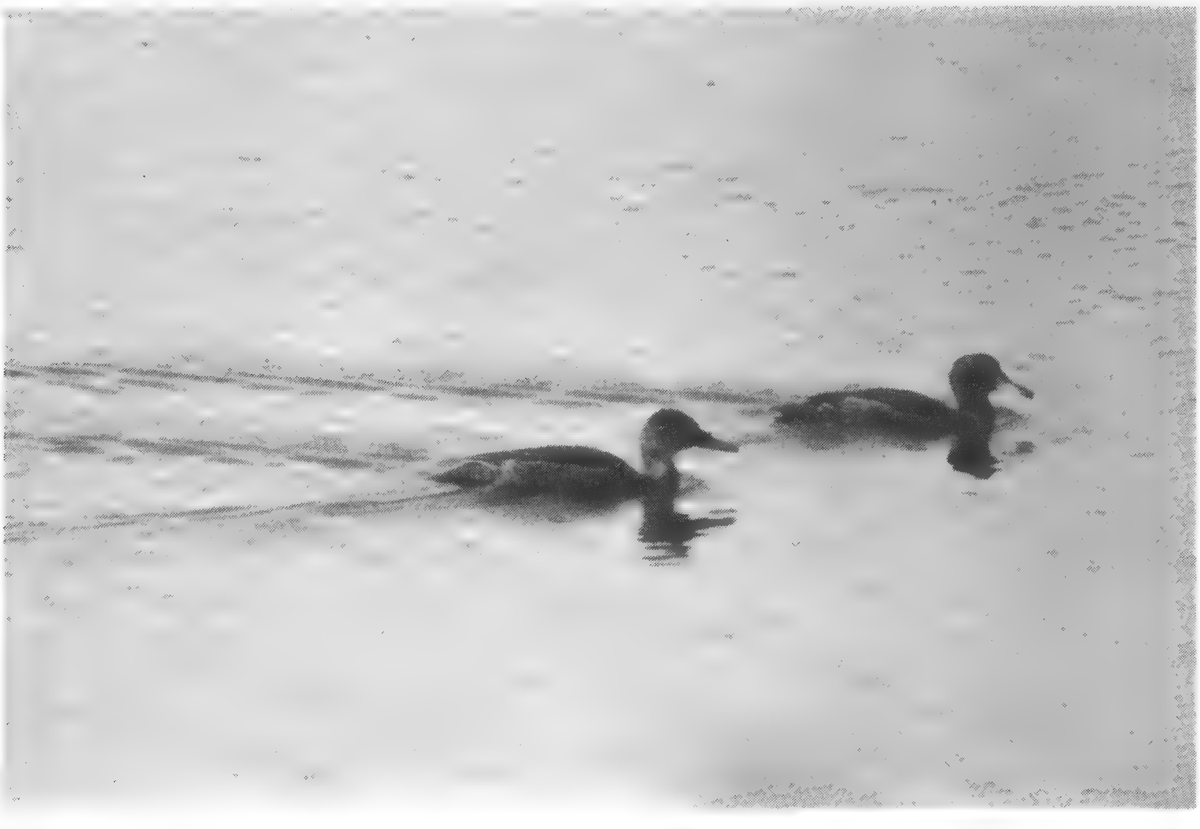


Figure 4. A pair of Black-headed Ducks swimming. The tail is frequently held in a horizontal position on the water, as shown here.

Figure 5. Behavior of the Black-headed Duck. (*A*) Note the tilted tail of the sleeping birds. These ducks swim easily through dense floating vegetation in a "scooting" position (*B*). I saw the extreme wing-up, tail-up posture (*C*) only several times as an alarm response. Black-headed Ducks are excellent divers, jumping fairly high *(D)* before submerging. They dive in water only two to three feet deep and remain submerged for 11.4 seconds (average of 76 dives). Typical feeding postures include up-ending (*E*) in water too deep for dabbling and treading (*F*) in shallow water.

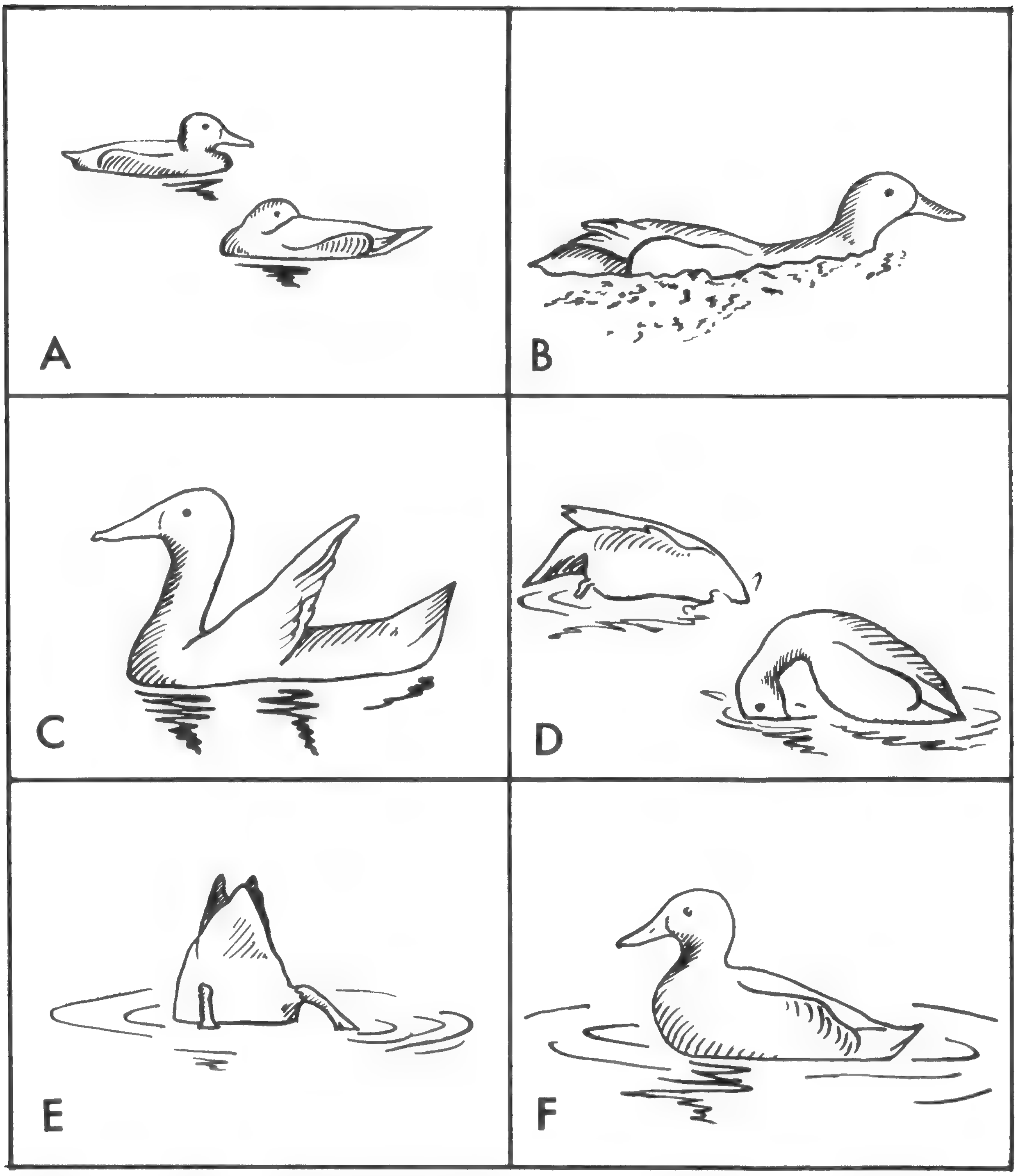


Figure 5. Behavior of the Black-headed Duck. (*A*) Note the tilted tail of the sleeping birds. These ducks swim easily through dense floating vegetation in a "scooting" position (*B*). I saw the extreme wing-up, tail-up posture (*C*) only several times as an alarm response. Black-headed Ducks are excellent divers, jumping fairly high *(D)* before submerging. They dive in water only two to three feet deep and remain submerged for 11.4 seconds (average of 76 dives). Typical feeding postures include up-ending (*E*) in water to deep for dabbling and treading (*F*) in shallow water.

ported seeing a male Cinnamon Teal courting an immature *Heteronetta* (the sexes are erroneously reversed in Delacour's, 1959, reporting of this incident) and I saw a similar one.

Foods and Feeding Habits

The food habits of both young and adults have been virtually unknown. In fact, I found only a single report of foods of an adult in the literature (Zotta, 1934) — of a bird which contained unidentified seeds, as well as some vegetable material and sand. Delacour (1959) noted that the species had a somewhat spatulate, strainer-type bill (Figure 7). In total, I examined 27 full-grown *Heteronetta* specimens (10 adult males, 12 adult females, 2 immature males, 3 immature females) for foods at various seasons.

Figure 6. Black-headed Ducks fly swiftly and can be identified in flight by the rapid beats of their small wings and by their elongate body and low head posture.

Throughout the year, seeds of the tules evidently are the main food, being found in 24 of the 27 birds and making up almost the total volume of food in 20 birds. In summer, the ducks also take snails (five of 27 birds); three individuals had fed almost entirely on snails. Black-headed Ducks swallowed snails whole, whereas a young Argentine Ruddy Duck, collected in the same area, had crushed the snails in its bill before swallowing them. Diving and water-treading (Figure 5F) suggested that other benthic organisms constitute part of the diet, but I identified no animal foods other than snails. The straining of duckweeds also may produce microscopic crustaceans. However, the presence of tule seeds in nearly every specimen suggests that seeds are the major food and that the well-developed lamellae of the bill function mostly in seed-getting. The ducks occasionally eat small unidentified seeds other than those of tules and one bird had eaten a few seeds of cut-grass. Some birds ate duckweeds, especially smaller varieties like *Wolfiella oblongata* and *Lemna valdiviana*. The unidentified green material found in the gizzard probably was duckweed.

The manner of feeding varies with the water depth. When surface-feeding in duckweed, the bill is held nearly horizontal as in most dabbling ducks.

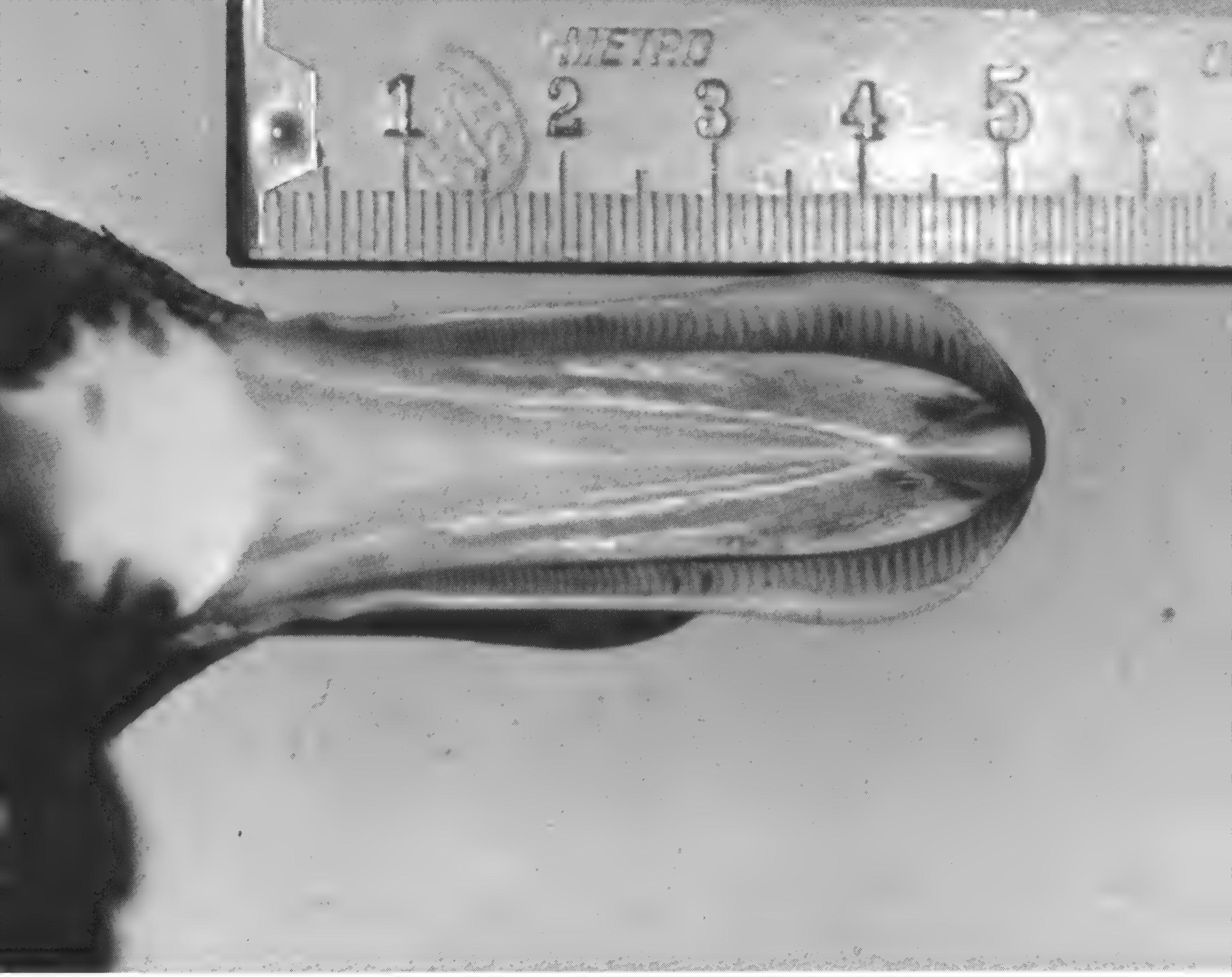


Figure 7. Ventral view of a Black-headed Duck showing the slightly spatulate, strainer-type bill.

When straining mud in shallow water, the bill is held at an angle of 45 degrees unless the water is extremely shallow. In slightly deeper water, feeding is swan-like with the head and neck under. When the water is too deep to reach the food by dabbling, the birds up-end (Figure 5E). During the summer months, full grown juveniles and adults dived in water two to three feet or more in depth.

Annual Cycle and Sex Relationships

I have found no nests of Black-headed Ducks and observed no females behaving as though they had nests or broods hidden from me. Despite the fact that I spent considerable time in areas where Black-headed Ducks parasitized nests of other birds, I saw no broods. On the basis of these observations and the absence of documented reports by other observers, I assume that the Black-headed Duck is completely parasitic.

In east-central Argentina, I watched birds in pairs regularly from mid-September to early December. I have no data on pair bonds of marked birds but the pairs behaved much as do other species of ducks. Some pairs were close-knit while others seemed to be less definite and even switched partners temporarily without great animosity. I saw several lone females during the laying period. Such birds became involved in courtship groups but the stage of their sexual cycle was unknown.

The sex ratio of 548 adults observed in the area near General Lavalle was 58 per cent males to 42 per cent females.

Daguerre (1922) stated that the species was found in pairs or groups of pairs throughout the year. I found no such relationship during the post-laying period of January to March when there were few birds in pairs — 5 per cent as compared with 60 per cent from early October through December.

After the laying period ended in late November and early December, lone females and small groups of *Heteronetta* became conspicuous. Because I saw few birds in December, I presume such groups underwent the flightless period together. The groups were common again in early January. The first birds with fully regrown primaries were collected on 31 December (a male) and 1 January (a female), but the majority of the birds probably molted somewhat later. The postmolting groups gradually increased in size so that in February and early March such gatherings numbered from 10 to 15 birds.

I saw no evidence of courtship during the fall — March to June in the southern hemisphere — and winter as occurred in the Argentine dabbling ducks. In fact, no pairs, or signs of courtship, were evident in late July; nor were they observed by Peter and Martha Miles who watched for such behavior in the nearly 150 birds that they observed on 28 August 1965 at Iturralde Marsh, Murphy, Santa Fe. Presumably, as in both the North American and Argentine Ruddy Ducks, Black-headed Ducks pair relatively late — in early September — despite the fact that laying may start in late September.

Table 1 shows data on the size of the gonads for specimens collected or observed from hunters' bags from October 1964 to July 1965. I collected few specimens during the breeding season to avoid the possibility of disturbing the birds at this time. As a result, there is little noticeable variation in the size of the gonads except between immatures and adults. Obviously, the specimens taken in July were not yet in breeding condition.

Although I have no proof that yearlings breed, I assume that they do because all the birds that I saw in spring were in breeding plumage and courting. However, I noted considerable variation in depth of the bursa of Fabricius. Most adults during the non-breeding period had either no bursa or one that measured up to 12 millimeters in depth (pocket only). This is a rather large variation. Moreover, two birds, a male and female collected at General Lavalle in July, had nearly adult plumage characteristics yet had bursas from 15–17.5 mm in depth. I assume that these birds were yearlings which still had a bursa even though the female had an open oviduct and the male had an adult-sized penis.

In the more northerly parts of its range the Black-headed Duck seems to breed in the fall, timing its cycle to coincide with the nesting of other water birds. Fall nesting of subtropical water birds seems to be regulated by the late summer flooding of marsh areas which are normally dry in spring and early summer. From one fall breeding area in central Paraguay, where the host species are unknown, two specimens were collected in March, 1937: a newly-hatched duckling (University of Michigan, Number 93120) and an adult male with enlarged gonads (Steinbacher, 1962). In addition, Dr. C. Olrog told me that he captured flightless young in May at the Banada de Figueroa, 40 miles northeast of La Banda in the province of Santiago del Estero. Dr. Olrog and I tried to find the host species there in late March but water conditions were not conducive to nesting. Several potential host species, seen in the area, were White-winged Coots *(Fulica leucoptera)*, Common Gallinules *(Gallinula chloropus)*, and Little Waterhens (*Porphyriops melanops*), birds which apparently nest in flooded cornfields as well as marshes.

TABLE 1

Gonad Sizes of Black-headed Ducks* Collected or Observed in Argentina from 31 December 1964 to 16 July 1965

Adult males			*Adult females*		
Date	*Testes size (mm)*		*Date*	*Ovary (mm)*	
	Left	*Right*		*Size*	*Largest*
31 December 1964	4.3 x 14.2	4.1 x 16.0	29 October 1964	–	25.0
26 January 1965	4.0 x 12.5	2.8 x 14.0	18 December 1964	–	4.2
28 February 1965	4.2 x 13.8	4.3 x 15.2	1 January 1965	10 x 22	2.7
1 March 1965	4.2 x 12.1	4.0 x 11.7	11 January 1965	10 x 20	2.8
18 March 1965†	2.4 x 9.0	1.9 x 9.6	5 February 1965	11 x 18	3.3
6 May 1965	4.7 x 11.9	3.2 x 11.1	1 March 1965	8 x 23	3.0
15 July 1965	2.6 x 9.6	2.6 x 10.5	18 March 1965†	10 x 23	2.5
16 July 1965	4.3 x 9.1	–	28 March 1965‡	12 x 20	3.0
16 July 1965	3.6 x 10.7	2.8 x 11.9	17 April 1965	12 x 22	2.6
16 July 1965	3.3 x 11.2	3.5 x 13.0	16 July 1965	9 x 25	2.8
16 July 1965	3.6 x 9.6	3.9 x 11.0	16 July 1965	11 x 22	2.8
			16 July 1965	9 x 23	2.5
Immature males			*Immature females*		
18 January 1965	1.9 x 9.0	2.0 x 7.5	6 January 1965	7 x 20	–1
16 April 1965	2.2 x 7.3	2.3 x 8.9	11 January 1965	8 x 12	–1
			28 February 1965	7 x 12	1.0

*All are non-breeding birds, except the female taken on 29 October 1964, and are from the Province of Buenos Aires except where noted.

†Province of Santiago del Estero.

‡Province of Tucumán.

Courtship

I saw courtship displays in the parasitic Black-headed Duck from the time I observed the first birds in mid-September until the ducks stopped laying in early December. Possibly courtship starts somewhat earlier in some areas. We did not notice it in July 1965 at General Lavalle or during August 1965 at Venado Tuerto, Sante Fe Province.

Displays. — The males responded to the presence of females or, to a lesser degree, to human intruders by a display which involved several movements and a call. Because the male inflates his throat as part of this display, the common name of the species is "pato sapo" or toad duck. Thus I have termed the entire display *Toad-call.* Wetmore (1926) described this display as: "neck down in and throat puffed out, at intervals raising the point of the bill and giving a low note *quah quah,* barely audible at 45 meters." The Toad-call actually involved several movements given almost synchronously. Some of its components also are given separately and may function as separate displays.

Males in groups and, in some cases, paired males were seen in a posture I termed the *toad-posture* which possibly functions as a threat as well as a

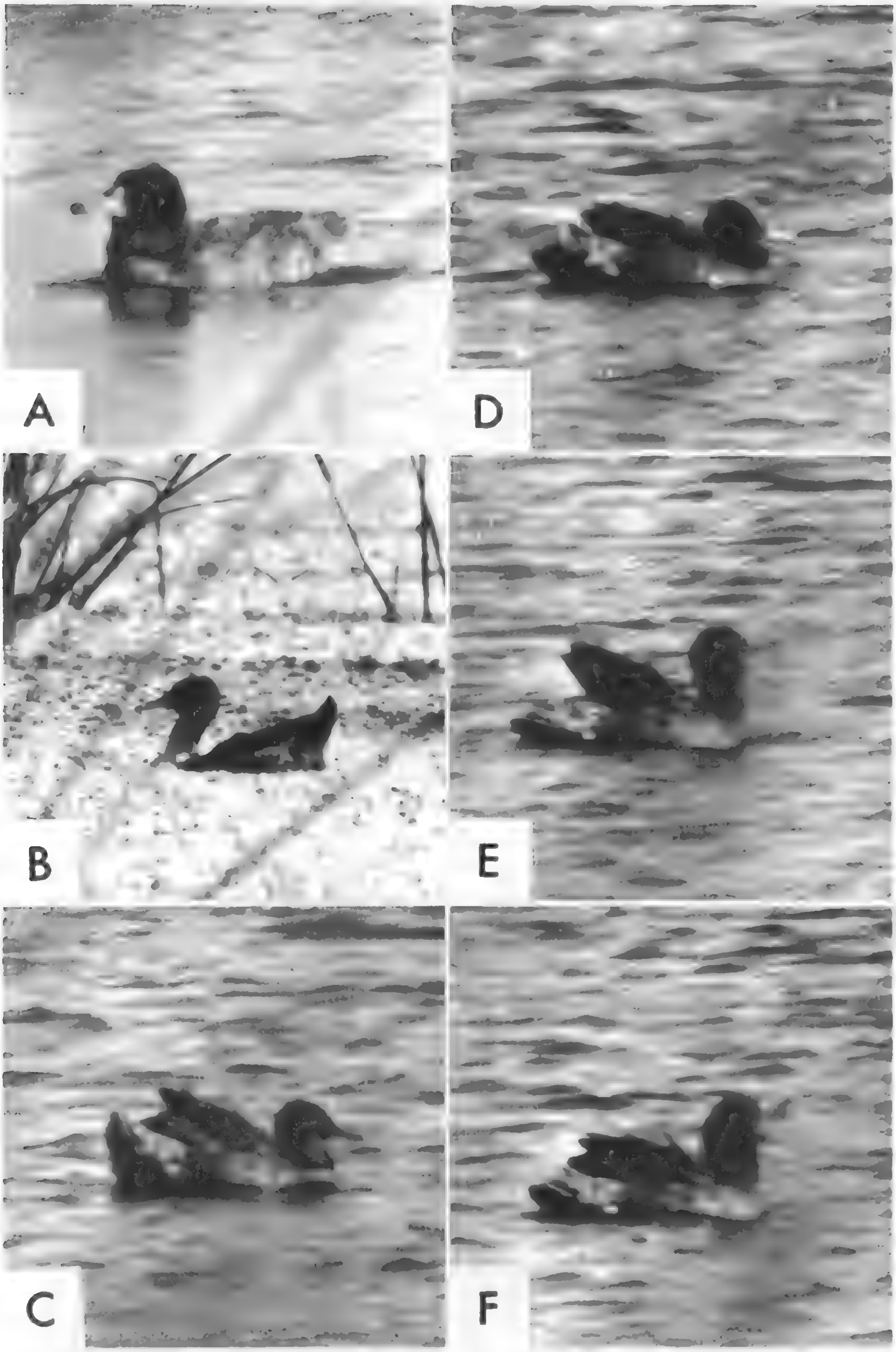
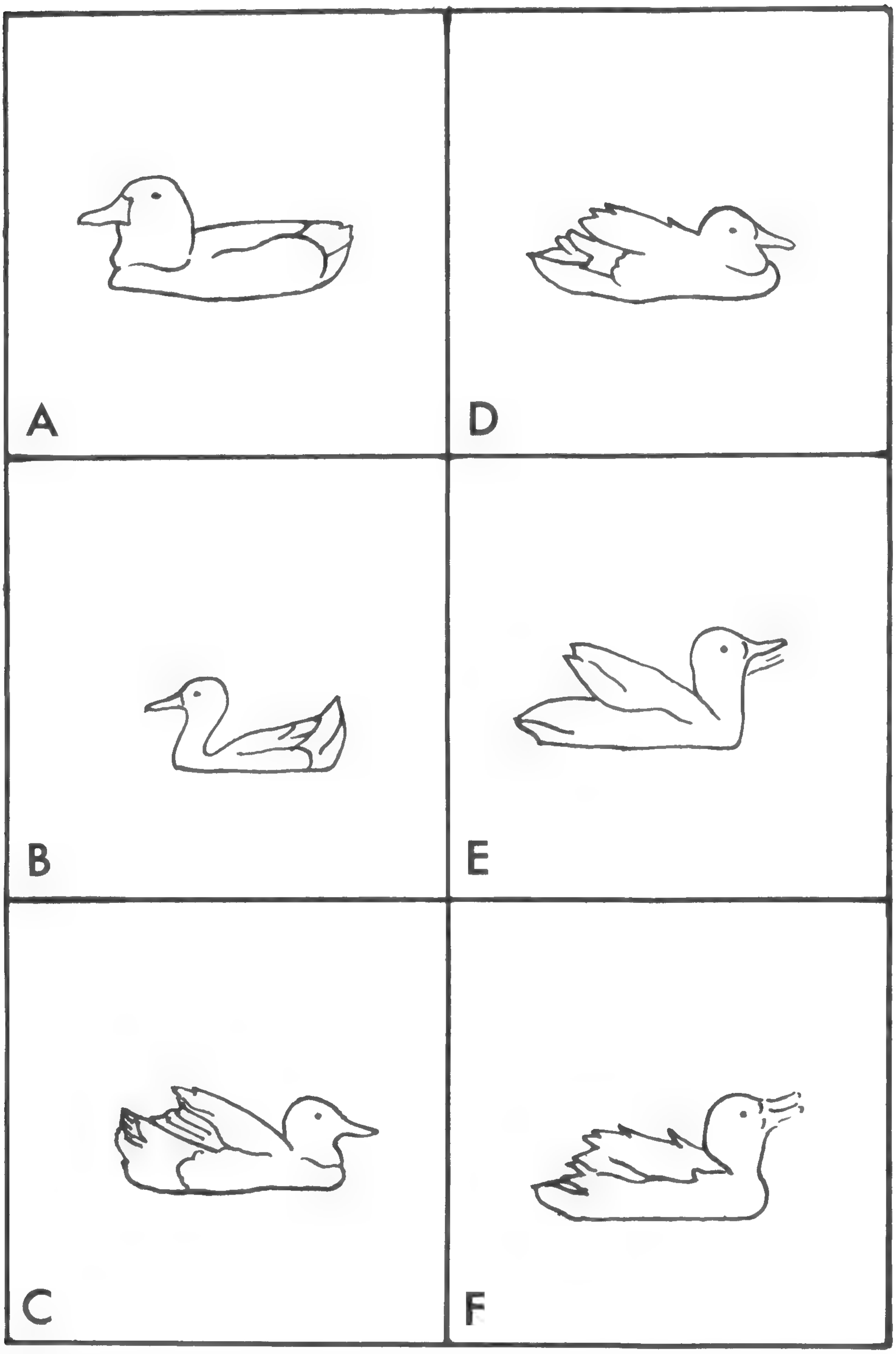


Figure 8. Courtship postures of the Black-headed Duck. *(A)* Toad-posture of a male characteristic of males courting in a group. It precedes the Toad-call and may also function as a threat display. Note the inflated neck. *(B)* The tail-up, tail-wag posture usually follows the toad-posture and Toad-call, which, in turn, is followed by a wing-up, tail-up (*C*). Now the male draws the bill close to the breast and partially lowers the wings and tail (*D*). The male then raises his head quickly with up-tilted bill, inflates the throat, raises the wings above the back (*E*). Finally (*F*), the male pumps his head rapidly. These are all moves of the Toad-call display.



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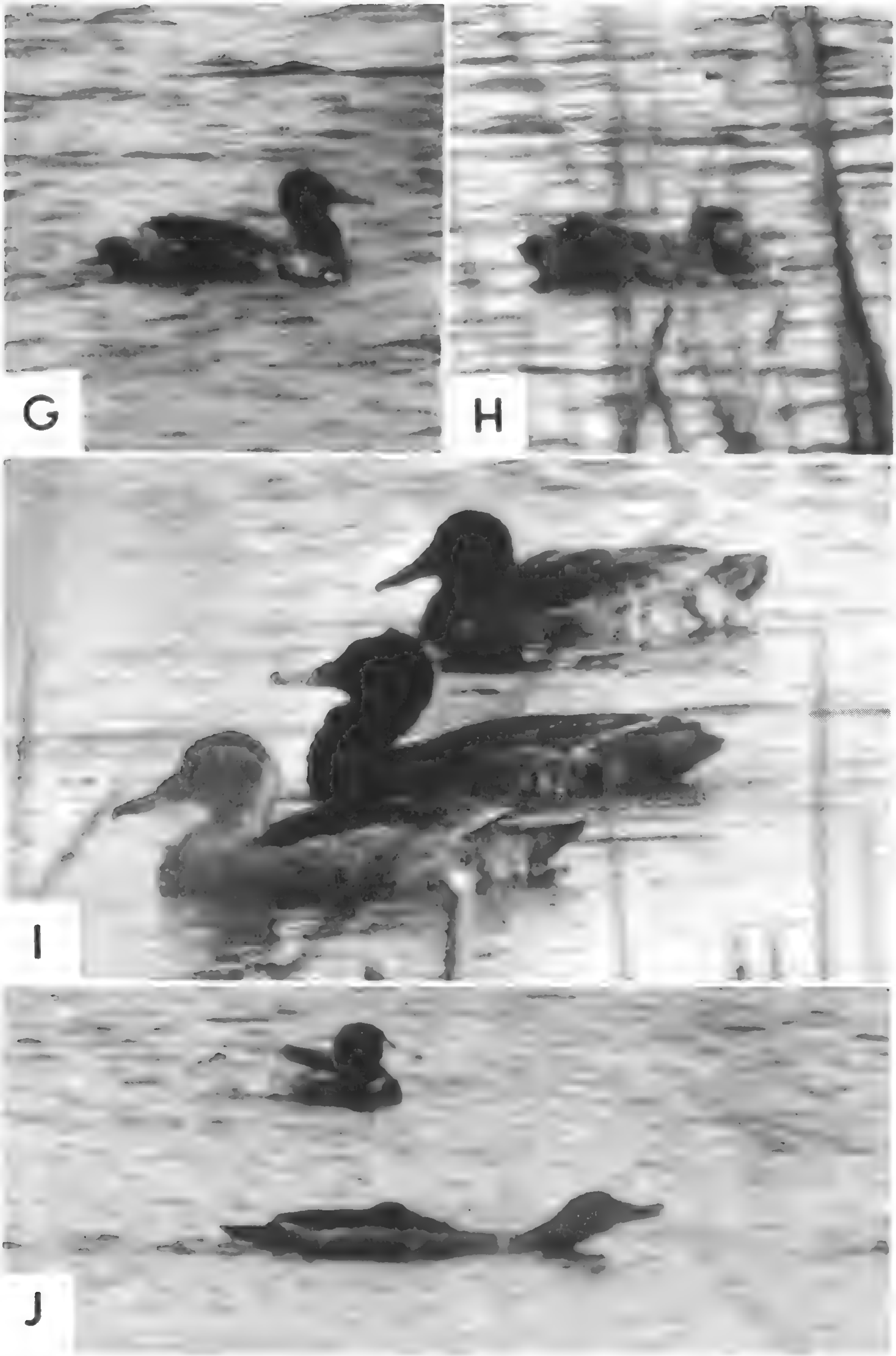

Figure 8. (*G*) The head-back high position sometimes follows the bill-up, head-pumping movement of the Toad-call display. (*H*) An extreme toad-posture. (*I*) The head-back high position is highly variable among individual males. Here, a male (middle) erects the feathers on the occiput and neck. (*J*) A female shows high-intensity aggression as she attacks a male with her neck outstretched and head lowered, mouth open, and a rushing movement.

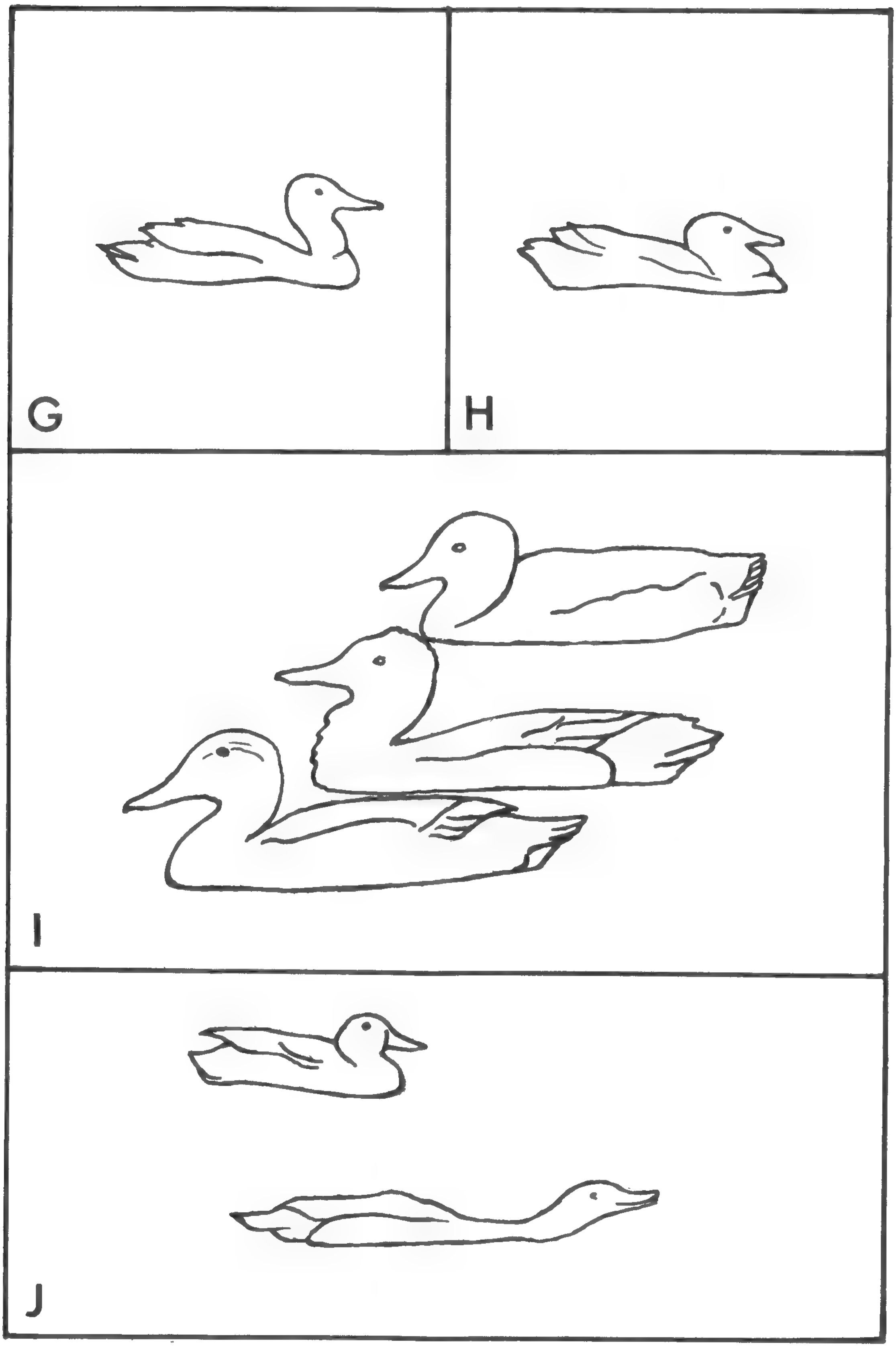

Figure 8. (*G*) The head-back high position sometimes follows the bill-up, head-pumping movement of the Toad-call display. (*H*) An extreme toad-posture. (*I*) The head-back high position is highly variable among individual males. Here, a male (middle) erects the feathers on the occiput and neck. (*J*) A female shows high-intensity aggression as she attacks a male with her neck outstretched and head lowered, mouth open, and a rushing movement.

preliminary to the Toad-call. Such males holding the head lower than normal inflate the throat and probably the cheeks and erect the feathers of the head, cheeks, and neck so that the swelling of the neck emphasizes the black-feathered area (Figure 8A). This posture, held for several seconds, is often followed by the Toad-call. Lone males also gave this call when disturbed but the movements never seemed as extreme as when the call is part of the courtship display.

The Toad-call involves the following moves: The male may or may not fully inflate the neck and cheeks. Most birds assume a toad-posture. This is followed by a *tail-up, tail-wag* (Figure 8B), then a *wing-up, tail-up* (wing-lift one) with the head held at near-normal level (Figure 8C). The secondaries and scapulars show prominently as the male lowers his head and tail. The bill comes very close to the breast as the wings and tail are partially lowered (Figure 8D). Then, the head is raised quickly with the bill 20 to 30 degrees above the horizontal; the throat seems to be inflated further as the wings again are lifted to a more extreme posture than during the first wing-lift (wing-up, bill-up — shown in Figure 8E). The tail is not raised during wing-lift two. The male now pumps his head very rapidly (Figure 8F), too rapidly to be stopped by a movie camera with a shutter speed of 1/160th of a second. Presumably, the pumping of the head produces the sound. The wings are lowered more slowly and completely and there is at least one tail-wag synchronized with these wing movements.

In some instances, the bill-up, head-pumping is followed by a head back-high position (Figure 8G) which varies considerably in degree among individuals. At times, the head feathers seem depressed on the crown but erected on the occiput, forming a crest (Figure 8I). The neck feathers also seem to be erected in most individuals. The head is pulled back in an angular posture strikingly different from the rounded appearance of the head during most displays.

One of the four males that I filmed performed an extreme toad-posture with the head very low and back (Figure 8H).

It seems probable that the male's plumage with its distinctive patterns and colors, the black head and neck so conspicuous when the head feathers are erected, the inflated cheeks, and the moving head may reinforce the Toad-call. The wing-bars are conspicuous when the wings are raised; the rufous under-tail coverts are obvious when the tail is elevated. The bill-up position may show the rose-colored spots and also a white area on the chin and throat that is present in almost all males.

A bill-dip and side to side head-shake may precede the Toad-call. Wing-flapping and swimming-shakes also occur regularly during courtship.

The duration of this display in four filmed sequences was about 1.3 seconds in one sequence and only 0.7 second in another.

The call is an unduck-like two-note grunt followed by a whistle which may be syllabized as *gr-rump-freet.* Wetmore (1926) apparently did not detect the whistle but Johnsgard (1961) noted it. Wetmore reported that the call was extremely soft and that 45 meters is the maximal distance one can hear it even on a quiet day. The sources and causes of the sounds are uncertain but Wetmore noted cheek air sacs and an esophageal swelling but no tracheal air sacs or osseus bullae. The male emits the grunt with the head in a lowered position and with the wings either up or starting down; and the whistle as the wings are lowered and the tail-wag starts. The regular rhythm of the calls — at 10- to 12-second intervals — suggests that the air sacs must be refilled after each call. I suspect that males can inflate the air sacs and call only during the breeding season. I had no specimen of post-breeding males with air sacs in the cheeks, and it was impossible to prepare the specimen by passing the skin over the head as Wetmore (1926) did with a male collected during the breeding season.

Johnsgard (1961) also noted a *Turn-the-back-of-the-head* display during courtship. I did not observe this behavior.

Threat Behavior. — Males exhibit threat and possibly sexual interest by a bill-down position which resembles the bird in a toad-posture. However, the head is held at the normal level, is less inflated, and the crown is directed forward by the low bill position. This posture needs further study as I saw it only five times; it may represent individual or motivational variation in the toad-posture such as in Figure 8H. I saw this posture in lone birds approaching groups of Black-headed Ducks in which there were females. Paired males also gave it in groups. One paired male approached me in this position, then turned and gave the Toad-call.

Black-headed Ducks expressed more clear-cut aggressive behavior when they moved toward the intruder with one of the following postures, each manifesting a higher intensity of aggression: (a) swimming-forward with head only slightly lower than the normal swimming posture, (b) a head-low threat with the neck outstretched, (c) mouth-open threat, and (d) attack, normally with the mouth open and a rushing movement (Figure 8J).

Display Sequences. — Lone males in search of females were conspicuous by their alert appearance, active swimming, occasional Toad-calls, and their tendency to fly, apparently seeking females. Such males often gave Toad-calls as they approached pairs, inducing similar behavior in the paired male. Usually the mated male attacked and successfully chased the intruder, but highly aggressive (presumably unpaired) males sometimes returned again and again. Such males wing-flapped and gave head-shakes, swimming-shakes, and head-flicks between encounters. Males avoiding attacks, but persistently maintaining a position by the females, took flight briefly to rise above the attacker. In a few cases, where several lone males as well as a paired male were fighting, the attacker also took flight so that a brief aerial attack occurred. Courtship battles always were brief, involving intense rushing, splashing, and flapping. I noted one possible shallow diving attack but, generally, diving played no part in courtship; nor did I see aerial chases or displays.

When several lone males pressed the same pair, the female often attacked calling males (Figure 8J). In a few cases, females and even males attacked their mates but seconds later allowed them to retain a position by their side, between them and the intruders. I did not observe inciting movements by females but, because courtship observations were mostly at long range, I could have missed such displays. Females nibble-preened the sides of their necks.

The largest courtship group observed contained five males and four females. In one case, a male drifted toward cover leading a female. When the female did not follow, the male returned to her side and drifted off again, whereupon the female followed him to an isolated pool. I witnessed no copulation during this study.

Apparently, females have almost no vocalizations. In several cases of alarm or threat, I suspected that the male responded to a low call by a female but I never actually heard a sound.

Hosts and Laying

During the laying season, pairs of *Heteronetta* frequented pools in areas used by many other nesting marsh birds. The lone males, seen occasionally

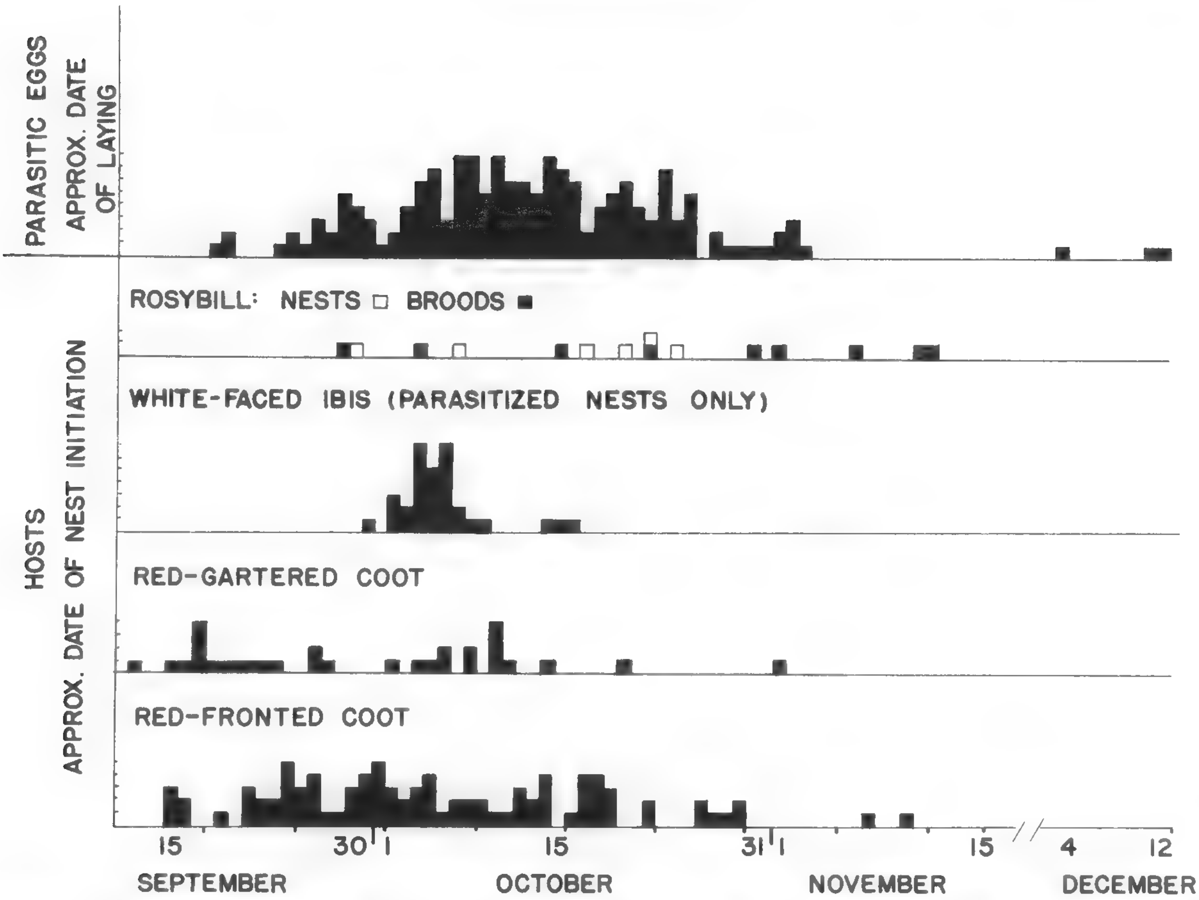

Figure 9. Chronology of nesting of hosts and of parasitic egg-laying by the Black-headed Duck, based on observations at two study areas near General Lavalle, Buenos Aires Province, Argentina. Height of bars indicates the number of eggs (parasite) and nests (host).

in the pools, may have been awaiting laying females. Although I also observed lone females at this time of year, the birds more commonly moved about in pairs through the semi-open tules as if in search of nests. When alarmed at this season, the female sometimes seemed to have difficulty rising from the water, possibly because of the extra weight of the reproductive tract during the laying period.

The prevalence of pairs in the late morning and afternoon and of lone males in the early morning suggests that laying normally occurs in early morning as it does in most ducks.

I never observed the parasitizing act. Host species were shy and deserted nests; female Black-headed Ducks avoided areas where we put up blinds. Nest parasitism in this species probably will be observed only as a result of several years of patient efforts, or of a chance observation such as that of McKinney (1954) on a Redhead *(Aythya americana)* parasitizing a Canvasback *(A. valisineria)*. Indirect evidence — the fact that we found no eggs cracked or knocked into the water — indicates that *Heteronetta* lay their eggs in the nest when the host is absent. The two parasitic eggs, found outside a nest, had been incubated and probably were accidentally pushed out by the host. There was no duck down in the nests of the hosts.

The laying chronology of the Black-headed Duck was well synchronized to the nesting chronology of the Red-fronted and Red-gartered Coots *(Fulica rufifrons* and *F. armillata)*, encompassing most of the nesting period of the former and all of the latter (Figure 9). It was also well synchronized to the early nests of Rosybills. Most laying occurred from 15 September to 13 November, but undoubtedly some females laid throughout November and early December, because three fresh *Heteronetta* eggs were found in a gull nest on 12 December. Also, the presence of a few very young juveniles in late February suggests that hatching occurred in late December or early January.

Information on dates of nest initiation and laying for *Heteronetta* eggs is derived from nests both at El Palenque and the Vanini Estancia (Figure 9). Laying dates for parasitic eggs probably are less accurate because the backdating depended on estimated incubation period of the *Heteronetta* egg. In cases where eggs contained dead embryos, this estimate is minimal. Possibly the minimal incubation estimates exaggerate the peaks of parasitism which are, in general, six to ten days later than the peaks of nest initiation by the hosts.

The list of host species seems to include any marsh bird that nests in fairly dense marsh emergents regardless of the color or size of the hosts' eggs or the type of nest. Table 2 lists the host species recorded in the literature. Most unusual is the nest parasitism of predaceous birds like the Chimango and huge marsh-nesting birds like the Crested Screamer *(Chauna torquata).* We tried to locate nests of various marsh birds and determine the relative incidence of parasitism of various species and the success of eggs in nests of different hosts. In this way, we hoped to determine the most significant host species. Unfortunately, we found relatively few nests of Rosybills and Fulvous Whistling Ducks *(Dendrocygna bicolor).*

Figure 10. The parasitized nest of the White-faced Ibis. The bowl of the nest is nearly 20 inches above the water. The parasitizing Black-headed Duck probably used its wings as well as its feet in reaching the nest.

Parasitism proved highest on the species nesting in the dense marsh areas (see Table 3): the Red-fronted Coot (55 per cent of 133 nests) and the Rosybill (83 per cent of six nests). Red-gartered Coots, which use the open marsh and semi-open emergent, were parasitized less often (16 per cent of 51 nests). In the huge colony (15,000 to 18,000 nests) of White-faced Ibis (Figure 10), the percentage of parasitism was low (1.5 per cent of 2,071 nests). However, since this is the only colony of the species in that part of Cape San Antonio, its birds were probably very important hosts for Black-headed Ducks.

Although data are not available to appraise the abundance of marsh-dwelling species in the Cape San Antonio area, there can be little doubt that the coots greatly outnumber the marsh-nesting ducks and probably most other

TABLE 2

Host Species of the Black-headed Duck Reported in the Literature

Host Species	*Location*	*Observer or reference*
White-faced Ibis (*Plegadis falcinellus*)	Rosas, Buenos Aires, Argentina	Daguerre, 1920
Black-crowned Night Heron (*Nycticorax nycticorax*)	Rosas, B.A., Argentina	Daguerre, 1934
Black-crowned Night Heron	Chile	Goodall, Johnson and Philippi, 1951
Roseate Spoonbill	General Lavalle, B.A., Argentina	Pereyra, 1937
Crested Screamer	Rosas, B.A., Argentina	Daguerre, 1920
Coscoroba Swan (*Coscoroba coscoroba*)	Rosas, B.A., Argentina	Daguerre, 1920
Coscoroba Swan	General Lavalle, B.A., Argentina	Gibson, 1920*
Rosybill	Rosas, B.A., Argentina	Daguerre, 1923
Limpkin (*Aramus guarauna*)	Rosas, B.A., Argentina	Dabbene, 1921
Spotted Rail (*Pardirallus maculatus*)	Rosas, B.A., Argentina	Daguerre, 1920
Maguari Stork (*Euxenura maguari*)	General Lavalle, B.A., Argentina	Gibson, 1920*
Red-gartered Coot	Venado Tuerto, Santa Fe, Argentina	Wilson, 1924
Red-gartered Coot	Chile	Goodall, Johnson, and Philippi, 1951
"Coots" (probably Red-fronted)	Rosas, B.A., Argentina	Daguerre, 1920
Chimango	Venado Tuerto, S.F., Argentina	Wilson, 1923b
Brown-hooded Gull	Rosas, B.A., Argentina	Daguerre, 1920
Brown-hooded Gull	Venado Tuerto, S.F., Argentina	Wilson, 1923a

*Identified as Rosybill eggs

TABLE 3

Incidence of Parasitism, Nest Success, and Success of Black-headed Duck Eggs in Two Marsh Areas near General Lavalle, Argentina, September–December 1964

Potential host species	*Total number nests observed*	*Incidence of parasitism in total nests observed*	*Total nests observed to termination*	*Incidence of parasitism in terminated nests*	*Nest success of all nests terminated*	*Nest success of parasitized nests*	*Nest success of parasites in terminated nests*	*Nest success of unparasitized host nests*	*Egg success of parasites (total number hatched of total laid)*
				Estancia El Palenque					
Red-fronted Coot	114	62 (54%)	46	31 (67%)	38 (83%)	25 (81%)	10 (22%)	13 (87%)	10 (18%)
Red-gartered Coot	51	8 (16%)	49	8 (16%)	28 (57%)		0 (0%)		0 (0%)
Crested Screamer	15	0	6	0	6 (100%)		—		—
Rosybill	6	5 (83%)	6	5 (83%)	1 (13%)		1 (17%)		1 (9%)
Fulvous Whistling Duck	2	0	2	0	0 (0%)		—		—
				Vanini Estancia					
Red-fronted Coot	19	11 (58%)	12	9 (75%)	10 (83%)		5 (41%)		6 (64%)
Brown-hooded Gull	7	1 (14%)							
White-faced Ibis	2071	32 (1.5%)	—	—	—				—
Roseate Spoonbill	22	0							
Common Egret (*Casmerodius albus*)	15	0							
Snowy Egret (*Leucophoyx thula*)	4	0							
Black-crowned Night Heron	8	0							

birds. Coot nests are common, easily found, well cared for, and have a high nest success (83 per cent for 46 Red-fronted Coot nests and 57 per cent for 49 Red-gartered Coots as compared with 13 per cent for six Rosybill nests; see Table 3). I found coots to be the most important host for *Heteronetta.* The abundance of different hosts probably assures the success of *Heteronetta* eggs. Most of the host species are solitary nesters but breed in dense populations because the habitat suitable for nesting is restricted. At least two major hosts are colonial — the White-faced Ibis and Brown-headed Gull. In addition to employing a wide spectrum of hosts, Black-headed Duck females probably vary in time of laying. Most females seem to deposit eggs in October when most of the hosts are nesting. Whether imprinting of young influences subsequent host selection is a challenging, but presently unanswerable, question.

Although *Heteronetta* eggs have been reported in heron nests, we found none in heron, egret, or Roseate Spoonbill (*Ajaia ajaja*) nests. Parasitized nests were mostly low. However, we found several 15 to 20 inches above water, and, unless there had been a drastic decline in the water level, the parasitizing females must have used their wings as well as their feet to enter them (Figure 10).

As noted for Redhead parasitism (Weller, 1959), the Black-headed Ducks parasitized nests in certain areas more intensively than others. These areas usually were associated with large *Azolla-* or *Lemna*-covered pools where, presumably, numerous parasitic females loafed and fed.

Eggs and Egg Success

Egg Shape, Size, and Texture. — The eggs of the Black-headed Duck closely resemble those of the Rosybills. Daguerre (1922, 1923) reported that *Heteronetta* eggs differed in shape, had a finely pitted surface (which can be felt when rubbed, as well as seen), and were whiter in color. He also stated that *Heteronetta* eggs usually were wider for their length than were those of Rosybills. We measured too few Rosybill eggs to allow a sound analysis but the differences, shown in Table 4, were not significant at the 0.05 level. Moreover, the measurements are too similar and variable to provide a practical field technique for distinguishing individual eggs of the two species. However, shape differed considerably in most cases. Eggs of the Rosybill were "longelliptical" or "subelliptical" (terms from Palmer, 1962) while those of Black-headed Ducks were "short oval." In addition, the shell of the *Heteronetta* egg, when candled, has a more granular density than those of Rosybills and the Fulvous Whistling Ducks. In this character the *Heteronetta* eggs resemble the eggs of Ruddy Ducks yet are not as rough, while the eggs of dabblers and inland divers have more translucent and less granular shells. A few *Heteronetta* eggs were found which resembled those of Rosybills in shape but not in shell texture. The shells of four eggs from which Black-headed ducklings hatched varied considerably in shape and color. For this reason, I suspect that many eggs, still attributed to Rosybills, are, in fact, those of *Heteronetta.* The only case I noted of interspecific parasitism by a Rosybill was an active ibis nest containing one Rosybill egg and one *Heteronetta* egg.

Number of Eggs per Nest and Time of Laying.—We found one parasitic egg per nest in 55 per cent of the successful nests of Red-fronted Coots at El Palenque, and in 82 per cent of 11 nests at Vanini Estancia. Thirty-two per cent of the nests at El Palenque had two eggs (Table 5). Up to five eggs were found in one Red-fronted Coot nest. The maximum—eight eggs—was found

TABLE 4

Measurements in Millimeters of the Length and Width of Six Rosybill and 23 Black-headed Duck Eggs

Species	*Measure-ments*	*Sample size*	*Mean*	*Standard deviation*	*Range*
Black-headed Duck	Length	23	58.05	1.85	55.1–62.6
Rosybill	Length	6	58.35	2.27	55.8–62.0
Black-headed Duck	Width	23	43.23	1.66	39.5–45.9
Rosybill	Width	6	42.37	1.15	40.5–43.3

at various levels in another Red-fronted Coot nest where later one *Heteronetta* egg and five coot eggs hatched. In some cases, coots buried the *Heteronetta* eggs and incubated their own eggs on the layer of "foreign" eggs. Rodriquez (1918) reported seven *Heteronetta* eggs in one nest.

I do not know whether some mechanism limits the number of eggs deposited in a nest or whether laying is random, as appears to be the case in cowbirds (Mayfield, 1965), as data are insufficient for a statistical analysis of randomness of distribution. Apparently no visual stimulus limits laying if one egg already is present. Probably no elaborate mechanism is involved. Hens frequent certain areas and tend to lay one egg per nest. Actually, since the laying period of the host is about the only time the Black-headed Duck can visit a nest inconspicuously, it seldom has an opportunity to lay in a nest more than once — unless, of course, its laying period coincides exactly with that of the host.

TABLE 5

Frequency Distribution of Black-headed Duck Eggs in Nests of Marsh Birds at Estancias El Palenque

Number of Black-headed Duck eggs in nest

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Red-fronted Coot (El Palenque)	17* (55%)	10 (32%)	2		1			1
Red-fronted Coot (Vanini)	9 (82%)	1	1					
White-winged Coot (El Palenque)	6	2						
White-faced Ibis (Vanini)	28	4						
Totals	60 (73%)	17 (21%)	3 (4%)	0	1	0	0	1

*Number of nests observed followed by per cent of total number of parasite eggs for the host species.

Figure 11 (*above*). Coot nests are heavily parasitized. This Red-fronted Coot nest has a single Black-headed Duck egg in the bowl. One of three buried eggs of the Black-headed Duck is visible.

Figure 12 (*below*). A "dump" nest containing 22 Rosybill eggs and four Black-headed Duck eggs (white).

There was no evidence that parasitizing birds destroyed or removed eggs of the host or battled with host females for a laying position on the nest. I found no cracked eggs or eggs in the water as I did in nests parasitized by Redheads (Weller, 1959). Obviously, the parasite has evolved a more efficient and successful mechanism for timing its egg-laying during the period when the host is least likely to be present — the laying period. This also assures a full incubation period. The fact that the females lay in nests of large and predatory birds supports this hypothesis. Nocturnal laying is a possibility.

Egg Success. — Because of the problems of maintaining a small nest with a large number of eggs during times of fluctuating water levels, the chances of egg and nest success probably are lower in nests containing several parasitic eggs. The relative density of hosts and parasites may affect the success. With numerous hosts in relation to parasitic females, success may be high because the eggs are well dispersed and well synchronized. When hosts are less numerous the number of eggs per nest may increase and lower the success of the parasite. Population size also must be directly related to habitat quality in marshes which regulates the abundance of host species. Obviously, the parasite can never exceed its host in abundance without creating a problem of availability of laying sites.

In the El Palenque marshes, 23 of the 62 parasitized Red-fronted Coot nests had at least one *Heteronetta* egg that was half buried; some were completely out of view. At the Vanini Marsh only one of 11 parasitized nests had a partly buried *Heteronetta* egg. The tendency of coots to bury parasitic eggs suggests that, although they recognize such eggs, they do not attempt to eliminate them from the nest (Figure 11). The burial of eggs may be unintentional as Pereya (1938) suggested, or it may be the result of fluctuating water levels — of the host species attempting to raise its own eggs above the rising water and neglecting the foreign ones.

It is doubtful whether Rosybills or other ducks distinguish the similar *Heteronetta* eggs from their own, and thus losses of eggs due to burial are unlikely. However, too few nests of these species were observed to determine this.

The system of Black-headed Ducks laying in active rather than deserted nests, possibly by chance alone, results in high hatching success. Whether they can or do determine the status of such nests is uncertain. It seems unlikely that warmth of the eggs could be the stimulus since the first three or four eggs of a coot and the entire clutch of a duck are deposited before intensive incubation starts. Moreover, Black-headed Ducks do lay in Rosybill "dump" nests as shown by a Rosybill nest of 26 eggs, of which four were *Heteronetta* eggs (Figure 12). Possibly, the Black-headed Ducks follow the host females when they are nest building or laying, as parasitizing Redheads seem to (Weller, 1959), and thereby visit only active nests. Black-headed Ducks deposited no eggs in eight artificial nests containing chicken eggs.

Black-headed Ducks usually parasitized nests in which the host had already laid three to five eggs; one parasitized nest of a coot had only two cold eggs. Many eggs were laid after the host began incubation and some even after intensive incubation was well under way. In a few cases fresh Black-headed Duck eggs were found in coot and ibis nests containing eggs which were near hatching. At Estancia El Palenque, the synchrony of 76 *Heteronetta* eggs in 43 Red-fronted Coot nests could be judged from information gathered from candling eggs in nests. Of these, 40 (53 per cent) obviously were deposited during the hosts' laying period (a considerably better percentage than in the parasitic Redheads according to Weller, 1959); 25 (35 per cent) appeared to be about two to five days late and may have hatched when the young coots were being brooded on the nest; and 14 per cent were laid so late there was no chance of survival. In spite of this fair synchrony, hatching success at Estancia El Palenque was low, being only 18 per cent for the most important host species, the Red-fronted Coot. I believe that this low hatching success was due to the high rate of burial of eggs.

At Vanini Estancia the hatching success was higher. But possibly the figures are biased because we observed only late nests of coots there. At El Palenque we found that coot nests started late in the season were more successful than the early nests. Of 14 eggs in 19 Red-fronted Coot nests at Vanini Estancia nine (64 per cent) were well synchronized and hatched; five (36 per cent) were not well synchronized and did not hatch. In ibis nests, 12 of 36 eggs (33 per cent) were within a few days of perfect synchrony and probably would have hatched. Thus, the species may have a high egg success under ideal conditions.

Hatching and Incubation Period

The incubation period of *Heteronetta* eggs was determined by reference to incubation periods of the host. In three cases, *Heteronetta* ducklings hatched in nests prior to the hatching of young coots. In one case, a duckling hatched a full day before the first coot. Because coots begin intensive incubation in the middle of the clutch (found in this study to be the fourth egg in Red-fronted and Red-gartered Coots), the incubation period differs for early and late-laid eggs. The first egg of both Red-gartered (one nest) and Red-fronted Coots (two nests) required 28 to 29 days from laying to hatching, while the last egg required only 24.5 to 25 days. Thus, an egg of a Black-headed Duck may be deposited after the first two coot eggs (the earliest record in this study) and be incubated in the nest for 27 days. Or, it may be laid with the host's last egg and have only 25 days incubation. Apparently, *Heteronetta* eggs may hatch in as little as 24 or 25 days. Observations of a Rosybill nest in which incubation of all eggs starts simultaneously and appears to last about 28 days supports this suggestion; the single *Heteronetta* egg in the Rosybill nest hatched two and one-half to three days before the Rosybill eggs. Thus, it appears that the eggs of Black-headed Ducks have a relatively short incubation period.

In one case, a *Heteronetta* hatched in a coot nest nearly four days after the last of the coot's brood. I found this duckling dead in the water. The egg probably hatched because of the warmth created by the coot's brooding of the young on the nest. Both Red-fronted and Red-gartered Coots often reline their nest for use as a brood ramp. Thus, the total warming period for unhatched eggs may be 30 to 33 days. It also is possible that *Heteronetta* eggs may hatch after the hatching of the host's eggs in ibis nests where the young are brooded for several weeks (Figure 13).

Responses of Hosts to Parasitism

Judging from observations at five Red-fronted Coot nests, one Rosybill nest and one ibis nest, all of which contained a *Heteronetta* duckling, foster parents brood *Heteronetta* ducklings as if they were their own. In two cases I saw Red-fronted Coots eating *Heteronetta* eggshells. On the other hand, I found shell fragments commonly in nests where Black-headed ducklings had hatched. Presumably, Rosybills eat or carry away shells as do other members of the family (Weller, 1959), and ibises carry off *Heteronetta* shells as they do shells of their own eggs. At least I found no shells in ibis nests where ducklings had hatched. Eighty-seven per cent of the unparasitized nests and 81 per cent of the parasitized nests of the Red-fronted Coot were successful. We had too few nests of the other host species for comparative figures. There was no egg breakage and only twice were eggs of the Black-headed Duck found outside nests — one of a Red-fronted Coot and one of a Red-gartered Coot. Because I saw egg ejection so rarely and because we found at least one coot egg outside a nest, I do not believe that the *Heteronetta* eggs were pushed from the nests.

Based on egg and nest success, there was no apparent increase in predation due to the conspicuous, white *Heteronetta* eggs. Presumably, hosts incubated steadily, never leaving the eggs exposed to predators.

To observe the response of a host to a parasitic egg, I added a *Heteronetta* egg to an unparasitized nest containing four Red-fronted Coot eggs. As I watched from a blind both adults visited the nest; one looked into the nest and got on without hesitating; the second bird looked but did not get on. The *Heteronetta* egg as well as the coot eggs eventually hatched.

Behavior of Ducklings

I collected data on the behavior of ducklings by observing young in nests from blinds, by recording behavior of ducklings found in or near nests, and by attempting to rear five captive ducklings.

Wild Ducklings. — I saw ducklings only in or near the nests of hosts and never in the broods of host species or alone in the marsh. We never observed female Black-headed Ducks with young or even behaving as though they had broods. After leaving the nest, the young apparently lead solitary and secretive lives in the emergent vegetation until able to fly. I saw only two flightless juveniles during the summer. They fed very close to the vegetation and were extremely wary.

Ducklings, hatched in coot nests and, presumably, in nests of other hosts, are brooded and cared for by the host as if they were their own and evidently remain in the nest one to two days (Figure 14). In one Red-fronted Coot nest, the duckling hatched during the night and left when between one-and-one-half to two days old. In a second case, the duckling hatched in early morning and was gone the next morning. There is no evidence that young return to be brooded at night but we need more observations. How long the host parent broods the young parasite may depend upon the hour of hatching and upon the synchronization of the parasite's hatching with that of the host. Because the incubation period of the Black-headed Duck is shorter than that of the ducks they parasitize, and since hatching is more closely synchronized in clutches of ducks' eggs than in coots', *Heteronetta* ducklings will hatch in advance of the hosts' young if laying occurs prior to the start of incubation. If it hatches in advance of the host's young, the *Heteronetta* duckling presumably leaves the nest. In nests of ibises and other marsh birds, its only hope of survival would be to leave the nest and feed independently.

Young *Heteronetta,* like most ducklings, show no fear of humans during their first three to five hours of life but they seem to dislike being gripped in the hand. In three cases, I observed that wild ducklings, disturbed in the nest, "froze" with neck outstretched and head low. In one case, the duckling left the nest after I moved away. When I returned it to the nest, it again froze — at least temporarily. Ducklings moved rapidly through the floating duckweed using the same "scooting" actions as the adults and swam toward emergent vegetation where they froze. Ducklings were handled in all cases and two, apparently older birds, squirmed and pecked and swam off when I freed them. However, in no case did the ducklings dive.

Figure 13 (*above*). A Black-headed duckling in a nest with a young White-faced Ibis. Note the distinctive, dark, vertical bar above the eye running through the superciliary line.

Figure 14 (*below*). A Black-headed duckling shares a nest with its host, the Red-fronted Coot. Two young coots have recently hatched. The duckling will remain in the nest for one or two days.

Captive Ducklings. — Because of the secretiveness of the young ducklings out of the nest and because it was impossible to observe them being brooded, we made observations on five captive ducklings, four hatched by a domestic chicken and one taken from an ibis nest. Three, including the wild bird, were kept in captivity to allow closer observation and to compare their behavior with that of other species. In general these birds were intolerant of confinement after the age of one day and were difficult to keep in cages. All died by the time they were four to seven days old, despite the fact that they ate well.

Imprinting. — The psychological attachment of a duckling to a parent normally assures a long-lasting bond which provides warmth and protection for the young during the preflight stage. But does imprinting occur in the parasitic species? Very quickly it was apparent that the Black-headed ducklings show no clear-cut following reaction and that they are not innately equipped to follow a parent or host.

Of the three Black-headed ducklings "imprinted" to humans, one taken from the hen at the age of two hours showed the best recognition of man and the least fear. Only this duckling tended to move toward both the human voice and figure after an intensive effort to teach it to follow. It gave contentment calls when several feet from human shoes and voice and moved toward them, but it would not follow any more distant or rapidly moving object. Neither of the other two, trained less intensively, showed even this slight inclination to follow.

Two ducklings reared by a domestic hen led generally independent lives. They left the nest, fed alone, and returned to it regardless of the whereabouts of the hen. In most cases they did not attempt to follow the hen when she left to feed or sunbathe. However, one duckling, failing in its repeated efforts to leave the enclosure, gave up normal feeding and nibbled on the hen's feathers instead. Becoming very weak at about three days of age it did follow the domestic hen several feet and once even left the box to seek her — presumably for warmth. It died a short time later.

Despite some attachment to the domestic hen, or to the human parent, at least four of the five ducklings (the fifth bird escaped before this point could be clearly observed) made efforts to leave the parent. Two ducklings, which gave contentment calls on seeing a human, ran away when placed outside their boxes. A one-and-one-half day-old duckling that did not run unfortunately escaped from its cage before further tests could be made. The captive ducklings liked the natural foods they were given so this desire for independence was not a result of foods.

My observations agree generally with those of several members of the Runnacles family of General Lavalle who have attempted to rear *Heteronetta* ducklings with other species and found that they do not remain with the broods in which they are hatched.

Data from the five ducklings demonstrate some variability but all showed the same tendency to leave the foster parent rather than to remain with it as has been reported for semi-parasitic ducks (Weller, 1959). Thus, the Black-headed Duck is unique in being the only truly parasitic species which is precocial.

The same domestic hen reared two Rosybill ducklings. Their behavior with this hen was typical of the young of most northern hemisphere anatids. There was no need to keep them in a cage. Although they also made some short excursions away from the hen, they kept close contact with her at all times, never displayed a tendency to escape if she was near, and did not fear humans nearly so much as did Black-headed ducklings.

It appears from these observations that the inclination to leave the host is strong soon after the parasitic duckling is dry and mobile. If for some reason it is not able to leave or is confined in the same general area as the host, the duckling apparently uses the host for warmth as did one captive duckling. Peña (1962) had a similar experience. He reared ducklings of this species by use of a foster parent, a domestic Muscovy Duck (*Cairina moschata*). The ducklings apparently returned to the female to be brooded at night. Generally, however, they reared themselves independently in a small pond where natural foods were available. In this situation there were several young and the behavior of a group may have influenced their response to the female since, normally, young are hatched singly.

Alarm Reactions of Ducklings. — *Heteronetta* ducklings soon developed reactions to foreign objects. When cornered, young Black-headed Ducks threatened with the neck-stretch and mouth-open hissing display, seen in both juvenile and adult Ruddy Ducks. Ducklings, imprinted to the chicken, feared humans and hesitated to show themselves when people were present. This was not true of young Rosybill ducklings imprinted to humans; these ducklings showed escape reactions toward humans only when the humans surprised them or moved quickly. All the hand-reared *Heteronetta* ducklings gave alarm calls when held in the hand. In general, however, the ducklings seemed to render fewer alarm calls as they grew older. Several ducklings of one-and-one-half days of age, when left in new cages, gave a few distress notes that lasted not more than a few seconds. The two ducklings reared by humans showed no distress reactions to low temperature and, when only three days old, slept, preened, and fed alone in outdoor temperatures varying from 50°F at night to 80°F in the daytime.

Feeding. — When ducklings were two-and-a-half hours old, I observed a nibbling action of the bill which eventually seemed to serve two purposes: preening and feeding. Nice (1962) observed this type of action in other duck species while the ducklings were still in the shell. Ducklings occasionally nibbled at irregular surfaces as ducklings of other species do, but they did not peck at spots. The tip of the bill seemed especially sensitive and nibbling often started as the head of a sleeping bird moved downward and the bill touched some surface. When water was placed under such a duckling, even the youngest, only seven hours old, responded to the contact immediately by dabbling. The head was held with the bill at approximately a 45-degree angle or less to the surface of very shallow water. The efficiency of this feeding action increased rapidly. The first captive bird fed when 13 hours of age and its nibbling created clear-cut swirls of water on each side of the bill (Figure 15). Water apparently enters the tip of the bill and is forced out each side, forming two circular currents which bring food organisms to the tip. The effectiveness of the straining undoubtedly increases greatly as the lamellae develop. Veselovsky (*in* Nice, 1962) reported that the lamellae do not develop in either divers or dabblers until ducklings are six to seven days old. Rosybills of six days had only the slightest trace of lamellae, but Black-headed Ducks, less than three days old, showed prominent and apparently functional lamellae.

Because the major food source of wild ducklings probably is in the duckweed mat found almost universally in these marshes, we presented the first captive bird with water containing some small duckweed. At its first contact with water it nibbled, then drank, and soon swirled and strained the water. During the first hour of feeding, the ducklings made the dabbling movement

Figure 15. A captive Black-headed duckling two days of age strains crustaceans from duckweed. Prominent and apparently functional lamellae appear in ducklings of this species when they are less than three days old.

with their bills whether water was present or not, suggesting that they learn where to feed by the intake of food. When it soon became apparent that they were eating very little duckweed, we added some chopped hard-boiled egg to the water. They consumed this eagerly, favoring the small bits of albumen especially, perhaps because of their more solid consistency. Then we separated macroscopic crustaceans from the duckweed mat and added them to the water-duckweed-egg solution. The ducklings took in the crustaceans easily with the effective swirling-straining action of the bills, and, by "searching" with the bill, covered the water area effectively and extracted all the amphipods of less than five or six millimeters in size.

We fed other ducklings by placing duckweed in water and they, too, soon learned to obtain food by trial nibbling and ate eagerly, effectively eliminating nearly all of the crustaceans from a shallow dish.

At first ducklings fed at the edge of the water but within a few minutes they entered the water and fed with a sweeping action of the bill from side to side. Several perfected this feeding action within 10 to 15 minutes after their first feeding. Within several hours they fed again and then quickly turned around to feed in the area immediately behind them. This was effective because the crustaceans tended to collect behind them away from the water currents. When two or more days old, several ducklings kicked in the water after feeding and then usually turned to feed behind them. This kicking action resembled the water-treading of adults in shallow water.

The first feeding periods lasted from five to ten minutes and were interspersed with preening and rest periods lasting 45 to 60 minutes. Later, when two or more days old, they fed almost continuously for 15 to 20 minutes with shorter rest periods in between. The ducklings often uttered delicate contentment notes as they fed, at least during their first two days of life, and, after each feeding, they preened and oiled thoroughly, especially in the ventral region.

Comfort Movements. — When less than three hours old (two hours and 45 minutes in one case) the ducklings began to nibble-preen the sides, breast, and lower back in the region of the oil gland. Such preening undoubtedly occurred earlier as noted in other species by Nice (1962), but I made no observations on these birds until they were virtually dry at two-and-one-third to four hours of age. Within the period of two-and-one-half to three hours of age I saw all the comfort movements. The ducklings were adept at keeping their plumage dry and spent time in the water only when feeding. None survived over seven days and I recorded no bathing activities during this period.

Summary of Behavior in Relation to Breeding Biology of Species. — Ducklings of this species seem highly precocial. They are innately and anatomically equipped to feed and care for their plumage at an early age. They give a minimum of alarm calls and even tolerate low temperatures without apparent distress. They display a high degree of independence and, in the wild, leave the parent host when one or two days old. In captivity, they do not, in most cases, remain with the foster parent. Since they are not seen in broods of other ducklings, all evidence suggests that they rear themselves. We do not know whether the ducklings leave the nest during their first day to feed (as other ducklings do) and then return. Such behavior would be possible in nests of coots and Rosybills but impossible in nests of ibises or herons because of their height above the water. This unique system of self-rearing is dramatically different from that of semi-parasitic Redheads and Ruddy Ducks where the ducklings are reared with the brood of the foster parent.

Discussion

Taxonomic Position of the Black-headed Duck

The systematic position of the Black-headed Duck has posed problems since its discovery. It has been classified in several different tribes. Delacour and Mayr (1945) recognized its uncertain position but placed it with the tribe Oxyurini (stifftails) on the basis of Wetmore's (1926) observations on both behavior and anatomy. Specifically, Wetmore pointed to the presence of: air sacs, loose skin of the neck of males, lack of an osseus bulla, diving ability, shiny plumage, small wings, and similarity of the sexes in the pattern of the adult plumage. Salvadori (1895) earlier had noted the similarity of its plumage with that of *Oxyura ferruginea* (Peruvian Ruddy Duck).

At the time of Wetmore's study, the literature contained no description of the plumage of the duckling although there were five specimens in museums. Observations of two of these specimens by Delacour and Mayr (1946) provided no simple solution, but they cited several similarities between *Heteronetta* and typical stifftail ducklings. My observations confirm these similarities. *Heteronetta* ducklings have the large head, heavy body, and wide-legged stance of Ruddy Ducks. Although they share the basic coloration with the dabblers, they are darker in color and have long down which gives them a "woolly" appearance. They have, in addition, a unique vertical line above the eye. Furthermore, the contour feathers of the juvenal plumage and the large rhachis and blunt ends of the juvenal tail feathers are similar to those of young Ruddy Ducks (Weller, 1967a).

The penes of Black-headed Ducks and Ruddy Ducks also are similar, having isolated "papillae" rather than "rings" as I noted in several species of Argentine dabblers of the genus *Anas. Heteronetta* and the stifftails (Oxyurini) show strong similarities in their skeletal features (Woolfenden, 1961); but the Black-headed Duck with an elongate body is highly modified for a coot-like existence while the Ruddy has a broad body and is a highly adapted diver.

Both *Heteronetta* and *Oxyura* lay large eggs in relation to the size of the female. However, the *Heteronetta* egg is smooth whereas the eggs of both the Argentine and North American Ruddy Ducks are rough in texture.

Some behavioral similarities between the two groups exist, but are less clear cut than are morphological likenesses. Black-headed Duck females, like Ruddy Duck females, are silent. Males call only during the breeding season, using the air sacs. In the parent-young relationships Black-headed Ducks have achieved the ultimate in precocial behavior among the Anseriformes. It is worth noting that female Argentine and North American Ruddy Ducks regularly abandon their young, or the young leave the brood. These seem to be able to survive well.

The distinctive courtship behavior of Black-headed Ducks does not provide a simple guide to the taxonomy of the species; but elements of its breeding behavior resemble displays of both Oxyurini and Anatini. Like Ruddy Ducks, Black-headed Ducks have air sacs in the head region and perform a vertical pumping head movement that resembles the sound-producing pump of the North American Ruddy Duck. Similar pumping movements are common to many dabblers. Other dabbler-like components of display include the grunt and whistle (no homology with the Grunt-whistle of *Anas* is implied; nor can it be denied) and wing-up, tail-up followed by a tail-wag. Unfortunately the copulatory behavior is still unknown.

In a number of characters, both anatomical and behavioral, Black-headed Ducks resemble the dabbling ducks, tribe Anatini. In general, both are marsh dabblers and strain their food through mud and water by surface feeding and up-ending. Black-headed Ducks dive expertly as well. Although Ruddy Ducks differ markedly among themselves, similar diversity occurs in other tribes. Argentine and North American Ruddy Ducks surface-feed (at least the young do) and dive, but rarely up-end or dabble. Black-headed Ducks lack the large flap on the hind toe characteristic of typical stifftails and other divers, and they apparently lack the ability to submerge gradually as do the stifftails. They fly easily and rapidly and rise directly from the water without preliminary "water-walking." Presumably, this is an adaptation to life in small pools where a steep take-off is necessary. Another morphological similarity to dabblers is in the presence of double white wing-bars, although no colored speculum is present.

The similar behavior and precocity of the young, the laying habits of females, the plumages of young and adults, and the anatomical similarities of skeletons and the male copulatory organs seem to link the Black-headed Duck more closely with the stifftails than with any other group. Systematically there are two possible alternatives: (1) leave the species with the Oxyurini, recognizing that it may be an ancient species which links the dabblers and stifftails, or (2) place it in a separate tribe (Heteronettini) between the Anatini and Oxyurini because of its unique combination of physical and behavioral characteristics. The former system seems more in keeping with the efforts made by Delacour and Mayr (1945) to link the genera into meaningful tribes despite the fact that it places together birds of diverse form and habits.

Evolution of Parasitism in *Heteronetta*

At the present time, there is no indication that Black-headed Ducks nest. Phillips (1925) suggested and local residents supported the idea that the species may nest in an inconspicuous site such as trees. However, one does not encounter the species in wooded areas but rather in marshes where trees are not common. There have also been suggestions that females may collect the ducklings after they hatch, but there are no well-documented reports of females with broods. Moreover, no one has found females with brood patches or observed brooding behavior as in females of non-parasitic species.

As with all parasitic birds the present breeding pattern presumably represents a modification of the normal nesting pattern. The pattern of pair formation, temporary pair-bond, and pair-defense seem to remain unmodified by the parasitic way of life.

Any theory of the origin of parasitism in the Black-headed Duck is difficult to postulate and preferably should be based on additional years of nesting data. However, in comparison with the semi-parasitic Redhead (Weller, 1959), there are some clear-cut differences which have resulted in successful parasitism in *Heteronetta* while a state of partial parasitism remains in Redheads and possibly North American Ruddy Ducks. The major difference is that the Black-headed Duck parasitizes nests of birds regardless of the egg color or shape while Redheads and Ruddy Ducks rarely do so. In addition, the evolution of self-rearing in the young is unique among parasites.

A key to success of a brood parasite entails the location of a suitable host species which: (1) is within the preferred habitat of the parasite, (2) is sufficiently abundant so that a clutch or several clutches of eggs may be distributed without placing a detrimental excess of eggs in one nest, (3) has a high rate of nest success, (4) will accept and normally incubate foreign eggs, and (5) will care for the young until they are able to care for themselves. For the Black-headed Ducks, coots (especially the Red-fronted Coot) seem to meet these requirements in Argentina. As a broody and abundant species with high nesting success, coots seem to be much better hosts than any species of duck could be. The ranges of the Black-headed Duck and the Red-fronted Coot coincide closely and their habitat preferences and adaptations are strikingly similar. Ecologically, numerically, chronologically, and from the standpoint of egg and nest success, coots seem the best host and the species most likely to have played a key roll in the evolution of this behavior in the Black-headed Duck.

There is little doubt that part of the success of the parasitic behavior is due to the fact that the species parasitizes a variety of hosts, five of which probably hatch and brood their young regularly: the Red-fronted and Red-gartered Coots, White-faced Ibis, Brown-hooded Gulls, and Rosybills. Local residents also reported *Heteronetta* eggs in nests of the Fulvous Whistling Ducks. Certainly Black-headed Duck eggs are highly successful in ibis and gull colonies, yet such colonies are very few in number. The Black-headed Ducks apparently parasitize Rosybills and probably other ducks regularly, but these species are not universally abundant and do not seem to be nearly as successful as are coots.

Parasitism of *Heteronetta* in Comparison with Other Parasitic Birds

Although obligate parasitism is found in only one anatid, it is distinctive among the five families with parasitic members because it is the only precocial

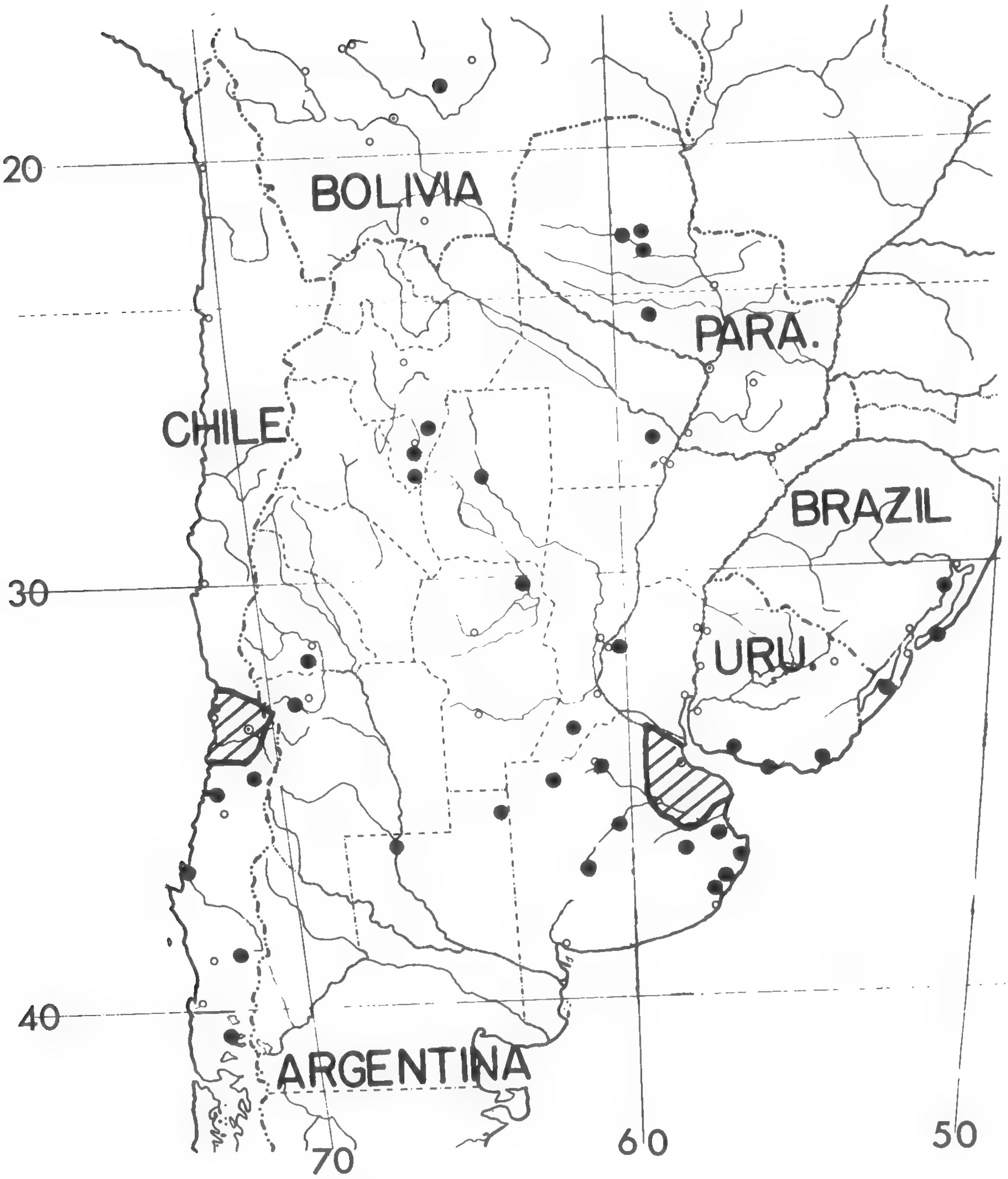

Figure 16. Distribution of the Black-headed Duck. Dots represent specimen records or sight records by professional ornithologists. Diagonal lines represent areas with numerous records.

species and appears to be the least damaging to its host. In this sense it is the most perfected of the brood parasites. The parasitic female does no damage to the eggs or nest of the host and, based on limited data, barely influences clutch size or nest success. Its young do not take food intended for the hosts' young. In fact, its behavior borders on commensalism rather than parasitism. Although highly specialized anatomical developments are non-existent, they do not seem necessary since the system functions simply and effectively. It appears that this is the only anatid in which the female is larger than the male (Weller, 1967a), but we clearly cannot attribute this fact to parasitism. For the above reasons, it is difficult to relate the chronology of evolution of this behavior in this group to that of other parasitic birds, based on the characters Friedmann (1955) has used — i.e., percentage of the species of the family which are parasitic with anatomical and behavioral specializations. The Black-headed Duck is neither abundant nor widespread (Figure 16), partly because it is habitat- and host-limited and partly because the system of self-rearing may produce a high rate of juvenile mortality.

Summary

A study was made of the breeding biology of the Black-headed Duck *(Heteronetta atricapilla)* with special reference to its parasitic laying. Observations on laying were made mostly at two marshes near General Lavalle in the Cape San Antonio region of the Province of Buenos Aires, Argentina.

The Black-headed Duck was found to be adapted to dense marsh vegetation where it fed mainly on seeds of marsh plants and occasionally on snails and duckweeds. It is rarely seen on land but flies easily and rapidly and dives as well as dabbles for food. It forms pairs during the breeding season but becomes social during the fall and is migratory. Sex ratio seems to be about 58 per cent males to 42 per cent females.

Courtship behavior is distinctive. Some components resemble displays of stifftails while others resemble those of dabblers. The main courtship display involves a Toad-call with a head-pumping movement which produces a grunt-and-whistle followed by a wing-up, tail-up display. Pair bonds are formed and tested in courtship groups in a manner similar to that of other species.

Parasitism appears to be the sole means of reproduction as no nests or brood care is known in the species. Hosts are birds which nest in dense marsh vegetation with the highest incidence being Red-fronted Coot *(Fulica rufifrons)*, Rosybills *(Netta peposaca)*, Red-gartered Coot *(Fulica armillata)*, and White-faced Ibis *(Plegadis falcinellus)*. There was a tendency for the parasitic female to lay during the hosts' laying period without disturbing the nest or eggs. Egg success was 18 per cent and 64 per cent of eggs observed on two study areas. Losses were due mostly to egg burial by coots. Eggs hatched in 24 to 25 days.

Ducklings were cared for by the host during the first 24 to 36 hours of life. Both wild and captive ducklings left the parent host at less than two days of age. They proved impossible to keep and rear under artificial conditions because of their tendency to leave the brooding site. They showed little of the following reaction common to other species of ducks. They were remarkably precocial in the development of feeding and maintenance behavior and were not alarmed by isolation or cold.

The plumage, anatomy, and behavior of Black-headed Ducks suggest that they are most closely related to the stifftails and probably should be maintained in that tribe. However, since they share several behavior traits of the dabblers, they may be ancient birds of dual affinities.

The success of parasitism in *Heteronetta* seems to be due to the selection of coots and a variety of marsh birds as hosts. Such birds are more numerous and successful in nesting than most ducks. The Black-headed Duck has achieved success not by specializations in laying behavior or egg color but by the random placement of eggs in nests containing eggs of any color. Survival of the young in the nests of these divers is possible because the young rear themselves after only a brief period of parental care. Because it is the least damaging to the host, it may be considered the most perfect of avian parasites; indeed, it is nearly commensal.

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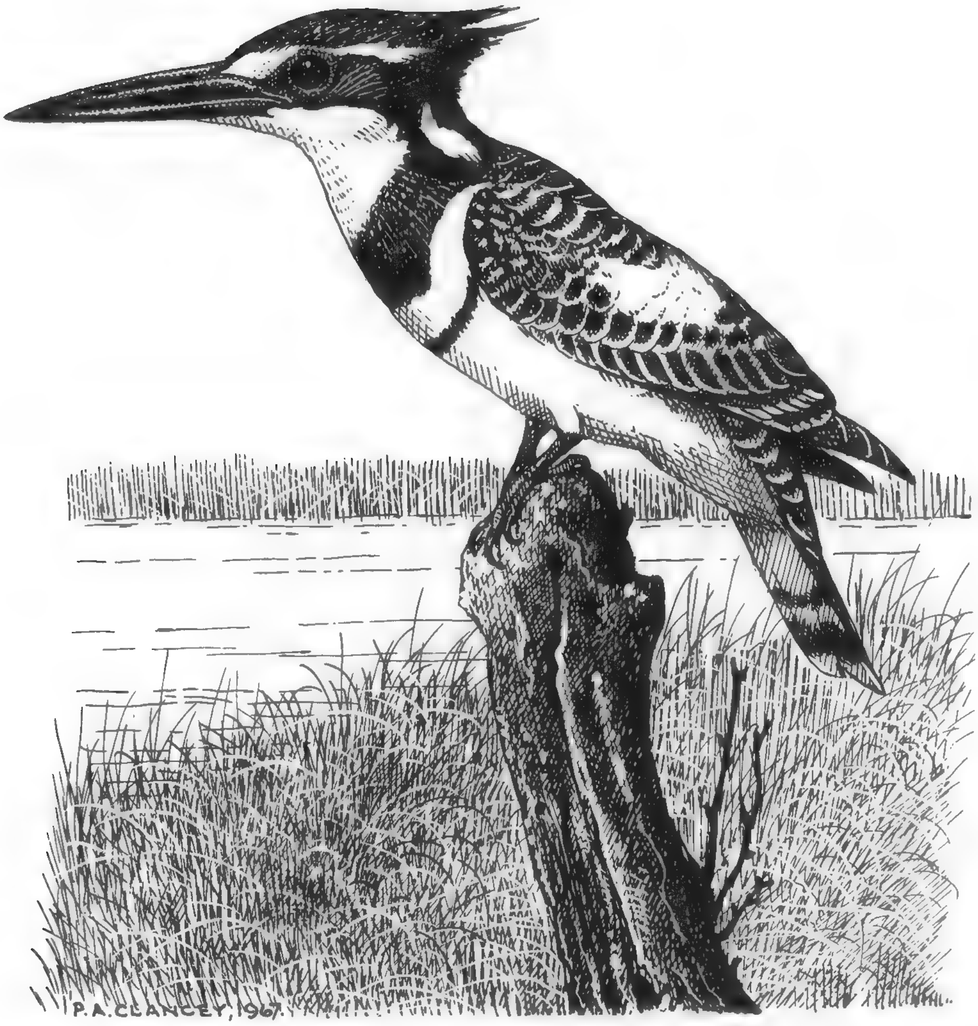


Pied Kingfisher, *Ceryle rudis*. Drawing by Phillip A. Clancey.

FIELD STUDIES ON THE SANDGROUSE OF THE KALAHARI DESERT

GORDON L. MACLEAN

From October 1964 to April 1966, I made a detailed study of the sandgrouse (Pteroclidae) in the Kalahari Gemsbok National Park, South Africa. In a paper resulting from this study (1967a) I reviewed the family and demonstrated clearly the lack of data on the behavior of the sandgrouse. In this paper I shall fill the gap to some extent on two species, the Namaqua Sandgrouse (*Pterocles namaqua*) and the Spotted Sandgrouse (*P. burchelli*), from my observations in the Kalahari and from my earlier studies in South West Africa (Maclean, 1960). The review of the Pteroclidae by Hüe and Etchécopar (1957) showed that few of the 16 species have been more than cursorily examined from a biological point of view. Even the observations of Meinertzhagen (1954) were of a rather casual nature, containing certain inaccuracies especially with regard to the method of transporting water by the adult birds to their young. Aldrich (1943), Baker (1921), Bump and Bohl (1964), Christensen and Bohl (1964), and Marchant (1961, 1963) all presented some very useful biological data. The more comprehensive account which follows may, I trust, serve as a basis for future field work on the sandgrouse.

Sandgrouse Habitats in the Kalahari

There are two distinct types of habitat in Gemsbok Park (Figure 1): the extensive dune country of red sand that supports a good cover of grasses (mainly *Aristida ciliata, Stipagrostis amabilis,* and *Asthenatherum glaucum*), shrubs, and bushes (Figure 2); and the more restricted stony flats of grayish calcrete or limestone, covered with sparse low shrublets (Figure 3) and confined to the eastern banks of the Auob and Nossob Rivers. The avifaunas of the dunes and calcrete differ markedly in composition and, in the case of terrestrial species, in coloration. The birds of the dunes, including the Spotted Sandgrouse (Figure 4), are characteristically reddish. The birds of the calcrete tend to be gray, although the Namaqua Sandgrouse is buffy or greenish brown (Figures 5 and 6). The adherence of *namaqua* to the rocky calcrete despite its brown color reflects its ancestral habitat, the rocky brown doleritic and sandstone areas to the south and west of the Kalahari sandveld, where the species is most abundant (Macdonald, 1957; Maclean, 1960).

In the Kalahari it is easier to study *namaqua* than *burchelli* because *namaqua* are concentrated in a more restricted habitat, because it is easier to drive a motor vehicle on calcrete than on sand, and because the smaller area of calcrete can be covered more thoroughly than the enormous area of dunes.

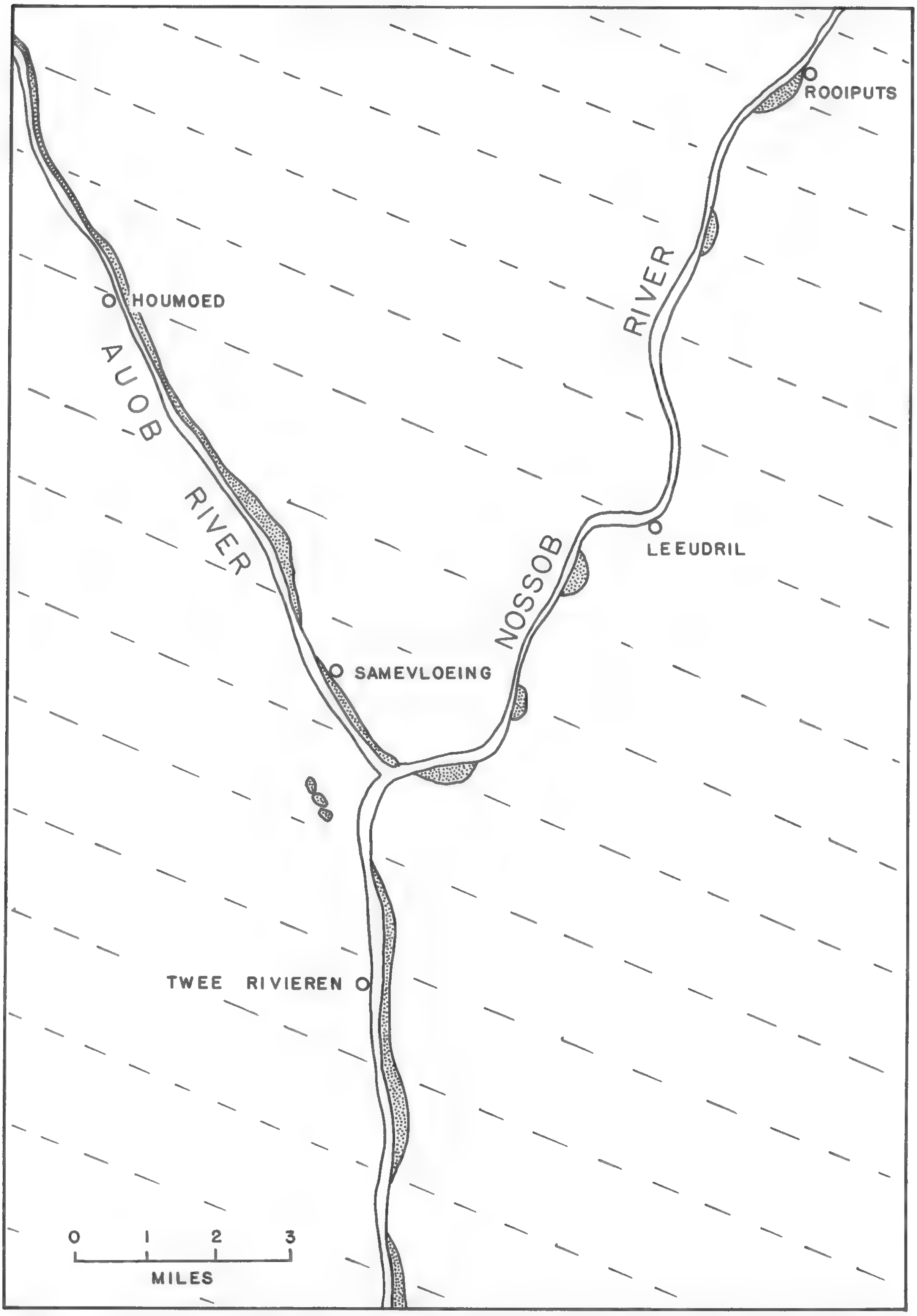


Figure 1. Map of the southern end of Kalahari Gemsbok National Park, South West Africa. The broken diagonal lines show the extent of the dunes. The shaded areas, on the east bank of the rivers, mark the calcrete.

Then too, in Gemsbok Park most of the game wells are on or near the calcrete. The sheer vastness of the dune country, the shyness of *burchelli,* and its rather fewer numbers make a study of this species most discouraging. Counts of sandgrouse drinking at water holes indicate a ratio of five *namaqua* to three *burchelli* on an average. *Namaqua* sometimes feed, especially in winter, and even nest in the dunes; *burchelli* come to the calcrete only for water.

Figure 2 (*above*). Typical dune habitat of the Spotted Sandgrouse. The grass in the dune trough is mostly *Asthenatherum glaucum* and on the dune crest *Stipagrostis amabilis*. The dark bushes on the dune slope are *Acacia detinens*.

Figure 3 (*below*). The author on the calcrete. This hard gray rock is the typical habitat of Namaqua Sandgrouse.

Figure 4 *(above)*. A male Spotted Sandgrouse at a water hole. He is about to soak his abdominal feathers in the water. When the feathers have absorbed the water, he will fly back to his chicks.

Figure 5 (*below*). A male Namaqua Sandgrouse showing his chest bands. His feathers are raised after a bout of preening and body-shaking. The long pointed tail is also visible.

Figure 6. A female Namaqua Sandgrouse with a small chick. Note how the plumage pattern of the female differs from that of the male in Figure 5.

Food

Both *namaqua* and *burchelli* appear to feed exclusively on seeds throughout their lives. I have never found anything but seeds in the crops of several dozen adults of both species, taken at all times of the year, and I have no indication that either species takes any animal food at any time. The one chick, examined for crop content, was less than a week old, and its crop contained

1,400 tiny, hard seeds — nothing else. The seeds most frequently eaten by both species are those of *Lophiocarpus burchelli* (Chenopodiaceae), one of the commonest annuals of the dunes. *Namaqua* depends for much of its food on seeds blown from the dunes onto the calcrete and seeds found in the more open dune troughs at the edge of the dunes.

A cursory examination of the dune troughs after *Lophiocarpus* has finished flowering, following the rains, reveals such an abundance of seeds that small depressions in the sand, such as antelope hoofprints, are full of them. I found other seeds in the crops of sandgrouse as well—all small, usually less than 2.5 mm, and hard. I have also seen a *namaqua* male pecking at a stubble tuft of dry grass but I could not make out whether it was eating anything or not; possibly it was feeding on young shoots emerging from the center of the tuft.

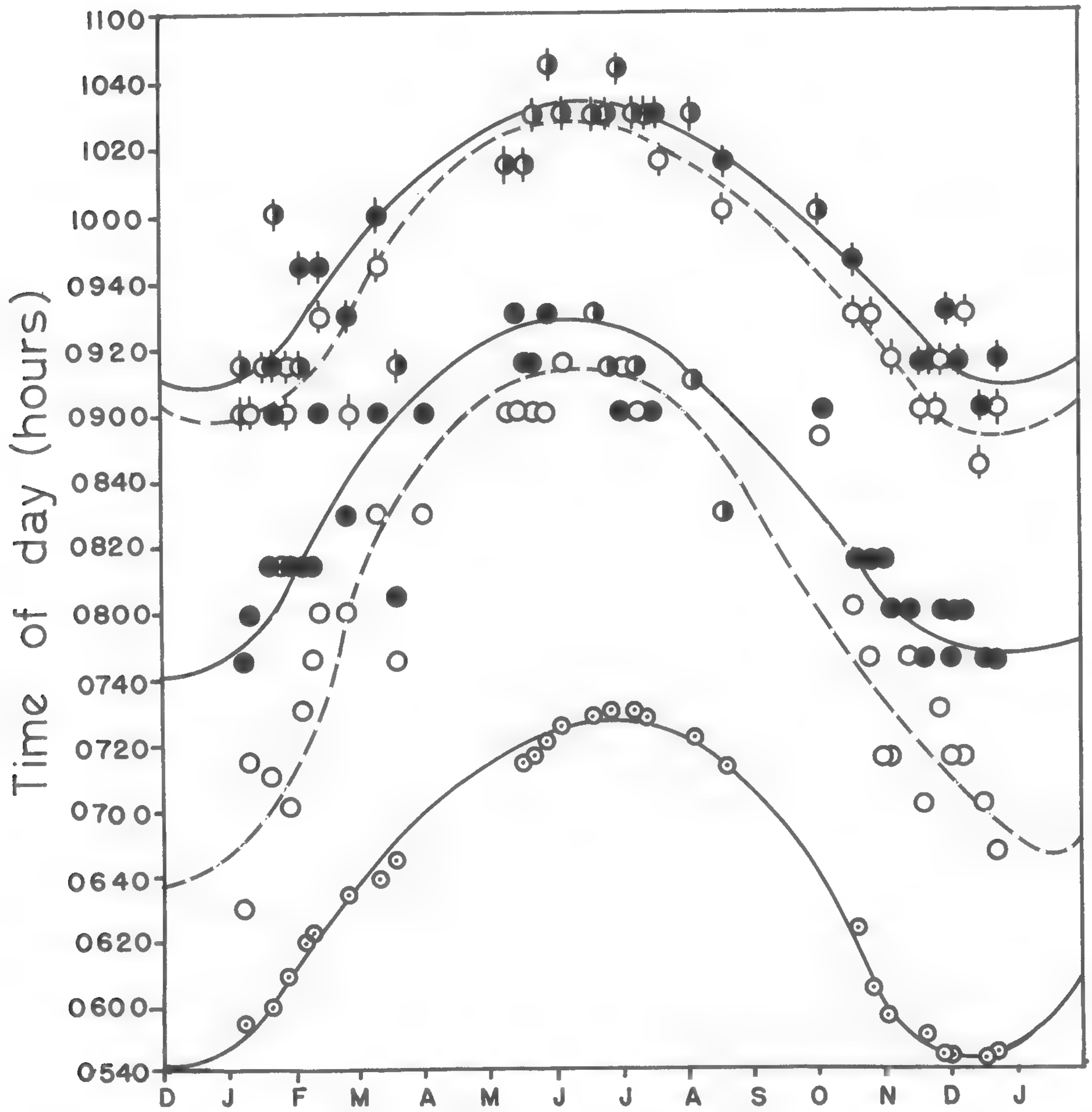


Figure 7. Graph showing the monthly variation in drinking times of the Namaqua and Spotted Sandgrouse in the Kalahari. Solid lines with solid circles indicate Spotted Sandgrouse; broken lines and open circles, the Namaqua Sandgrouse. In each case the lower curve is the beginning of the drinking time and the upper curve the end of drinking time. The bottom curve with the dotted circles is the time of sunrise.

Drinking

Time of Day.—The drinking habits of sandgrouse are sometimes spectacular (Bump and Bohl, 1964; Cade *et al.*, 1966; Meinertzhagen, 1954). Most species drink at rather regular times, either morning or evening, sometimes both, and sometimes at night. The birds usually gather in large flocks before flying to the water. Groups of birds flying to the water are joined by others along the way, and, in the case of *namaqua,* these groups assemble on the calcrete overlooking the water hole until the flock may number a thousand or more birds. The flocks of *burchelli* coming to drink are usually smaller, seldom numbering more than 40 or 50 birds. They gather in the dunes many miles from water before flying to the water hole.

Both *namaqua* and *burchelli* drink in the morning from one to two hours after sunrise and from two to two-and-a-half hours after sunrise, respectively (Figure 7). On cloudy mornings the birds drink somewhat later. *Burchelli* is less affected by overcast skies than *namaqua* probably because it ordinarily drinks later, at a time when the light intensity in the Kalahari is considerable, even on cloudy days. A few *namaqua,* mainly females, may drink again in the evening about an hour and a half before sunset. In the morning most of the late drinkers are males. The different drinking times of the sexes are correlated with the incubation patterns of sandgrouse, about which I shall say more below.

The end of the drinking period in the morning is more clearly defined than the beginning (Figure 7). Stragglers may arrive up to half an hour or more after the main flocks have departed, but seldom does a bird of either species arrive after 0945 hours in summer and after 1045 hours in winter. However, there may be some regional variation in drinking times, possibly dependent upon the distance over which the birds have to fly to water. In the Namib Desert at Gobabeb, Cade (pers. commun.) saw *namaqua* drinking as late as 1200 or 1300 hours in winter. On cloudy mornings the flocks drink for shorter periods than on sunny mornings. Likewise, in winter the average drinking period is shorter by 15 to 30 minutes than in summer.

Distance Traveled to Water.—There is little recorded evidence regarding the distance that sandgrouse in the Kalahari will fly to water. I have records of *namaqua* living and breeding from one-half mile to 15 miles from the nearest water. None of the water from the wells for a distance of 70 miles south of Twee Rivieren (Figure 1) is available to sandgrouse; and, since the overflow of water at Samevloeing is erratic, the next available water to the north of Twee Rivieren is at Houmoed. Thus sandgrouse living halfway along this 80-mile stretch between the two watering places have a maximal distance of 40 miles to fly to drink each day. However, *burchelli* does not drink at the more southerly of these water holes which is on a farm and too close to human habitation for these shy birds. Yet *burchelli* occurs all through the red dunes to well south of the Molopo River, some 50 miles south of Houmoed. And I have seen these birds flying at heights of up to 1,000 feet in the direction of Houmoed, over points several miles south of Twee Rivieren, at such a time in the morning that their arrival at Houmoed would coincide with the drinking time for the species.

Height and Speed of Flight.—As a rule *namaqua* flies lower than *burchelli,* but both fly higher when going long distances. I have timed both species flying alongside a Land Rover at 45 mph, about their normal cruising speed. At the end of October 1964, when the main flocks of *namaqua* were drinking at Houmoed between 0745 and 0800 hours, I saw birds flying northwards past

Figure 8. A flock of over 200 Namaqua Sandgrouse at the Houmoed water hole. Most of the birds have just flown in and landed several feet from a pond scooped out of the Auob River bed. Note that the river bed is very bare compared with the rather well vegetated dunes in the background.

Twee Rivieren at 0730 hours. If they covered the 10 miles to Houmoed in 15 minutes, they arrived at just the right time for the morning drink. Given a cruising speed of 45 mph and assuming that a flight of one hour in each direction is feasible, it is quite possible that sandgrouse may fly 45 and possibly even 50 miles to water each day — a maximal estimate based on present evidence.

Behavior at the Water Hole.—Once the flocks of *namaqua* have gathered on the calcrete before drinking time, the birds rise suddenly in a cloud, calling noisily, and descend to the ground a few feet to several yards from the water's edge (Figure 8). Here they wait for a few seconds or several minutes before running to the water to drink. The length of the wait is usually inversely proportional to the size of the flock of birds. In contrast to this, incoming groups of *burchelli* land right at the water's edge, or even in the water, drink quickly, and depart at once. Birds, which land in the water, float like ducks and take off from the surface without difficulty. After drinking, Namaqua Sandgrouse may fly straight from the water, or they may walk away a foot or so and wait until the group is ready to depart. The pair bond in *namaqua* must be strong because members of pairs always wait for each other. During trapping operations I have seen a bird take off and then suddenly land again and wait for its mate which has been caught in the mist net.

The two species of sandgrouse usually arrive at the water in separate flocks. However, if, as occasionally happens, one or two *namaqua* arrive with a flock of *burchelli,* they will land with the majority of birds right at the water's edge, although they are less nervous than the *burchelli* and often remain on the ground after the flock of *burchelli* has departed. The Spotted Sandgrouse are extremely wary at the water; flocks sometimes circle for several minutes before finally landing to drink. In their haste to depart, some may not drink at all. This may also be true of *namaqua* but much less often. I have seen non-drinkers leave the departing flock and turn back for a drink, but many non-drinkers may not drink at all that day. The non-drinkers are usually the last birds of the flock to land; in the same way, the first one or two *burchelli* to land frequently takes off again without drinking if the rest of the flock fails to land.

An account of the actual drinking process is given by Cade *et al.* (1966). Figure 9 illustrates the fact that the head is raised after each draft. The number of drafts taken by a bird probably depends on the volume of water in each draft and on the fullness of the bird's crop. One morning a male *namaqua* with a perforated crop (possibly the result of flying into a telegraph wire) came to drink. As fast as he swallowed the water, it ran out of the hole in his breast. He took about 20 drafts, more than twice the mean for male *namaqua* (Cade *et al.,* 1966), walked away from the water, and then returned for another 10 drafts before taking off with a flock of departing birds.

Number of Birds at the Water Hole.—The numbers of sandgrouse drinking at Houmoed varied with the season, the rainfall, and the condition of the water. The water, pumped by windmill into a reservoir, overflowed into a large "pond" in the river bed (Figure 8). Here, the sandgrouse drank only at the pond. During a hot, dry period of high winds, when the overflow of water into the pond was strong, the sandgrouse could number 6,000 birds in a morning. In the absence of wind, when the water became very brackish as a result of high evaporation and often thick with unicellular algae, the number of birds might be only 160. This means that the majority must have flown farther afield to seek more potable water. Similarly, after rain the sandgrouse did not visit the game wells at all, preferring to drink the rain water in the pools scattered in the river beds.

Pond Preference.—Sandgrouse did not visit the more brackish waters in Gemsbok Park as often as the fresher ones. They clearly demonstrated a preference for fresher water at Rooiputs where a trough leading from the reservoir overflowed onto flat ground across which the water ran for a few yards into a large pond. The water at the Rooiputs reservoir was about 100 times as saline as tap water (Table 1) and unpleasant to my taste so it is hardly surprising that the sandgrouse did not drink in the pond where the water was even more saline and had an offensive odor. Many sandgrouse dipped their bills into the pond, apparently testing the water, then walked around to the inlet and tested the water seeping from the trough. Most of the birds tested the water by bill-dipping progressively closer to the trough where they finally drank the water that had had the least time to evaporate.

Breeding Biology

Most of the data in this section concern *namaqua.* It was all but impossible to locate nests of *burchelli.* I found only one during the 19-month study period in the Kalahari, despite the fact that, from evidence of paired birds

Figure 9. *Above,* Spotted Sandgrouse drinking. The female in the right foreground has immersed her bill and is taking a draft of water; the male in the background has raised his head after a draft in order to swallow. The open bill while swallowing is typical. *Below,* Namaqua Sandgrouse drinking. Both birds have their heads down and the male, in the foreground, has his bill immersed.

in the dunes and males soaking their feathers at the water holes, we knew when and approximately where the birds were breeding.

Breeding Seasons.—Although one finds nests and other signs of breeding activity, such as males soaking their abdominal feathers (Cade and Maclean, 1967; Maclean, 1966a), almost every month of the year, *namaqua* showed peaks of breeding in July and November (Figure 10), both dry months in 1965. The only nest I found of *burchelli* was in April 1966, but counts of soaking males increased in winter as with *namaqua;* and the finding of two large young of *burchelli* on 27 July 1965 was further evidence of winter breeding.

Pair Formation.—Among the many curious and so far unexplained behavior patterns of the Namaqua Sandgrouse is one I have termed "strutting," in which a male follows a female (occasionally *vice versa*), both birds with their tails raised vertically and fanned, and their heads hunched in towards the body. This display may have something to do with pair formation.

A female usually runs away from a strutting male, or she may turn and attack him. Strutting often ends in what appears to be an attempt at copulation in which the female may be literally "bowled over" by the male. No doubt strutting is sexually motivated; whether or not it is part of the courtship behavior of sandgrouse is not clear. I have not seen strutting in *burchelli,* but this is not surprising since the species is so shy at the water and difficult to observe in the dunes.

Nests and Nest Sites.—Of 36 *namaqua* nests found in the Kalahari all were on the calcrete except three in the dunes and three in the river bed. A nest,

TABLE 1

The Salinities of Some of the Game Wells in the Kalahari Gemsbok National Park—with Tap Water and Sea Water for Comparison—Showing where the Sandgrouse Drink*

Source of water	*River*	*Molarity* *Na+*	*K+*	*Cl−*	*Drunk by sandgrouse*
Tap water (Pretoria)†	—	0.50	0.06	0.17	
Sea water†	—	470.00	9.90	448.00	
St. John's Dam	Nossob	0.40	0.21	0.13	++++
Houmoed	Auob	30.00	0.10	7.10	+++
Rooiputs	Nossob	42.00	0.21	15.00	+++
St. John's Well	Nossob	58.00	0.55	34.00	++
Monro	Auob	64.00	0.25	38.00	++
Kasper se Draai	Nossob	168.00	0.77	108.00	+
Kameelsleep	Nossob	250.00	1.00	174.00	+
Kij Kij	Nossob	272.00	0.98	197.00	−
Kransbrak	Nossob	824.00	8.10	665.00	−

*The popularity of the wells with the sandgrouse is shown by a plus sign (+); the more saline waters are less popular as drinking places. Those marked by a minus sign (−) are not used at all by sandgrouse for drinking purposes.

†For comparison.

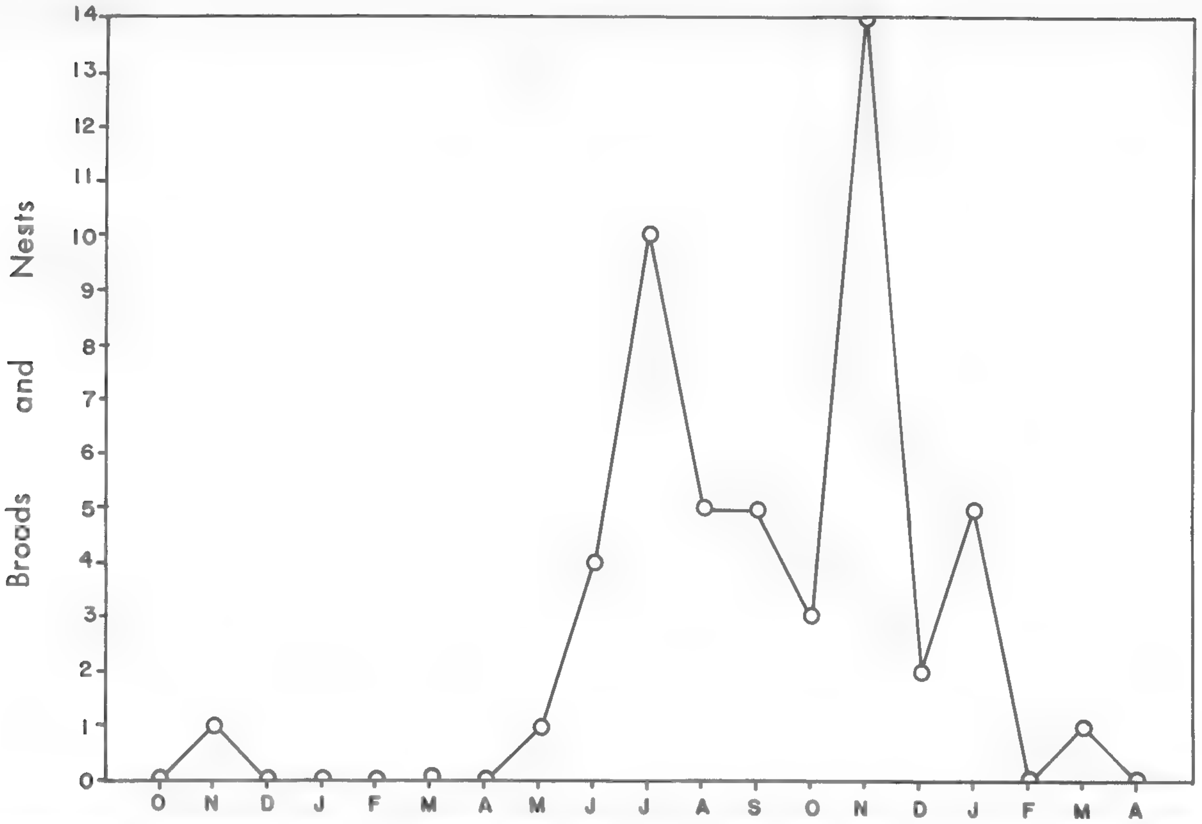


Figure 10. Combined counts of broods and nests of Namaqua Sandgrouse from October 1964 to April 1966, showing the peaks in July and November.

found in South West Africa near Keetmanshoop, was among dolerite boulders at the foot of a low hill. The single *burchelli* nest was found in the dunes as might be expected. Four of the *namaqua* nests were on gently sloping ground, the rest on flat ground; unlike the Double-banded Courser (*Rhinoptilus africanus*) of the same habitat (Maclean, 1967b), the Namaqua Sandgrouse did not show any tendency to nest on sloping calcrete or in hollows.

Both species of sandgrouse make simple nest scrapes on the ground (Figures 11 and 12). Two scrapes of *namaqua* measured 11.4 cm and another 10.2 cm in diameter. Nest scrapes varied in depth according to the terrain, being rather deeper on sandy soil than on hard calcrete, but they usually were not more than three or four cm deep. One nest was in the old hollow of a lark nest at the foot of a small woody shrub; 24 nests (66.7 per cent) were in completely exposed sites; and the rest were close to shrubs but were not orientated for shade as was the lark nest (Maclean, in press). In one case, a *namaqua* attempted a nest scrape on hard rough calcrete at the base of a shrub and laid two eggs. Three days later the full clutch of three eggs had been moved about a foot to a more suitable, yet more exposed, scrape.

Eggs.—The eggs of the Namaqua Sandgrouse have been described in the literature. The texture is smooth with a waxy gloss, and I found two distinct color types, a "green" and a "red." Red eggs, less common than green, occurred in only three of 34 nests. The red effect, due to a tinge of pink on the pale stone ground color, is accentuated by dark reddish brown smeared markings. Green eggs, a pale greenish stone in ground color, are marked with olive-brown. There are darker and lighter variations of these shades and the markings may or may not be in the form of a ring around one end. The eggs of one clutch were capped with apple green at one end.

The three eggs of *burchelli* were indistinguishable from those of *namaqua,* having a pale olive-cream ground color with olive-brown blotches.

Figure 11 (*above*). Typical nest of Namaqua Sandgrouse, a simple scrape with clutch of three eggs. The accumulation of small stones in the scrape is the result of the birds' side-throwing at nest-relief.

Figure 12 (*below*). Nest of Spotted Sandgrouse with three blotched glossy eggs, the typical clutch of the genus *Pterocles*. The bits of vegetation in the scrape probably accumulated during side-throwing by the birds.

The measurements of 93 *namaqua* eggs ranged from 31.0 to 38.8 mm long, 22.5 to 27.1 mm wide, with a mean of 35.8 by 25.2 mm, comparable to those in McLachlan and Liversidge (1957) and in Mackworth-Praed and Grant (1962). The mean of three *burchelli* eggs was 34.7 by 23.5 mm. In *namaqua* I found no difference in size between the first egg of a clutch and the last.

Namaqua almost invariably lays a clutch of three eggs and I suspect the same is true of *burchelli.* Of 32 complete clutches of *namaqua,* 31 had three eggs and one had two eggs. Possibly one egg was lost from this last clutch before I discovered it. As a rule, the females appear to lay the eggs at 24-hour intervals; one female laid the first egg of a clutch at 1220 hours.

Incubation and Nest-relief.—Incubation in *namaqua* started with the first egg of the clutch and, in five out of six cases, until the clutch was complete, the males incubated the one or two eggs regardless of the time of day. After the completion of the clutch the male incubated at night and the female during the day.

In the morning after sunrise, the female feeds and then flies to drink at the nearest water hole. She returns directly to the nest and takes over incubation from the male. He then flies to drink and returns to the vicinity of the nest to feed. Thus, most of the late-drinking birds at the water holes are males, probably those relieved at the nest by the female. The male spends the midday hours in the shade of a shrub near the nest, sometimes only two feet from the incubating female. He may feed again before taking over from the female an hour or two before sunset.

In the evening, after being relieved at the nest, the female flies again to the water to drink. She probably returns to feed before sunset and remains near the nest until she takes over from her mate after feeding and drinking the next morning. Neither parent leaves the nest during its period of attendance unless it is disturbed.

The nest-relief ceremony is simple but of interest as an indication of the systematic position of the sandgrouse (Maclean, 1967a). When the female *namaqua* returns from the water hole in the morning, she lands a few feet to several yards from the nest where the male may greet her with the "kelkiewyn" contact call (the word "kelkiewyn" is Afrikaans for a wine goblet and is the onomatopoeic name of *namaqua* in that language). The female then walks toward the nest. When she is ten feet away or less, the male begins to pick up small stones and other objects which he tosses into the nest scrape around his body. Hall (1959, 1964) called this "side-throwing." The male may also turn the eggs. He then gets up and, still side-throwing in the direction of the nest, moves away as the female settles on the eggs. She may make a few side-throwing movements, too, until the male takes off for the water hole.

The evening nest-relief is much the same except that the female is impatient to depart. Probably thirsty after sitting for a whole day in the hot sun, she seldom waits until the male is near the nest before she gets up to go. However, as soon as she sees the male approaching, she always side-throws before leaving the nest. Then she usually walks no more than a foot or two from the nest before taking off for the water hole. The male walks quickly to the nest and settles down to incubate.

As a result of side-throwing, the nest scrape becomes filled with small stones and bits of vegetable matter as incubation proceeds, until the eggs, by the time they are due to hatch (Figure 11), lie on a substantial pavement of material.

In summer the female incubates from about 0800 to 1800 hours (10 hours) and the male from 1800 to 0800 hours (14 hours). In winter the female's atten-

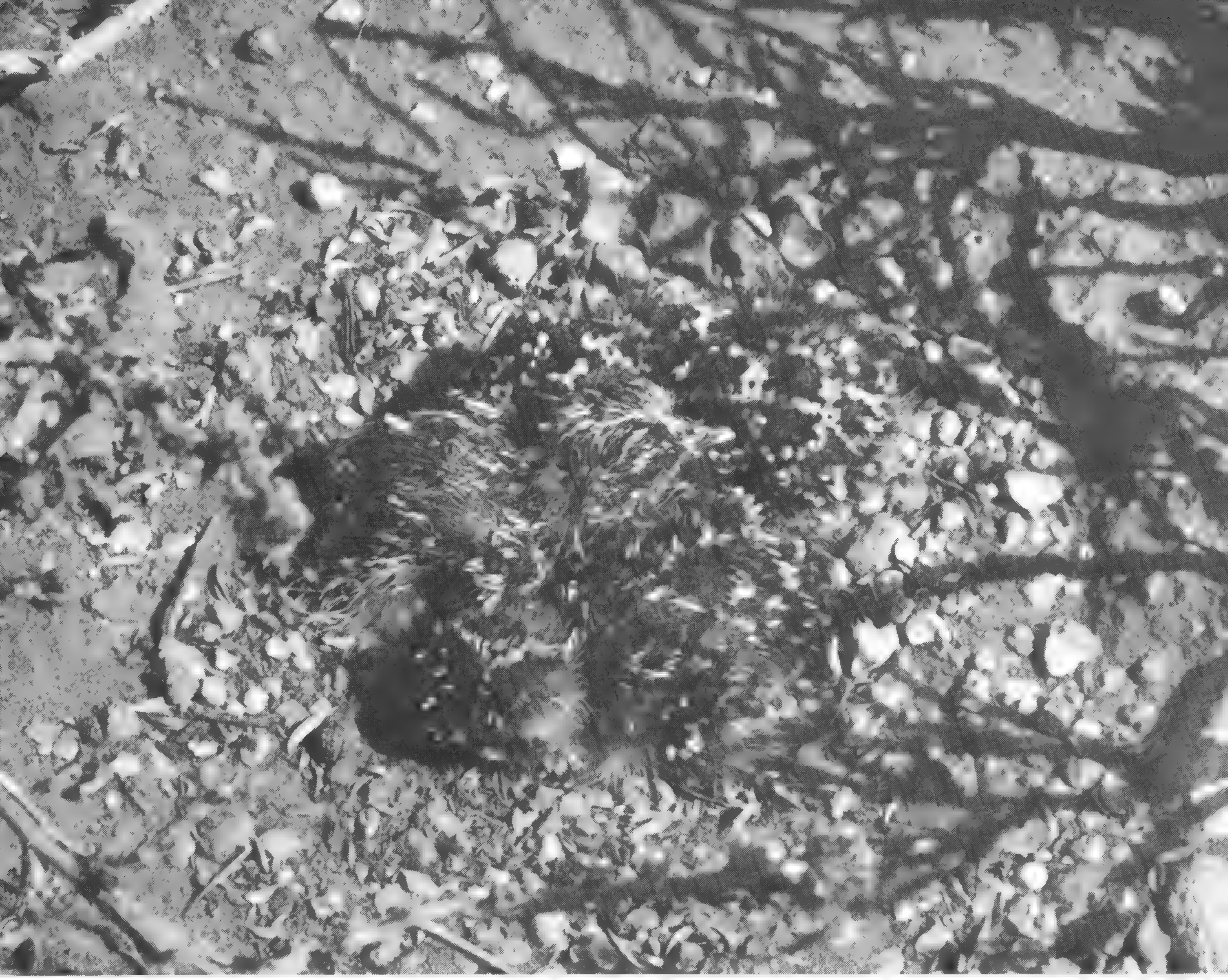


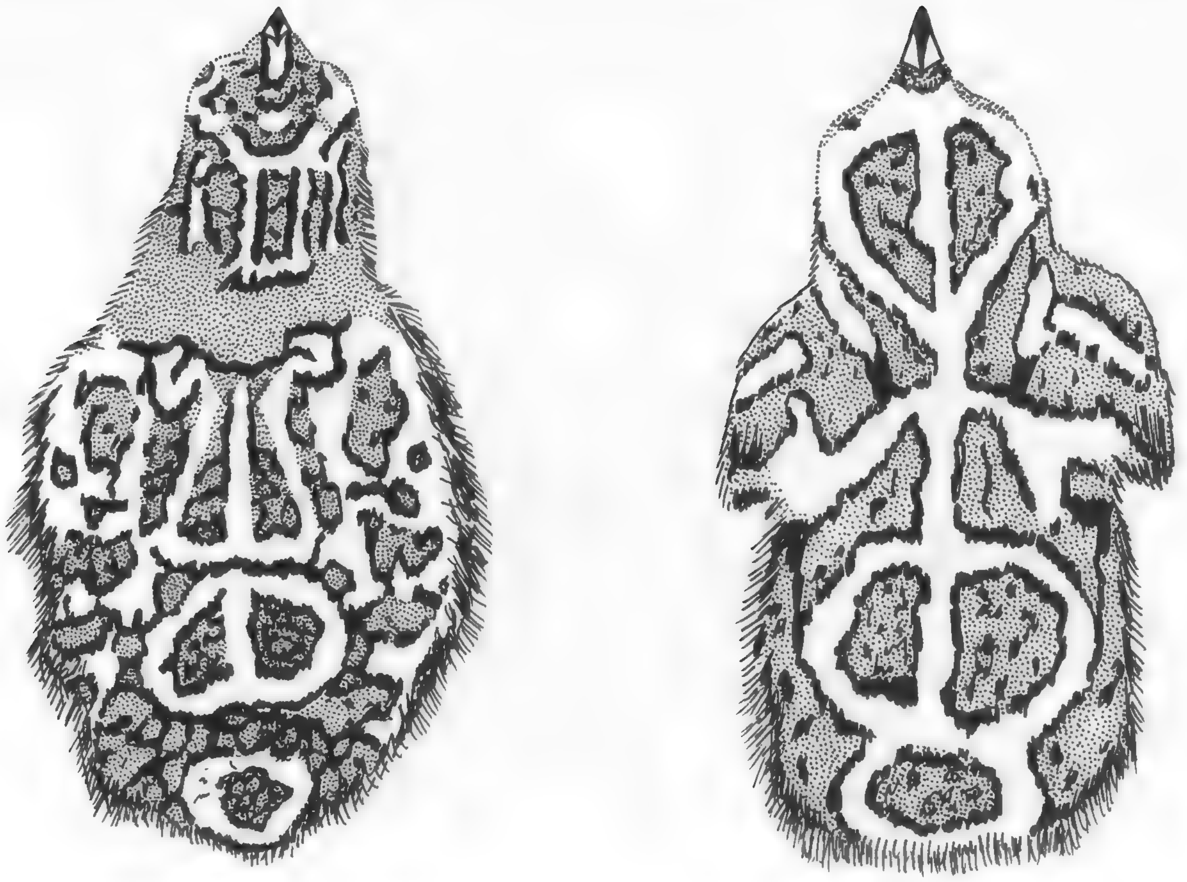
Figure 13. Three newly hatched chicks of Namaqua Sandgrouse still in the nest. The chick at the top of the photograph is already dry, the nearest slightly damp, and the middle one still quite wet, having just hatched. The white pattern on the back of the oldest chick (*top*) is partly visible.

tive period is about two hours shorter and the male's two hours longer. The incubation period, determined from the day the last egg was laid to the day the last chick hatched, was 21 days in four nests of *namaqua*.

Hatching and Development of the Chicks.—The chicks may all hatch on the same day, or they may hatch on three successive days. Usually one of them hatches a day earlier or later than the other two. The chicks usually remain in the nest until all are dry (Figure 13) although an adventurous chick may make exploratory movements up to two feet from the nest even before the others have hatched. The parents carry the eggshells away and may drop them as close as three feet from the nest, but they usually carry them farther.

Out of 69 eggs (23 clutches of three eggs each), whose fate was known, 47 (68.1 per cent) hatched. One egg was infertile; the other failures were due to predation. I could not calculate the losses of young after they left the nest but it was rare to find more than two large young in a family group. Probably rather more than a third of the chicks that leave the nest do not survive. If so, about 23 per cent of the eggs laid may give rise to flying young. And this estimate is perhaps too high.

The color pattern of the downy chicks makes them extremely difficult to see (Figure 15). The back (Figure 14) has an intricate pattern of black and white down on a background of mixed black and brown. The ventral down is a uniform buff and the hind neck is rufous-buff. I have not seen the downy young of *burchelli*.



Pterocles namaqua Pterocles bicinctus

Figure 14. Downy chicks of Namaqua Sandgrouse and *P. bicinctus* showing the characteristic patterns on the back. These patterns compare with similar patterns shown in color plates of *P. alchata* in Bartlett (1866) and of *P. gutturalis* in Fisher and Peterson (1964).

The chicks begin to feed after about 24 hours, appearing to eat only seeds. Both parents look after them except when one is away drinking; sometimes both parents go to drink together, leaving the chicks crouched under shrubs on the calcrete. The male brings water to the chicks in his abdominal feathers. Although we (Cade and Maclean, 1967) have already described this behavior in detail, I shall mention it briefly here. As the male returns from the water hole where he has soaked his feathers, the chicks gather round his abdomen and strip the water from the wet feathers with their bills. Marchant (1961, 1962) appropriately termed this "litter of puppies" behavior. We seldom saw female sandgrouse soaking their feathers; they probably do so only in the event of the death of the male parent.

At the age of three weeks the half-grown and almost fully feathered young still cannot fly (Figure 16). They do, however, use their wings for balance when running away from danger (Figure 17). When about one month old the *namaqua* chicks can fly a few yards at a time and at the age of six weeks can fly capably. The chick probably does not fly to the water hole to drink until almost two months old since it is rare to see young sandgrouse at the water in full juvenal plumage. Most of the young birds at the water have begun to molt into their more boldly marked adult plumage. Four or five months after the peak of breeding most of the *namaqua* of the year are in full adult plumage. They are probably capable of breeding at the age of one year.

Intruder-reactions of Breeding Adults and Chicks.—Both male and female *namaqua* sit very closely on the nest and do not flush easily. An incubating Namaqua Sandgrouse will remain on its nest only six feet from a passing motor vehicle. If the vehicle passes closer than six feet, the sitting bird flies

Figure 15 (*above*). A week-old chick of the Namaqua Sandgrouse crouched on the calcrete. Note how well this chick blends into the background of gray stone.

Figure 16 (*below*). An almost fully feathered chick of the Namaqua Sandgrouse about three weeks old. During the heat of the day the chick remains in the shade of a shrub.

Figure 17. The same chick as in Figure 16. Although this chick is not yet able to fly, it uses its wings for balance as it runs away from the photographer.

up at the last moment. If a human approaches on foot, an incubating *namaqua* walks off the nest for several yards before taking wing. *Burchelli,* also, always seem to walk away from the nest before flying, even when approached in a motor vehicle. I found the nest of the Spotted Sandgrouse only by tracing the footprints back to the nest. Even so, I did this many times without success because the birds trace a zig-zag path as they walk and their footprints criss-cross with others. *Burchelli* may walk up to 20 yards from the nest before taking off.

My observations indicate that *burchelli* breed in loose groups on the dunes. At the time I found the one nest of this species there were other *burchelli* in pairs scattered over areas of perhaps 20 acres each in the dunes, and between these areas there were no *burchelli* at all.

Even at the approach of a natural predator an incubating *namaqua* will sit tight on the nest until the last moment. Once a sitting female flew up from her nest when a bat-eared fox *(Otocyon megalotis)* ran by only a foot or two away. This attracted the attention of the animal which promptly found the eggs and ate them. A Chanting Goshawk *(Meliërax musicus)* flying overhead causes an incubating *namaqua* to crouch on the nest.

A non-predatory intruder such as a horse or a motor vehicle at first elicits an "upright-alert" posture (Brown, 1962) with stretched neck, but when the intruder gets closer, the sandgrouse crouches. A common intruder-reaction of both *namaqua* and *burchelli,* either at the nest or at the water hole, is head-bobbing. Bobbing is always performed in the conflict situation of depart/approach, such as when the incubating drive tends to force the bird towards the nest, or thirst forces it toward water, yet fear of an intruder tends to hold it back. Bobbing invariably precedes departure, either by walking or flying.

When a nesting *namaqua* is finally forced to take wing, it often flies off with dangling legs and a loud *ki-kiiii ki-kiiii* alarm call. The bird then lands a few yards away and performs a distraction display of the "injury-feigning" type, both wings fluttering or quivering and the fanned tail pressed to the ground. A *prrr prrr* distraction call sometimes accompanies this display. The parents display with greater intensity when they have young or eggs close to hatching than when incubation is in its early stages.

The nesting territory of *namaqua* is small; adjacent nests may be less than 20 yards apart. From this territory the bird drives off members of its own species and other harmless terrestrial birds with a threat display.

Intruder-reactions of Chicks.—At the alarm notes of the parents, the chicks of *namaqua* crouch and lie still. If the disturbance is sudden, they crouch where they are (Figure 15); otherwise they run to the nearest shrub or stone and crouch in the shade (Figure 16). The chick utters a distress call, a two-syllable note *ki-chik* or *chi-wrr,* while being chased or when separated from its parents too long. As soon as the young bird is fully able to fly, it no longer gives this call.

Behavior

Vocal Behavior

Both *namaqua* and *burchelli* have calls with a nasal quality. *Namaqua* has at least five distinct calls.

1. *Contact call.* The common flight call of *namaqua,* a striking three-note *kel-kie-wyn* with the last syllable accented and slightly drawn out, is one of the most characteristic sounds of the dry western regions of southern Africa north of the Orange River. The bird utters the call at intervals of a few seconds. I have heard a male *namaqua* sitting on a nest give it to its mate as she flew in to take over incubation. The corresponding flight call of *burchelli* is a staccato *quok-wok* with the accent on the second syllable which may be a quarter tone higher. In contrast to the highly vocal *namaqua,* the Spotted Sandgrouse call infrequently when in flight; a flock of 50 or more of this species may arrive at and depart from a water hole in complete silence.

On the ground at the water hole very large numbers of *namaqua* (flocks of over 500 birds) keep up a continual muttering sound of low *kip kip* notes, which also seems to be a form of contact call. Smaller groups of *namaqua* are usually silent.

2. *Take-off call.* Both species have similar take-off calls – a quick burst of sharp *quip quip quip* notes. Again *namaqua* uses this call far more than *burchelli.* The take-off call of *Pterocles bicinctus,* which I have heard in the Gamsberg Mountains of South West Africa, is a rather similar but harsher *chuk chuk chuk.*

3. *Following-call.* The following-call, used by parents to summon their chicks mainly out of hiding after a disturbance, is a rather special type of contact call. In *namaqua* it is a soft *quip quip* not at all unlike the muttering notes mentioned for the large flocks at the water.

4. *Alarm call.* Namaqua Sandgrouse render a strident *ki-kiii* when flushed from the nest or brood.

5. *Distraction call.* This call, a high-pitched purring sound, is heard only from birds performing an injury-feigning distraction display near the eggs, or, in the case of the Namaqua Sandgrouse, the young.

Threat Displays

1. *Aggressive threat.* An adult displays aggressively by running or hopping rapidly toward an intruder with lowered head and tail. I have seen this display in a male *namaqua* which drove off a finch-lark *(Eremopterix verticalis)* and another male of its own species that had approached to within about six feet of his two small chicks near the nest scrape. I have also seen female Namaqua Sandgrouse drive off strutting males in this way; another female successfully drove a Crowned Plover *(Vanellus coronatus)* away from the vicinity of her nest, accompanying the display with slightly spread wings that probably indicated high-intensity aggression. The sandgrouse and the plover had nests only 25 yards apart, again indicating the limited size of sandgrouse territories.

2. *Defensive threat.* The defensive threat display of both *namaqua* and *burchelli* appears to be a ritualized flight-intention movement in which the bird faces *away* from the stimulus, usually a bird of a harmless species — other sandgrouse, dove, sparrow — flying low overhead, lowers the breast to the ground, raises the head, flicks the wings open, and raises and spreads the tail. I have seen both species of sandgrouse give this display to the flickering shadows of a rotating windmill wheel and a female *namaqua* react in this way to a Land Rover passing near her nest.

Maintenance Behavior

Behavioral Heat-loss Mechanisms.—Air temperatures in the Kalahari often exceed 40°C in summer. Namaqua Sandgrouse solve the problem partly by seeking shade. The off-duty member of a breeding pair stands in the shade of a shrub near the nest; non-breeding birds may gather in small groups in the shade of a tree; and *namaqua* chicks walk in the shade of their parents' bodies, sometimes right between the parents' legs, when the sun is high.

But what of the female sandgrouse sitting on an exposed nest in the hot sun all day? Unlike the Double-banded Courser which nests in similar sites, she is not relieved by her mate at intervals throughout the day (see Maclean, 1967b). Sandgrouse have developed gular fluttering as a means of evaporative cooling. Sandgrouse chicks, if overheated, pant from the moment they hatch and do not appear to use gular flutter as a cooling mechanism until they are older.

Comfort Movements.—I shall use the term "comfort movements" as defined by McKinney (1965). Once again, I made most of the observations which follow on *namaqua.*

1. *Shaking movements.* (a) Body-shake. As in most birds a raising of all body feathers accompanies the body-shake. Wing-shake is not a separate movement, but rather a follow-through movement from body-shake during which the wings remain in their "pockets" (Figure 5). (b) Wing-flap. A both-wings-stretch with open hand always precedes wing-flap and a hop accompanies it. This "flap-hop" movement is probably more of a stretching movement than a shake, but I have kept to the categories of McKinney (1965).

2. *Stretching movements.* (a) Wing-and-leg stretch. This is a common stretch pattern among sandgrouse as among most birds. The pattern is fully developed in *namaqua* chicks of less than a week old. (b) Both-wings-stretch. Apart from the stretch with open hand already mentioned, there is a both-wings-stretch with closed hand. In the both-wings-stretch with open hand the bird holds the body high and almost vertically, while in the both-wing-stretch

with closed hand (which is the most common among birds) the bird leans downward with the neck stretched forward.

3. *Cleaning movements.* (a) Preening. Both *namaqua* and *burchelli* preen frequently, oiling their feathers with the secretion from well developed uropygial glands. *Namaqua* chicks preen when only 24 hours old. (b) Scratching. Namaqua Sandgrouse and probably all sandgrouse scratch the head indirectly (by bringing the leg over, or behind, the wing). (c) Bathing. I have never seen sandgrouse bathing in water, although it has been suggested that the feather-soaking pattern of male sandgrouse may be derived from bathing movements (Cade and Maclean, 1967). I have, however, watched both *namaqua* and *burchelli* dust-bathe in the same way as do domestic chickens.

Rather different is a movement I have termed "belly-rubbing," which occurs only in male sandgrouse prior to feather-soaking and after the chicks have finished drinking from the wet feathers. In belly-rubbing, the bird rubs the abdominal plumage on the ground with yawing movements of the body about a vertical axis, using the legs as a pivot. This movement probably serves to "de-oil" the plumage before soaking the feathers and to dry it after the chicks have finished drinking.

Displacement Activities and Intention Movements

Displacement feeding and displacement brooding are not uncommon in *namaqua,* and occur in the conflict situation involving an approach to the nest in the presence of an intruder or an unfamiliar object. I also saw displacement feeding in both species of sandgrouse near water; usually it accompanied walking, while bobbing was performed when the birds were standing still. The nature of bobbing has already been dealt with (Daanje, 1950; Maclean, 1966b, 1967a, 1967b; Simmons, 1953) and seems to be a ritualized departure-intention movement. The nature of side-throwing is less clear; it is definitely ritualized, but its origin is obscure. I have already described the ritualized flight-intention movements of the defensive threat display.

An interesting case of vacuum activity can be seen in male sandgrouse which arrive at a habitually used water hole to find it dry. Those that come to soak their feathers squat where the water should be and go through the movements of soaking their feathers. Intention-soaking movements may also be incorporated in the belly-rubbing movements prior to actual soaking in water.

Predators of Sandgrouse in the Kalahari

Probably the commonest predators on the eggs and young of Namaqua Sandgrouse are the bat-eared fox and the silver fox (*Vulpes chama*). A number of other small carnivorous mammals may prey on sandgrouse, but direct evidence is lacking for all but the bat-eared fox. Snakes may also take a toll of eggs and young birds.

The commonest predator on adult sandgrouse is the Lanner Falcon *(Falco biarmicus)* which, singly or in groups of up to 20 individuals, hunts around the water holes. I have also seen the Chanting Goshawk and the Gabar Goshawk *(Micronisus gabar)* eating sandgrouse which were killed by flying into telegraph wires. I doubt that either of these hawks could catch an adult sandgrouse under normal circumstances; the former is too large and ungainly, the latter is too small. For the same reason I doubt whether in the Kalahari any of the three remaining species of *Falco (tinnunculus, chiquera,* and *rupi-*

coloides), all smaller and more lightly built than the Lanner Falcon, ever catch adult sandgrouse.

Although I examined many sandgrouse in the Kalahari, neither *namaqua* nor *burchelli* was ever found to have Mallophaga on their feathers, nor any visible ectoparasites on their skin. Bump and Bohl (1964) mention the lack of internal parasites in a sandgrouse *(P. orientalis).* This may be a feature of arid environments.

Discussion

One of the most striking facts which emerges from this study is the complete dependence on free surface water of a group of birds that are otherwise so well adapted to an arid environment. This raises the question of what effect the water, provided artificially since the advent of man, has had on the distribution of sandgrouse in the Kalahari. It seems likely that, since the sinking of wells and boreholes in the Kalahari Gemsbok National Park, *Pterocles namaqua,* a species so common in and so well suited to the rocky areas to the south and west of the Kalahari sandveld, has spread into the sandveld by way of the limited stretches of calcrete.

The situation with *Pterocles burchelli* is very different. The dune country lacks naturally occurring surface water except for brief periods after rain, and then only in the few pans and river beds. Where would *burchelli* have obtained its water before the sinking of wells? The nearest permanent sources of natural water to Gemsbok Park are the Fish River 200 miles to the west and the Orange River 200 miles to the south, as well as a very few springs between the sandveld and these rivers. It is possible that *burchelli,* once a bird of the dune country fringes, has now been able to colonize more extensive dune areas as water is provided deeper and deeper into the heart of the sandveld. It is a pity that we have no adequate records of sandgrouse ranges in the Kalahari before the 1930's when farming began there on a large scale.

Sandgrouse overcome the problem of water-dependence largely by their excellent powers of flight and endurance. Heim de Balsac and Mayaud (1962: 165) say of *Pterocles senegallus:* "Les oiseaux ne s'établissent pour nicher que dans un perimètre de 30 a 50 km. autour d'un point d'eau accessible. . . ." In this connection, Christensen and Bohl (1964) mention that *P. exustus* flew up to ten miles to water, while Bump and Bohl give distances of 15 to 20 miles for *P. orientalis.* Otherwise there are no adequate data on the distances sandgrouse fly to drink, and published records are vague, e.g., "very many miles" (Buxton, 1923), "Hunderte von Kilometern" and "gewaltige Strecken" (Hoesch, 1955), and "considerable distances" (Schmidt-Nielsen, 1964). I doubt that the birds would fly hundreds of kilometers daily as claimed by Hoesch, but I do not think that my estimate of 50 miles, or a round trip of 100 miles daily, is excessive.

Dependence on water must limit the breeding range of sandgrouse (Cade and Maclean, 1967). A statement by Macdonald (1957), who collected a family of *burchelli* (male, female, and "1 juv.") in the Northern Cape, runs: "The chick disgorged a large amount of water, which must have been fed to it by its parents for there was no open water within miles." Unfortunately he does not mention the age of the chick, how much the "large amount" of water was, nor how far the nearest water could have been; but it is fairly certain that *burchelli* has to fly farther to water as a rule than *namaqua.* This observation nevertheless demonstrates the efficiency of the water-carrying mechanism of sandgrouse.

Selection has favored the evolution of water transport by only the male parent, possibly to free the female for brooding the chicks on cold mornings while the male's feathers are still wet. Although females may very occasionally be seen soaking their feathers, it is most probably just an emergency measure adopted when the male parent has been killed.

Their good powers of flight also enable sandgrouse to move about in search of better feeding areas or drinking places (*cf.* Heim de Balsac and Mayaud, 1962), although they have capitalized on what is probably the most plentiful food in most semi-deserts at all times of the year — dry seeds. There is little doubt that sandgrouse seldom eat animal food. The only record of their doing so is that of Baker (1921) who writes that *P. indicus* "certainly eat termites . . . and one correspondent says that he found them feeding on ants." The most thorough analysis of sandgrouse food is that of Faruqi, Bump, Nanda, and Christensen (1960) on *P. exustus* in which they found only seeds at all times of the year, except for a few grass blades in spring and summer. Other food items mentioned in the literature (Andersson, 1872; Bump and Bohl, 1964; Fairbairn, 1952; Hoesch and Niethammer, 1940; Smith, 1849) include seeds, "fruits of desert plants," grain, berries, roots, small bulbs, and salt, augmented with quartz, grit, gravel, stones, and sand.

Living in the desert requires a compromise. Sandgrouse have locally abundant food, but have to drink water. Coursers, on the other hand, are independent of water because they feed largely on insects whose fluctuating abundance necessitates some local migration in these birds. Bird species, numerically most abundant in the Kalahari, are those that depend on a permanently abundant food supply, such as the sandgrouse and the Sociable Weaver, *Philetairus socius* (Maclean, pers. observ.), or those that are nomadic, moving into areas where food is temporarily abundant, such as the coursers and larks (Maclean, pers. observ.).

The drinking times of sandgrouse seem to be very constant for a given species over its whole range. Published records of *namaqua* drinking time in the morning agree closely with mine: "eight or nine in the morning" (Andersson, 1872); "almost exactly one and a half hours after sunrise" (MacDonald, 1957); "about 8 or 9 a.m." (Mackworth-Praed and Grant, 1962); "about two to three hours after sunrise" (Meinertzhagen, 1950). There is less agreement, however, on the evening drinking time of *namaqua*. Macdonald (1957) tells of "large numbers" of *namaqua* drinking at dusk in South West Africa, while Meinertzhagen (1950) says that they "do not water in the evening." Whether they do or not probably depends on whether or not the birds are breeding, and, possibly to some extent, on the immediate availability of highly potable water. The only time I saw large numbers of *namaqua* drinking in the evening was when good rains left pools of fresh water all along the Nossob River. I have never seen *burchelli* drinking in the afternoon or evening.

Although Cade *et al.* (1966) described at length how the sandgrouse raises its head after each draft, we should note that Bump and Bohl (1964), who actually observed *P. orientalis* in the field at their watering places, write: "sandgrouse and pigeons are unique in that they immerse their bills and actually suck up the water without the necessity of raising their heads between swallows." Is it possible that *P. orientalis* drinks differently from other sandgrouse? Similarly surprising is the conclusion of Christensen and Bohl (1964) that the practice of soaking the belly feathers to take water to the young is still a matter of speculation, particularly since Marchant (1962) had already confirmed the earlier statements to this effect. Old ideas do indeed die hard.

Next to the limited availability of water, excessive heat is probably one of the most important problems besetting the sandgrouse of the Kalahari. Cowles and Dawson (1951) and Lasiewski and Dawson (1964) clearly show the effectiveness of gular fluttering as a cooling mechanism in other avian species; and Lasiewski and Bartholomew (1966) demonstrated that gular fluttering is more economical energetically than panting. Gular fluttering is the only outward sign of overheating in sandgrouse and may partly explain why a sandgrouse can stand sitting in hot sunshine for eight hours at a stretch. On the other hand, the Double-banded Courser, which only pants, has evolved a pattern of frequent nest-relief throughout the day. Sandgrouse cannot use their short, feathered legs as heat loss centers as do many other species (King and Farner, 1961; Maclean, 1966b). However, their thick undercoat of downy feather-bases may help protect them against solar radiation. The Pteroclidae are clearly worth a detailed physiological study.

Although sandgrouse chicks seem to be less sensitive to heat than other precocial birds in the Kalahari, they still seek shade whenever possible. This is in contrast to Buxton's statement (1923) that sandgrouse chicks "run about, even during the hot hours, near their parents but not sheltered by them, as I have myself seen."

The factors governing the breeding seasons, such as they are, in the Namaqua Sandgrouse are obscure. The bird seems to breed during the driest times of the year, but our knowledge of the ecology of these birds is still too inadequate to allow any speculation. One may suggest that breeding in winter allows the birds to transport water in their feathers to their young more efficiently because of less evaporation, but since they are able to breed quite successfully in summer, some other factors must be involved.

Although the clutch size of *namaqua* is a constant three eggs, most writers give the clutch sizes of all species of *Pterocles* as two or three eggs (Andersson, 1872; Bump and Bohl, 1964; Fairbairn, 1952; Heim de Balsac and Mayaud, 1962; Mackworth-Praed and Grant, 1962; McLachlan and Liversidge, 1957; Roberts, 1940). In view of my own findings and those of Baker (1921), Christensen and Bohl (1964), and Marchant (1963) I suggest that most of the recorded clutches of two eggs were incomplete and that the normal clutch size for *Pterocles* is three eggs.

The incubation of incomplete clutches of eggs by the male parent may be of selective advantage in allowing the female a chance to feed adequately during the time when she is under considerable physiological strain. After the completion of the clutch, the pattern of attentive periods still allows the female to feed in the morning and evening during daylight. This is important because *namaqua* is strictly diurnal. The incubation pattern seems to be the same in other species of sandgrouse (Kendeigh, 1952), except for that in the nocturnal *Pterocles bicinctus*, which has not yet been determined. The fact that the female *namaqua* can find enough to eat in the short hours available to her illustrates the abundance of seeds in the Kalahari.

The incubation period of 21 days in *namaqua* is a little shorter than 25 days recorded for *P. alchata* (Bartlett, 1866) and 28 days for *Syrrhaptes paradoxus* (Blaauw, 1890), but is much longer than the incorrect period of 16 days given by McLachlan and Liversidge (1957).

My observations regarding the predation on sandgrouse while drinking confirm the studies of Cade (1965): The Lanner Falcon is the main predator and the Chanting Goshawk will take injured birds. Meinertzhagen (1960) mentions that Lanners, Tawny Eagles (*Aquila rapax*), and crocodiles also prey on sandgrouse. Although the Tawny Eagles were common in the Kalahari, I never saw one attempt to capture a sandgrouse. Meinertzhagen's data are from East Africa where this may be a common occurrence.

I have already dealt with the taxonomic significance of the behavior of the Pteroclidae (Maclean, 1967a), species which show remarkable similarities to the Charadrii. A similar study of the seed-snipes (Thinocoridae) of South America, a charadriiform family which seems to have evolved along much the same lines as the sandgrouse of the Old World, may throw considerable light on the true systematic position of the sandgrouse.

Summary

A 19-month field study was undertaken on two species of sandgrouse (Pteroclidae), the Namaqua Sandgrouse (*Pterocles namaqua*) and the Spotted Sandgrouse (*P. burchelli*) in the Kalahari Gemsbok National Park, South Africa. *P. namaqua* is a bird of rocky terrain, while *P. burchelli* inhabits the red sand dunes; each species wears a plumage similar to the background on which it lives. Both species feed exclusively on vegetable matter, mostly small, hard seeds. They fly each morning to water to drink; *P. namaqua* may drink again in the evening. The distance of their flights to water may be up to 50 miles. The provision of game wells in the Kalahari has no doubt extended the birds' range.

P. namaqua may breed at any time of the year, but shows peaks of breeding activity in the dry periods (mainly July). The factors governing the onset of breeding are unknown. The normal clutch size is three eggs. Males incubate incomplete clutches; after completion of the clutch, the female incubates during the day and the male at night. The incubation period of *P. namaqua* is 21 days. The highly precocial chicks leave the nest as soon as they are dry and feed on seeds from their first day. The male brings them water in his abdominal feathers until they are able to fly to water at the age of six to eight weeks.

The nest, eggs, and young are described; also the nest-relief ceremony and other behavior associated with breeding. Calls, comfort movements, displays, heat-loss mechanisms, and displacement activities are described and discussed. A brief account of predators is given.

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Peregrine Falcon, *Falco peregrinus*. Drawing by Tony Angell.

THE GYRFALCON AND FALCONRY

TOM J. CADE

Largest of the long-winged hunting hawks, the Gyrfalcon *(Falco rusticolus)* is a bird of circumpolar distribution and breeds in subarctic and arctic wildernesses, south from roughly 55° to 60°N Lat. in limited areas of Ungava, southwestern Alaska, the Komandorski Islands, and even farther south in the Altai Mountains, northward over the greater part of the tundra regions to 82°N in Greenland. Despite man's long history of involvement with the Gyrfalcon as a hunting partner, the species is still inadequately known biologically. It nests in regions difficult of access, and it begins breeding early in the season — typically laying its eggs in April — at a time when snow still covers the land and harsh winter conditions often prevail. For these reasons biologists know little about the early phases of courtship, nest-site selection, egg-laying, or incubation. Does the Gyrfalcon sometimes build its own stick nest? No one seems ever to have been on hand at the right time to find out.

The most detailed accounts of the Gyrfalcon's biology and life history are contained in various writings of the Russian ornithologist and one-time falconer, Professor G. P. Dement'ev. His Russian monograph, "Sokola Kretcheti," published in Moscow in 1951, is the most complete and authoritative study to be found between the covers of one book. Most of the biological information in this monograph also appears in various sections of Volume 1 of "Ptitsy Sovetskovo Soyuza," also published in 1951 and now very fortunately available in English translation through the Smithsonian Institution and the National Science Foundation under the title, "Birds of the Soviet Union." A German version of the "Sokola Kretcheti," somewhat updated, was published in 1960; and this work has also recently been rendered into English by the Foreign Languages Division, Bureau for Translations, Department of the Secretary of State, Ottawa, Canada. In this translation the English reader has available to him for the first time Dement'ev's fine essay on the cultural history of the Gyrfalcon and the use of this bird in falconry. His information on the uses of the Gyrfalcon in Tsarist Russia is especially interesting.

The English name, Gyrfalcon, comes from the Latin *gyrfalco* or *girofalco,* which is of uncertain derivation and meaning. Writing in the 13th Century, the Emperor Frederick II of Hohenstaufen, ardent student of the Gyrfalcon and falconer *par excellence,* tells us that *girofalco* is a low Latin corruption of *hierofalco,* which means "sacred falcon." The latter name reflects the high position that this noble bird has held in man's esteem down through the ages. Whether called *gyrfalco* or *hierofalco* by the Latin scholars of Europe, Jaktfalk or Jagdfalke (hunting falcon) in Germanic and Scandinavian tongues, Kretchet in Russian, Schumkar or Sonkar among the Tatar tribesmen, this strong-beaked, heavy-footed falcon, capable of pulling down swans, cranes, and other birds of prey in full flight, has always been the most prized of the hunting hawks. The Altai race of Gyrfalcon—called Turul—appeared as the emblem on the shield of Attila the Hun, and after him the sons of Genghis Khan hunted with these falcons on the plains near Samarkand. White gyrs, such as the one painted by Louis Agassiz Fuertes on the cover of this issue of *The Living Bird,* were the most coveted of all and were quite literally worth a king's ransom, as they had to be obtained in trade from such remote places as Greenland, Iceland, and northeastern Siberia. (White birds do not occur uniformly through the range of the Gyrfalcon.)

The commerce in Gyrfalcons was very considerable right up to the end of the 18th Century. Even though Greenland was known at an early date as the home of the White Falcon, few Gyrfalcons came from there because the voyage was too long for the birds to survive. Russia, Sweden, Norway, and Iceland supplied most of these falcons, particularly Iceland.

The existing records concerning Iceland are especially detailed and are most instructive as an example of sustained, heavy exploitation of a local falcon population without evident reduction in the breeding stock. The wild Gyrfalcons were rigidly protected by law, and the trapping was carried out under royal patents issued by the Danish kings. Each trapper had his own territory, knew all the nesting sites in it, and was responsible for the delivery of a specified quota of birds each year.

After Iceland came under Danish rule in the 13th Century, according to the records compiled by G. Timmermann (1938; cited by Dement'ev, 1960), exploitation of the island's Gyrfalcons became a royal monopoly in Copenhagen and continued more or less unabated until about 1775. The last order for 30 Gyrfalcons was issued by the Danish treasury in 1805, and by 1809 only one Gyrfalcon remained in the historic, old mews in Frederiksborg near Copenhagen.

During most of this long period the records, which refer mainly to the era of declining interest in falconry in the 17th and 18th Centuries and so may bias any overall estimate toward the low side, indicate that 100 to 200 Gyrfalcons were shipped annually from Iceland. Most of these were young, trapped as newly independent fledglings in their first summer of life, although some were migrants from Greenland. Considering the small size of Iceland — only about 39,709 square miles — and the large uninhabitable areas occupied by glaciers and lava fields, this was a staggering harvest and certainly must be reckoned as one of the heaviest, sustained predation pressures ever exerted on a geographically circumscribed falcon population. I personally doubt that there could ever have been more than 200 pairs of Gyrfalcons nesting on Iceland even during the best "ptarmigan years," probably considerably fewer than that number in most years. If one allows a generous average of two young fledged per pair, it appears likely that human depredations alone removed something on the order of 25 to 50 per cent — or more — of the annual production of fledged young. Yet there is no evidence that this degree of molestation had any depressing effect on the breeding population over several centuries.

This remarkable record of resilience by a falcon population to direct human depredation stands in such marked contrast to the current, widespread loss in numbers of breeding Peregrine Falcons *(Falco peregrinus)* as to emphasize once again the truly insidious nature of the agent responsible for the Peregrine's decline. Down through the centuries, not all the falcon trappers, egg collectors, war ministries concerned for their messenger pigeons, or misguided gunmen have been able to effect a significant reduction in the numbers of breeding falcons. But the simple laboratory trick of adding a few chlorine molecules to a hydrocarbon and the massive application of this unnatural class of chemicals to the environment can do what none of these other grosser, seemingly more harmful agents could do.

Evidently the falcon populations long ago evolved a social organization that strongly buffers the breeding pairs against numerical reduction, through the production of a large reservoir of sexually competent non-breeders, able to replace losses in the breeding population rapidly. Thus, under normal conditions the breeders, even with a low rate of reproduction, produce a large surplus of individuals with respect to total breeding opportunities. These surpluses have protected the falcons from the acquisitiveness of falconers and egg collectors for centuries. But when suddenly and continually subjected to a new class of chemical compounds in their food, chemicals that somehow reduce reproductive rates to levels so low that breeders are not replaced as rapidly as they are lost, the Peregrines have had no chance to evolve physiological resistance or any other effective countermeasures. Large segments of the Peregrine's former, nearly worldwide population seem doomed to extinction. Those who find pleasure in the lives of wild creatures can but hope that some local populations will remain free of the contamination, or that some falcon's will eventually be selected for resistance to chemical poisons, unlikely though that prospect seems at the moment.

For the time being at least, the status of the Gyrfalcon looks much more secure. It breeds in remote regions where direct application of chemical poisons is of very limited occurrence. More importantly, Gyrfalcons feed mainly on ptarmigan — an herbivorous food species low down in the food web and only one trophic level removed from the primary production of vegetation. Hence, there is limited opportunity for pesticide residues to accumulate in the Gyrfalcon's diet, as contrasted to the situation with the Peregrine, which feeds on insectivorous and carnivorous birds in whose bodies the residues have already had a chance to become concentrated. I was most encouraged in the summer of 1967 to find that breeding Gyrfalcons in arctic Alaska were as common as they have ever been during the past 15 years.

As the Peregrine and other desirable hawks become reduced in numbers in the more heavily populated parts of the world, modern falconers and would-be falconers will undoubtedly direct their attentions more and more to the Gyrfalcon. Contrary to what one reads in history books, falconry is not a dead sport. Many people tend to think of it as having been the chief pastime of the Middle Ages and to have died out with the advent of guns. One must keep several facts in mind about the Middle Ages, the human population, and falconry. In former times falconry was mostly the pastime of a privileged few, the nobility and the landed aristocracy, although it must be admitted that some ardent devotees like the Kublai Khan and the Emperor Frederick II employed hundreds of falconers and kept thousands of birds. But every man did not keep a hawk. Moreover, the total human population of the Middle Ages numbered only a few hundred million persons. Today it approaches 3.5 billion.

Since World War II there has been a great resurgence of interest in falconry, particularly in Europe and in the United States, where the old traditions of social restrictions on the use of hawks have never been known. Except among the oil-rich Middle East aristocracy, falconry is today mainly the hobby of an increasingly leisured middle class. No one knows how many falconers or keepers of hawks there are in the world, but 10,000 is probably the right order of magnitude (certainly there are more than 1,000 but fewer than 100,000). I think it is reasonable to assume that persons interested in falconry will continue to increase in some direct fashion with the overall increase in human population (currently predicted to double by about the year 2000). Clearly some point will be reached in time when uncontrolled demand for birds will outstrip the sustained yield of the falcon populations. At the present time we do not know for a single species of falcon or hawk what the safe level of harvest is.

The time has come when national governments should give consideration to the problems of man's relation with the birds of prey. It is not just falconers who are concerned. The plight of the Peregrine, how to regulate falconry on some equitable basis for falconer and non-falconer alike, how to insure the continued existence of rare and highly valued species like the Gyrfalcon — these are all problems involved in the larger concern for the kind of world in which we will live in the future. If we human beings are willing to exercise some judgment and some restraint, there is no reason why wild Gyrfalcons and Peregrines, and all their marvelous cohorts with hooked beaks and taloned feet, cannot be a part of the world of the 21st Century.

Hopefully, too, falconry will be able to survive the present excesses of some of its practitioners and, under legal regulations based on biologically sound estimates of harvestable surpluses, assume its proper role as the avocation of a few specially qualified and devoted experts. At the moment, a number of North American falconers — working through the Raptor Research Foundation, Inc. — are devoting considerable effort, and no little personal expense, to develop methods for breeding falcons in captivity. If successful, they may solve their own problem of a continuing supply of hunting birds, while at the same time providing scientists with a new means of studying problems relating to reproductive physiology, social behavior, and the influence of external factors like pesticides on the functioning of the birds of prey.

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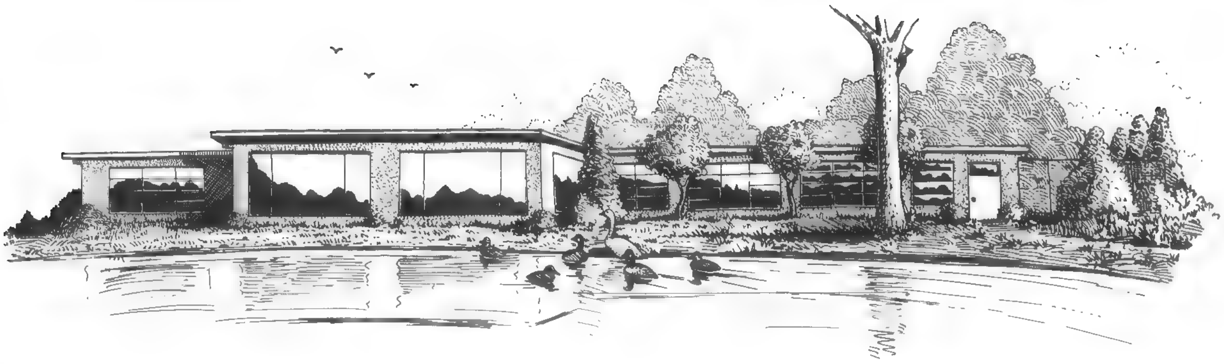
Black-and-white Warbler, *Mniotilta varia*. Drawing by Orville O. Rice.



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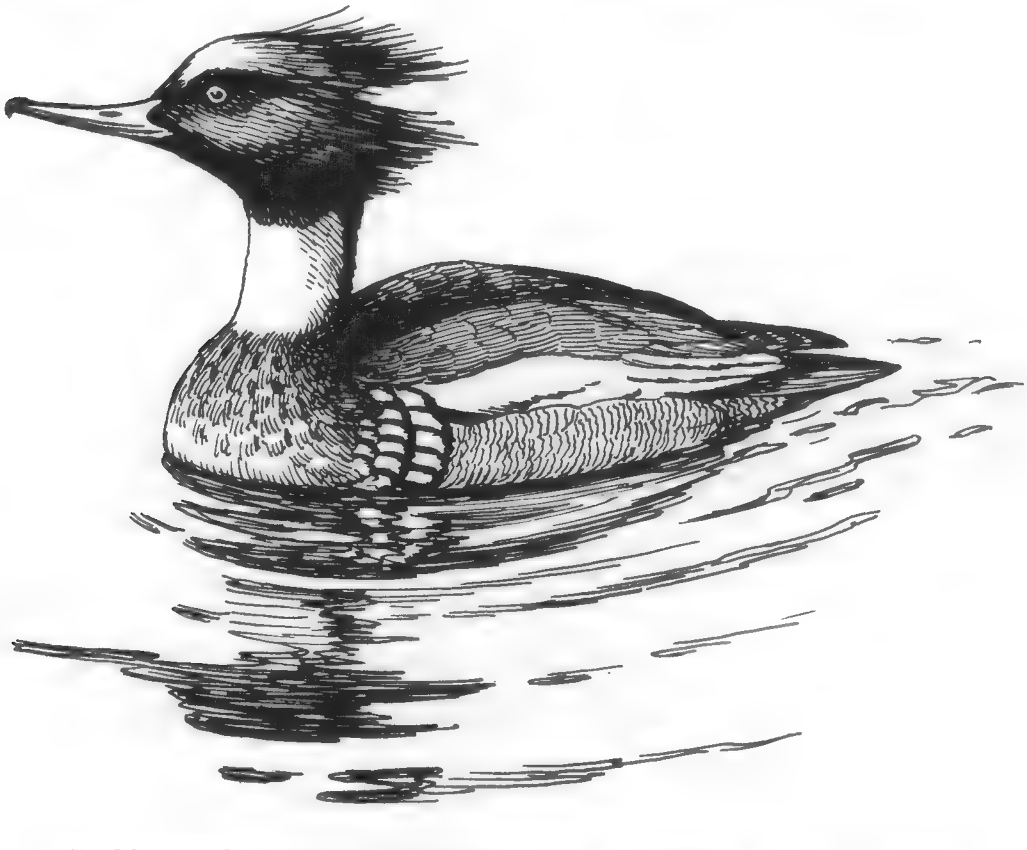

Red-breasted Merganser, *Mergus serrator*. Drawing by Orville O. Rice.

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Snowy Owls, *Nyctea scandiaca*. Drawing by John Busby.

Sparrow Hawk, *Falco sparverius*. Painting by Tony Angell.

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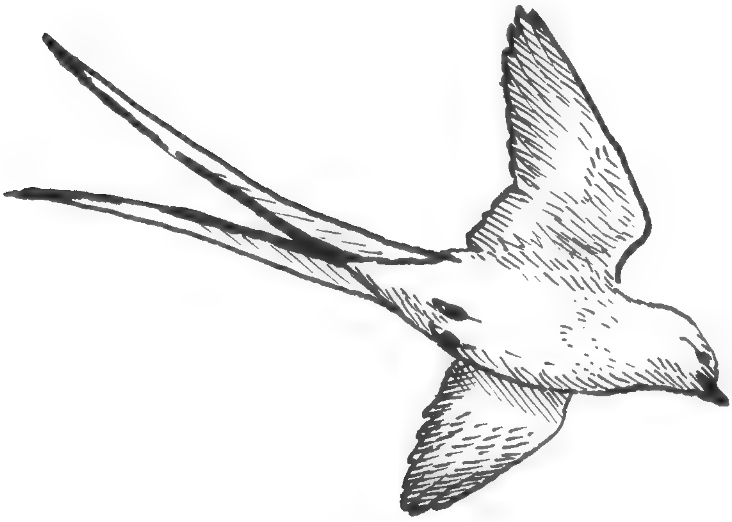

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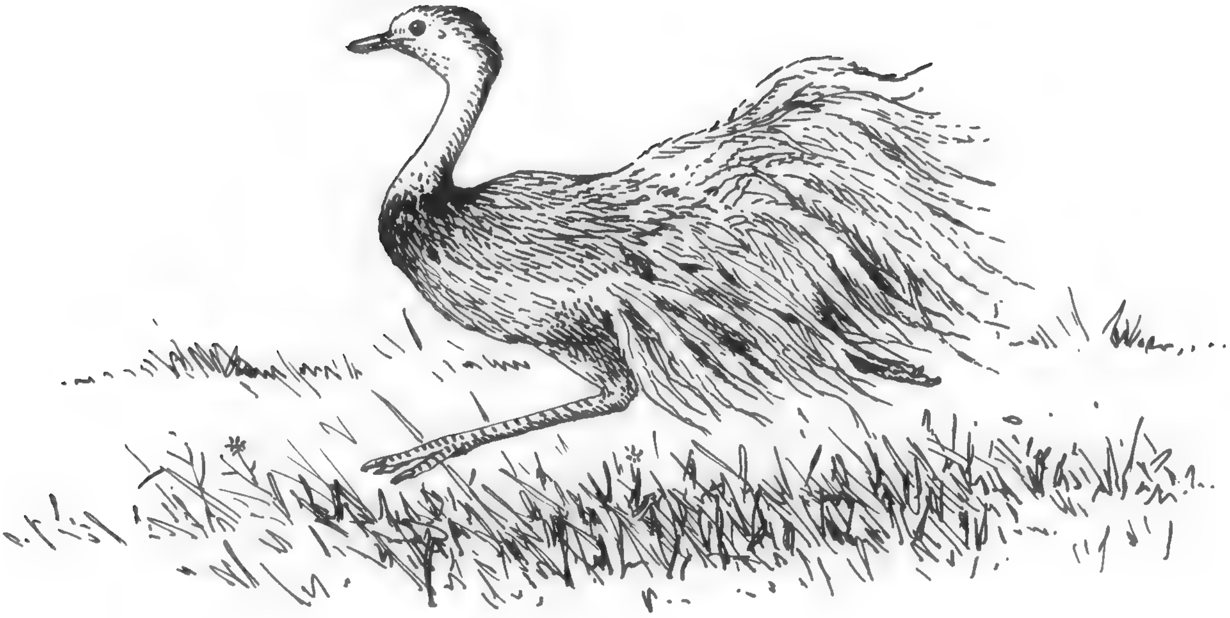

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Cape Robin, *Cossypha caffra.*
From a transparency by Peter Johnson.

A STUDY OF THE CAPE ROBIN IN SOUTHERN AFRICA

Mary K. Rowan
Photographs by Peter Johnson

The little "robins" of the genus *Cossypha* are particularly attractive members of the Ethiopian avifauna. Brightly marked in shades of orange and chestnut, they have the pert and lively manners typical of small Turdidae and often enrich their songs with sounds that mimic other animals including man. White (1962) recognizes 15 species, of which about two-thirds are true forest-dwellers and the remainder inhabitants of thick cover. Because the dense vegetation of the type they require occurs unevenly across the face of Africa, some of the species of *Cossypha* have a discontinuous distribution. The ranges of several overlap quite extensively, and, where this happens, the different species may live together or replace each other in an ecologically bewildering manner.

Sometimes a given species is inexplicably absent from places where we might reasonably expect it to occur. Elsewhere we may find the same species sharing a single habitat with one, two, or more of its congeners. These differences might be explained in terms of competition for their predominantly invertebrate food, but Oatley (1966) has argued that "optimum" nest sites in hollow stumps form the resource in short supply and that massive nest-predation is a "paramount factor limiting population increase." He believes that food is seldom, if ever, a serious problem in the "serene environments" of the tropics, to which most of the Cossyphas are confined.

There is, however, one exception. The Cape Robin (*Cossypha caffra*) is the only species widely distributed in the truly temperate environments at the southernmost end of Africa where it is very successful. It adjusts readily to man-made changes in the environment and commonly inhabits gardens in towns and villages throughout the Republic of South Africa. Yet, as with so many other familiar local birds, we have no detailed account of its biology.

Study Areas and Methods

This paper, resting largely on personal observations made during the past 17 years in the country between 22 and 34 degrees S Lat., attempts to fill the gap. The bulk of my notes are from four places in the extreme southwest: Tokai and Hout Bay in the Cape Peninsula up to 1956; subsequently, Claremont in suburban Cape Town and the farm Troughend at Stellenbosch (Figure 1). All these localities have a Mediterranean climate with rainy winters and warm dry summers. Stellenbosch and Tokai have been intensively

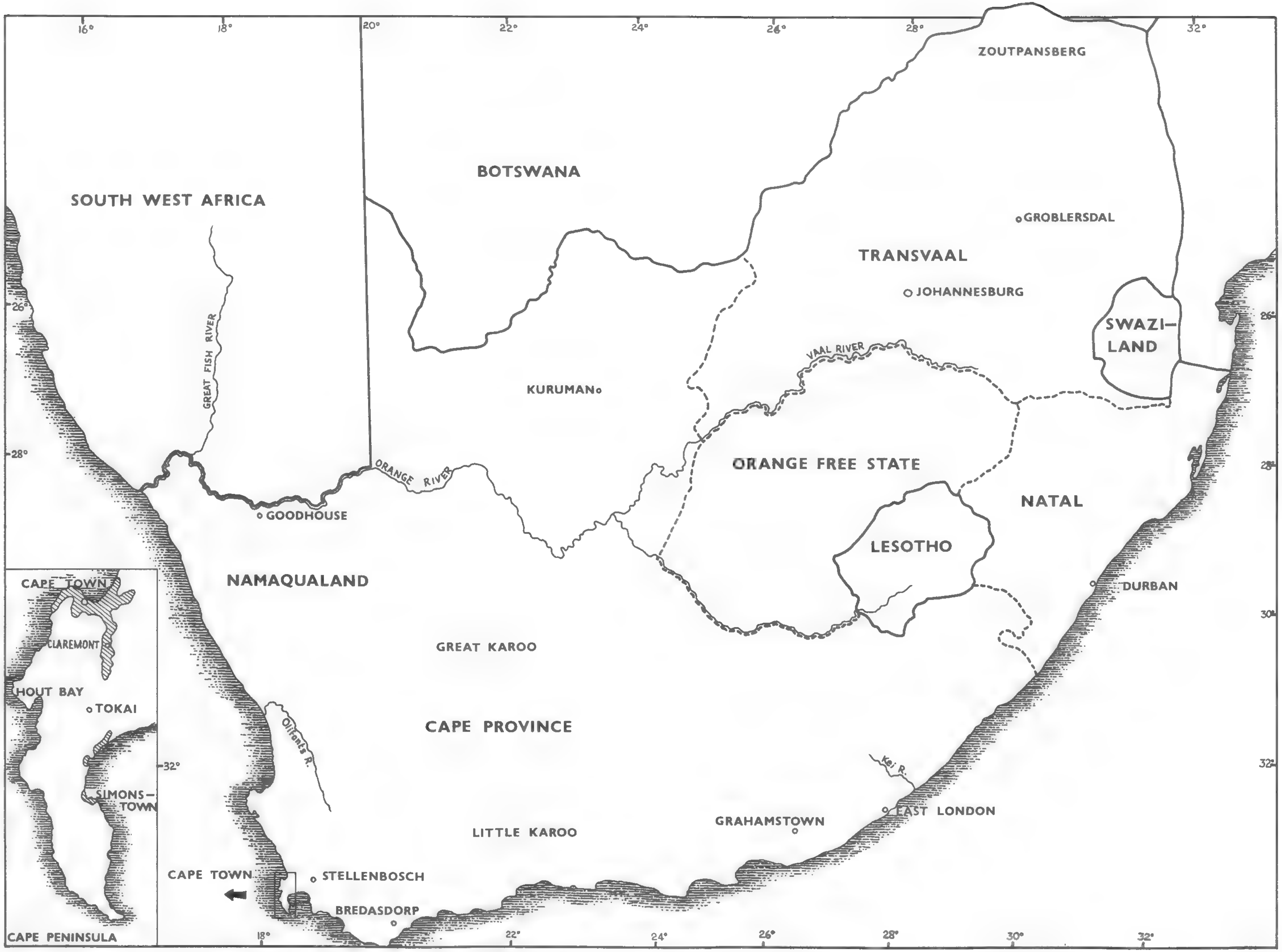

Figure 1. Map of South Africa showing places mentioned in the text. Inset: Cape Peninsula, in which three of the four main study areas were located.

cultivated in mixed-farming and fruit-growing for about 300 years; Claremont, with an average of four or five houses per acre, is a typical "garden suburb," but the mountain valley that formed my main study area at Hout Bay is probably little changed from its virgin state. Apart from a few acres of indigenous forest and a few groves of introduced trees, the slopes are clothed in the unique Cape sclerophyll vegetation, *fynbos,* dominated by proteas and heaths.

For further data I have drawn on many sources—notes contributed by friends, manuscripts from the Percy Fitzpatrick Institute of African Ornithology, and numerous fragmentary items scattered through the literature on African birds. In addition, the South African Ornithological Society has kindly allowed me access to its collection of nest-record cards, which provided the basic data for an analysis of breeding seasons and nesting success.

Description of the Cape Robin

The Cape Robin is small; a full-grown bird weighs about one ounce and the average of 40 weighed alive was 28 grams. Mainly olive-brown above and clear bluish gray below, it wears a bright orange bib and has a dark streak through the eye and a conspicuous white "eyebrow" extending from the base of the bill towards the back of the head. As in all species of the genus *Cossypha,* the Cape Robin (see Frontispiece) has a rich chestnut tail with two darker central rectrices—brown in this species, black in some others. The rump and vent are rufous.

Adult males and females are similar. Young birds, at fledging and for several weeks thereafter, possess a distinctive plumage—dark brown spotted with orange above and pale buff underparts finely speckled with brown. They lack the black feathering through the eye and have no superciliary stripe. Only their tails, absurdly short at fledging, have the typical adult coloring from the start.

Characteristic Behavior

Cape Robins hop on the ground, where they do much of their foraging, and are nimble on the wing, darting rapidly for cover if disturbed while feeding in the open. On alighting, the Cape Robin flicks its wings and momentarily fans its tail, revealing the dark central stripe (Figure 10).

Highly covert in undisturbed habitats, the Cape Robin often becomes remarkably confiding where it lives in association with man, making regular use of bird baths and food tables in suburban gardens. There is much local folklore concerning wild robins that have learned to take mealworms (*Tenebrio*) from the hand, that enter houses to steal butter from the table, or that boldly share with the family dog fragments of meat and porridge from its dish.

Distribution and Habitat

The Cape Robin occurs throughout the Republic of South Africa and in the enclaves of Lesotho and Swaziland. It is found in southern South West Africa and, from the Transvaal, extends northwards into eastern Rhodesia, Malawi, Tanganyika, Kenya, and the extreme south of the Sudan. However, it is not continuously distributed over this vast range. In the extreme south, it is found at all levels down to the coast. In the moister (mainly eastern) parts of the interior it is similarly general and widespread; but in the more arid areas to the west it is confined to the denser vegetation found only along drainage channels or in sheltered valleys. In the high grasslands of the Transvaal and the Orange Free State, it is probably a comparatively new component of the avifauna, since these areas formerly afforded no suitable habitat; but today it is widespread in the parks and gardens developed by man. On the east coast, from about Port St. Johns northwards, the species is known only as a nonbreeding winter visitor, but its status here is unique. Throughout the rest of its range, the Cape Robin occurs as a resident, with settled pairs to be observed in their territories all through the year.

From Rhodesia northwards, this species, like some of its congeners, is not generally distributed, but is restricted to a series of "island" populations, all at high altitudes. This has led some workers (e.g., Liversidge, 1959) to suggest that high temperatures may limit its range. However, for reasons to be developed elsewhere, I cannot subscribe to this view and believe that other explanations must be sought. Possibly competition with its relatives is important, and there is a possibility, suggested by Warner's (1968) work on Hawaiian honeycreepers (Drepanididae), that arthropod-borne diseases of wildlife may be a limiting factor in these tropical environments.

In all parts of its range the Cape Robin exhibits a wide tolerance towards climatic and floristic variables. It lives and breeds successfully in the widely divergent regimes of South Africa's summer and winter rainfall regions, and also in those areas where rain may fall at any season. It occupies almost every broad botanical association, wherever growth is thick and lush enough, whether the vegetation is predominantly sclerophyllic, karoid, or a part of the main African flora. However, unlike other Cossyphas, it is not a forest bird, although it often occurs along the forest fringes. The main features of its preferred habitat seem to be: a good deal of dense cover from ground level to height of four feet or more; some trees or other vegetation of sufficient height to supply prominent songposts; and ideally, but not essentially, some open ground over which to forage. Thus, the Cape Robin, like man, tends to seek places affording sun, shadow, and privacy in adequate admixture, which is perhaps why it is so consistently present in gardens from the Cape to the Transvaal.

Food

Cape Robins feed predominantly on insects although they often take other invertebrates as well: earthworms, amphipods, spiders, centipedes, and the exotic snail, *Theba pisana*. In coastal areas birds may venture right down to the edge of the sea where they feed on small Crustacea in the tangled masses of seaweed cast ashore (Robinson *et al.*, 1957). Occasionally even small frogs and lizards fall prey to these vigorous little hunters (Liversidge, 1955), and seasonally they may take a limited amount of fruit: garden mulberries or the drupes of indigenous plants such as wild peach (*Kiggelaria*) and wild fuschia (*Halleria*). They also eat the succulent red seedstems of an introduced Australian wattle (*Acacia cyclops*) and in so doing may assist in the alarming spread of this exotic plant.

Songs and Calls

Belcher (1930) described the Cape Robin as "the sweetest singer of all African birds." Although some of its forest-dwelling congeners vie for title, *C. caffra* performs ably and generously, singing for the greater part of the year.

Typically, song consists of a series of short passages, each beginning with a muted whistle that slurs down the scale and is audible only at close quarters. This is followed by a musical phrase of four to ten sweet clear notes and a momentary pause before the next passage. The bird may use a succession of entirely different phrases or repeat a single one several times, often with slight changes in pitch, volume, or rhythm. The most versatile singers have a number of themes with many variations.

The most sustained song occurs early in the morning or in the evening with bursts of up to 20 minutes duration. Intermittent singing normally continues throughout the day unless the weather is windy or very hot.

Although less given to mimicry than other members of the genus, *C. caffra* quite often uses the notes of other birds, including mousebirds, *Colius* spp.; bulbuls, *Pycnonotus* and *Andropadus;* various thrushes of the genera *Turdus* and *Monticola;* Boubou Shrikes (*Laniarius ferrugineus*); certain starlings (*Sturnus vulgaris* and *Onychognathus morio*); several sunbirds, *Nectarinia* spp.; White-eyes (*Zosterops virens*); and some "canaries" (*Serinus canicollis* and *S. albigularis*). Doubtless we could extend the list. C. J. Skead (pers. commun.) told of one Cape Robin in his garden at King William's Town in whose songs he could recognize the notes of over 20 different species. The birds are specially prone to imitate cuckoos, in particular the Red-chested (*Cuculus solitarius*), the Didric (*Chrysococcyx caprius*), and Klaas's (*C. klaasi*) Cuckoos, often in winter when cuckoos are absent or silent.

Some Cape Robins will engage in whistling contests with a human being, often copying and occasionally learning the sequence of notes used. One regularly reproduced my neighbor's whistle for his dog so faultlessly that the bewildered beast often came running at the bird's bidding. However, banding reveals that individuals vary greatly in the extent to which they borrow sounds from other species. Some Cape Robins seldom, if ever, imitate; others do so constantly.

Close observation of paired robins suggests that full song is mainly, perhaps entirely, by one partner, presumably the male; and that it functions primarily in territorial advertisment and defence. Two marked individuals, believed to have been females on the basis of their nesting behavior, occasionally uttered brief, muted phrases, but never indulged in the sustained singing regularly heard from their mates. Song seems to serve little, if at all, as a means of communication between the sexes.

Both members of a pair regularly use an alarm call, low-pitched, guttural, and usually trisyllabic, which seems to be important in maintaining contact in the dense vegetation they inhabit. Its utterance by one bird normally brings the other promptly to its side. Cape Robins sometimes render a distress call rather like the quiet ticking of a clock. I have heard it from adults while I handled their chicks for banding, and also from birds engaged in territorial or interspecific skirmishes. It is audible only at close quarters.

Juveniles have a thin whistling call, uttered persistently once they leave the nest, often for minutes at a time. I suspect that it serves to advertise their whereabouts to the parents. Normally the juveniles fall silent at the sound of a parent's warning cry.

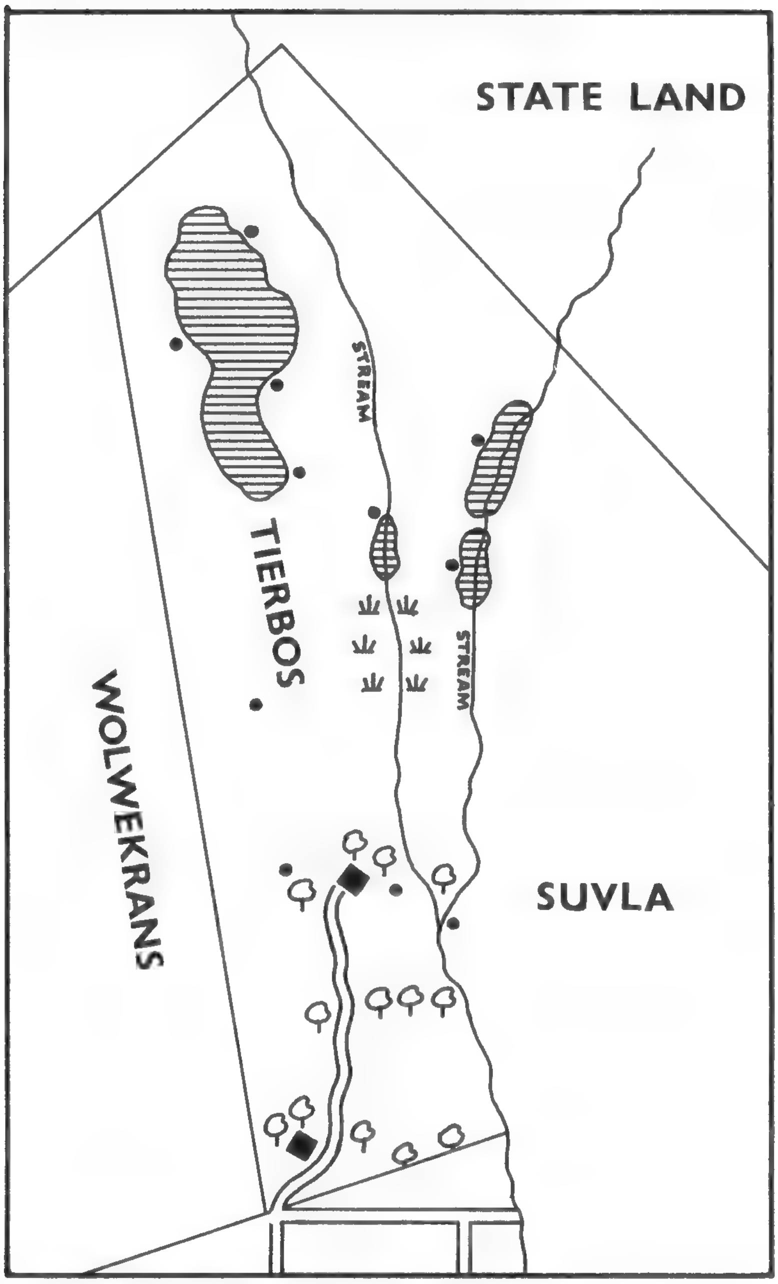

Figure 2. Sketch map of "Tierbos" where Hout Bay observations were made. The area, about 100 acres in extent, lies in a mountain valley from 300 to 1,000 feet above sea level. Dots represent the approximate centers of 13 known Cape Robin territories. Cross-hatching indicates remnants of indigenous forest. Vertical lines mark the marsh. Silhouettes of trees show introduced trees, scattered or in windbreaks. Solid blocks indicate dwellings.

Territory

Tenure of Territory

Mated Cape Robins are highly territorial. The pairs remain together on their territories all year round. Observations of a limited number of color-banded birds at Hout Bay and Stellenbosch suggest that these unions endure as long as both birds live. If one dies, the surviving male or female normally remains on the territory and soon secures a new partner which evidently learns and accepts the boundaries observed by its predecessor.

The history of territory A at Hout Bay illustrates the usual sequence of events. A banded robin AL, believed to have been a female on the basis of singing and nesting behavior, occupied area A for three and a half years. I last saw AL's original, but unbanded, mate during May of the second year. By June, AL had another mate ED, a bird caught and banded as a juvenile during the preceding summer at a point about half a mile from area A. When

AL disappeared about 15 months later, ED remained on the territory with another unbanded mate for at least one more year.

In three other instances banded birds, two males and a female, disappeared, but the surviving mate quickly obtained a new partner without disturbance of neighboring pairs or of territorial boundaries. Thus, individual holdings tend to continue for years without significant changes in size or shape. A similar state of affairs in which pairs remain settled on territory all year round has been reported for other species—e.g., the South African Crowned Hornbill, *Tockus alboterminatus* (Ranger, 1949-1952); the South African Black Crow, *Corvus capensis* (Skead, 1952); the South African Red-winged Starling, *Onychognathus morio* (Rowan, 1955); the American Plain Titmouse, *Parus inornatus* (Dixon, 1956); and the Australian Blue Wren, *Malurus cyaneus* (Rowley, 1965).

Source of Recruits

The source of birds filling vacancies in the ranks of territory-holders is difficult to determine. The fact that replacements always move promptly into available vacancies, without disrupting neighboring pairs, implies a nonbreeding reserve of territory-less birds. This is a contentious conclusion (see arguments in Lack, 1953:145), but some field evidence supports it. For instance, during the past 12 years I recorded 21 territorial skirmishes between single birds and settled pairs. These occurred in every month from February to October with the highest frequency in April, indicating that territory-less individuals may challenge territory-owners at all times of the year except from November to January, the height of the austral summer which is the molting season for this species in the southwest Cape.

However, such incidents are rather rare and banding activities indicate a greater number of robins without territory than the 21 skirmishes suggest.

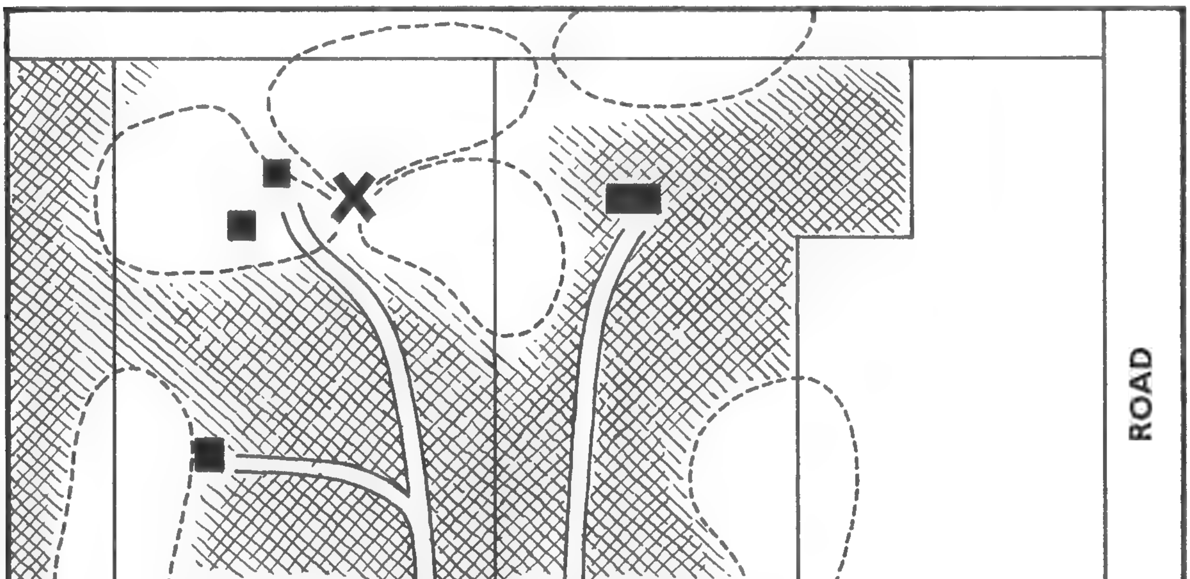

Figure 3. Sketch map of study area at Tokai. Rose Farm and Charnwood are each about five acres in extent. Solid blocks indicate dwellings. Solid lines represent fences and hedges separating properties. Dotted lines show the approximate boundaries of Cape Robin territories. Cross-hatching indicates open lawns, pastures, and vineyards, affording no suitable habitat. X marks at point at which there was much territorial skirmishing.

This first emerged during a "Field School," conducted by the Fitzpatrick Institute at Bredasdorp, Cape, in September, 1962. We stretched mist nets across two known territories, and caught and color-banded six Cape Robins, none of them residents of the two territories. The four birds in possession of the area evidently perceived the nets at once and evaded them. At first, I considered the six marked birds as trespassers from neighboring territories. However, we soon discovered that all adjacent areas were held by unmarked birds. Although teams of students quartered all the surrounding habitat suitable for robins for a radius of about one mile and searched for five days, we never saw any of the marked individuals again.

At the same locality, in September 1965, we netted and color-banded five more Cape Robins. And, as before, they all disappeared after release while the unmarked territory-holders remained in possession of the area. MacLeod (1964) reported a similar experience on a farm near Somerset West where he banded the astonishingly large total of 103 Cape Robins between February to May 1963. Later, he returned to the farm and spent three weeks searching especially for the banded birds. He failed to find one although Cape Robins seemed as plentiful in the area as before.

From these observations it appears that any stretch of suitable habitat, occupied by settled pairs, may also harbor a fair number of nonresident birds, which behave so secretively that their presence would not be suspected, but for some special circumstance, such as the netting activities described above.

Quite probably the reserve of nonresident Cape Robins is composed mostly, or entirely, of birds of the year. Presumably, this age-group also supplies the migratory fraction of the population—those birds which recur seasonally in regions such as the Natal coast where the species is not known to breed. Indeed, because established territories are so continually occupied, at least in the southern part of the range, it seems impossible to account for regular migratory movements in any other way. The birds that migrate to nonbreeding areas are evidently quite bold, often singing in their winter quarters, in contrast to the silent and secretive behavior of the floating population in other parts of the range. This seems to support the view that any reserve of unmated birds must live somewhat precariously in areas where the habitat is already parceled out among permanently settled pairs.

Size of Territory

The size of the areas defended by territory-holders varies considerably from place to place. I have satisfactory measurements from only three types of habitat. The largest territories known to me cover 5,000 to 9,000 square yards in the *fynbos* at Hout Bay where some are adjacent and others separated by tracts of apparently unclaimed and usually treeless land (Figure 2). At the other end of the scale are the small and crowded holdings in the orchard-and-garden environment at Tokai. Here, in a 10-acre area, six territories, varying in size from 600 to 620 square yards, occupied every scrap of suitable habitat (Figure 3). A similar high density of small territories occurs in the same sort of environment around the farm homestead at Troughend. Intermediate in size are the territories in mature coastal scrub at Bredasdorp. Nine averaged 3,000 square yards with extremes of 1,700 to 5,000 square yards (Figure 4).

The largest territories were more than 10 times greater than the smallest. In other songbirds of similar size and habits differences of the order of three to five times are more usual (Lack, 1953). In her studies of the Wrentit

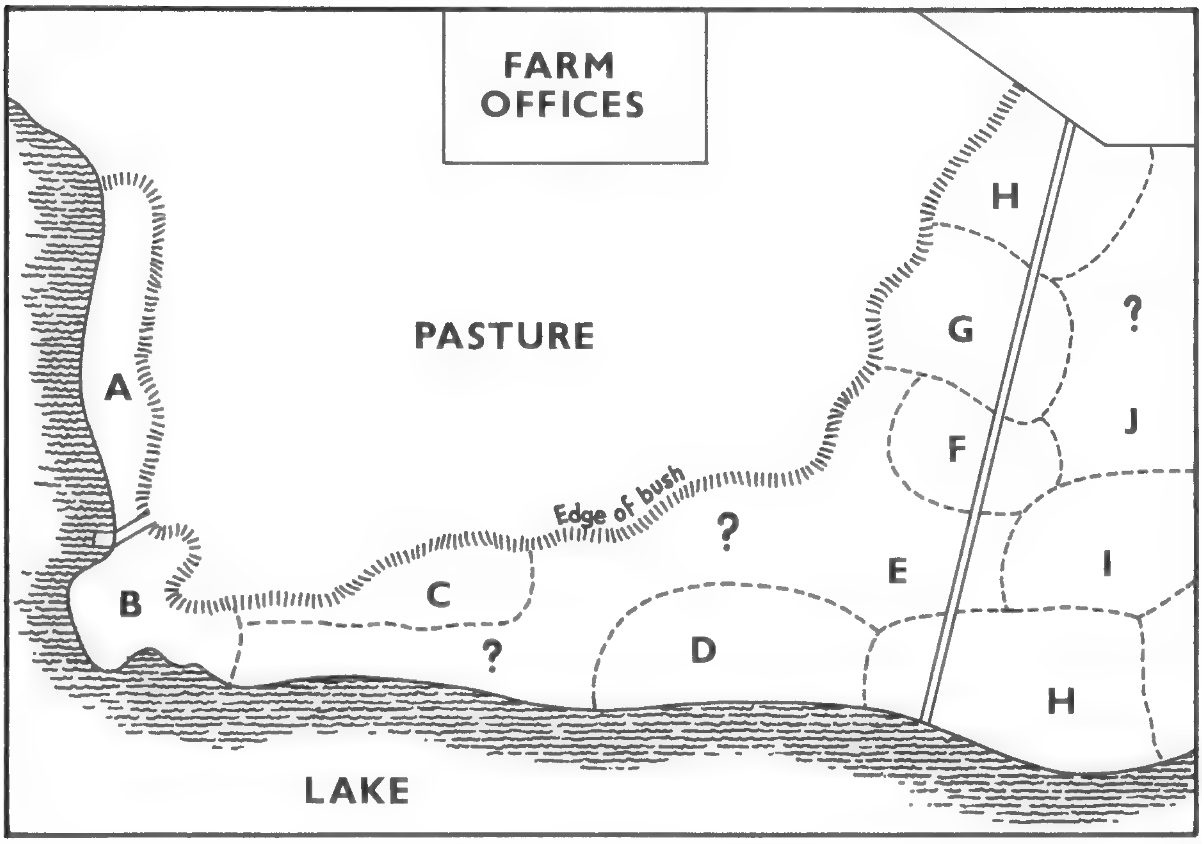

Figure 4. Sketch map of a portion of the Cape Nature Conservancy's farm, De Hoop, at Bredasdorp, showing the approximate boundaries of nine Cape Robin territories, located in a stretch of mature coastal scrub on the shores of a lake. Pairs E and J occupied territories at the points shown, but their boundaries were not determined and there may have been two or three further pairs in the areas marked with queries.

(*Chamaea fasciata*), Erickson (1938) related the variation in territory size to the length of the defended border. In the Cape Robin also, territories tend to be smaller when surrounded on all sides than when they have a boundary that need not be defended. However, the most striking result of this study of territory size is that the variation in size within any one of the three habitats is never as great as it is between the habitats. This suggests some relationship between the extent of the defended area and the productivity of the environment.

In the past the hypothesis that the size of the territory may be related to the amount of food available has frequently been suggested and frequently disputed (Lack, 1966), the arguments for and against being centered around birds with fairly rigid habitat requirements. The Cape Robin, occupying different botanical associations, affords opportunities for comparison at another level. The *fynbos,* in which we find the largest territories, is the poorest environment for mammals as well as birds, having comparatively few species per acre and few individuals per species. Mature coastal scrub, as at Bredasdorp, is much the richest in number of species; and orchard-and-garden environments have the highest number of individuals among birds that have adjusted to man-made changes. Winterbottom (1965) and Siegfried (1968) have summarized relevant figures. Thus, territory size in the Cape Robin varies in different habitats in accordance with the density of the avifauna as a whole, again supporting the conclusion that size may be related to the productivity of the environment.

Advertising in Defense of Territory

Only one member of the pair, presumably the male, engages in territorial advertising, and vigorously proclaims ownership for the greater part of the year. While some birds may sing from any point within the territory, most have from one to six favored songposts. In the Cape region, song usually wanes towards the end of the breeding season (October) and dies away altogether by the middle or end of November when adults start to molt. In crowded areas, as at Tokai, intermittent song may persist throughout the molt, but usually territory-holders are silent, apart from regular exchange of alarm calls, for a period of six to eight weeks.

Once Cape Robins are in fresh plumage, it seems to depend largely on the weather when they start singing again. For instance, at Hout Bay in 1953 I noted the first few song phrases of the year in the evening of 13 January and then heard no more until 20 January when, following a heavy overnight rain, Cape Robins suddenly came into full voice throughout the valley. The following year the weather was cool and overcast on 4, 5, 19, and 23 January. Although I heard desultory phrases on all four days, song did not become general until 28 January when there were light showers. Similar, but less detailed, records for other years and places confirm that resumption of singing is usually associated with cool overcast days or with rain and suggest that the species may respond to changes in humidity.

Territorial encounters between neighboring males rarely amount to anything more than singing bouts, but physical displays and even fighting do sometimes occur, mainly when a single bird persistently intrudes on a territory.

The owner may threaten an intruder with a display in which it holds the body upright, fluffing out the rufous rump feathers, and moving the half-fanned tail up and down, from the vertical to horizontal, very slowly in contrast to the normal rapid flick. Sometimes skirmishes consist of singing bouts alternating with chases and may be remarkably prolonged. One such incident, observed at Tokai in February 1952, started at 7:45 AM and was still in progress at 4:00 PM. As usual the female accompanied her mate throughout the encounter but took no active part in it.

Occasionally Cape Robins behave aggressively toward other species. At Hout Bay one marked bird regularly attacked Orange-breasted Sunbirds (*Nectarinia violacea*) and usually, but not always, drove the sunbird away. Most remarkable, however, was an incident at Tokai. A pair of Malachite Sunbirds (*N. famosa*) entered a small orchard where the territory-owner perched in song. The robin stopped singing at once, flew at the male sunbird, and chased it, both birds twisting and turning among the trees. Whenever the robin caught up with the sunbird, it struck with its bill; the sunbird retaliated. Finally locking claws, they fell fluttering to the ground where they struggled in the long grass for a few seconds. Then the sunbird escaped and flew off followed by its mate and, for a short distance, by the robin. During the encounter the female sunbird perched on a branch, uttering sharp little cries and bouncing up and down; the female robin was nowhere to be seen.

Other observers have recorded robins attacking White-eyes (*Zosterops virens*) and doves.

The Breeding Season

For this study I analyzed about 850 breeding records, chiefly for the years 1954 to 1966. Almost three-quarters were from the southwest Cape and the rest from elsewhere in the Republic.

Table 1 shows the number of monthly breeding records, expressed as percentages of the totals for each climatic area. In most parts of the range, laying is restricted to a four-month period, five months in the eastern Cape, but there are regional shifts in timing. The season is earliest, July to October, in the winter rainfall area; intermediate, August to November, in the eastern Cape; and latest, September to December, in the summer rainfall areas. Thus the breeding tends to follow, or coincide with, the wet season and in most parts is also associated with rising temperatures. In the southwest Cape, however, egg-laying begins in the coldest month of the year.

TABLE 1

Breeding Seasons of the Cape Robin

Climate and region	*Number of nests*	*Percentage of nests with eggs**							
		June	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*
Winter rainfall**									
Southwest Cape	573	x	9	30	34	24	3	x	–
Summer rainfall**									
Highveld: Orange Free State and Transvaal	94	–	–	4	15	35	29	15	2
Natal midlands	57	–	–	–	14	25	33	28	–
Rain at any season**									
Eastern Cape	100	1	3	11	21	22	32	8	–
Rhodesia and Malawi***	22	–	–	–	5	27	59	19	–

*Included are brood records, adjusted to dates when eggs were probably in the nest.

**Data largely from nest-record cards of the South African Ornithological Society and supplemented from personal files and the literature.

***Data from Benson *et al.* (1964).

x Less than 0.5 per cent.

Curiously, regional differences in the months showing maximum breeding activity do not exactly match regional differences in the breeding season as a whole. A September peak in the southwest is followed by an October peak in the Highveld and a November peak in all other areas. I am unable to suggest any reason for this deviation which, of course, may be no more than artifact. It also is curious that, although the Cape Robin is double brooded at least in the southern part of its range, none of the breeding frequency curves is bimodal—i.e., shows two peaks. This is possibly because many nests fail, and numerous "repeat" nests are begun well before the bird would normally undertake a true second brood.

The Cape Robin builds at rather low levels and conceals its nest well. Only 35 per cent of all records are for nests three feet or more above the ground, the highest at 11 feet. About 40 per cent ranged between one and

Figure 5. A Cape Robin standing on the edge of its nest. The tangle of dead grasses and sticks, left by a flood in a poplar copse, offered the bird an ideal site for a nest—an accumulation of debris not too far above the ground. Over three-quarters of the nests were hidden in dense vegetation of great variety; others were in dead brush or hollows in earth banks. A few robins occasionally build nests in artificial sites—cartons on rubbish dumps, empty tins in garden sheds, or even in potted plants on a veranda.

Figure 6 (*above*). A Cape Robin coming to its nest with food. This nest, like the one opposite, was built in a pile of flood debris rather close to the ground. Johannesburg, 1968.

Figure 7 *(below)*. A closer view of the Cape Robin pictured above. In the nest, which is more exposed than is usual in this species, are two downy young waiting for the food.

three feet, and the remaining 25 per cent were on or very near the ground. Roughly 80 per cent were hidden in dense vegetation of different kinds: rank grass and weeds, clumps of arum or calla lilies (*Zantedeschia*), leafy bushes such as *Protea* and *Rhus,* the crowns of tree ferns, the axils of *Aloe* leaves and palm fronds, and a variety of garden shrubs, hedge plants, and creepers.

About seven per cent of nests were built in heaps of dead brush (Figures 5, 6, and 7), and a similar proportion in hollows in earth banks, often beside streams. However, if sorted geographically, the records show that Cape Robins used such nesting sites more frequently in the Natal midlands, 40 per cent, than in the southwest Cape, eight per cent. Perhaps this is because the vegetation of the interior is partly deciduous, and cover may be thin at the onset of the breeding season, whereas the evergreen coastal vegetation of the Cape provides adequate shelter all year round.

Occasionally robins use artificial situations and build in potted plants on verandas, in old cartons on rubbish dumps, and in discarded tins or sheltered corners of open garden sheds. Very few of the recorded nests, less than three per cent, were in holes in trees. This is relevant to the contention of Oatley (1966) that hollow stumps provide "optimal" nest sites for the forest-dwelling Cossyphas of the tropics, and that competition for this resource constitutes a major limiting factor in their population ecology. In the light of the data reviewed above, it seems unlikely that the same considerations apply to *C. caffra* which is clearly adjustable in its nesting behavior and brings off young in a wide variety of situations.

The Cape Robin's nest is a fairly solid structure resting on an untidy foundation of twigs, roots, bits of bark, moss, and dead leaves. On this the bird builds a small pile of dry vegetation in which it forms a cup by shuffling and wriggling its body into the mass. It then lines the bowl neatly, and smooths the rim with thin pliable grasses, rootlets, finely shredded bark, hair, and similar materials. From start to finish building may occupy from six to 14 days, occasionally longer. In an average of 21 measurements the final structure had an internal diameter of 7 cm, with extremes of 6 to 8 cm, and an internal depth of 5.5 cm, with extremes of 5 to 6.5 cm.

Like many other small passerines, the Cape Robin builds in spurts, most busily in the morning and least so at midday. During an active spell, it visits the nest every two or three minutes. Then for an hour or more the nest may receive no further attention. Some birds seem to abandon work at the least disturbance or sign of adverse weather; others continue building even in pouring rain. Although both members of the pair occasionally go to the nest together as in four out of a series of 25 visits recorded at Tokai, the male's participation seems to be limited to infrequent escort duty. I never saw any of my banded males contribute any material. Advertising song occupies much of the male's time while the female works on the nest.

Egg-laying usually starts from one to four days after the nest is finished, but may be delayed for as much as a fortnight. It is unusual, but not unknown, for a nest to be used more than once; and there are occasional records of nests, built and abandoned in one season, being used in the next.

Eggs, Clutch Size, and Laying Rate

The eggs of this species are beautiful and highly variable in color. Occasional clutches are immaculate turquoise, buff, or creamy pink; but most eggs are speckled, blotched, or penciled in shades of fawn, reddish brown, or chocolate on a ground color that varies from off-white to buff, pink, or pale green.

Sometimes the markings are fine and sparse, sometimes concentrated at the larger end, and sometimes so densely distributed that the entire egg appears brown. Average measurements for 106 fresh eggs in 46 clutches are: 23.5 (21.0 to 25.8) by 16.8 (15.5 to 18.3) millimeters.

The small clutch never numbers more than three eggs and two-egg clutches are recorded about twice as frequently as one-egg and three-egg clutches combined. One-egg clutches are probably incomplete. None on record survived to hatching and most were deserted before incubation began. There is a tendency for the size of the average clutch to increase with decreasing latitude from 2.17 eggs in the southwest Cape to 2.50 in the Transvaal and 2.57 in Natal (Table 2). This is a reversal of the normal situation found in birds, but it could be explained in terms of Cody's (1966) "general theory of clutch size," if we postulate simply that the winter rainfall region provides the species with the most stable of all the environments that it occupies—a hypothesis which is probably true.

The nesting records also show a tendency for clutch size to increase as the breeding season advances, reaching a maximum in November in all parts of the country, except the southwest Cape, where there is no significant seasonal change.

TABLE 2

Average Clutch of the Cape Robin

Region	*Months*						*Totals*
	July	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	
Southwest Cape							
Two-egg clutches	27	80	106	65	7	–	345
Three-egg clutches	3	9	24	23	1	–	
Total eggs	63	187	284	199	17	–	750
Average clutch	2.1	2.1	2.2	2.2	2.1	–	2.17
Eastern Cape							
Two-egg clutches	–	4	11	10	13	1	62
Three-egg clutches	–	–	1	6	14	2	
Total eggs	–	8	25	38	68	8	147
Average clutch	–	2.0	2.1	2.4	2.5	2.6	2.37
Natal							
Two-egg clutches	–	–	3	6	3	4	38
Three-egg clutches	–	–	2	3	10	7	
Total eggs	–	–	12	21	36	29	98
Average clutch	–	–	2.4	2.3	2.8	2.6	2.57
Highveld							
Two-egg clutches	–	–	5	15	6	7	66
Three-egg clutches	–	–	3	11	15	4	
Total eggs	–	–	19	63	57	26	165
Average clutch	–	–	2.3	2.4	2.7	2.4	2.50

Females usually lay at the rate of one egg a day until the clutch is complete. The first is most often laid an hour or more after sunrise, for example, between 8:00 AM and 10:00 AM in September in the southwest Cape, and the second two or three hours later than this on the following day. The third, if there is one, is a little later still, so that intervals between eggs tend to be slightly in excess of 24 hours. However, R. A. Reed (pers. commun.) reports two exceptional nests on the Witwatersrand in which the third eggs were deposited at least 40 hours and perhaps as much as 60 hours after the second.

Incubation

Since it is impossible to see rings worn by a sitting bird, I found it difficult to establish in this sexually monomorphic species whether the male and female share incubation. Thus, although I suspected that the male Cape Robin took no part, I could not prove it until, at Hout Bay, I discovered an individual always recognizable by a small imperfection in its plumage—a smudge of black feathers marring the otherwise immaculate white of its left "eyebrow." This bird built its nest unaided by its mate, incubated the eggs by itself, and covered the young after hatching (Rowan, 1953). Similarly, at a nest parasitized by a cuckoo, Liversidge (1955) noted that one of the foster parents, which he distinguished by a damaged tail, did all the incubating and later all the brooding of the chick. Thus is seems probable that in *C. caffra,* the female normally discharges these duties.

Attentive periods during incubation tend to be fairly prolonged and absences brief—a few minutes at a time, except in the early morning and late afternoon when the female often leaves the nest for 20 minutes to an hour or more. There is, of course, considerable individual variation in incubation behavior, but many of the birds, observed in the course of this study, spent so much time on their eggs that it seems doubtful whether they foraged as much as four hours a day. In several related African Turdidae, the males contribute to the incubating female's diet, but I never saw a male Cape Robin bring food to its mate on the nest.

At four out of six nests, observed closely during the laying period, the females started incubating as soon as their clutches were complete; at two others there was a definite delay. The details are best known in the case of the female with the imperfect eyebrow. She laid her last egg between 9:00 AM and 5:00 PM on 19 September. When I visited the nest after dark that night, I found no incubating bird, and the clutch of three was cold. All through the next day and night the eggs were unattended and when the eggs were still cold at 8:00 AM on 21 September, I feared she had deserted the nest. However, at 4:00 PM that afternoon, the eggs felt warm to the touch, and from then on the female sat closely. The 48-hour interval between clutch completion and the start of incubation did her offspring no harm. All three hatched between 10:00 AM and 6:00 PM on 6 October.

Observing the convention that incubation is measured from the laying to the hatching of the last egg (Moreau and Moreau, 1940), the period at this nest was 17 days and one hour plus or minus eight hours. However, if we allow for the female's initial neglect, the actual incubation was almost exactly two days shorter—i.e., 15 days and one hour plus or minus nine hours.

Among the nest records of the South African Ornithological Society, 16 provided sufficient information for calculating the interval between the laying and hatching of last egg. These data, combined with my own for six nests, show an average incubation period of 16 days plus or minus one hour, with extremes of 14.5 days at one nest and 17.5 at three others. (Possible errors vary from six to 24 hours either way.) The three-day difference between extremes seems very large in relation to the total period. Furthermore, a closer examination of the data suggests that the average is an artificial value, because at only one of the 22 nests was an interval of 16 days actually recorded. The rest of the readings fall into two groups clustered around periods of 15 to 15.5 days and 17 to 17.5 days (Figure 8).

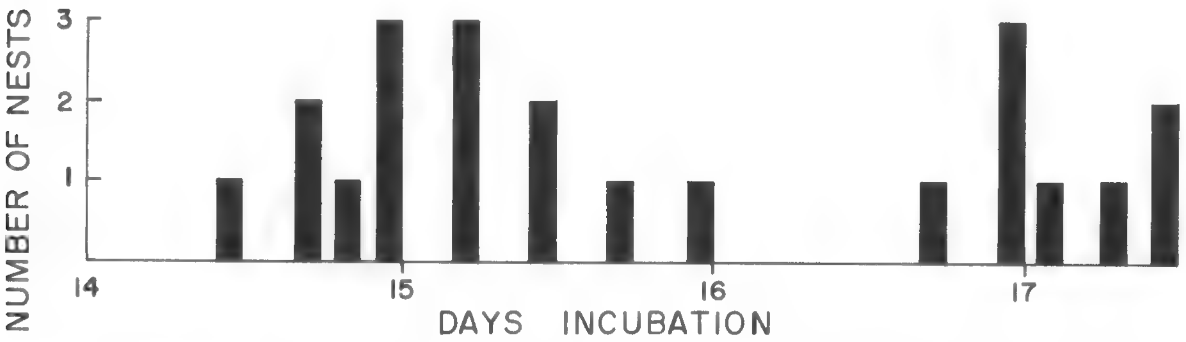

Figure 8. Incubation periods. Sixteen nest records from the files of the South African Ornithological Society, combined with six of my own, provided the information for calculating the interval between the laying and hatching of the last egg in the clutch.

The most likely explanation for this variation in incubation periods seems to be that a proportion of Cape Robin females, roughly 40 per cent of the sample available, behave in the same way as the bird with the imperfect eyebrow, deferring the start of incubation for about two days after laying the last egg. Why they should do so is far from clear. We must presume that the delay relates (proximately) to the physiological state of the bird since a shift in the hormonal balance is required before full "broodiness" occurs. Skutch (1962) showed that "normal constancy in incubation" often takes a day or two to develop, especially in tropical species with small clutches. However, this differs from an interval in which *no* incubation behavior is evident. One might expect natural selection to operate ruthlessly against physiological laggards, prone to leave their eggs exposed to predators for two days after completing the clutch, unless there is some other important (ultimate) factor involved. Conceivably, the females, best nourished at the start of incubation, enjoy the best chance of hatching their eggs. Unfortunately, we have too few data for a valid comparison of the hatching success with the length of the incubation period.

The Nestling Period

Sometimes one of the eggs in a clutch hatches in the late afternoon, even as late as 6:00 PM, and the other, or others, early next day. Most often, however, the whole clutch hatches on the same day, usually early in the morning. The adults carry the empty shells away, dropping them at some distance from the nest, 35 yards in one case.

For the first few days after hatching the female broods the chicks, intermittently during daylight and continuously after dark. The female's brooding behavior is probably influenced to some extent by the weather since she tends to sit more consistently during rainy spells than at other times. Also, in the southwest Cape where it is often cold and wet during the early breeding season, females covered their young at three September nests for eight, nine, and 11 nights after hatching; but another female, raising two chicks in warm November weather, ceased brooding the young after the fifth night.

The chicks are fed mainly on larval and adult insects although other soft-bodied invertebrates, such as spiders and earthworms, are often included in their diet (Figures 9 and 10). The adult brings such small insects to the newly hatched young that it is frequently difficult to decide whether it is carrying any food at all. Later, parents bring items an inch or more in length, often well thrashed against a stone or branch before delivery at the nest.

Both parents feed the young, but in the early stages of the nestling period, the female may do so two to four times as frequently as the male. Gradually, however, he assumes an increasing share of the feeding. At two of the nests under observation the marked males were clearly bringing more food than their mates by the time the young were ready to fly. In both cases, the male's greater contribution resulted from an increase in the amount of food carried to the nest per visit rather than from an increased number of visits. To illustrate: during one hour each parent of a brood of three nine-day-old chicks came to the nest eight times. The male always fed at least two chicks and often three; the female never fed more than one chick at a time. As a result, there were 30 "meals" delivered — 10 per chick — during that hour instead of 16 as a count of visits might imply.

Because Cape Robins nest in dark places, it is often impossible—short of gross disturbance—to distinguish between meals and visits; and I did not appreciate the need for such a distinction until the later stages of this study. Thus, most of my data, accumulated at about a dozen nests over the years, refer to the visiting rate. For what they are worth, these figures indicate that the Cape Robin, like many other birds, increases the number of visits to the nest with an increase in brood size, but not proportionately. The visits average from 10 per hour with one chick to 16 per hour with broods of two and three chicks.

Combining all data for all brood sizes and computing the number of visits per chick, the average is six per hour during the first four to five days. Thereafter it increases to about eight per hour. This results partly from the male's increasing participation and partly from the fact that the female gradually gives less time to brooding and more to feeding. During the course of any one day there is also an hourly variation in the visiting rate. It declines from an overall average of 7.5 per hour per chick in the early morning to 5.8 at midday and then rises again to 7.2 per hour per chick in the late afternoon. However, as noted, the actual number of meals delivered seems likely to be greater than these figures suggest, especially later in the nestling period.

Young Cape Robins tend to leave the nest prematurely if disturbed by predators or over-zealous observers. I have, therefore, discarded several records of unduly short nestling periods, clearly associated with the banding of advanced chicks. Twenty-five records remain, 19 from the South African Ornithological Society, and provide sufficient data for calculating the average nestling period at 16.5 days with extreme values of 15 and 17.5 days. These data are within a maximum error of one day either way.

Sometimes the chicks are curiously hesitant about their departure. They perch on the rim of the nest for extended periods, often leaving their droppings on its edge before finally hopping and fluttering into the undergrowth. At all other times nest sanitation is meticulous, with the adults either removing feces or swallowing them. However, when fledging is imminent, the parents generally do not approach their offspring closely, but move restlessly about in the neighborhood of the nest, sustaining a chorus of alarm calls, until the chicks are safely away, dispersed, and hidden in dense vegetation.

Figure 9 (*above*). A Cape Robin returning to its nest with a beakful of insects. Both parents feed the nestlings, bringing an assortment of insects, spiders, and earthworms. When an item of food is large, the parent may thrash it well on a branch or stone before presenting it to the young birds.

Figure 10 (*below*). Back view of the Cape Robin pictured above. Note the darker central rectrices. On alighting, the bird flicks its wings and momentarily fans its tail, revealing the darker central stripe. See also the Frontispiece.

Development of the Young

As with other songbirds, the newly hatched chick is blind and helpless, and only sparsely clothed in long iron-gray down, mainly on the head, sides, and tail. By the time the chicks are 12 days old, they have attained their typical juvenal coloring, and now grow so fast that, at 14 days, the average nest seems far too small to hold two chicks, let alone three. Usually, however, they remain tucked within its confines although sometimes nestlings perch one on top of the other, instead of snuggling side by side.

Data from various sources show some interesting deviations in the development of behavior patterns. For instance, at three nests for which I have detailed notes, eight-day-old chicks showed no fear of me and still responded by gaping to the least tactile stimulus. "Fear-crouching," which replaces this reaction and usually accompanies full vision, developed at nine days in two of these nests and at 11 days in the third, despite the fact that feathering proceeded at about the same rate in all nests. By contrast, Blaker (*in litt.*) recorded a brood in which the gravity-gaping response to tactile stimuli disappeared after the sixth day and noted that the chicks started to utter begging calls at about the same time. I have no record of any sound produced by nestlings, except for an occasional squeak when I banded them.

By the time the young birds are ready to leave the nest, much of their down has rubbed off, except for a few tufts on the head. Their bills are still rather broad and edged with soft creamy skin at the gape, and their tails are absurdly short—about 2 cm as against the adult's 8 cm. The juvenal plumage, described above, is quite unlike that of the parent, except for the tail, and is so highly cryptic that within the undergrowth a motionless fledgling is barely visible against the background of dappled sunlight and shadow.

The Post-nestling Period

Through feather growth and abrasion, the plumage of the young Cape Robin undergoes some minor changes while it is still in the care of its parents. On the under surface a light speckling of gray-brown develops; on the rump and vent the rufous coloring characteristic of the adult becomes more noticeable; and the tail grows rapidly, almost reaching its full length by the time the young bird has been out of the nest two weeks. At this stage it also is much stronger on the wing. Initially, the fledglings can hardly fly at all; and, although they hop and flutter agilely through the vegetation, I have caught banded young by hand without much difficulty up to six days after fledging.

Once out of the nest, the juvenile becomes increasingly noisy, uttering its thin piping calls with growing insistence, often for minutes on end. About five weeks after fledging, it begins to add to its vocal repertoire, producing its own three-syllabled warning cries, *wa-de-da,* in response to the adult's. Initially, the young bird depends entirely on its parent for food, but when about three weeks out of the nest, its aimless pecking and probing seems to become more functional, and I have seen juveniles of this age gather an occasional insect. Despite their increasing ability to forage, the young continue to beg insistently and remain in the care of their parents for some time. I regularly recorded the juveniles from four banded broods within their respective territories from 32 to 38 days after fledging. A member of another marked brood solicited food from its parent when 42 days out of the nest, and yet another received food from the male when 50 days fledged (Rowan, 1953). The last observation represents the longest period of parental attention.

The young birds probably disperse five to seven weeks after leaving the nest. At this stage they are still in juvenal plumage, and it seems remarkable how rarely one notices such birds away from their natal territories. Farkas (1966) described the ornithological changes accompanying the development of a garden in the grassveld of the western Transvaal and mentioned that, out of nine Cape Robins which prospected or settled in the newly available habitat over a period of three years, only three were in juvenal plumage when they arrived. In areas already occupied by territorial pairs, juveniles are probably seen even less frequently.

There are a few observations to indicate the age at which adult plumage is assumed. One bird began to molt in captivity at 11 weeks (Spence, 1957) and was in almost full adult plumage at 12.5 weeks, except for the white superciliary streak, the last marking to appear. The molt was complete at 15 weeks.

My own record is for a banded chick noted in the parents' territory at Hout Bay about five and one-half weeks after hatching and recovered some 12 weeks later when it killed itself in a fight with its own reflection in the window of a house about half a mile away (Rowan, 1953). The bird was then, in early February, just starting to molt. Of three young Cape Robins, raised in the Transvaal and recaptured at intervals after banding in the nest (R. A. Reed, pers. commun.), two, from the same nest, were still in juvenal plumage at an age of 14 to 15 weeks; a third, from another nest, was in full adult dress when approximately 13 weeks old.

These data, although meager, indicate considerable individual variation in the timing of the first molt, which evidently may start from 11 to 18 weeks after hatching. Further, both Farkas's observations and the recovery of the chick banded at Hout Bay suggest that young birds may try to take up territory while still in juvenal plumage.

Second and Repeat Broods

If robbed of their eggs, Cape Robins will build and lay again, often completing the second clutch 10 to 20 days after the loss. Such replacements may occur at any time during the breeding season provided the date is not too far advanced. Some pairs have laid as many as three and four clutches in succession without hatching a single chick. If young are brought off at the first attempt, the whole process of building, incubation, and raising the nestlings to fledging occupies about six weeks within the four-month breeding period of this species. Most successful pairs embark on a second clutch, the usual interval between the fledging of the first brood and laying the second set of eggs being again 10 to 20 days.

This means, of course, that the female commences her new nest well before the juveniles of the first brood have dispersed. Observations of marked pairs indicate that at this stage of the post-nestling period, the male assumes most, if not all, of the feeding responsibilities for the first brood, and there is a noticeable decline in the amount of song. When second broods are brought off late in the season, the male may have lapsed into silence altogether by the time the chicks leave the nest. This raises an interesting question in regard to the development of song in the young. Since Cape Robins are good mimics, it seems probable that at least a part of their vocal repertoire is learned; however, there must be many a chick from a second brood that never hears its male parent sing.

TABLE 3

Hatching Success in the Cape Robin

Region and clutch size	*Number of clutches*	*Total eggs*	*Number hatched*	*Percentage of eggs hatched*		*Percentage of clutches failing*
				*Excl**	*Incl***	
Southwest Cape						
Date completed						
July, Aug.	59	116	73	97.4	62.9	37.2
Sept.	62	130	60	99.2	46.1	54.8
Oct.	51	108	42	95.3	38.8	58.8
Clutch size						
One egg	10	10	0	–	–	100.0
Two eggs	142	284	142	97.8	50.0	47.8
Three eggs	20	60	33	95.0	55.0	40.0
Totals	172	354	175	97.4	49.4	50.0
Eastern Cape						
Clutch size						
Two eggs	25	50	25	96.1	50.0	48.0
Three eggs	14	42	19	90.4	45.2	50.0
Totals	39	92	44	93.6	47.8	48.7
Transvaal and Orange Free State						
Clutch size						
Two eggs	18	36	22	100.0	61.1	38.8
Three eggs	18	54	29	87.8	53.7	38.8
Totals	36	90	51	92.7	56.7	38.8

*Excluding clutches that were complete failures.

**Including clutches that were complete failures.

Nesting Success

In the breeding records available for the southwest Cape the histories of 172 nests can be traced from start, or near it, to finish; the details are summarized in Tables 3 and 4. Similar data from other regions, though meager with none from Natal, have been included in the tables for comparison. However, since some of the samples—for example, data on broods from three-egg clutches—are probably too small to be representative, I have excluded them from the following analysis.

In all areas, losses are greater at the egg stage, involving 40 to 50 per cent of the nests, than at the chick stage when 20 to 30 per cent are lost. Only 30 to 35 per cent of the eggs laid produce flying young. Most failures are due to predators, the exceptions being 13 nests with eggs that failed through desertion, and three in which all chicks died from an undetermined cause. Excluding the effects of these factors (column 5 in both tables), it appears that hatching success is lowest in clutches of three—they presumably have proportionately more infertile eggs.

TABLE 4

Fledging Success in the Cape Robin

Region and clutch size	*Number of broods*	*Number of chicks hatched*	*Per cent of broods failing*	*Number fledged*	*Young fledged as per cent of young hatched*		*Young fledged as per cent of eggs laid*
					*Excl.**	*Incl.***	
Southwest Cape							
Date of completed clutch							
July, Aug.	37	73	29.7	46	94.5	63.0	39.6
Sept.	28	60	35.7	37	96.6	61.6	28.4
Oct.	21	42	38.0	29	100.0	66.6	25.9
Clutch size							
Two eggs	74	142	36.4	83	95.7	58.4	29.2
Three eggs	12	33	16.6	28	100.0	84.8	46.6
Totals	86	175	33.7	111	96.5	63.4	31.3
Eastern Cape							
Clutch size							
Two eggs	13	25	23.0	19	100.0	76.0	38.0
Three eggs	7	19	14.2	15	93.7	78.9	35.7
Totals	20	44	20.0	34	97.1	77.2	36.9
Transvaal and Orange Free State							
Clutch size							
Two eggs	11	22	18.1	18	100.0	81.8	50.0
Three eggs	11	29	45.3	16	94.1	55.1	29.6
Totals	22	51	31.8	34	97.1	66.6	36.6

*Excluding broods that were complete failures.

**Including broods that were complete failures.

In the southwest Cape the proportion of chicks that fledge improves slightly as the season advances, possibly in relation to a corresponding improvement in the average weather conditions. However, these small gains are more than offset by seasonal changes in the level of predation which increases steadily from August to October so that nearly twice as many young fledge from early nests as from late ones. Clutches of two and three seem to be about equally successful in surviving predation, but may differ regionally in overall success. On the face of things three-egg clutches appear to produce a larger proportion of fledged young than two-egg clutches in the southwest Cape, about the same proportion in the eastern Cape, and a smaller proportion in the Transvaal. This is in inverse relation to the incidence of three-egg clutches which is highest in the Transvaal, 50 per cent of records; intermediate in the eastern Cape, 37 per cent; and lowest in the southwest Cape, 17 per cent. However, until there are more reliable data for success during the nestling period, it is probably unwise to attach any significance to these values.

Predators, Parasites, and Mortality

Occasional Cape Robins are remarkably long-lived. One, banded in 1954, was recaptured in the same place seven years and 10 months later (Middlemiss and Skead, 1962). Reed (1967, 1968) recaptured several birds many times, one eight years and five months after banding. Another was at least nine years old at its seventh and final capture.

However, few birds live as long as this. For instance, R. A. Reed's results (*in litt.*) show that only one-quarter of 35 adult robins, banded in the six years ending in 1959, repeated in a following breeding season. My observations of a smaller sample of color-banded birds at Troughend, Stellenbosch, also suggest a survival rate of roughly 25 per cent from one breeding season to the next. Most of the similarly marked birds at Hout Bay were two or more years old by the time they disappeared. Middlemiss and Skead (1962) indicate that only eight out of 198 Cape Robins banded in a 10-year period (total from the Sanctuary's privately published report) were known to have survived as long as two years.

None of these figures agrees satisfactorily with the mortality rates suggested by nesting success. Given a stable population, the figures in Tables 2, 3, and 4 imply that 40 to 50 per cent of flying Cape Robins must perish every year — a substantially lower mortality than is suggested by banding results. Plainly, we need more reliable data. Because of the covert behavior of adults in the often impenetrable thickets that they inhabit, work with banded birds may indicate too low a survival rate. On the other hand, the figures for nesting failure may be too high, Nests under observation are probably more exposed to predators, both because they are less well-concealed than those escaping notice and because the breeding birds are more frequently disturbed.

As always, the causes of mortality vary with age and are difficult to ascertain. The band of one juvenile, banded in the nest, was found in the pellet of a Barn Owl (*Tyto alba*) about three weeks after the robin fledged (R. A. Reed, *in litt.*). Another drowned in a rain-water butt a few days after leaving the nest (data from nest cards). And a third, as reported above, killed itself in a battle with its own reflection. Broekhuysen (1965) and Siegfried (1955) have shown that, along major highways, collisions with fast-moving traffic must account for a fair number of adult deaths, perhaps as many as one or two per 1,000 vehicle miles in suitable environments. However, these figures are hardly significant in relation to total mortality, which presumably lies somewhere between 40 and 70 per cent. We must admit that we have no idea how or why most Cape Robins die once they have left the nest.

By contrast, the predators taking eggs or chicks have been identified surprisingly often. Among those caught in the act are rats and several mice, especially introduced *Rattus* spp. and the indigenous *Rhabdomys pumilio*. Most rodents have been indicted at the egg-stage, but they may take nestlings as well. Domestic cats, the boomslang or tree snake (*Dispholidus typus*), a kestrel (*Falco tinnunculus*), and a shrike (*Lanius collaris*) are all on record as carrying off young, the kestrel once only, but the others several times apiece. Another shrike (*Laniarius ferrugineus*), which shares Cape Robin habitats generally, has been observed robbing different nests of both eggs and young, and may prey heavily on the species during the breeding season. The same is probably true of various mongooses and meerkats (Herpestinae). None of these small mammals has been seen taking eggs or chicks, but they often leave telltale tracks beside robbed nests.

Another cause of losses during the nestling period seems likely to be the anthomyd fly, *Passeromyia heterochaeta.* Taylor (1949) recovered these insects in some numbers from nests of *C. caffra* and of several other songbirds in which all young died mysteriously. He considers that the blood-sucking larvae of this fly, which pupate within the nest fabric, may be responsible for much unexplained nestling mortality.

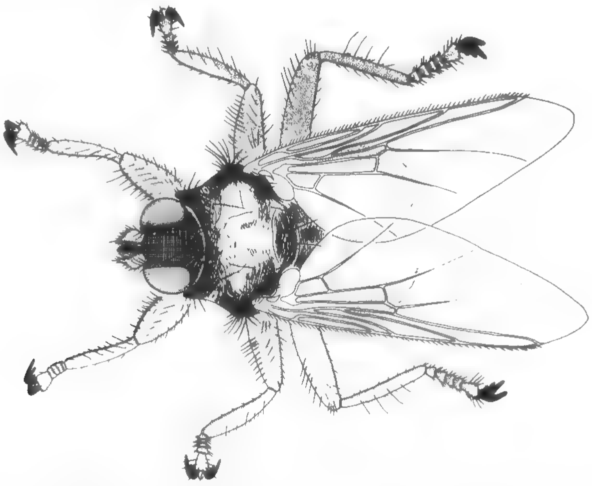

Figure 11. *Ornithoctona laticornis,* a common and widespread parasite in sub-Saharan Africa, recorded from more than 50 species of birds. Drawing by J. A. Ledger of the South African Institute for Medical Research.

On other invertebrate parasites of the Cape Robin, information is meager. For the following data, a review of what exists, I am indebted to Mr. J. A. Ledger of the South African Institute of Medical Research. There are no records of mites from *C. caffra,* although other Cossyphas have yielded mites of seven different genera. At least some of these genera may be expected from the Cape Robin in time. A hippoboscid, *Ornithoctona laticornis,* infests *C. caffra* (Figure 11). These viviparous insects feed on blood as adults and are believed to be vectors, or intermediate hosts, of other avian blood parasites, such as protozoa of the genus *Haemoproteus.*

The Cape Robin also suffers brood parasitism, being the main host of the large Red-chested Cuckoo (*Cuculus solitarius*), which weighs 70 to 80 grams, against the robin's 28 grams. The parasitic chick evicts its nest mates within a day or two of hatching, so that the foster parents have no chance of raising any young of their own during the seven weeks or so—three weeks in the nest—that the cuckoo is dependent on them (Liversidge, 1955; R. A. Reed, 1969). However, the cuckoo is an inter-African migrant, rarely recorded in the Republic before mid-September, and its first eggs are probably not deposited until a week or two later. Thus, robins in the southwest Cape with their early breeding season have an opportunity to bring off a first brood before the cuckoo arrives; the same may not be true for robins in the Transvaal.

Payne and Payne (1967) have recently made a study of the proportions of various songbird nests parasitized by African cuckoos. Their analysis shows that about one per cent of the Cape Robins' nests are affected in the southwest Cape, 8 per cent in the eastern Cape, 17 per cent in Natal, and 22 per cent in the Transvaal, with an average of 4.5 per cent in southern Africa as a whole. Except for remarking that, within a restricted locality, the number of parasitized nests may be higher than average, the Paynes do not discuss these regional differences. It seems to me that they must be attributable, in part at least, to regional differences in the host's breeding season. In fact, in the southwest Cape, only about 28 per cent of Cape Robin nests are still active by the time the cuckoo starts to lay (see Table 2) which is not altogether in accord with the Paynes' argument that parasitic cuckoos in general choose hosts that are abundant and whose nests are thus easily found. On the other hand, considering the matter from the point of view of the host, for *C. caffra* as a whole, brood parasitism is probably of minor importance in limiting nesting success when compared with predation. For local populations, as in the Transvaal, it may be a significant factor.

Summary

Of 16 members of the African genus *Cossypha* (family Turdidae), the Cape Robin (*C. caffra*) is the only species widely distributed in temperate habitats at the southernmost end of the continent.

Cape Robins evidently pair for life, and mated birds remain together on their territories all year round. If one dies, the survivor soon obtains a new mate without disruption of neighboring pairs or disturbance of territorial boundaries. The source of birds filling such vacancies is difficult to determine, but banding studies indicate a fairly substantial reserve of unpaired wandering birds. These presumably supply the migratory fraction of the population, those birds which appear seasonally on the Natal coast. Where the habitat is already parceled out among settled pairs, unmated birds appear to lead a precarious existence, skulking in the territories of others.

Territory size, in three types of habitat, ranges from about 600 square yards in favorable cultivated areas to as much as 9,000 square yards in the Cape sclerophyll vegetation or *fynbos*. However, size variations are much larger between habitats than within any single habitat, and they are in accordance with variations in the density of the avifauna as a whole, which suggests that the extent of the defended area may be related to the productivity of the environment. Advertisement and defense of the territory seems to be entirely by the male, which sings consistently for about nine to ten months of the year, falling silent during the molt, November to January.

The breeding season is restricted to four months of the year, during which successful pairs normally bring off two broods. However, the timing of the season varies regionally, being earliest in the southwest Cape and latest in the Transvaal and Natal. The shift may bear some relation to rainfall regimes. The birds build cup-shaped nests low down, zero to three feet in 65 per cent of records, usually in dense vegetation. Egg color is variable and clutches small. In the Cape two-egg clutches occur nearly six times as often as three-egg clutches, but in Natal and the Transvaal records of two-egg and three-egg clutches are about equal. All incubation is by the female and intervals between the laying and the hatching of the last egg vary from 14.5 to 17.5 days. This spread may be due to a tendency of some females to delay the onset of incubation for as much as two days after the completion of the clutch. No advantages for such behavior are evident.

Both parents feed the young, mainly on insects, at an average rate of about eight visits per hour per chick. The female broods the young intermittently by day and consistently at night for periods which vary at different nests, possibly in accordance with the weather. The chicks normally leave the nest on the 16th day after hatching but are prone to depart prematurely if disturbed. After fledging the young birds remain in the care of their parents for a further five to seven weeks and then disperse while still in their speckled juvenal plumage which is highly cryptic. The molt into adult plumage has been recorded as beginning from 11 to 18 weeks after hatching.

Many nests fail, mainly through predation, which accounts for about half of those recorded at the egg stage and up to 30 per cent of the survivors at the chick stage. Thus, only 30 to 35 per cent of eggs laid produce flying young. These figures imply a mortality rate of 40 to 50 per cent in a stable population, but banding results suggest that only about 25 per cent of the adults marked survive from one breeding season to the next, although individuals are known to have lived for as long as eight or nine years. Possible reasons for the discrepancy are considered.

Causes of mortality among flying birds include predation and accidents of various sorts, but it is unknown how or why most adult Cape Robins die. Nest predators, identified fairly often, include small mammals such as rodents and mongooses, a snake, and various birds, in particular two shrikes. Additional causes of breeding failure arise from blood-sucking fly larvae, which infest the nest, and from brood parasitism by the Red-chested Cuckoo (*Cuculus solitarius*).

Acknowledgments

In this study I received help from several people, most of whom are named in the text. In addition, I wish to acknowledge my debt to my husband, A. N. Rowan, for long-suffering assistance in the field and at the desk; to Mr. and Mrs. G. A. S. Lipp for generous and enduring hospitality at Troughend, Stellenbosch; and to Mr. and Mrs. R. A. Reed for similar kindness in the Transvaal and for the wealth of Mr. Reed's field experience, generously placed at my disposal. My colleagues, Professor J. M. Winterbottom and Mr. W. R. Siegfried, kindly read and criticized the paper in draft.

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A STUDY OF SEEDSNIPE IN SOUTHERN SOUTH AMERICA

GORDON L. MACLEAN

"L'avifaune du Chili est peu connue, même dans le monde savant." Although a keen group of amateur ornithologists has done a certain amount of biological work in various parts of Chile in the meantime, this statement by Housse (1948) is almost as true today as it was 20 years ago. The biology of the birds of Chile remains an almost untouched field to which, only now, the eyes of professional ornithologists in other parts of the world turn, drawn by the richness and intrigue of the many problems.

This paper is concerned primarily with a biological study of the seedsnipe of the genus *Thinocorus* in the field; it will serve also as a review of the literature, often rather old and in relatively obscure journals. Since I located most of the earlier works in South America, it may be profitable to assemble them here. Most of the published work on seedsnipe consists of brief notes on distribution and habitat, or accounts of calls, together with a little information on feeding. Goodall (1964) summarized all the available references on seedsnipe to date. Further biological data are sadly lacking.

It was partly to fill this gap that I ventured into some of the drier parts of Chile and Argentina to look at seedsnipe in their natural habitat; and partly to compare seedsnipe, Thinocoridae, with sandgrouse, Pteroclidae, another vegetarian family of charadriiform desert-dwellers that I have studied in the Kalahari Desert of South Africa (Cade and Maclean, 1967; Cade *et al.,* 1966; Maclean, 1967a, 1968). I worked in South America (see Figure 1) near Vallenar in the Chilean province of Atacama; in the Andes of the province of Santiago; at Río Verde and Cerro Castillo in the province of Magallanes; at Fuentes del Coyle and Las Vegas, on the Argentine side of the Andes, in the province of Santa Cruz; and at Viamonte and Harberton on the island of Tierra del Fuego.

My study period covered the months of September through December 1967. I spent the longest single time at Vallenar where, for seven weeks in September and October, I made an intensive study of the Least Seedsnipe (*Thinocorus rumicivorus*). For one week in October-November, I worked on the Gray-breasted Seedsnipe (*T. orbignyianus*) in the Valle del Yeso of the Andes in Santiago, at an elevation of 3,000 meters. The rest of the time I was in Magallanes, Santa Cruz, and Tierra del Fuego, doing further comparative study on the Least Seedsnipe.

Most of the general works on the birds of Chile and Argentina contain accounts of the geography and climate of the two countries (Goodall *et al.,* 1957; Johnson, 1965; Olrog, 1959). De Agostini (1960) and Vial *et al.,* (1959-1960) wrote good descriptions of the southern regions.

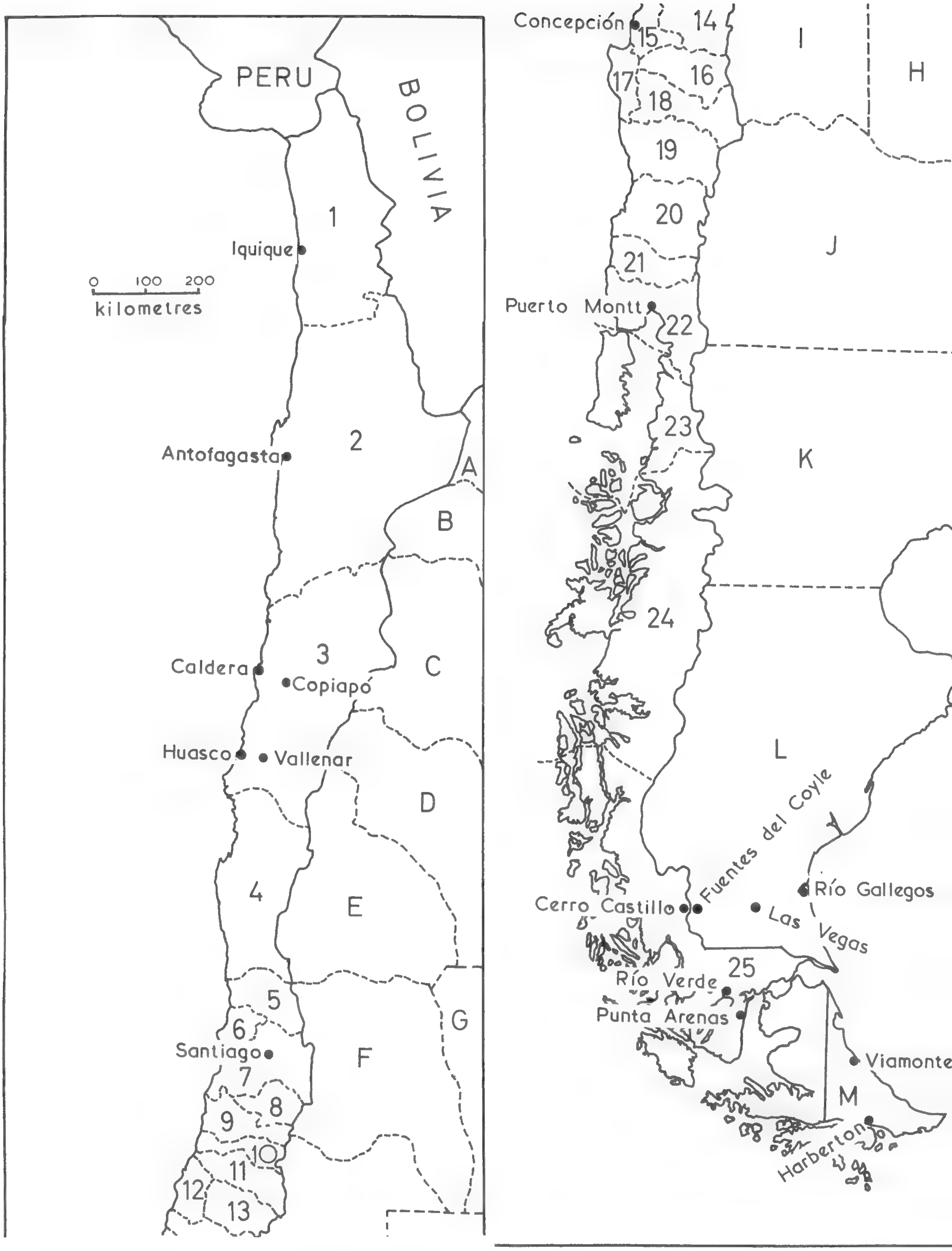

Figure 1. Map of Chile and part of Argentina showing the main localities mentioned in the text. The Chilean provinces are numbered: 1. Tarapaca, 2. Antofagasta, 3. Atacama, 4. Coquimbo, 5. Aconcagua, 6. Valparaiso, 7. Santiago, 8. O'Higgins, 9. Colchagua, 10. Curico, 11. Talca, 12. Maule, 13. Linares, 14. Ñuble, 15. Concepcion, 16. Bio-Bio, 17. Arauco, 18. Malleco, 19. Cautin, 20. Valdivia, 21. Osorno, 22. Llanquihue, 23. Chiloe, 24. Aysen, 25. Magallanes. The Argentine provinces are lettered: A. Jujuy, B. Salta, C. Catamarca, D. La Rioja, E. San Juan, F. Mendoza, G. San Luis, H. La Pampa, I. Neuquen, J. Rio Negro, K. Chubut, L. Santa Cruz, M. Tierra del Fuego.

I made my field observation mostly on foot, occasionally in a Land Rover or on horseback. In the province of Atacama I collected specimens of adult and young Least Seedsnipe, Numbers 786639 to 786644 in the American Museum of Natural History. I preserved the stomach contents in formalin for the laboratory where they, as well as dry feces collected from roosting scrapes, have been examined microscopically. I collected no specimens of the Gray-breasted Seedsnipe.

Distribution of Thinocorus

The Least Seedsnipe (*T. rumicivorus*) occurs from Ecuador and Perú to northern Tierra del Fuego (Koepcke, 1964; Meyer de Schauensee, 1966; Taczanowski, 1884-1886). Within the borders of Chile this species ranges from Tarapacá (Behn *et al.*, 1957; Hellmayr, 1932; Lane, 1897; Reed, 1933) through Antofagasta (Amenábar and Millie, pers. commun.), Atacama (Hellmayr, 1932; Peña, 1961), Coquimbo (Lane, 1897), Curicó (Barros, 1928), Llanquihue (Hellmayr, 1932), and Aysén (Philippi, 1938) to Magallanes including Tierra del Fuego (Bernath, 1965; Crawshay, 1907; Cunningham, 1871; Johansen, 1966; Olrog, 1948; Philippi, 1964; Philippi *et al.*, 1954; Sclater and Hudson, 1889). The species is mainly confined to lower elevations near the coast, except in Patagonia where it occurs far inland on the open steppe—the "pampa"—and is partly migratory in the southern part of its range, moving north in winter, mainly on the Argentine side of the Andes, as far as Buenos Aires (Durnford, 1877b; Serié, 1918), Uruguay (Meyer de Schauensee, 1966), and Santa Fé (Wilson, 1926). Johansen (1966) suggests, however, that it is also a year-round resident because Bernath (1965) recorded the Least Seedsnipe in Tierra del Fuego in April and May. It appears that, in the south, some Least Seedsnipe migrate and others do not.

Though the Least Seedsnipe is definitely a bird of the drier regions, there is a limit to its tolerance of dry conditions. It is absent from most of Antofagasta where it has been recorded only once, in November 1967, after local rains. In the extreme southern part of its range it occurs almost exclusively in the region north and east of a line marking an annual rainfall of 500 millimeters, the 500 mm isohyet, which is also the boundary between pampa and forest (Figure 2). The Least Seedsnipe is most common north and east of the 250 mm isohyet; on the pampa of eastern Santa Cruz it is perhaps the most numerous bird. The increase in its numbers is most striking when one drives eastward from Fuentes del Coyle, near the Chilean border, to Río Gallegos on the Atlantic coast. The western limit of the Least Seedsnipe in Patagonia is the Fitzroy Channel at Río Verde, just east of the 300 mm isohyet. In Tierra del Fuego it occurs as far south as Viamonte, just north of the 500 mm isohyet.

The Gray-breasted Seedsnipe, a montane species particularly in the northern part of its range, occurs from the Andes of Perú (Koepcke, 1964; Morrison, 1939) and Bolivia (Meyer de Schauensee, 1966) through the Chilean provinces of Tarapacá (Behn *et al.*, 1957; Lane, 1897; Reed, 1933), Antofagasta, Atacama (Peña, 1961), Aconcagua (Barros, 1921, 1928), Santiago (Olrog, 1948), Colchagua (Hellmayr, 1932; Reed, 1933), and Concepción to Tierra del Fuego (Crawshay, 1907), and on the Argentine side of the Andes from Jujuy in the north (Budin, 1931) all the way to Santa Cruz (Hellmayr, 1932). The Gray-breasted Seedsnipe seldom descends below 700 meters except in the extreme southern part of its range; elsewhere it occurs up to an elevation of 3,500 meters (Housse, 1948).

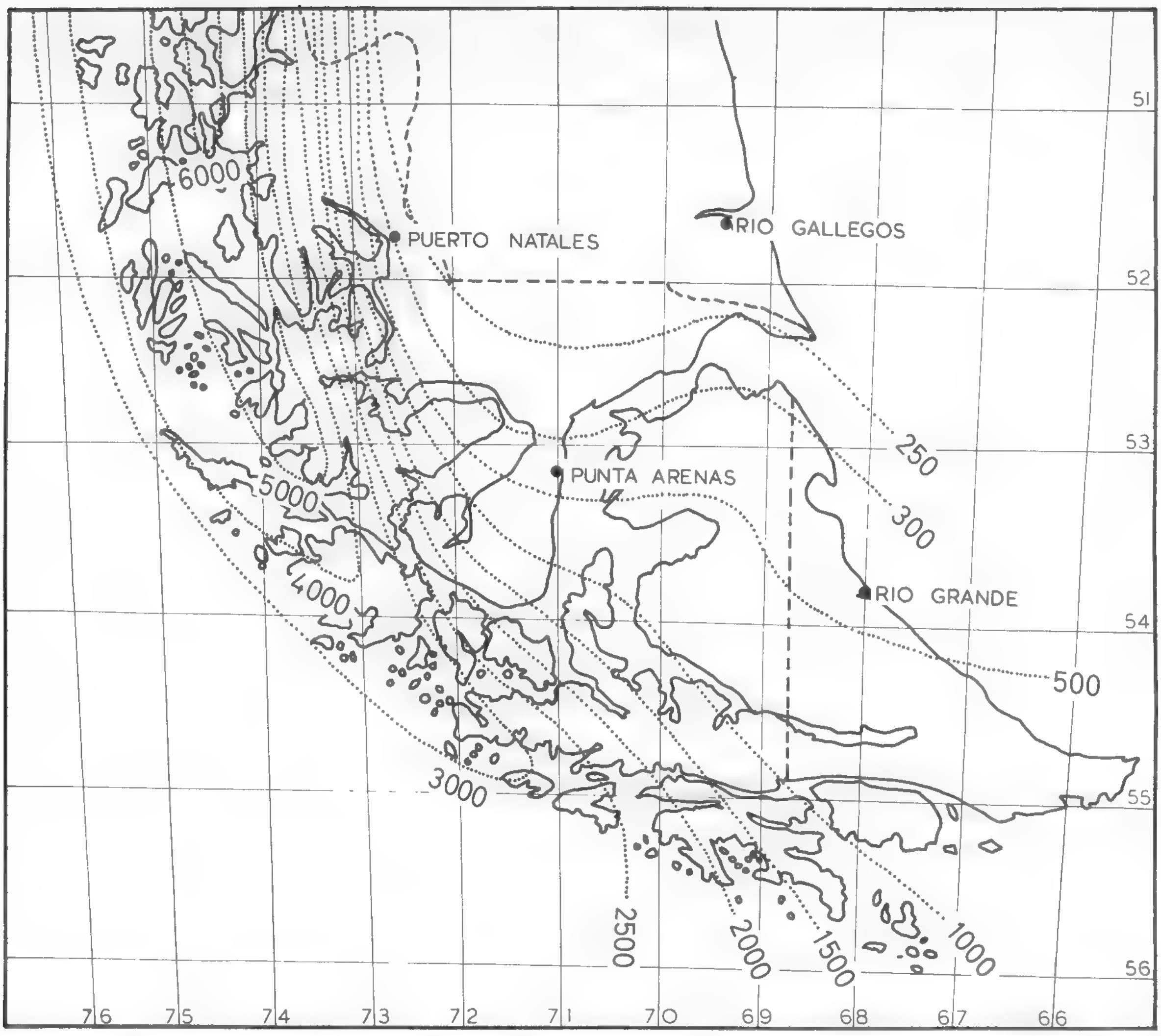

Figure 2. Map of Patagonia and Tierra del Fuego on the extreme southern tip of South America. The isohyets—lines connecting areas of equal annual rainfall—are after Vial, Sommers, and Roberts (1959-1960); the figures are in millimeters. The 500-millimeter isohyet marks the boundary between the pampa and the forest.

Several authors have called attention to large local fluctuations in populations of both the Least and Gray-breasted Seedsnipe in the Patagonian region (Johansen, 1966; Philippi *et al.*, 1954). In fact, the Gray-breasted is so decidedly rare in Tierra del Fuego, where it used to be common (Crawshay, 1907), that it seems all but to have disappeared. Johansen (1966) did not see any; I was fortunate enough to see one in high open country about 20 kilometers east of Porvenir on the western side of the island. The local inhabitants ascribe the disappearance of the Gray-breasted to sheep farming which has probably changed the ecology of the open areas sufficiently to make them unsuitable for this seedsnipe.

We have no satisfactory explanation for the fluctuations in numbers of the Least Seedsnipe. William Waldron of Punta Arenas suggested the following possibility: the populations of Least Seedsnipe, formerly fairly common in the Patagonian region, increased rapidly after the imposition of a bounty on the gray fox (*Pseudalopex gracilis*), locally called "zorro plateado"; with the lifting of the bounty, the increase in foxes was followed by a corresponding decrease in seedsnipe. We need more concrete evidence to support this idea.

Habitats

My own observations on the Least Seedsnipe confirm the statements of earlier workers that it is a bird of flat open country with low sparse vegetation, from the seashore inland as far as the open areas extend (Barros, 1928; Behn *et al.*, 1957; Bernath, 1965; Crawshay, 1907; Durnford, 1877a; Hellmayr, 1932;

Johansen, 1966; Koepcke, 1964; Peña, 1961; Philippi *et al.*, 1954; Wilson, 1926). Philippi *et al.* (1954) and Johansen (1966) drew attention to the fact, and I noticed too, that the Least is particularly common along the roads in the Patagonian region. No doubt the roads provide the most open habitat and the birds can find the seeds, on which they feed, most easily there.

Figure 15 shows how the Least Seedsnipe favors bare country in Atacama; it was entirely absent from the cultivated fields where there were standing crops unless there was a small patch of bare ground (Nests M, N, O, P). I did, however, find it on fallow fields which had not been recently irrigated and where the vegetation had all but disappeared. The bird also frequented the narrow, non-arable slopes of the old river terraces (Nests G, I, J, K, L) even though fields of tall green wheat bordered the bare areas. Thus, the very bareness of the ground, more than the extent, determined whether or not the seedsnipe would inhabit it.

Figure 3 shows the typical habitat of Least Seedsnipe in Atacama where these open stony flats are known as the "llano," and Figure 4 the Patagonian habitat.

Just as the Least Seedsnipe is essentially a bird of the lowlands, the Gray-breasted Seedsnipe is a bird of the mountains. In the northern part of its range it inhabits the Puna region, a high-elevation semi-desert (Koepcke, 1964), almost always near water and where there is some vegetation (Behn *et al.*, 1957; Hellmayr, 1932; Morrison, 1939; Peña, 1961; Pereyra, 1951). My own observations of the Gray-breasted confirm this. In the northern part of their range these seedsnipe occur at well over 4,000 meters (Peña, 1961). Barros (1928) states that Gray-breasted Seedsnipe move down to the valleys at the foot of the cordillera after heavy snows, even to below 2,000 meters in the province of Aconcagua. In the southernmost part of its range the Gray-breasted is still more a bird of higher elevations than the Least (Crawshay, 1907) although the inhabitants of Argentine Patagonia assured me that in winter the Gray-breasted is common on the pampa. There is thus some local movement of the Gray-breasted but the extent has not been properly determined.

The typical Andean habitat of the Gray-breasted is shown in Figure 5. On Tierra del Fuego it used to occur somewhat south of the 500 mm isohyet in the grassy valleys, between the *Nothofagus* forests on the slopes. This is no longer true.

Systematics of the Thinocoridae

Systematists long ago established the position of the Thinocoridae within the Charadrii (the suborder of the order Charadriiformes) which includes all the shorebirds. This position is determined on the basis of anatomy (Garrod, 1877; Hanke and Niethammer, 1955). The evidence from their biology and egg-albumin proteins supports this. Egg-albumin proteins, analyzed electrophoretically as described by Maclean (1967a), and the resulting profiles (Figure 6) are typical of the Charadrii. Analyses of the malic dehydrogenase and other enzymes of the heart and breast muscle of the Least Seedsnipe by Allan C. Wilson of Berkeley, California, also confirm this position. As Wilson (*in litt.*) writes: "On the basis of this electrophoretic work with the three enzymes, I am inclined to suggest that seedsnipe are *bona fide* members of the order Charadriiformes and that their closest relatives may be the Glareolidae (or possibly the Scolopacidae)." Dr. Joseph R. Jehl of San Diego (pers. commun.) suggested that the seedsnipe may be distantly related to the sheathbills, but there is no electrophoretic evidence from egg albumin or muscle enzymes to prove it.

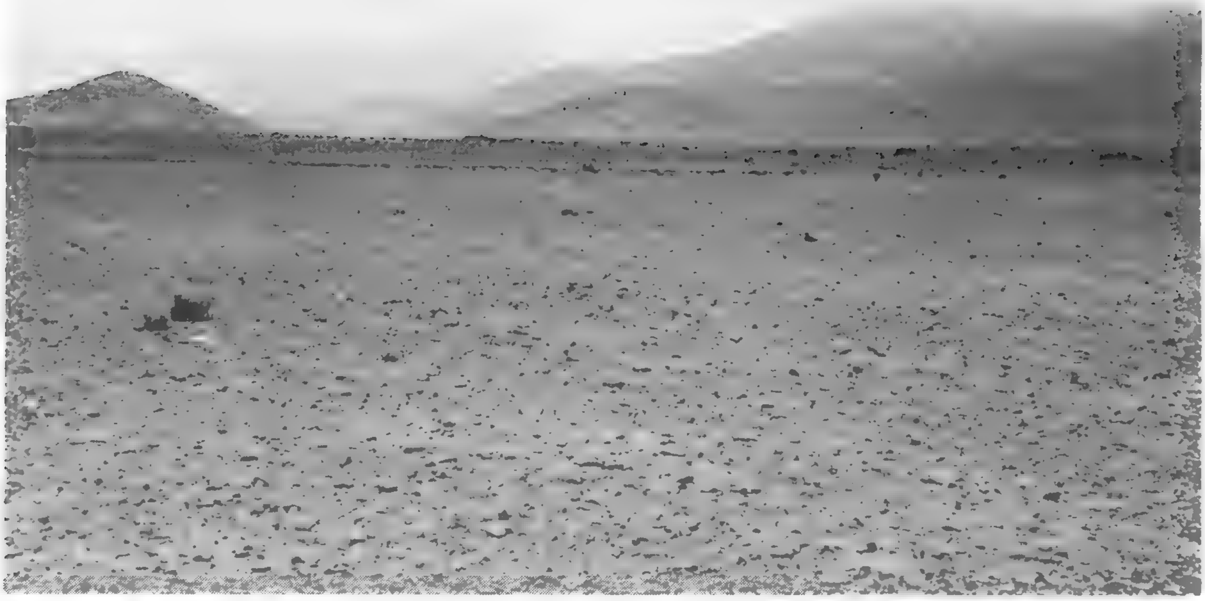

Figure 3. A typical llano, the habitat of the Least Seedsnipe in the Atacama Desert near Vallenar, Chile. Only a few tufts of vegetation appear on the flat, stony plain; a coastal mist enshrouds the mountains in the background.

Figure 4. The habitat of the Least Seedsnipe on the Patagonian pampa in the Argentine province of Santa Cruz. Although stony and rocky as in Figure 3, there is more ground cover. The single shrub is *Berberis buxifolia.*

Figure 5. In the foreground, the floor of the Valle del Yeso, in Santiago, Chile. This habitat of the Gray-backed Seedsnipe lies in the Andes at an elevation of about 3,000 meters above sea level. Note the bare, stony ground and the almost complete lack of vegetation. Gray-backed Seedsnipe occur well above 4,000 feet in the northern part of their range.

Although some earlier workers (Barros, 1921; Budin, 1931; Fiora, 1933) used the family name of Attagidae for the seedsnipe, the presently accepted name is Thinocoridae. The genus *Thinocorus* has 12 rectrices while the genus *Attagis* has 14 (Pereyra, 1943). This difference is almost certainly just a function of the larger size of the two species of *Attagis,* the Rufous-bellied Seedsnipe and White-bellied Seedsnipe.

The two species of *Thinocorus* are very similar to each other in appearance and habits and, as Crawshay (1907) remarked, the Gray-breasted is merely a larger edition of the Least. Both are characterized by the light blue-gray chest with black markings in the male (Figures 10, 11, 13, and 35). These markings are rather variable in the male Least; the vertical black stripe may be broad, narrow, or absent (Figure 7). The females of the two species are almost identical in coloration. The two species have no doubt diverged from a common stock quite recently, the Gray-breasted keeping to the mountains and the Least to the plains. In between their respective habitats a strip of deeply dissected, and often wooded or scrubby valleys forms an effective barrier. The only place where their ranges may to some extent overlap is in the Fuegian region, but even there they are, in large measure, altitudinally separate.

Data on the weights and measurements of both species of *Thinocorus* are presented in Table 1.

Various general works (Austin, 1961; Goodall *et al.,* 1951; Taczanowski, 1884-1886) give good descriptions of the Least Seedsnipe. Workers have tried to divide this species into a number of subspecies, *rumicivorus, boliviana, cuneicauda,* and *patagonia,* on the basis of size or coloration. Because weights and measurements vary so greatly between individuals of even a single population of this bird and because size is erratic and difficult to reconcile with given

TABLE 1

Weights and Measurements of Adult Least Seedsnipe and Gray-breasted Snipe

Sex	*Weight in grams*	*Millimeters*						*Reference*
		Body length	*Wing*	*Tail*	*Culmen*	*Tarsus*	*Middle toe*	
				Species: Least Seedsnipe				
both		180	113.7	58.0	10.4			Goodall *et al.* (1951)
both		190						
both			117.0					Olrog (1948)
male			112.0					Philippi *et al.* (1954)
male			112.0					
male			122.0					
female			118.0					
male			107.0	50.0	12.0	15.0	16.0	Taczanowski (1884-1886)
female		160	100.0	49.0	12.0	15.0	16.0	
male	49.0	175	111.6	55.3	10.3	14.6	20.6	Original
female	60.0	182	117.0	53.5	11.9	14.7	20.8	
Means	54.5	177	113.0	53.2	11.3	14.8	18.4	
				Species: Gray-breasted Seedsnipe				
male	125.0							Crawshay (1907)
male	142.0							
female	125.0							
female	125.0							
?	110.0							Fiora (1933)
?	115.0							
both		200	140.0	64.0				Goodall *et al.* (1951)
female			140.0					Olrog (1948)
?		200	146.0		13.0	19.0	28.0	Pereyra (1951)
male		212	133.0	62.0	15.0	22.0	23.0	Taczanowski (1884-1886)
male			140.0					
female			140.0	57.0	15.0	23.0	23.0	
Means	123.6	204	139.8	61.0	14.3	21.3	24.7	

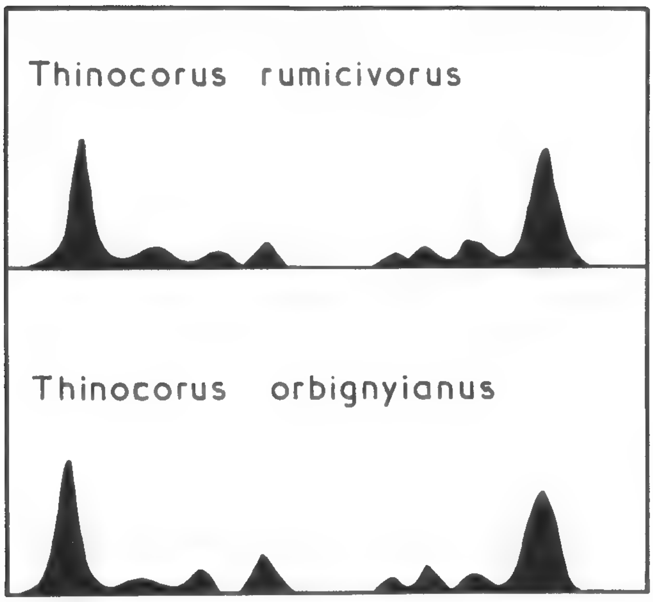

Figure 6. Profiles of egg-albumin proteins of the Least and Gray-backed Seedsnipe. The profiles, made from electrophoretic analyses by Dr. W. R. Spofford, are typical of the order Charadrii, a suborder of the order Charadriiformes, that includes all shorebirds.

geographical areas, Philippi *et al.* (1954) claim that most of the described races of *Thinocorus rumicivorus* are unsatisfactory. Subspecific variation almost certainly exists in such a terrestrial species with such a wide range, but the picture is complicated by the fact that at least part of the southern populations is migratory and all populations are highly nomadic. Regional differences in song and egg color are detectable, but not constant. Subspeciation in *T. rumicivorus* is probably more incipient than accomplished at present.

Descriptions are also available for the Gray-breasted Seedsnipe (e.g., Pereyra, 1951; Taczanowski, 1884-1886) and a colored figure appears in Thomson (1964:513). This figure is not particularly accurate, however, since the throat within the black border should be white and the black chest band is lacking.

Published measurements of the Gray-breasted are hard to come by; the few available ones are summarized in Table 1. The weights, given by Crawshay (1907) in ounces and converted to grams, seem to be too large although there may be a real size difference between different populations with the largest birds occurring in the south. There seems to be no dispute about the two subspecies that have been described, *T. o. orbignyianus* and *T. o. ingae,* the latter occurring in Perú (Behn *et al.,* 1957; Hellmayr, 1932; Koepcke, 1964; Morrison, 1939; Peña, 1961; Pereyra, 1951; Reed, 1933).

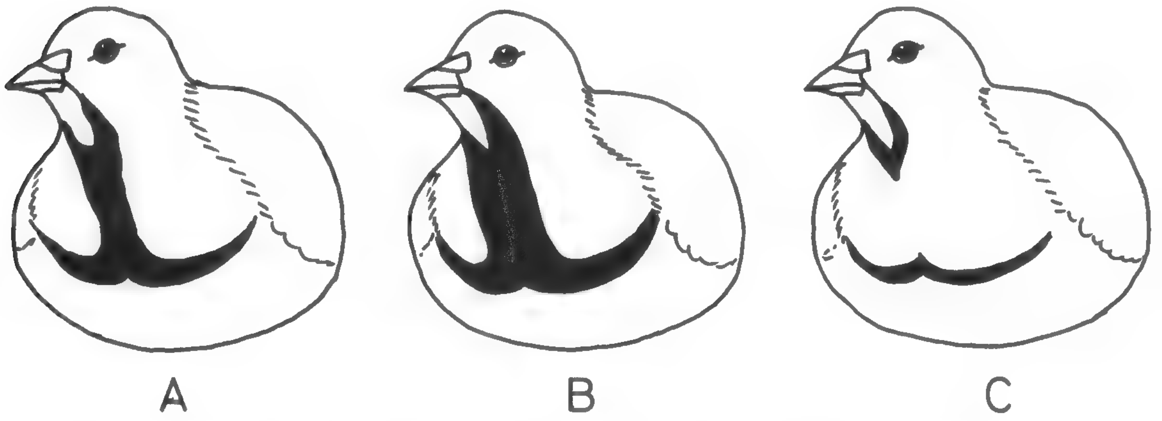

Figure 7. Variations in the chest markings of male Least Seedsnipe in the province of Atacama. The vertical black stripe may be broad as in Bird B, narrow as in Bird A, or missing as in Bird C. Bird A shows the most common type; Bird C, the least common and one seldom found.

Figure 8 (*above*). "Pata de guanaco" (*Calandrinia grandifolia*) growing in a habitat of Least Seedsnipe in Atacama. Seedsnipe eat only vegetable food and drink no water. A bird has been feasting on the leaves of this succulent that provides water as well as nourishment.

Figure 9 (*below*). *Taraxacum officinale* growing in the Valle del Yeso, a habitat of the Gray-breasted Seedsnipe. Note that the tips of some of the leaves have been nipped off—the work of a seedsnipe.

Food and Feeding

From direct observation in the field and from microscopic examination of stomach contents of adults and chicks and of feces collected from roosting scrapes, we know that the Least Seedsnipe eats only vegetable food. The crops and stomachs of adults, collected at Vallenar in October, contained seeds, cactus flower buds, unidentifiable pieces of succulent vegetation, small stones, and some tiny feathers. The bird had no doubt swallowed the feathers during preening. Direct observation at Vallenar revealed that adult Least Seedsnipe also feed on: (1) green seeds picked off an unidentified herb, (2) leaves of the succulent portulacaceous "pata de guanaco," *Calandrinia grandiflora* (Figure 8), (3) green leaves of the legume, *Medicago* sp., and (4) succulent tips of the flower buds of a small pincushion cactus, not yet identified, that grows commonly on the llano.

In Patagonia the Least ate the leaves of the common dandelion (*Taraxacum officinale*) as well as seeds off standing grass inflorescences 10 to 12 centimeters tall.

Published accounts of the food of the Least include only vegetable matter — seeds, leaves, buds, plant stalks, "weeds," green grass, and "fibrous vegetable matter" (Durnford, 1877a,b; Hanke and Niethammer, 1955; Johnson, 1965; Lane, 1897; Philippi *et al.*, 1954; Sclater and Hudson, 1889; Wilson, 1926). Philippi (pers. commun.) tells me that J. C. Johow of Santiago has seen adults and young feeding on the succulent leaves of the "doca," *Carpobrotus chilensis*, on the coast of the province of Ñuble. In captivity these birds will eat seeds and grains of various types (Barros, 1928). Francisco Fuchslocher and Jürgen Rottmann of Santiago kept the Least Seedsnipe in captivity on a diet of dry mixed birdseed, lettuce, bread soaked in water, and, twice a week, mealworms. The birds ate the mealworms avidly, a fact that seems most unusual when one considers their natural, and apparently exclusive, vegetable diet. It is doubtful that seedsnipe take any animal food in the wild. Sclater and Hudson (1889) probably summed up the feeding habits of the Least fairly accurately when they wrote that the Least Seedsnipe was "exclusively a vegetable feeder"; and Hudson added: "I have opened the gizzards of many scores to satisfy myself that they never eat insects, and have found nothing in them but seed (usually clover-seed) and tender buds and leaves mixed with minute particles of gravel."

The diet of the chicks is essentially the same as that of the adults. I will deal with it more fully in the section on breeding biology.

One of my most important questions was: Do seedsnipe drink water? There are statements in the literature that lead one to believe that the Least may drink. Lane (1897) heard that these seedsnipe "could be shot wholesale near the water-springs at certain hours" around Huasco and Coquimbo and, although he never saw them drinking, he believed that they probably did. The fact that they are often found near water seems to strengthen this belief. I never saw a Least Seedsnipe drink, even when it was actually walking through water. There was absolutely no question of their gathering in flocks to drink; they did not.

According to the literature, the diet of the Gray-breasted is "a thick succulent leaf with uneven edges" (Crawshay, 1907), "yerbas frescas," probably meaning green leaves (Barros, 1928), and green shoots (Morrison, 1939). Housse (1948) found small seeds and masses of fragmented plant material in the stomachs of five specimens. Barros (1928) states that the Gray-breasted Seedsnipe eats grain and green alfalfa in captivity.

My own observations in the Valle del Yeso showed that the Gray-breasted eats vast quantities of green grass leaves and green marsh vegetation, as well as the leaves of *Taraxacum officinale* (Figure 9). On present evidence, Johnson's (1965) statement that it feeds "mostly on seeds" does not hold good for the bird's summer diet, but it is quite probable that seeds may form the bulk of the winter diet when green vegetation is scarce or absent.

I have never seen the Gray-breasted drink nor can I find any indication in the literature that it does so.

Breeding Biology

Breeding Season

Seedsnipe breed in summer. The Least Seedsnipe nests from late August to January or even February (Durnford, 1878; Goodall *et al.,* 1951; Johansen, 1966; Johnson, 1965; Koepcke, 1964; Philippi *et al.,* 1954). Although Behn *et al.* (1957) collected a male with inactive gonads in February, Durnford (1878) has found chicks as late as March which suggests that this seedsnipe may have two or more broods a season.

I found half-grown chicks of the Least at Vallenar on 12 September; they had hatched from eggs that must have been laid at the beginning of August or even at the very end of July, an estimate based on my data relating to incubation periods and growth rates of the young. In Patagonia, the Least still had nests with eggs in December. Unfortunately, I left before the end of the breeding season so I could not determine its full extent. Durnford's (1878) remarks are without doubt quite acceptable; he appears to have been a most reliable observer.

The information on the breeding season of the Gray-breasted is patchy, but the indications are that this species breeds rather later than the Least, starting in September in the northern part of its range and ending as late as April (Johnson, 1965). Other authors mention January or February (Goodall *et al.,* 1951; Hellmayr, 1932; Housse, 1948; Lane, 1897). The Gray-breasted was already nesting in the Valle del Yeso at the beginning of November, 1967. Dr. Philippi tells me, however, that summer was early in 1967 because of the drought. Nevertheless, Barros (1921) states that this species breeds in the Andes of Aconcagua as early as the end of September so the nest in the 1967 season may not have been abnormal.

There appeared to be some degree of synchrony of egg-laying in the Valle del Yeso population. Five nests in the study area had fresh eggs at the same time and there was no sign of chicks anywhere.

Male Breeding Displays

Arriving in Atacama as I did, after the breeding season of the Least Seedsnipe had started, I missed pair formation. The males, though, frequently performed territorial display flights, associated with a song which they also uttered from a perch—a stone, a wall, or a bush (Figure 10). The territorial flight display of the Least takes the following form: The bird flies up from the ground or from a perch, rises steeply to a height of about 15 to 20 meters, then glides with stiffly decurved wings for a few seconds as he utters the first part of the song, a rapid *wikiti wikiti wikiti* repeated six to eight times, and finally dives almost vertically toward the ground uttering the second part of the song, a far-carrying hooting *puku puku puku;* as he approaches the ground he levels out and glides again on stiffly decurved wings and upturned tail for a few meters before landing. The *puku* notes may be replaced at times by an

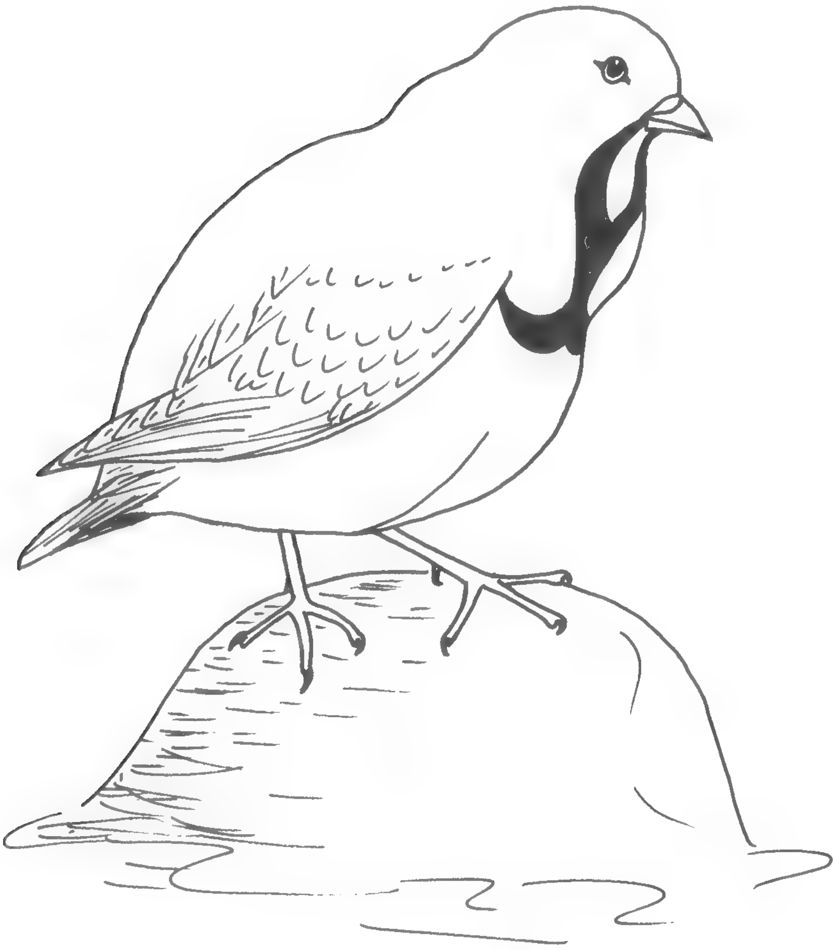

Figure 10. A male Least Seedsnipe in typical singing posture. Note how the bird inflates the region of the neck. The males sang during territorial display flights or from a slightly elevated perch—a stone as in the drawing or, perhaps, a wall or bush.

even richer *whoop-whoop-whoop* phrase, alternated in some instances by three or four *wikiti* phrases.

The Least Seedsnipe performs another display flight, a "butterfly flight," during which it may fly high in the air or just skim over the ground, beating stiff wings in an exaggerated arc above and below the body and, at times, uttering the *wikiti* notes only.

I am fairly certain that these songs and displays are territorial in nature; the functional difference between them is not immediately apparent. Some light may be shed on the problem from observations of birds using isolated and possibly slightly modified parts of the typical song. I saw two male Least Seedsnipes engaged in an aerial chase during which I heard only the flight call. The pursued bird (B) landed at times and the pursuer (A) would then also land and chase B with the head-down aggressive threat posture. Bird A eventually perched on a bank of earth and began to call a deep *kru kru kru,* repeating the note as many as 30 times in each burst of calling. B stood just below A, called *puku puku* from time to time, and eventually ran off to join a female standing on the adjoining territory.

I interpret these events as follows: A was clearly dominant; B was intruding on A's territory because he left later to join what was probably his rightful mate on his own territory. The *kru* note may be a challenge, issued to an intruder of the same species, while the other components of the song, *puku,* are more simply in the nature of territorial advertisements.

Figure 11 (*above*). A male Least Seedsnipe standing on a stone perch. The female, just barely visible, is feeding on the ground to the right of the male. This small patch of bare ground in Atacama is typical habitat.

Figure 12 (*below*). A male Least Seedsnipe singing from a high perch. The top of the "calafata" (*Berberis buxifolia*) is about two meters above the ground in a characteristic habitat in Santa Cruz. Note the same shrub in Figure 4.

In the Patagonian region there are two main dialect differences in the song of the Least Seedsnipe. The first is a rapid *pu-pu-pu-pu-pu,* derived from the first syllable of the more commonly heard *puku.* The second is a rolling variation of the *wikiti* notes that sounds like a very rapid *krikikru kriki-kru.* Southern males also utter the *puku* notes much more rapidly than do the northern birds. In many cases, however, I could not distinguish the song of the southern birds from that of the northern.

The song perch of the male Least varies according to the type of objects available. In Atacama the males normally used a stone of perhaps 20 to 30 cm high (Figure 11); they also perched on fence posts and stone walls as high as one and a half meters and on the dry inflorescences of the "cardo," a thistle, *Carduus pycnocephalus,* which may be almost a meter tall. In Patagonia, Least Seedsnipe males often perched on the topmost branches of the bush "calafate," *Berberis buxifolia,* over two meters high (Figure 12).

The Gray-breasted has a song essentially similar to that of the Least but much simpler. What the song lacks in complexity, it makes up for in length. Usually it is a simple *puku puku puku,* uttered from a rock perch or in a display flight at the rate of 160 to 170 per minute. When given from a perch, a single song lasting up to five minutes may have as many as 850 *puku* notes and is one of the most characteristic and monotonous sounds of the high Andean valleys.

The *puku* song may be introduced by a series of growling notes thus: *prrkrr prrkrr prrkrr puku puku puku.* Since the display flight seldom lasts more than 30 seconds, the *puku* notes, when uttered in flight, are usually not repeated more than 10 times. The Gray-breasted gives its song flight closer to the ground than does the Least, usually no more than five to 10 meters. The bird rises to its cruising height, begins to sing, and then drops toward the ground in a shallow dive, during which the tonal frequency of the song also drops. The song ends before the bird lands, but should it land on a rock perch, it may begin to sing again almost immediately, particularly if another male is in sight. The Gray-breasted has the same final glide after the display flight as does the Least with one difference—the Gray-breasted does not raise its tail.

Male Gray-breasted Seedsnipe are very aggressive among themselves. There are frequent clashes over territorial boundaries during which one male usually goes after another with the aggressive, head-down threat display (Figure 13). However, an intruding male may not always give up easily. I saw one extreme case of territorial conflict that is worth recounting.

At 0830 hours I came upon two males, A and B, on the same territory. After a number of display flights both birds landed on flat ground. Bird A at once threatened B with the head-down posture (Figure 13), sometimes with the wrists held slightly away from the body. After a few more display flights over the territory the two birds landed and began to fight, jumping at each other with spread wings and feet directed well forward. When the fighting stopped, A began to chase B. Neither bird ran fast and A geared his pace to that of B, keeping about 40 cm behind him. Every now and then B stopped and turned toward A with an upright threat posture in which the black wing linings were exposed by slightly opening the wrists (Figure 14). This behavior released the same posture in A and the two birds fought again.

Sometimes the fighting was merely "sparring" with the two birds jerking their heads from side to side. A head movement to one side by one bird was followed by a movement to the same side by the other. A variation of this was vertical head-bowing with alternating head-down and head-up movements in quick succession.

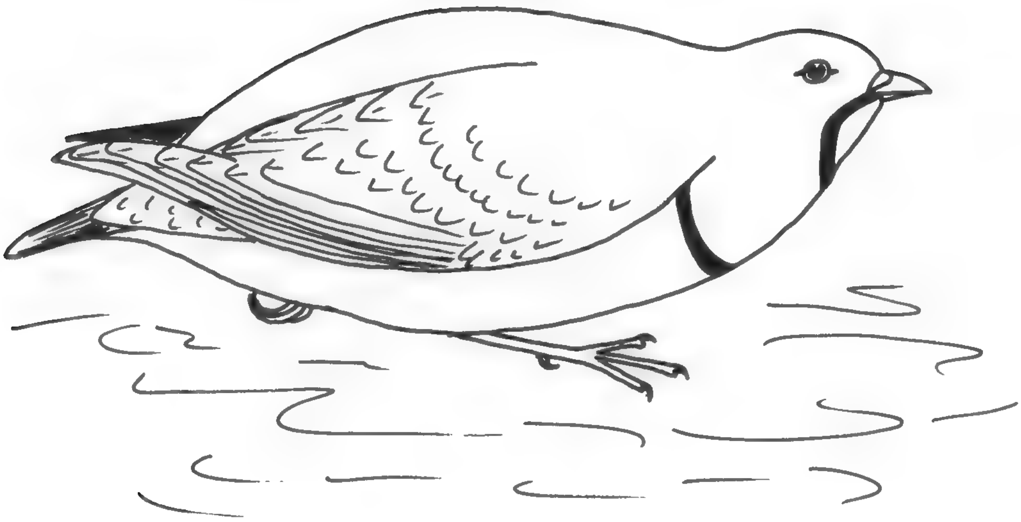

Figure 13 (*top*). The head-down threat posture of a male Gray-breasted Seedsnipe. Because the males are very aggressive toward other males of the same species, disputes over territorial boundaries are frequent. The male assumes this posture when chasing another male Gray-breasted Seedsnipe from his territory.

Figure 14 (*bottom*). The upright threat posture. The bird, preparing to fight, stands straight up and opens his wrists, exposing the black linings of the wings. His adversary does the same and usually a fight follows.

They then resumed chasing, A always chasing B. And so they battled until at least 1545 hours, more than 7 hours later, with chasing, sparring, occasional fighting, and even some exaggerated displacement feeding, rather reminiscent of grass-pulling in gulls.

While A and B were engaged in this seemingly futile combat, two other males gave display flights over the same territory. One of these landed next to the combatants, approached them with a high-intensity threat display, standing with body vertical, wings half-open and drooped, and tail partly fanned, and chased both A and B away. As they retreated, the third male lowered his head and followed them, holding his wings partly open.

One female Gray-breasted, apparently an occupant of this territory, performed the typical male display flight several times on successive days. This flight was remarkable in being accompanied by a song, shorter in length, having no more than six *puku* notes at one time, and squeakier in quality than the male's. This was the only female seedsnipe I saw display in this way.

Johnson (1965) writes of the Gray-breasted that the "calling goes on day and night." In my experience both species of *Thinocorus* were strictly diurnal in all their activities. The Gray-breasted usually began to sing at 0500 hours, just as dawn was breaking on 29 October, and continued singing until about 0800 hours when it slackened off somewhat. The birds resumed singing at about 1645 or 1700 hours and continued until dusk.

The Least, which also starts singing at about dawn, carries on intermittently throughout the day until dusk with a lull usually during the midday hours. Both species of *Thinocorus* utter the song with the bill open; they may give the lower cooing notes with the bill closed.

Breeding Territories

In Atacama, I found nests of the Least only where the ground was bare, open, and stony (Figure 15). Nest M was on a patch of ground, 80 by 30 meters, in the middle of a field of green wheat. The bare area on which Nest P was situated was even smaller. Seldom were nests on the open llano less than 250 meters apart. The two closest contemporary nests, I and J, were 60 meters apart. There was no question of the birds being semi-colonial in their nesting habits as suggested by Johnson (1965). The males strictly observed and always jealously guarded territorial boundaries.

Intraspecific threat in the Least occurred only between males, never toward a female or by a female. It resembles the head-down threat display of the Gray-breasted, also a highly territorial species.

Nest Sites

Eleven of the 16 nests of the Least, found near Vallenar, were completely exposed on stony ground littered sometimes with dry feces of domestic stock, dry cornstalks, and perhaps a little other plant material (Figure 16). Five nests were placed against small plants (Figure 17), four on the east side of the plant and one on the southwest side. Seven nests were next to or among dry feces of donkey, horse, or cow (Figure 18). The three nests in the Patagonian region were on flat ground and completely surrounded by low vegetation (Figure 19).

The nest sites of the Gray-breasted are essentially the same as those of the Least — all on flat ground, quite exposed from above, and unprotected by plants or surrounded by sparse, low vegetation. Of five nests in the Valle del

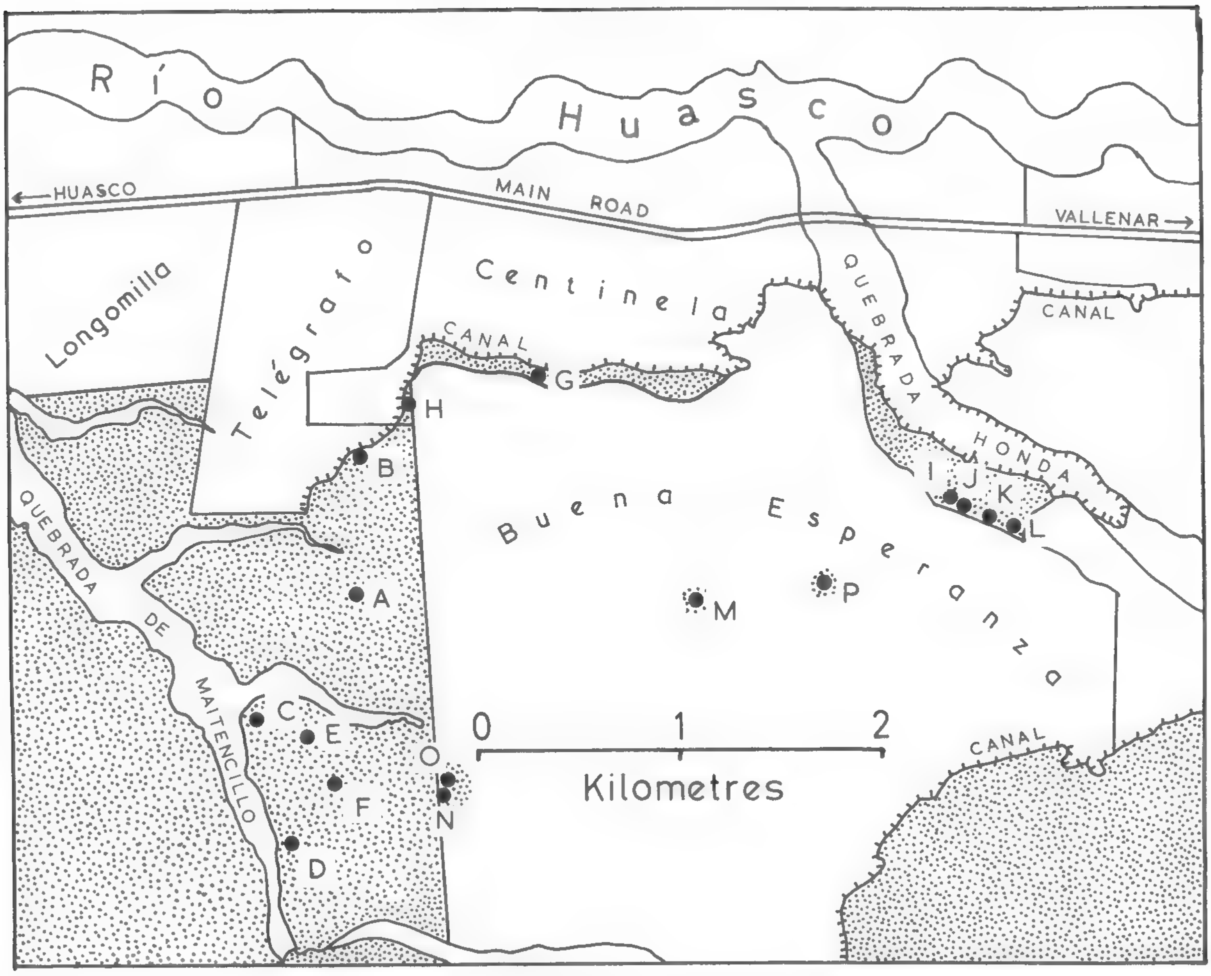

Figure 15. Map of the study area on the bank of the Huasco River at Hacienda Centinela near Vallenar in Atacama, Chile. The localities, lettered A to P, are the sites of 16 nests of the Least Seedsnipe found during the study period. The stippled areas are stony places and open llano; the white areas are valley bottoms, as in the two "quebradas," or cultivated fields.

Yeso, two were on the east side of low plants (Figure 20), one on the east side of a dry cow pat (Figure 21), one among plants and stones and not noticeably oriented to any particular object, and the fifth on top of a tussock of spiky marsh grass in a bare sandy patch.

The Nest

Typically charadriiform, the seedsnipe nest is a scrape in the ground, lined with almost any loose material available although mostly with organic matter (Figures 16 and 21). The nests of both species of *Thinocorus* are very similar, distinguishable only by size. Three nest scrapes of the Least measured on an average 113 mm in diameter by 41 mm in depth; one scrape of the Gray-breasted measured 160 mm by 50 mm. Both species, once they have completed the scrape, fill it to overflowing with pieces of dry organic material and an occasional small stone. As the eggs are laid, they become embedded in this loose lining, which the female also uses to cover the eggs when she leaves the nest.

Both Durnford (1878) and Johnson (1965) say that the nest of the Least is *sometimes* lined with material. It is my experience that the nest is *always* lined with material.

Within a single territory there are often four or five nest scrapes, some of them unlined, but the female lays eggs in only one. It seems as if the birds

Figure 16 (*above*). Nest A of the Least Seedsnipe in Atacama. The birds make a scrape on bare stony ground and line it with bits of soft material—dry feces of domestic animals, dry cornstalks, and dried pieces of other plants. The four eggs in the picture lie partly buried in the lining just as they do when the female incubates them.

Figure 17 (*below*). Nest C of the Least Seedsnipe in Atacama. Some nests are on completely open ground; others such as this are against small plants or bushes. This nest, at the base of a dried shrublet, has an ample lining of vegetable material.

Figure 18 (*above*). Nest B of the Least Seedsnipe in Atacama. This nest, on the open ground, is encircled by horse feces. The eggs are hidden, having been covered with the dry lining by the female before she left the nest.

Figure 19 (*below*). Nest Q of the Least Seedsnipe in Patagonia. All three nests in Patagonia were on flat ground and surrounded by green grass and herbs.

Figure 20 (*above*). Nest B of the Gray-backed Seedsnipe in Valle del Yeso, Santiago. Of the five nests in this valley two were on the east side of low shrubs. A dry shrublet with spiked leaves shelters this nest.

Figure 21 (*below*). Nest C in Valle del Yeso, Santiago. A third nest lies on the east side of a dry cow pat. Note the similarity of the vegetation to that in the picture above.

make several scrapes before deciding which one to use for the eggs. They line this one. Unlined nest scrapes differ from roosting scrapes (*q.v.*) in being much deeper and broader.

Eggs and Clutch Size

Johnson (1965) described the eggs of both *Thinocorus* species. Goodall *et al.* (1951) give mean dimensions of 42 Least eggs at 31.6 by 22.9 mm. These are a little larger than the means of 31.1 (standard deviation = 1.192) by 22.5 (SD = 0.660) for 49 eggs that I measured in Atacama; the extremes of these 49 eggs were from 28.1 to 32.9 by from 21.3 to 24.0. Measurements of 21 Least Seedsnipe eggs, in the collection of W. R. Millie and also from Atacama, have means of 31.5 by 23.2. The overall means from Mr. Millie's and my figures are 31.4 by 22.8, which compare more closely with those of Johnson (1965).

Goodall *et al.* (1951) give mean measurements of 20 eggs of Gray-breasted (*T. o. ingae*) as 38.4 by 27.0. More recently (1957) these workers give mean measurements of six eggs of the typical subspecies (*T. o. orbignyianus*) as 39.7 by 28.0. Taczanowski's (1884-1886) measurements of six eggs of this species give means of 40.3 by 27.0.

Out of 14 nests (with complete clutches) of the Least, 13 contained four eggs each; one had three. All five nests of the Gray-breasted in the Valle del Yeso had clutches of four. Johnson (1965) says that four is the normal clutch size of both *Thinocorus* species, although he adds that in the Gray-breasted "3 is not uncommon." He also records a clutch of two eggs for this species.

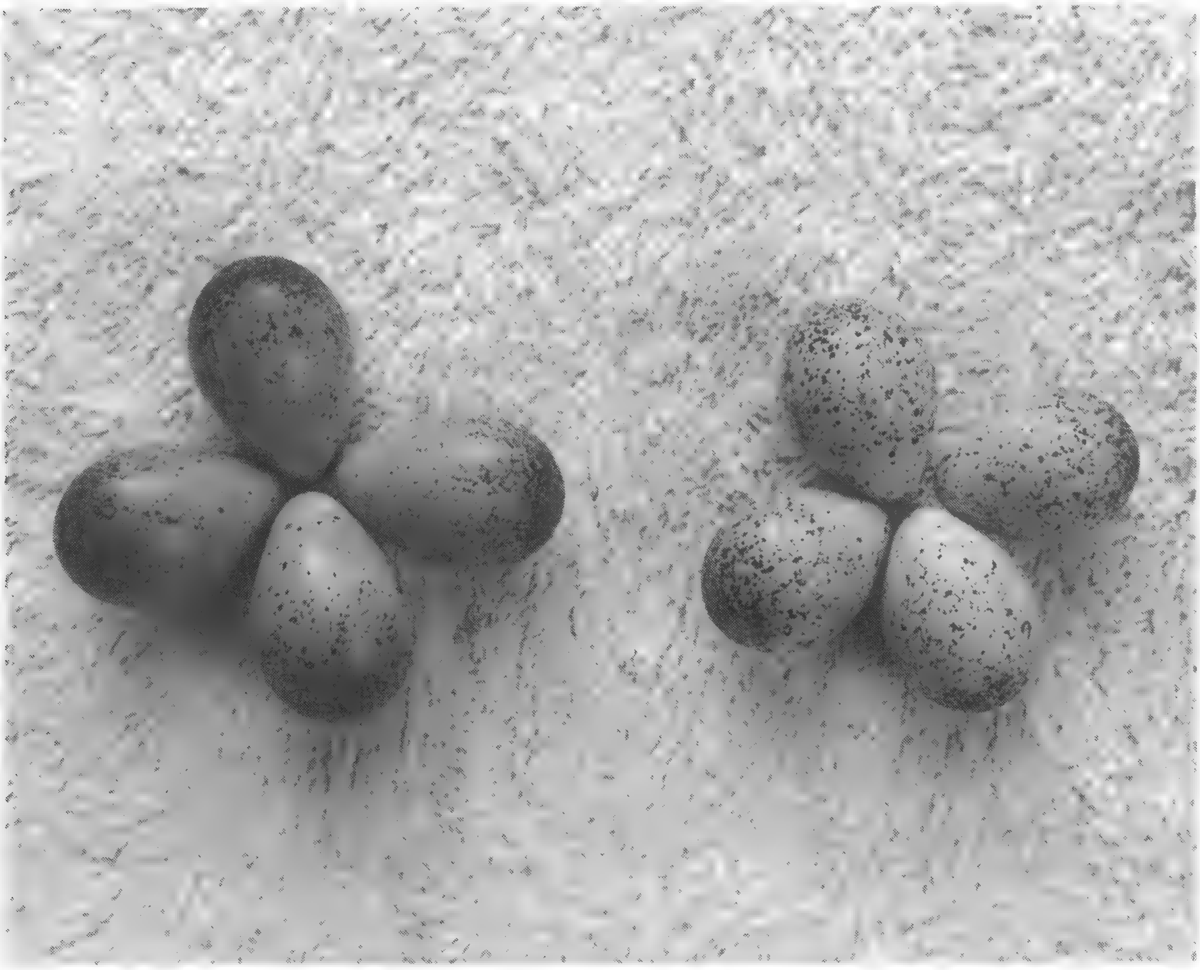

Figure 22. Clutches of eggs of the Least Seedsnipe. The larger eggs on the left are from Tierra del Fuego and are dull green with fine speckles around the thick end. The eggs on the right are from Atacama and are typically creamy pink in color. This difference in color has not been mentioned in the literature.

I believe that clutches of less than four eggs in *Thinocorus* are most unusual and in many cases due to the loss of one or more eggs after the clutch has been completed. More than likely the clutches of three eggs, recorded by Johnson, were either incomplete or one had been lost. Both Hellmayr (1932) and Housse (1948) also record clutches of four eggs for the Gray-breasted.

Records of clutches of more than four eggs in seedsnipe, such as a clutch of eight eggs of *Attagis gayi* (Housse, 1948) and the suggested possibility of six eggs in some species (Van Tyne and Berger, 1959) are almost certainly the result of confusion with the nests of other species or of two female seedsnipe laying in one nest.

Except for their size, the eggs of the two *Thinocorus* species are very similar. There is, however, an interesting color variation in the eggs of the Least from the Patagonian region. Some have a dull green ground color, instead of pink or cream, and are very finely speckled around the thick end (Figure 22). I first noticed this difference, not mentioned in the literature, while examining eggs in Mr. Millie's collection, where a single clutch of green eggs from Tierra del Fuego contrasted markedly with the creamy pink eggs from Atacama.

Mr. Waldron, who has lived for many years in the provinces of Magallanes and Santa Cruz, tells me that eggs of both pink and green types occur in the Patagonian populations of the Least, and that, in his experience, the green is much the commoner of the two. Of three nests of this species that I found in Patagonia, one contained green eggs, the other two pink. Len and Oliver Bridges of Viamonte, Tierra del Fuego, say that they have found pink and green eggs in about equal numbers of nests. In any case, I found green eggs only in the Patagonian region and nowhere farther north.

Incubation Period

There is no published information on the incubation period of any seedsnipe. The longest period during which I had a nest of the Least under continuous observation — from the completed clutch to the known hatching date—was 25 days. On the day I found the nest, 17 October, the four eggs were cool and fresh as though incubation had not yet begun. On 10 November, when I first heard the chicks, the eggs were not pipped. On 11 November, all four had hatched and the chicks were some six meters from the nest. Thus, the incubation period of the Least is at least 25 days and probably not more than 26 days.

I have no information on the incubation period of the Gray-breasted Seedsnipe.

Hatching and Development of Chicks

I heard the chicks of the Least Seedsnipe peeping inside the eggs up to two days before the pipping began. The length of time between pipping and emergence varied between nests, from less than 24 hours to just over three days, yet it did not vary within a single brood; all the eggs of one clutch took the same time to hatch. For instance, in Nest G all the eggs were pipped at 0855 hours on 7 October, and the chicks all emerged sometime between 0840 hours on 9 October and 0940 hours on 10 October. In contrast, none of the eggs in Nest P was pipped at 1850 hours on 10 November and all the chicks had hatched by 1810 hours on 11 November.

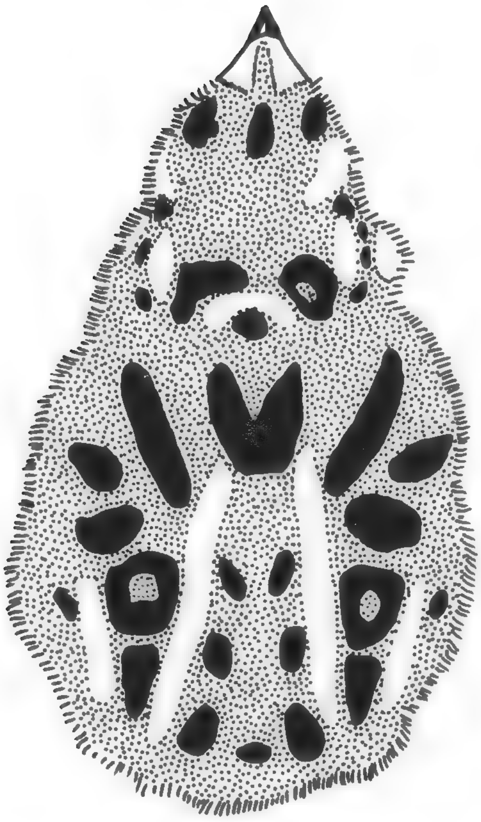

Figure 23. The pattern of the natal down on the back of the Least Seedsnipe chick. The black areas are black, the white areas are predominantly white, and the stippled areas are earth brown. This cryptic plumage of lines and patches on a mixed background of black and brown camouflages the chick most successfully.

TABLE 2

Measurements and Weights of Least Seedsnipe Chicks of Various Ages from Atacama, Chile; with Mean Weight and Measurements of Adults from the Same Locality Given for Comparison

	Age in Days									*Adult*
	2	*2*	*4*	*7*	*7*	*15*	*25*	*35*	*40*	
					Millimeters					
Body length	55.0	57.0	56.0	66.5	62.3	71.0	82.0	119.0	128.6	177.0
Wing			13.7			17.5	22.4	64.9	80.0	115.3
Culmen	5.0	5.0	5.4			7.8	8.6	11.4	11.5	11.1
Tarsus	9.4	10.4	9.1	10.1	10.9	11.6	13.0	14.5	14.1	14.5
Middle toe	14.0	15.0	15.6	15.4	14.5	17.7	15.6	17.1	18.2	20.8
Hind toe	3.2	3.6	4.0	4.5	4.4	4.2	4.2	4.7	5.0	5.0
Tail								12.0	14.2	54.1
						Grams				
Weight	5.0	5.5							36.8	52.8

The chicks, highly precocial, usually leave the nest within a few hours after hatching, the first waiting for the last as a rule and the brood departing together. However, since hatching in the Least Seedsnipe is so highly synchronized within the brood, the first chicks do not have to wait long. If the chicks are disturbed, they leave the nest even before they are dry.

At hatching, the chick of the Least weighs about 5 grams and is about 55 mm in length. The natal down, with a cryptic pattern of white lines and black patches on a mixed background of black and brown (Figure 23), conceals the chick well (Figure 24). The ventral down is off-white, and the soft parts colored as follows: bill, pale bluish gray with a black line down the culmen; egg-tooth, white and lost within 24 hours; cere, grayish pink; iris, dark brown to black; feet, grayish pink; and claws, smoky horn.

The changes in the dimensions of the chick are shown in Table 2 and Figure 25. I obtained these data by measuring chicks in the field and in the laboratory; in most cases I knew, or could closely estimate, the age of the chick. There is little change in the appearance of the chick during the first week of its life. At the age of 10 days (Figure 26), the scapular feathers have broken their sheaths and are about 10 mm long. No other feathers are visible. At 15 days the scapular, pectoral, and mantle feathers have all broken their sheaths, but the sheath bases persist for a few more days. At this age too, the outermost remiges are about 3 mm long and tipped with natal down; no other remiges nor any rectrices are visible. The soft parts may or may not have changed to the adult coloration. I saw 25-day-old chicks with the soft parts colored as they were at hatching.

At the age of 25 to 30 days (Figure 27) the scapular and mantle regions are fully feathered; the primary remiges have all appeared as quills; no secondaries are yet apparent. At 35 days, the chick is fully feathered dorsally and partly feathered on the chest; the tail is about 12 mm long. At 40 days (Figure 28) the chick is fully feathered with a plumage pattern resembling that of the adult female; the soft parts have the adult female coloration and the sexes are indistinguishable.

The Least Seedsnipe flies at the age of seven to eight weeks. A chick estimated to be seven and a half weeks old, give or take five days, flew for a few meters and landed clumsily. It could not have been able to fly at all for more than a day or two.

One question I hoped to answer was: What is the food of seedsnipe chicks? The stomach contents of Least Seedsnipe chicks of various ages, from less than 48 hours old to at least six weeks, consisted of seeds, including wheat grains, and green leaves of *Medicago* and other herbaceous plants. Very tiny chicks, even when barely dry after hatching, feed adequately by themselves and need no assistance from the parents either in the location of, or the picking up of, food. Chicks of less than a week old have no visible crop and I was unable to determine at what age the crop developed. There was no reason to suspect that young Least Seedsnipe ate animal food at any time or ever drank water. Never did I see a parent feed, or attempt to feed, a chick of any age.

The behavioral development of the Least Seedsnipe chick is fairly typical of the Charadriiformes (cf. Maclean, 1966; 1967b). The usual alarm reaction is crouching, sometimes with the eyes partly closed during the initial period (Figure 27) and slowly opening as time passes. When the chick begins to fledge, crouching may give way to escape running if an intruder approaches too closely. While running, the chick utters its distress call, an undistinguished *peep peep,* just like the young of many other precocial birds. Even before the

Figure 24. A brood of four Least Seedsnipe chicks. Only about 48 hours old, they have left the nest and are crouched among fallen stalks of dry wheat in a field in Atacama.

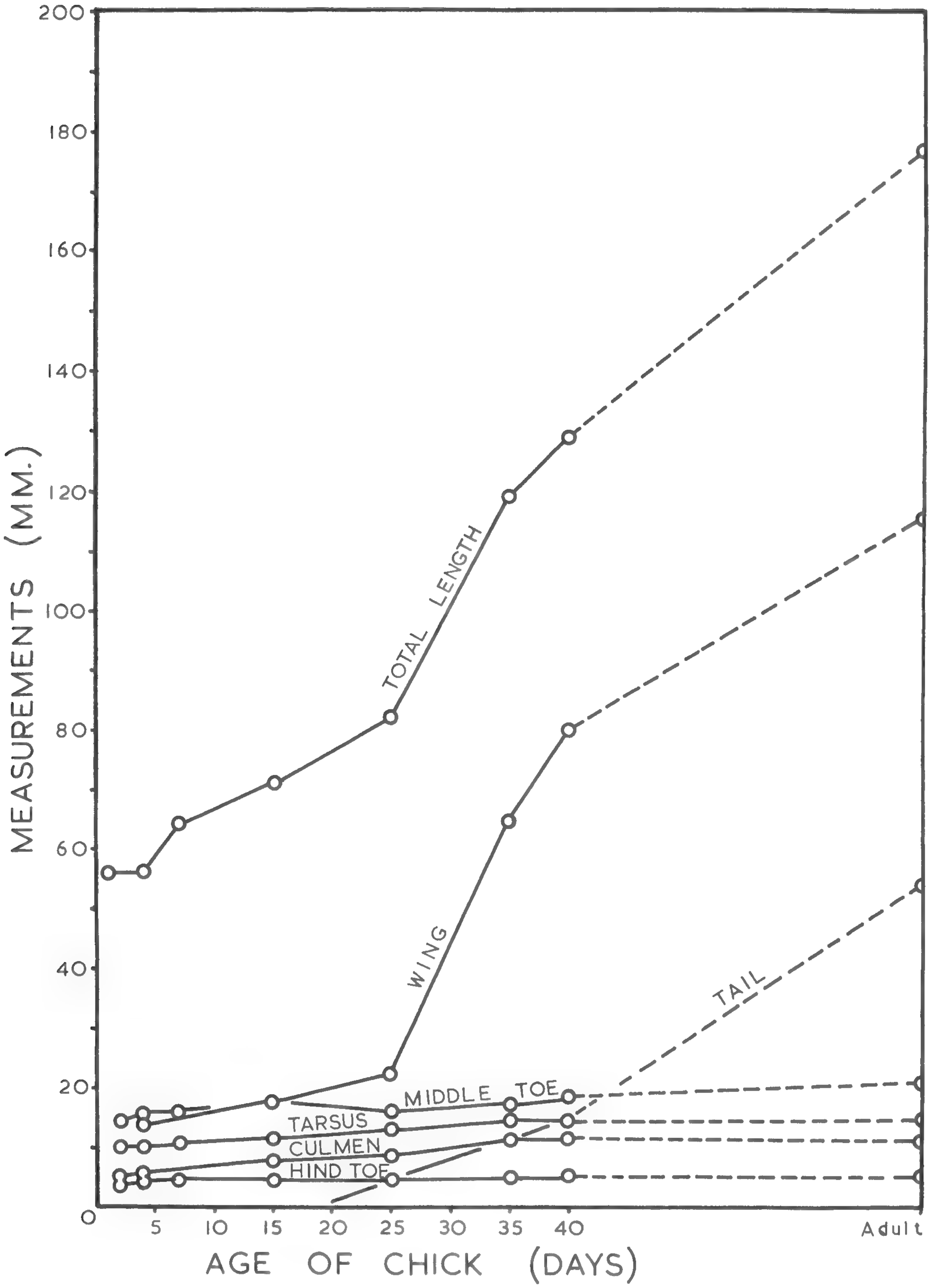

Figure 25. A graph of the growth rates of Least Seedsnipe chicks. The data for the graph come from Table 2.

Figure 26 (*above*). Chick of the Least Seedsnipe at 10 days of age. The chicks change little in appearance for the first week of life; after that they change rapidly. At 10 days of age the scapulars have broken their sheaths and are about 10 millimeters in length—just beginning to show.

Figure 27 (*below*). Chick between 25 and 30 days of age. The scapular and mantle regions are fully feathered; the primaries are only quills; there are no secondaries. This chick is crouching with eyes half-closed—an alarm reaction that may change to running if the observer comes too close.

Figure 28. Chick of the Least Seedsnipe at 40 days of age. Though traces of down still cling to the head, and the tail is very short, the chick is now fully feathered. Both sexes resemble the adult female in the pattern of their plumage and in the color of the soft parts.

remiges appear, it spreads the wings while running, particularly when dodging to avoid capture.

Parental Care

In both species of *Thinocorus* only the female incubates the eggs. Associated with this is the total absence of brood patches in the male. The female's brood patches are situated on either side of the abdominal midline and separated from each other by a narrow tract of feathers (Figure 29). Probably only the female constructs the nest; this requires confirmation. Incubation begins with the completion of the clutch. I was unable to determine the time interval between the laying of successive eggs. From the first egg the female covers the eggs with the soft nest lining when she leaves the nest. Females are prone to desert the nest before the clutch is complete; but I saw not a single case of a bird deserting a nest with a complete clutch. Once, while trying to photograph a female at the nest from a hide, I kept a Least Seedsnipe from her eggs for five and a half hours. After I removed the hide, she returned to incubate and all the eggs hatched 12 days later.

Although it was difficult to assess accurately, the female Least Seedsnipe appeared to have two long attentive periods in 24 hours. Except for two breaks when she left the nest to feed, she was on the nest all the time. A morning break is usually between 0900 and 1000 hours, but may be as late as 1030; an evening break, recorded at Vallenar in October, was between 1800 and 1900 hours, about sunset. At both of these breaks the female almost invariably left with the male.

The morning break in the Gray-breasted, between 0630 and 0800 hours, may be even earlier if it has snowed the previous night; the evening break occurs about 1700 hours.

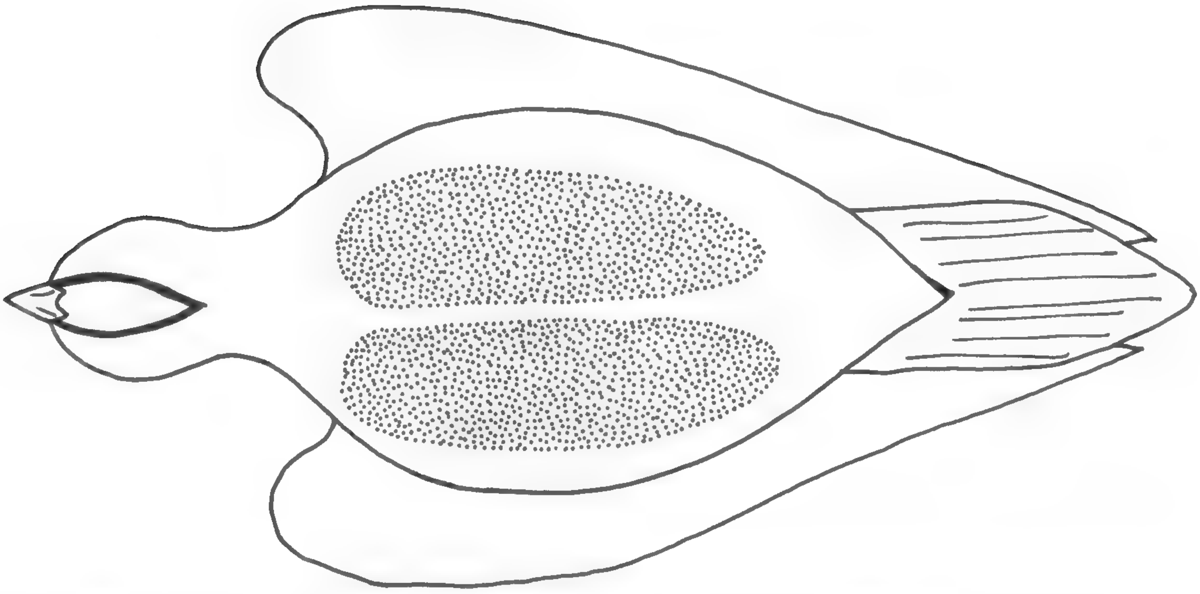

Figure 29. The brood patches on the abdomen of a female Least Seedsnipe. The stippled area shows the brood patches on either side of a narrow tract of feathers along the midline of the abdomen. The male, which never incubates the eggs, has no brood patches.

Both species of seedsnipe cover the eggs in exactly the same way. Before leaving the nest, the female raises her body slightly and kicks the nest material rapidly inward with her feet, covering the eggs completely (Figures 18 and 30). She does this in two or three seconds when disturbed suddenly or she may take rather longer when undisturbed and preparing to leave at the end of an attentive period.

Seedsnipe females, disturbed or calm, feed almost continually when not on the nest. This is in marked contrast to the male which spends most of the time, while the female is incubating, standing on a stone in the vicinity of the nest (Figure 11). The opportunistic feeding behavior of the female is of considerable biological significance because feeding time, normally available to her, is limited and the male never feeds her under any circumstances.

On returning to the nest, the female begins to remove the covering material with her bill (Figure 31), tossing it aside with the "side-throwing" movements typical of the Charadrii. She then works the remaining material aside with her abdominal feathers (Figure 32) and also, to some extent, with her feet (Figure 33). Once the tops of the eggs are exposed, she settles down to incubate (Figure 34). Even after starting to incubate, the female indulges in intermittent side-throwing, tossing the nest material along the sides of her body and working it outward to lie around the rim of the nest. This side-throwing behavior, intensified when she is alarmed, invariably precedes her departure from the nest.

Although the male never incubates, one incident occurred which may indicate that the roles of the sexes were at one time more equal. The female, incubating on Nest G, left when I set up a hide. The eggs were already pipped; I could hear the chicks peeping inside. Of the two adults, the male was the first to return to the nest. He pecked at the nest material, side-throwing just as the female did, and then he moved on to the rim of the nest as though preparing to incubate (Figure 35). At that moment, I photographed him. Alarmed a little by the click of the shutter, he walked away, and, as he did, he side-threw until he was about one and a half meters from the nest. He did not return to the nest again; the female arrived shortly and settled down to incubate.

Egg-covering is the rule whenever the female seedsnipe leaves the nest, except, of course, in a very sudden departure. Associated with egg-covering is the habit of leaving the nest surreptitiously when approaching danger is still many meters away. This distance varies considerably with the individual female. In the Least it is usually not more than 150 meters and seldom less than five meters. Some females of both species habitually sit tight (Figure 36) and leave the nest only when almost stepped on. One female Least almost allowed herself to be touched on the nest.

Precipitate departure from the nest was always accompanied by a distraction display in which the female fluttered low along the ground, her tail depressed and fanned, showing the white tips on the dark rectrices (Figure 37). She would flutter thus to the edge of the territory or just for a few meters before she either landed, ran away, or took to normal flight and possibly disappeared from view over a bank. This display was identical in both the Least and Gray-breasted Seedsnipe.

Some Least Seedsnipe females indulged in distraction flights even after covering the eggs and leaving the nest. In such cases, the female crouched three or four meters from the covered nest and then, when closely approached, fluttered away suddenly as if she were leaving directly from a nest. Usually, however, if the female had already covered the eggs, her distraction display was less intense, consisting merely in running away with the tail fanned, the wrists held slightly away from the body and the head drawn inwards. The wing on the side toward the intruder was usually dragged on the ground, a display similar to the "rodent-run" of the male.

Figure 30. Nest B of the Gray-backed Seedsnipe. Nothing shows. The female covered the four eggs with lining material before she left them. She can do this quickly—in two or three seconds if disturbed suddenly. Usually, when leaving for her regular feeding period, she takes much longer.

Figure 31 (*above*). Female Least Seedsnipe on her nest. She has just returned to incubate and is removing the nest-covering from the eggs with her bill. She tosses it to one side in a movement known as "side-throwing" and typical of the shorebirds.

Figure 32 (*below*). Following the side-throwing movements, she works the material aside with her abdominal feathers.

Figure 33 (*above*). She then pushes it aside with her abdomen and to some extent with her feet.

Figure 34 (*below*). And when the eggs begin to show, she settles down to incubate. While she is incubating, she may side-throw occasionally, tossing the material along the sides of her body and working it outward to lie around the rim of the nest.

Figure 35 (*above*). Nest G of the Least Seedsnipe. In one instance, after the observer had frightened a pair and the female had left the nest, the male, which never incubates, returned first. The eggs, already pipped, were still covered. He pecked at the covering, side-throwing a bit, and moved to the rim of the nest as though he might incubate. Unfortunately, any intention he may have had vanished with the click of the camera. He fled. The female returned and settled down to incubate.

Figure 36 (*below*). Female Gray-backed Seedsnipe. One must look carefully to find this bird, so effective is the camouflage of her plumage. This photograph was taken from a distance of two meters with a 50-millimeter lens. Some females will leave their nests only when about to be stepped on; one bird allowed the author to touch her on the nest.

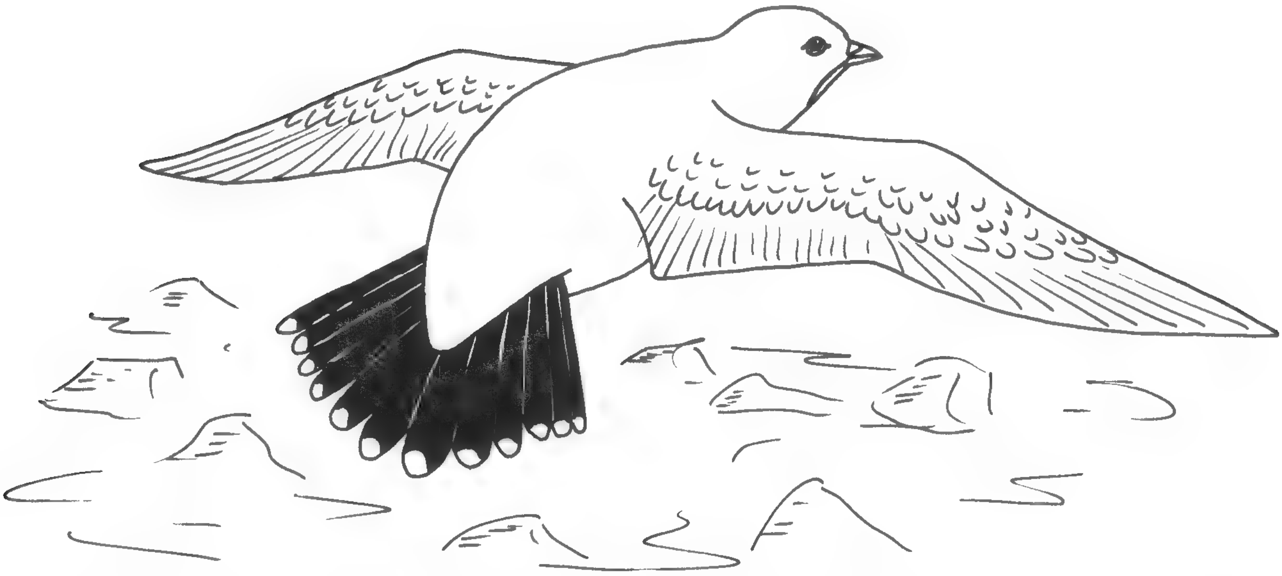

Figure 37. Distraction flight-display of female Least Seedsnipe. As she leaves her nest, when startled, she flutters low on the ground with tail depressed showing the white tips on the dark rectrices. The distraction flight-display is identical in the Least and Gray-backed Seedsnipe.

After hatching, there are never any traces of eggshells in or near the nest. The female probably carries them away. A female with young still in the nest will, when disturbed, cover them in the same way that she covers eggs. Once the chicks have left the nest, she may still cover them if there is any loose plant material available. For about two weeks after leaving the nest, the female broods the chicks when necessary. Although the male never broods the chicks, he becomes extremely solicitous of the welfare of the female and the chicks and performs two distraction displays to draw attention away from them. The first and commoner of these is the rodent-run display in which he runs quickly with back hunched and head tucked into the shoulders, sometimes dragging a wing. He may run to and fro about 10 to 15 meters from the intruder, or he may run toward the intruder, turning when just a few meters away to repeat the rodent-run display directly away from the chicks. He may repeat this maneuver several times.

The second type of male distraction display involves repeated take-offs accompanied by extremely exaggeratedly loud take-off notes, followed by a brief flight and ending with the stiff-winged downward glide with raised tail. After landing, the male generally runs towards the intruder and then repeats the distraction flight.

When the chicks are still very tiny, the female usually remains as inconspicuous as possible, but, if a chick is picked up and utters the distress call, her behavior changes radically. She gives very high-intensity distraction displays with spread tail, wings beating hard on the ground, and much rushing back and forth, often within less than a meter of a human observer. At lower intensity the display may consist merely in rodent-running with one dragging wing. Another high-intensity distraction behavior pattern of the female Least is displacement brooding in which she vigorously flings grass sideways with head-shaking movements and then shuffles her body on the ground as if she were on a nest. Very rarely she runs about with both wings held vertically open.

The role of the male parent throughout the breeding cycle is essentially that of sentinel and guard. During incubation he always accompanies the female back to the nest. Then he perches on a nearby stone for a period of from a few minutes to half an hour at a time. Sometimes he flies away as soon as he has seen the female safely settled on the eggs. The role of sentinel continues after the chicks have hatched. Although the male may sometimes feed while the rest of the family is feeding, he frequently jumps onto a rock and scans the area before continuing his feeding.

Intraspecific territoriality in the Least has already been mentioned; I have only once seen a female of this species react to a harmless bird that came too close. A Correndera Pipit (*Anthus correndera*) approached to within four meters of an incubating female Least; the seedsnipe stood up, shook herself, and flew at the pipit to chase it away.

The behavior of the Gray-breasted Seedsnipe at the nest is similar to that of the Least with one notable difference—on leaving the nest the Gray-breasted female frequently walks toward an intruder. In my experience, Least females always walk away from an intruder.

Post-breeding Activity

I was not able to follow the post-breeding activities of either species of seedsnipe. Mr. Millie (*in litt.*) has sent excellent records of the Least in Atacama for the end of the 1967-1968 breeding season. I can do no better than quote from his letter of 21 March: "These birds [i.e., *T. rumicivorus*] are now to be seen around the farmland, on the dry fields, in the potato field and almost everywhere except on the slopes and dry patches where you found the nests. They are in flocks or groups of five to eight. They apparently are eating seeds now because they are seen searching for certain things which they stop and pick up. They have stopped calling altogether. . . ."

The breeding season of the 1967-1968 summer ceased at about the end of February in Atacama, giving it a duration of some seven months in all.

There is no accurate information about post-breeding activity in the Gray-breasted. It appears, however, that this species also forms small flocks in winter (Housse, 1948; Peña, 1961) and that these flocks usually move to lower elevations (Barros, 1921; Reed, 1907).

Calls

Alarm Calls

Both sexes of the Least Seedsnipe, particularly parents with chicks, use three calls in stress situations. The first is a mournful, rising *piiiiii* and the second, a soft nasal *krim krim*. It is my impression that the *piiiiii* call indicates more intense alarm than the *krim* call, but the birds use both calls when retreating from a danger stimulus that is some distance from the nest and chicks. The third call indicates the highest intensity of alarm; a loud, sharp *kikikik kikik*, frequently repeated, is given by an adult advancing upon the danger stimulus that is very close to the nest or chicks.

I did not hear such high-intensity alarm calls in the Gray-breasted because the birds did not have young at the time. They do, however, have a *pik pik* call that is probably the homologue of the *kikik* call of the Least. There was also a high-pitched purring *krrr* which seemed to be homologous with the *krim* note of the Least. I heard no note from the Gray-breasted that could be homologized with the *piiiiii* note of the Least. This does not mean that it does not exist; the call, if it has such, is probably mainly associated with danger to the chicks.

Take-off Call

Both sexes of the two species of seedsnipe have very similar take-off calls, usually a single rasping *bzeep,* uttered as the bird leaves the ground. This call with its singularly snipe-like quality must have caught the fancy of the earliest observers and led to the common name of "seedsnipe."

Flight Call

The flight calls of both species are similar to their high-intensity alarm calls, but quieter. In the Least it is a disyllabic *kirik;* in the Gray-breasted it is a deeper *wuk-wuk.* The birds utter these disyllabic notes at irregular intervals as long as they are on the wing and the effect is highly reminiscent of flying sandgrouse.

Following Call

The following call is uttered by parents coaxing the chicks to follow them. In the Least Seedsnipe this call may be a trisyllabic *kiriki* note, indistinguishable from the flight call but so soft that it is inaudible to the human ear at a range of more than about 10 meters. Given only by the female, it brings the chicks together after they have been scattered by a disturbance and, of course, stimulates them to follow. I have no data on following calls in the Gray-breasted.

Table 3 summarizes the homologous calls of the two species.

TABLE 3

Homologous Calls of Least Seedsnipe and Gray-breasted Snipe

Call	*Least Seedsnipe*	*Gray-breasted Seedsnipe*
Alarm:		
(a) low-intensity retreat	*krim*	*krrr*
(b) high-intensity retreat	*piiiiii*	not recorded
(c) high-intensity advance	*kikik*	*pik-pik*
Take-off	*bzeep*	*bzeep*
Flight	*kirik*	*wuk-wuk*

Comfort Movements

The comfort movements of both species of *Thinocorus* are identical and are unremarkable in themselves. I observed the following movements (terminology largely after McKinney, 1965): (1) Body-shake. (2) Tail-shake. (3) Wing-and-leg-stretch. (4) Both-wings-stretch. (5) Tail-stretch. (6) Scratching. (7) Bathing.

During body-shake, the wings are kept in their pockets of the pectoral feathers. Tail-shake is common after an alarm situation has passed, be it a chase by a member of its own species, disturbance by a predator, or any other situation of stress. In both-wings-stretch the wrists are always kept folded, unless wing-raising is used as part of a distraction display. Tail-stretch is performed simply by fanning the tail symmetrically; asymmetrical tail-stretch accompanies wing-and-leg-stretch as in all birds.

Head-scratching is always direct, under the wing, as in the Scolopacidae. Dust-bathing is apparently not common; I saw it only once in a female Least Seedsnipe. Since dust-bathing is of short duration, the behavior may be more widespread than my observations suggest.

Locomotion

Although short-legged, seedsnipe run with great facility and speed. There is no foundation for the absurd statement by Sclater and Hudson (1889): ". . . the legs and feet of *Thinocorus rumicivorus* are extremely small and feeble, and scarcely able to sustain the weight of the body." Yet Hudson repeated this statement verbatim in 1920. As a matter of fact, the toes of the Least are relatively rather long, even longer than the tarsometatarsus (Table 1).

Seedsnipe are superb fliers. They hold their legs out behind, under the tail while in flight, as do all the other Charadrii. The wings are long and pointed. In flight the Least looks like a small sandpiper, frequently jinking from side to side, particularly shortly following take-off and just before landing. The Gray-breasted, with its proportionately heavier and stockier body, looks very like a sandgrouse in flight as well as on the ground, but it runs with greater ease than does a sandgrouse.

When flushed, both the Least and Gray-breasted have a habit of disappearing behind a rise or over a bank. If the nearest bank is too distant, often the case in the wide open habitat of the Least, they usually land behind rocks or shrubs. If they do land in the open, they pause and then run to hide behind the nearest object.

Heat-regulating Behavior

I did not often get the chance to observe heat-regulating, or thermoregulatory, behavior in seedsnipe since there was seldom any really hot weather in any of my study areas in Chile and Argentina. When incubating in hot sunshine, the female Least pants and raises the feathers of her back in exactly the same way as coursers do (Maclean, 1967b). I also saw a chick of the Least raise its head and begin gular fluttering after it had been lying in the sun for a couple of minutes. Although I did not notice gular fluttering in adult seedsnipe, it probably does occur.

Alarm Reactions of Adult Seedsnipe

The initial alarm reaction of both species of seedsnipe, whether on the nest or not, is to crouch flat. The bird may then take flight or run behind a stone to hide. The commonest alarm reaction of seedsnipe at any time is head-bobbing, also the common alarm reaction of all Charadrii. Both seedsnipe performed it usually immediately before departure and, as in sandgrouse, only bob the head. At high-alarm intensities both species also rocked the tail up and down. The head and tail movements are not synchronous. The head movements are fast and jerky; the tail movements are more deliberate.

Figure 38 (*above*). Roosting scrape of the Least Seedsnipe on the bare ground of the llano at Atacama. Both species roost on the ground in scrapes, smaller and shallower than nesting scrapes. Roosting scrapes may occur singly or in groups of from four to eight, not more than 50 centimeters apart.

Figure 39 (*below*). Roosting scrape of the Least Seedsnipe at the base of a cactus in Atacama. The roosting scrapes, sheltered by a stone, bush, or cactus, always seem to be on the south, east, or southeast side of the object, where, possibly, the birds have protection from the sun and, in certain areas, from the constant west wind.

Roosting

Both species of seedsnipe roost on the ground in small scrapes which they make for the purpose. In Atacama, the Least made its roosting scrapes on the llano. These depressions were smaller and shallower than nest scrapes and usually contained small amounts of dry feces (Figure 38). Often the scrapes are quite exposed but sometimes may be at the foot of a shrub, cactus, or stone (Figure 39), and, as with nest scrapes, tend to be oriented on the south, east, or southeast side of an object. Though roosting scrapes may occur singly, most were in small groups of four to eight, placed no more than 50 cm apart as a rule. The roosting scrapes of the Gray-breasted Seedsnipe in the Valle del Yeso occurred in groups of up to eight, were all on the east side of shrublets or grass tufts, and, like those of the Least, were smaller than the nest scrapes.

Predation

I have already mentioned the possible predation on the Least Seedsnipe by foxes. The only predators of which I have firsthand knowledge are the American Kestrel (*Falco sparverius*) and the Cinereous Harrier (*Circus cinereus*), both of which took small and half-grown chicks. I have no information on the predators of the Gray-breasted.

Discussion

I cannot decide which of the two species of *Thinocorus* is closer to the ancestral form. Since three out of four species of seedsnipe are montane, the Least Seedsnipe might have secondarily adapted to the plain. But the general trend in the family appears to be either toward an increase in size coupled with a decrease in sexual dichromatism, a difference in the color of the sexes; or, in a reverse direction, toward a decrease in size and an increase in sexual dichromatism. Kendeigh (1952) makes the basic assumption that equality in the parental roles of the sexes is the primitive condition; associated with this condition is the lack of sexual dichromatism.

The development of patterns of parental care and sexual dichromatism has gone in two very different directions within the suborder Charadrii. On the one hand in the phalaropes, the Phalaropodidae, the female is more aggressive and more brightly colored than the male, which assumes the major role in parental care. On the other hand, in the seedsnipe, *Thinocorus,* the brighter colored male takes very little part in parental care; at least he has a more indirect role than that of the female. The single case of the male Least at the nest indicates, however, that the male did at one time, during the course of seedsnipe evolution, share in the incubation of the eggs, especially since the evidence indicates that bi-sexual parental care in birds is the more primitive. In the isolated case of male parental care, it was most certainly the sounds of the chicks in the eggs that first stimulated the male to return.

We must learn more about parental care in the genus *Attagis* for we cannot assume that the roles of the sexes are equal in that genus. If the parental role is greater in the male *Attagis* than that in the male *Thinocorus,* we could suggest that *Attagis* is the more primitive of the two genera.

We can visualize an evolutionary trend by hypothesizing the Least Seedsnipe as the most primitive, and progressing through the Gray-breasted in which the vertical black stripe, part of the male's secondary sex characteristics, is lost from the chest pattern, the chest band becoming narrower and the song simpler; to *Attagis* with a total loss of differences in male plumage patterns that are externally visible. Incidental to the other revolutionary processes, would be the increase in size, probably associated with the progressively colder environments inhabited by the increasingly larger species, which is the situation as we find it today.

Introducing the section on parental care in the Charadriiformes, Kendeigh (1952) says: "No information is available on the . . . Thinocoridae . . . ." Gilliard (1958) states of the Least Seedsnipe that: "The length of incubation and the roles played by the sexes in rearing the young apparently remain unknown." The present study has advanced our knowledge, but we need more information on both species of *Attagis* and on the post-hatching parental care of the Gray-breasted before we can speculate on which species is closest to the ancestral type. The evidence points at present to the evolution of smaller, more complex forms from larger, less differentiated forms.

I have already mentioned the possible relationships between the seedsnipe and other members of the Charadrii. We know too little of these relationships to discuss them here. However, we can note the remarkable convergence between the seedsnipe, Thinocoridae, and the sandgrouse, Pteroclidae. We have evidence that the sandgrouse are merely highly specialized Charadriiformes (Maclean, 1967a), so we are hardly surprised to find morphological and behavorial convergence between two families within a single order. Both the seedsnipe and the sandgrouse have evolved into vegetable feeders, no doubt from a more generalized insectivorous charadriiform ancestor: hence the similarly stocky build, small head, simple bill, and short legs. In both groups the legs, short as they are, are still held under the tail in flight. Both have retained excellent powers of flight, the sandgrouse for their daily flights to water (Cade and Maclean, 1967; Maclean, 1968), the seedsnipe for their nomadic and migratory flights.

Both sandgrouse and seedsnipe tend to have colonized semidesert regions. The reason for this convergent similarity in choice of habitat is not immediately apparent. Probably both families evolved from deserticolous, or barren-montane, charadriiforms that took to a vegetable diet because of competition. Living as they do in the mountains of Chile, a narrow strip of land well provided with rivers and streams from the Andes, and also in the flat wastes of Patagonia with its frequent marshes and pans, the problem of water never became serious for the seedsnipe. Even though they do not drink water, they have sufficient green or semi-succulent vegetation on which to feed and thereby obtain their water preformed. Furthermore, the misty coastal belt of Chile supports a rich variety of true succulent plants of various families — Cactaceae, Aizoaceae, Portulacaceae among others—which provide the coastal Least Seedsnipe with water-rich food. Should these water-rich plant sources fail, the seedsnipe can easily move to more profitable areas and this is exactly what they do.

To what extent does the naturally available food of the Least provide water? Apart from the fact that the crushed leaves of such plants as *Calandrinia* and *Carpobrotus* literally drip with water, analyses of the leaves of *Calandrinia grandiflora* in Atacama by Mr. Millie revealed a mean water content of no less than 92.56 per cent (Table 4). We are certain that the succulent food of the Least Seedsnipe in the Chilean desert is an adequate source of preformed water and reason enough why these seedsnipe do not need to drink.

For the same reason, seedsnipe do not need to provide their chicks with water as do the sandgrouse (Cade and Maclean, 1967). There would therefore

TABLE 4

Water Content of Green Leaves of *Calandrinia grandiflora*[1]

Sample	*Weight before drying*	*Weight after drying*	*Weight of water lost*	*Per cent water content*
A	175.7	11.2	164.5	93.63
B	105.0	6.6	98.4	93.71
C	107.3	12.3	95.0	88.53
D	134.5	8.8	125.7	95.66
Means	130.6	9.7	120.9	92.57

[1] The leaves were weighed fresh, oven-dried for 72 hours to constant weight, and re-weighed. Weights are in grams. The samples consisted of 12 leaves each from four different plants from the Quebrada Maitencillo, Vallenar (Figure 8). Data from W. R. Millie *(in litt.)*.

have been no selective pressure on the evolution of such elaborate structural and behavioral adaptations for water transport as are found in the sandgrouse. With regard to the acquisition of food, however, the young of both groups are equally independent of their parents and are never fed by them. They show the same high degree of precocity in other ways, too.

A major difference between sandgrouse and seedsnipe, at least seedsnipe of the genus *Thinocorus,* is the marked inequality of the parental roles in the seedsnipe. In all sandgrouse, so far studied, the male helps with the incubation of the eggs and the care of the young (Maclean, 1968). This is of interest if only because the two families exhibit a similar degree of sexual dichromatism. In addition, the males of both families show a tendency towards the evolution of characteristic chest colors outlined with distinctive chest bands, although this tendency is also well marked in such related families as the Charadriidae, Glareolidae, and Scolopacidae.

Despite the considerable similarities between seedsnipe and sandgrouse, none can be used as a criterion for their close phylogenetic relationship. The differences are probably more fundamental than the similarities, which are nonetheless a classical study in convergent evolution within an avian order.

The tendency in both the Least and Gray-breasted Seedsnipes to place nests and roosting scrapes on the east, south, or southeast side of an object resembles a similar tendency in larks and some other ground-nesting birds of the Southern Hemisphere (Maclean, in press). The nest or scrape is not only sheltered from the sun for most of the day, but also from the cold west wind blowing in from the sea all down the Chilean coast and up into the Andes. In Patagonia where the "Roaring Forties" howl almost incessantly across the pampa, the problem of shelter for ground-dwelling birds is partly solved by the presence of a relatively good cover of grass that breaks the force of the wind at ground level.

The placing of the nest next to a plant or stone cannot have much function in concealing the nest or sitting bird. The plains of Atacama and Patagonia are covered with many extraneous objects, stones and grass tufts, giving the background a disruptive effect according to the principles outlined by

Maclean and Moran (1965). This is borne out by the number of Least Seedsnipe nests on the open llano without any cover or protection from nearby objects.

The habit of egg-covering by the female seedsnipe when she leaves the nest probably has little to do with protection of the eggs from cold or heat. Heat is seldom a problem in any seedsnipe habitat; the coastal and montane semi-arid regions of Chile and Argentina are more often cold than hot, even in summer. The covering material, used by the birds, does not provide adequate insulation against heat loss from eggs if there is a cold wind blowing. In any case, judging from a photograph of its nest, the Rufous-bellied Seedsnipe (*Attagis gayi*) of the high Andes does not cover its eggs simply because the nest appears to have no lining (Johnson, 1965:361). *A. malouinus,* the White-bellied Seedsnipe, probably does cover its eggs (Johnson, 1965:371). We need much more information on this genus.

Hall (1958, 1959) studied egg-covering in the Kittlitz's Plover (*Charadrius pecuarius*) in South Africa; Conway and Bell (1968) observed the same behavior among captive pairs nesting in the New York Zoological Park. Only the approach of a human intruder seems to elicit egg-covering in this bird. Cows and falcons do not, even though the plover may leave the nest when they approach. In the Least Seedsnipe, I saw egg-covering at the approach of man and of a dog. I did not observe the bird disturbed by any other animal. The adaptive significance of egg-covering would be to conceal the eggs from a predator hunting by sight. Man is the only animal in this category in Chile and Patagonia; the other mammals and the few snakes hunt largely by smell and it is highly unlikely that hawks or falcons prey on seedsnipe eggs.

How did egg-covering evolve? Armstrong (1942) suggested that it arose in Kittlitz's Plover and the "Patagonian" Seedsnipe (=the Least Seedsnipe) initially as a result of accidental kicking of material over the eggs as the bird hurriedly left the nest. My own suggestion is that it could have been an incidental result of the shuffling movements made by an incubating bird on the nest as it flattens itself out in order to become less conspicuous at the approach of an intruder (Figure 36). In either event, selection pressure would favor egg-covering until it became a fixed behavior pattern in the presence of certain sign-stimuli, such as man.

However, the situations in the plover and the seedsnipe are not quite parallel. In Kittlitz's Plover both sexes incubate so that the eggs are not usually unattended, and, during nest relief, the departing bird does not cover the eggs (Hall, 1958, 1959; Conway and Bell, 1968). In the seedsnipe only the female incubates and the eggs are unattended when she feeds. Whenever she leaves the nest, for whatever reason, she always covers the eggs. Even at the end of an attentive period when the only stimuli are hunger and possibly the position of the sun, she still covers the eggs. We need more experimental work to clarify this problem.

In the same way as selection for egg-covering against sight-hunters has developed in the seedsnipe, so presumably has the selection for egg color which almost certainly preceded egg-covering as an adaptive feature. The selection for green eggs in the southern populations of the Least is incomplete, yet the evolutionary pressure of the egg-covering habit would tend to reduce, or even eliminate, the evolution of cryptic egg coloration.

It is possible that green eggs in the Least are a vestigial feature of an incomplete evolutionary process, rather than a developing feature. The difference between pink and green eggs of the Least appears to be reflected within the genus *Attagis* between *A. gayi,* the Rufous-bellied Seedsnipe of the arid mountains, and *A. malouinus,* the White-bellied Seedsnipe of the green Fuegian tundra. All known eggs of the Rufous-bellied are pink and the four known eggs, a single clutch, of the White-bellied, are green (Johnson, 1965). I have seen these clutches in Mr. Johnson's collection in Santiago and the difference is truly remarkable. The number of clutches known, however, is too small to permit any more than a preliminary statement here. The suggestion is certainly there (cf. Goodall, 1964).

The similarity of intense-alarm, flight, and chick-following calls in the Least may seem surprising at first. However, each of these calls constitutes a contact-call in one way or another. The intense-alarm call serves to contact the mate in time of danger; the flight call acts as a contact-call to keep the pair or flock together in the air; and the following call serves to keep the family together. The three calls are apparently therefore just variations on the same basic theme. Sclater and Hudson (1889) and Hudson (1920) give an account of calls in flocks of Least Seedsnipes as follows: "If a person stands still close to or in the midst of the flock the birds will presently betray their presence by answering each other with a variety of strange notes, resembling the cooing of Pigeons, loud taps on a hollow ground, and other mysterious sounds, which seem to come from beneath the earth." I interpret this account with some reserve, and suggest that the calls he describes are merely flock contact-calls. I never had the impression of any "mysterious sounds" from any species of seedsnipe although the cooing and whooping notes of these species may at times be somewhat ventriloquial.

The brevity of my study period and consequent paucity of information on the seedsnipe allows only a limited amount of observation from which a longer discussion is not possible. I have sorted out the basic problems of seedsnipe biology and indicated where future investigation may most profitably lie. Although we have only scratched the surface in the study of this fascinating genus, we have a start. It is my hope that New World ornithologists will continue the investigation from where I left off and follow it through.

Summary

The literature on the genus *Thinocorus* is reviewed. This paper is a report of a four-month field study of the Least Sandsnipe (*T. rumicivorus*) and the Gray-breasted (*T. orbignyianus*) in Chile and Argentina. The distribution and habitats of these two species are described. The taxonomy of the genus is briefly dealt with and the systematics of the Thinocoridae discussed.

Seedsnipe of the genus *Thinocorus* feed exclusively on vegetable matter under natural conditions and never drink water; this applies to both adults and young of all ages. Chicks are never fed by their parents. Sufficient water is obtained from succulent and green leaves; this obviates the need to drink.

Both species of *Thinocorus* breed in summer. Nests are typically charadriiform and lined with dry organic matter. The clutch is invariably four eggs, which are covered by the parent when she leaves the nest. Only the female incubates. The male lacks brood patches, while the female has one on each side of the abdominal midline. Breeding displays and songs of the males are described. Breeding territories vary in size according to the terrain and the population density. Nesting is not colonial. The incubation period is 25 to 26 days in the Least Seedsnipe.

Chicks of the Least Seedsnipe leave the nest within 24 hours of hatching. The first feathers appear at between seven and ten days and the young fly at

between seven and eight weeks of age. Weights and measurements of developing chicks are given and their plumages and behavior described. Parental care is described and discussed from an evolutionary point of view. At the end of the breeding season the seedsnipe gather into small flocks that leave the breeding places and become nomadic.

Calls, comfort movements, and other behavior patterns are described. Predators include a harrier and falcon and probably foxes.

Acknowledgments

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A TECHNIQUE FOR REARING PASSERINE BIRDS FROM THE EGG

WESLEY E. LANYON AND VERNIA H. LANYON

There is a growing need among contemporary biologists for passerine birds that have been hand-reared from an early age, preferably from the egg stage. The behaviorist may wish to study the development of particular behavioral patterns in an individual under controlled aviary conditions. The physiologist functions more efficiently when he can maintain and study his experimental material within convenient range of laboratory equipment and facilities. The experimental systematist looks to hand-reared birds in studying hybrids of known parentage and for obtaining data on potential isolating mechanisms. But the problems associated with the hand-rearing of the altricial young of passerines have been so formidable as to discourage investigators and preclude the use of this experimental approach by most laboratories. Efforts over the past five years in our own laboratory — at the Kalbfleisch Field Research Station of the American Museum of Natural History in Huntington, New York — toward the development of a more reliable procedure for rearing passerines from the egg have been most rewarding. We now feel confident enough of our technique to make it available to other investigators.

Species that we have successfully reared from the egg include the Great Crested Flycatcher (*Myiarchus crinitus*), Blue Jay (*Cyanocitta cristata*), House Wren (*Troglodytes aedon*), Eastern Meadowlark (*Sturnella magna*), and House Finch (*Carpodacus mexicanus*). In addition we have raised Black-capped Chickadees (*Parus atricapillus*) and Blue-winged Warblers (*Vermivora pinus*) from an age of one to four days. Though our experience has been confined to birds of the order Passeriformes, we can see no reason why the same procedures would not be suitable with those non-passerines — e.g., cuckoos and woodpeckers—that have altricial young and that are largely insectivorous in their food habits. One might have to alter the diets slightly to allow for specific differences in nutritional requirements.

Incubation

Equipment

The requirements of many projects dictate that the young birds be hatched in an incubator under controlled environmental conditions. Since our particular interests included the effect of very early experience upon the development of vocalizations, we were obliged to incubate and hatch the eggs in an enclosure where we could regulate the sound environment. For this purpose we adapted a Hartshorne chamber to serve as a still-air incubator (Figure 1). The basic Hartshorne chamber consists of three wooden boxes nested within one another and separated by sound-insulating material. The inner box measures 19 by 19 by 13 inches and is equipped with microphone and speaker. Tests on our Hartshorne chambers, using a General Radio sound-level meter (Type 1551-B) and an audio-signal generator, revealed that those frequencies most characteristic of bird vocalizations (above 1,000 cycles per second) are attenuated by the time they reach the inner chamber by more than 70 decibels. (The decibel is a term expressing relationships in the loudness of sounds according to the ratio of their power levels. A difference of only 10 decibels between two sounds is roughly equivalent to our psychological concept of "twice as loud.") This means that in practice the reduction in sound energy is sufficient to prohibit any bird voice from reaching eggs within the closed chamber. Conversely, birds within the closed chamber cannot be heard from without. A thermostatically-controlled electric heating element, mounted in the ceiling of the inner box, heats the air within the chamber. We have found that the Number 4 heater assembly—manufactured by the Lyon Rural Electric Company of San Diego—is satisfactory for this purpose. To avoid overheating the woodwork, the unit is mounted so that there is about one-half inch of air space between heater and ceiling. The special design of this particular heater causes the heated air to circulate, without a fan, throughout the chamber and provides equal temperature at the bottom and at the top of the eggs, which we place in a suitable container, a "nest," in an accessible position at the front of the chamber. A thermostat mounted near the eggs regulates temperature. Two temperature-sensitive probes, one taped to the surface beneath the eggs and

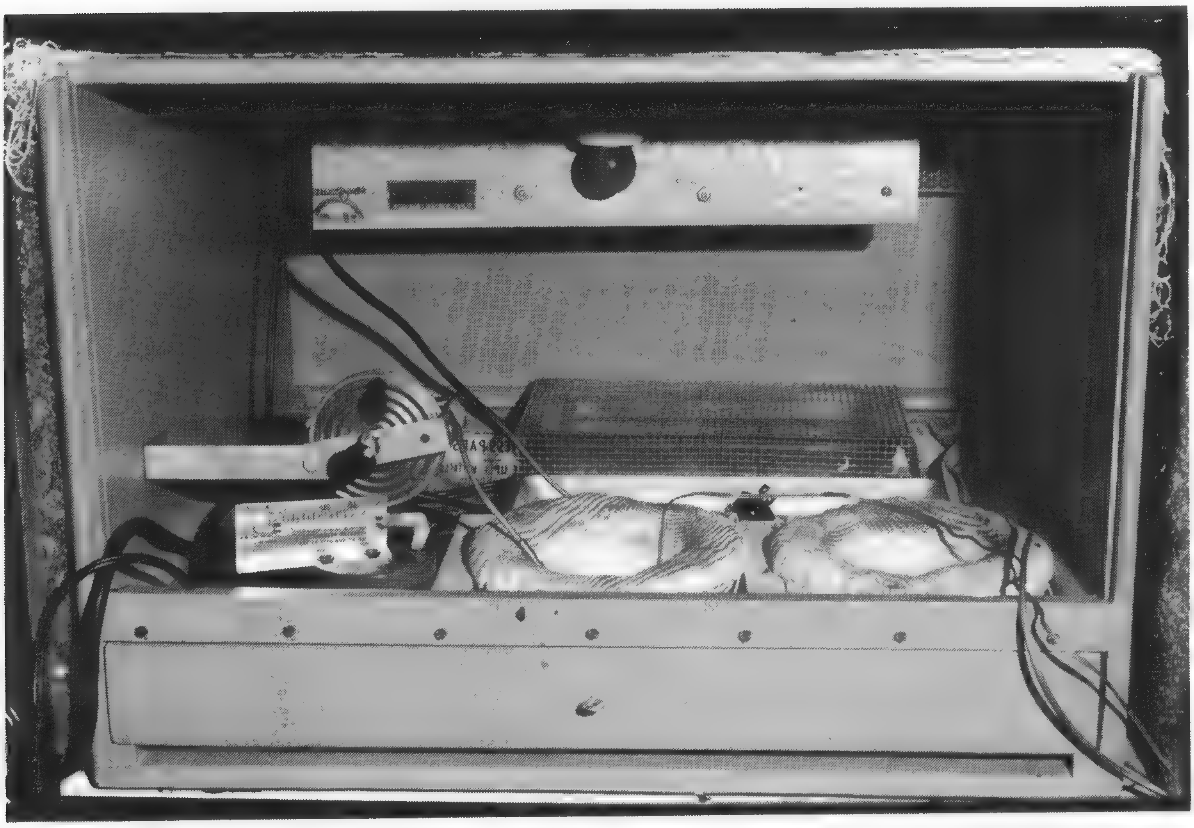

Figure 1. The interior of a Hartshorne chamber, adapted to serve as a still-air incubator. In this chamber the sound environment can be controlled, thus preventing any bird voice reaching the eggs from the outside.

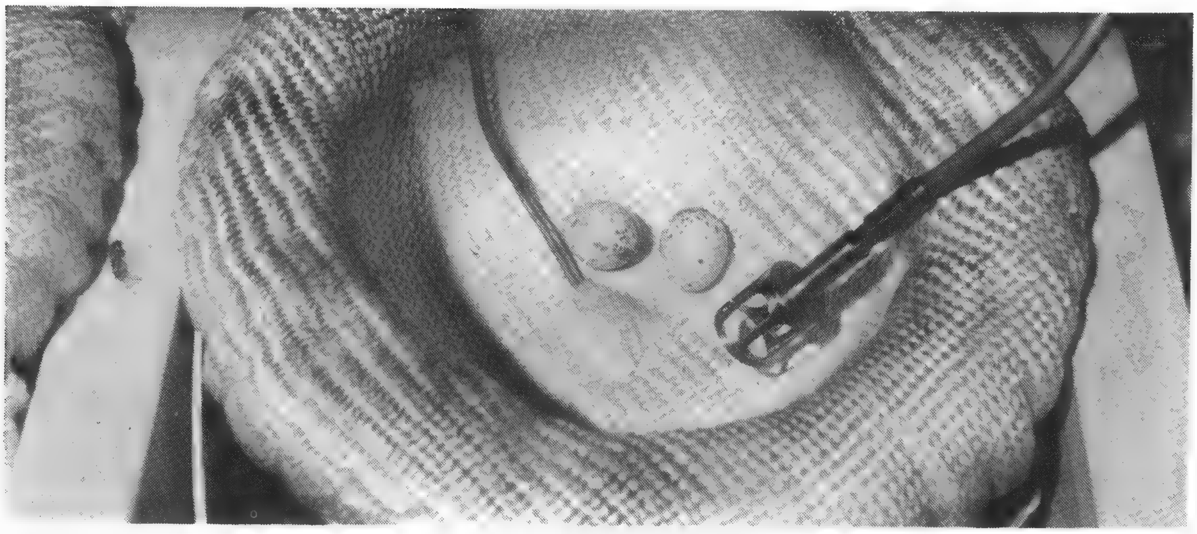

Figure 2. The eggs are placed in a suitable container at the front of the incubator. The effective incubation temperature, as registered by probes on the surface beneath the eggs and in the air above the eggs, is monitored by a remote-reading Tele-thermometer outside the incubator.

the other suspended in the air at the upper level of the eggs (Figure 2), register the effective incubation temperature and a remote-reading Tele-thermometer—from the Yellow Springs Instrument Company—monitors it outside of the chamber. Small holes, drilled in the walls of the chamber, permit the passage of the 110 AC power line to the heating element and cables to the two temperature probes in the nest. One may use a small red pilot light to indicate the "on and off" cycles of the heater, but this is not essential. The performance of the heater is at once apparent through the temperature monitor outside of the chamber. Containers of water placed within the chamber and spray from an atomizer provide humidity and a still-air hygrometer—from the American Lincoln Incubator Company, New Brunswick, New Jersey—placed as near to the eggs as possible, measures the relative humidity.

Discussion

The artificial incubation of non-passerine eggs, especially those of waterfowl and of galliform birds, is an exact science today and consequently there is a wealth of information to guide the neophyte experimentalist in that field. But we know comparatively little about the temperature and humidity requirements of passerine eggs and the frequency with which they need to be turned. While we were experimenting with this problem, especially with regard to an optimal incubating temperature, we had discouraging results except with those eggs that had been incubated naturally for nearly the full incubation period. Our technique has improved, however, and we recently fledged successfully a full brood of House Finches hatched from eggs that had been incubated in our chamber for nine days. This species has a normal incubation period of 13 to 14 days. As a general rule, we advise working only with eggs that have been incubated for at least half of the normal incubation period before removing them to the artificial incubator. Bear in mind, of course, that if development in a controlled sound environment is critical to the study, the embryo may be receptive to auditory stimulation several days prior to hatching (Gottlieb, 1965).

The thermostat in the incubating chamber should be adjusted to provide for a temperature ranging from 97° to 100°F throughout the on-and-off cycle of the heating element. No further adjustment should be required thereafter, providing the room temperature outside the chamber remains reasonably constant. Within the closed chamber there should be no significant difference between the temperatures recorded by the two sensor probes — i.e., the actual surface temperature of the nest beneath the eggs and the air temperature at the top of the eggs. When the chamber is opened for turning eggs and atomizing, the temperature at the eggs may fall to 90°F, thus providing periodic fluctuations that correspond crudely to the non-attentive periods of an incubating female.

A relative humidity of approximately 70 per cent should be maintained in the chamber. Evaporation from the water pans may be adequate but, if the humidity in the room outside the chamber is low, it may be necessary to spray with an atomizer. When the eggs begin to pip the moisture should be increased. The glass on the chamber door should show some moisture condensation during the hatch. If necessary, one can place sponges in the water pans at this time in order to increase evaporation. A little experience will determine the conditions under which the young birds appear to hatch with least difficulty. Too little moisture restricts movement within the shell and may make the membranes too dry and tough for the chicks to penetrate.

The eggs should be turned several times daily to prevent adhesion of membranes and provide exercise for the developing embryo. We routinely turn the eggs a minimum of five times per day and we have no data on the effectiveness of a fewer or greater number of turns.

As the young birds hatch, we remove them to a Hartshorne chamber that has been modified into a brooder.

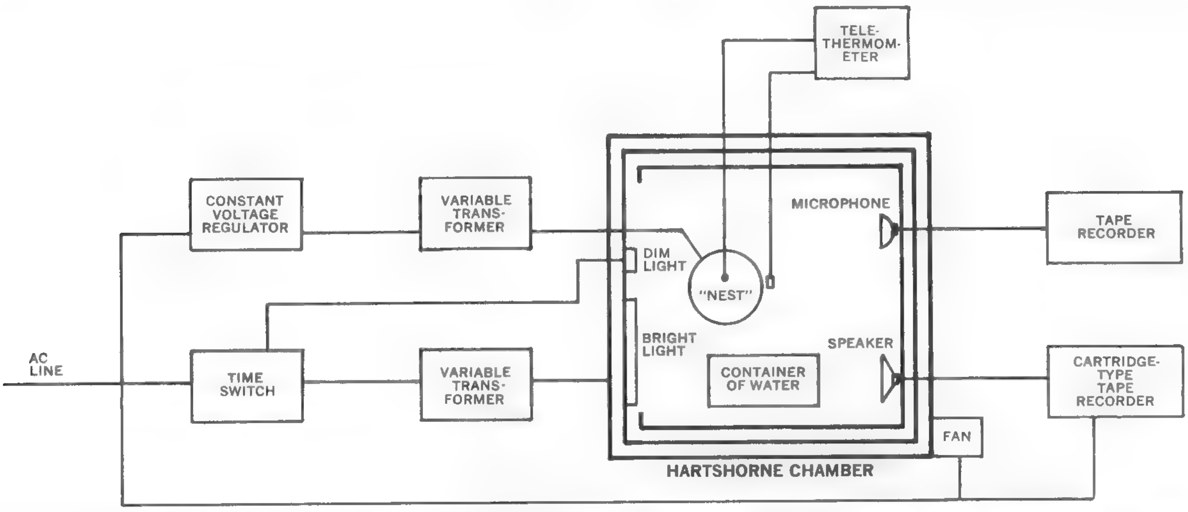

Figure 3. Diagram of components used for brooding nestlings in a Hartshorne chamber. A fan (*lower right*) maintains a circulation of fresh air. Actual brooding is through direct application of heat to nestling birds rather than by heating the air within the chamber.

Brooding

Equipment

The brooding chamber consists of a basic Hartshorne chamber modified and equipped with various accessory components as indicated in Figure 3. A fan maintains a circulation of fresh air from the air-conditioned laboratory throughout the chamber at all times. A container of water covered with wire screening provides moisture through evaporation. The actual brooding is accomplished through direct application of heat to the nestling birds rather than heating the air within the chamber. An incandescent tube illuminates the interior of the chamber and a time switch can regulate the photoperiod. The intensity of this lighting is controlled by a variable transformer. A dim circuit on the time switch allows for fifteen minutes of subdued light, permitting fledglings to assume roosting positions before total darkness ensues.

Nestling birds are brooded in a round-bottomed heating mantle, as used in the chemistry laboratory for heating flasks of inflammable fluids (Figure 4). We use mantles of two sizes—manufactured by the Glas-col Apparatus Company of Terre Haute, Indiana. The smaller of these (200 milliliters), with an inside diameter of 3.0 inches and a depth of 1.75 inches, is appropriate for birds of warbler size. We use a larger mantle (500 ml), with an inside diameter of 3.75 inches and a depth of 2.0 inches, for birds of meadowlark size. Other mantles are available in smaller and larger sizes. A variable transformer activates a heating circuit throughout the glass fabric of the mantle and the voltage setting of this transformer controls the brooding temperature of the nest. Since the heating element in the mantle is sensitive to the slightest fluctuation in line voltage, we found it necessary to use a constant voltage regulator in the main power line, thus insuring a constant power supply for the nest. A washable, open-weave cloth liner keeps the nest clean and yet permits the transfer of heat from the glass fabric to the nestlings. A separate piece of open-weave cloth, the brooding blanket, is placed across the opening of the nest to cover the nestlings.

A remote-reading Tele-thermometer monitors temperatures at two points within the chamber: (1) the surface of the bottom of the nest, and (2) the air at the lip of the nest, beneath the brooding blanket.

Discussion

Since altricial nestlings of passerines are unable to regulate their body temperature, or thermoregulate, for some days after hatching, some provision must be made for duplicating the function of the brooding parent bird. Our initial approach to the problem was to heat the air throughout the chamber, as in the incubating chamber, but we discovered that this invariably led to severe dehydration and intolerable losses in body weight, particularly overnight. We regard this problem of dehydration, associated with the usual method of brooding in a blanket of warm air, to be one of the principal reasons for the failures that most laboratories have experienced in hand-rearing passerines. It occurred to us that it might be preferable to apply heat directly to the body of the nestlings—i.e., simulate the role of the brood patch—and this led us to try the chemists' heating mantle (Figure 4).

The variable transformer is set to produce a temperature of 100° to 102°F at the surface of the glass fabric at the bottom of the nest. The effective brooding temperature is somewhat less than this, of course, for the open-weave cloth liner is interposed between the glass fabric and the nestlings. The air temperature at the lip of the nest, but beneath the brooding blanket, is generally about 80°F, thus creating a heat gradient of approximately 20°F within the immediate vicinity of the nestlings. When the nestlings achieve some capacity for thermoregulating themselves—at about the time the eyes open and feathers begin to emerge from their sheaths — the surface temperature beneath the cloth liner may reach as high as 105°F. At this time the voltage to the nest can be reduced by lowering the setting of the variable transformer, thereby maintaining only a minimum brooding temperature for prevention of chilling. The nestlings need no heat during the last two days of the nestling period. The brooding blanket remains in place over the nestlings for most of the first two to three days, except during feeding. Gradually, as the nestlings become more fully feathered, the use of the blanket is curtailed. During the latter part of the nestling period it need be in place only during the night, as a deterrent to premature fledging.

Figure 4. Nestlings are brooded in a round-bottomed heating mantle, as used in the chemistry laboratory for heating inflammable fluids. A washable, open-weave cloth liner keeps the "nest" clean and yet permits the transfer of heat from the glass fabric to the nestlings. There is a heat gradient of approximately 20° F between the surface of the nest beneath the birds and the air at the lip of the nest. This brood of House Finches, about four days old, is fed with forceps every 30 minutes.

The container of water, which must be kept filled, supplies moisture by evaporation until just prior to fledging, at which time we remove the container from the chamber. Since the air in the brooding chamber is relatively cool and there is no serious problem with dehydration, it is not necessary to atomize. Furthermore, we suspect that an increase in the relative humidity might lead to growth of fungi and possibly respiratory diseases.

If one wishes to control the sound environment experimentally within the brooding chamber, he must adjust the amplifier to provide for an appropriate playback volume through the chamber's speaker. A tape recorder, designed to accept a cartridge or endless loop tape, will introduce into the chamber a complete vocal repertoire which will repeat itself indefinitely. The investigator may monitor the vocalizations of the nestlings via the microphone in the chamber and record them as desired.

The brooding chamber requires no lighting during the nestling period because enough light penetrates through the one-way glass in the chamber's doors to provide the nestlings with a subdued light. When we are feeding the young, however, we find it helpful to have available good auxiliary lighting, directed into the chamber and on to the nestlings, thereby reducing the possibility of injury.

At time of fledging we remove the heating mantle, install wooden perches, and convert the brooding chamber to a cage (Figure 5). We discontinue the use of one temperature probe and relocate the other monitoring the air temperature within the chamber. We activate the lighting system and select an appropriate photoperiod by means of the time switch.

Diet

Ingredients

Paramount among the problems associated with the hand-rearing of passerines is the selection of a diet that is adequately nutritious and consists of ingredients that are readily available. Some workers have tried to solve the diet problem by feeding nothing but living invertebrates—mealworms, crickets, fly or moth larvae, etc. Such attempts usually have been unsuccessful, probably because the birds need a greater variety of food items. Furthermore, an exclusive diet of living food makes it difficult if not impossible to switch young birds to non-living ingredients when they require a more nutritional balance or when living food becomes scarce or unavailable. Faced with the additional problems of maintaining cultures of these living invertebrates, most laboratories sooner or later turn to the development of that notoriously elusive product, the "artificial" diet *sans* living food, for rearing nestlings. Like so many workers before us, we too had no success with this other extreme. As a result of much experimentation, our ultimate formula for a successful nestling diet is one that combines some living food with basic and essential non-living ingredients. At the same time our diet provides for a gradual phasing out of the live food by the time the young birds are feeding themselves. We have identified all of the ingredients of this diet in Table 1 and only certain items need additional comment.

In our search for a suitable living food we rejected such possibilities as mealworms (too chitinous for nestlings), adult moths attracted to "black lights" (too low in food value), wax moth larvae (too time-consuming to culture), geometrid larvae (natural supply too undependable), and various dipteran larvae (too disagreeable to culture). When a paper by Gary, Ficken, and Stein (1961) suggested the larvae of the honey bee (*Apis mellifera*) as suitable for bird food and recommended a technique for concentrating brood

Figure 5. The brooding chamber is converted to a cage at time of fledging. Fledgling Blue-winged Warblers here are induced to take soft bill mix from the forceps.

Figure 6. A frame containing honey bee brood of assorted ages is brought into the laboratory where the dietary mixtures are prepared. The capped cells are opened easily with forceps and the pupae extracted as needed.

within the bee colony and harvesting the larvae nine to eleven days following egg-laying, we established our own apiary. This soon became an ideal source of live food for nestling birds as well as one that required minimum supervision and attention. There are many good references on apiculture (Grout, 1949; Root, 1954) and we need not dwell on that discipline here.

We found the procedure advocated by Gary, Ficken, and Stein (1961) for harvesting bee larvae to be too time-consuming and wasteful of brood. Furthermore, we prefer to use bee pupae rather than larvae — i.e., those developmental stages following metamorphosis of the larvae but prior to the deposition of any substantial pigment in the thoracic and abdominal segments. These pupae develop in from 12 to 16 days from the date of egg-laying. Once the cells have been capped and metamorphosis has occurred, the development proceeds without further care of the brood by the worker bees. In practice, then, a frame containing brood of assorted ages is removed from the colony and brought into the laboratory where the capped cells are opened easily with forceps and the pupae extracted as needed (Figure 6). When the supply of brood has been exhausted, the empty frame is returned to the colony where the worker bees clean and ready it for egg-laying by the queen once again. Thus, the industrious bees perform all of the routine feeding and cleaning chores that normally make the culturing of live bird food so tedious and time-consuming. Our feeding formula does not require great quantities of bee pupae since the nestling birds are quickly shifted over to a diet consisting solely of soft bill mix. Hence we have never needed more than six hives, each with two or three standard 10-frame Langstroth bodies.

The soft bill mix is a modification of the mix fed to insectivorous birds at zoological parks and in aviaries by aviculturists around the world. It is made up in bulk, frozen in small plastic containers, and then thawed out as needed. The following recipe will make approximately four quarts of mix:

Six hard-boiled eggs with shells

Three 14-ounce cans of cooked, selected horse meat (not less than 25 per cent crude protein)

One 7.5-ounce jar of "Junior" grade carrots

Four cups of turkey starter mash (medicated poultry feed, consisting of not less than 28 per cent crude protein)

Two cups of dried "flies" (commercial preparation of assorted aquatic invertebrates)

One-quarter cup of crushed oyster shells

One-half cup of wheat germ

One-half 15-ounce box of seedless raisins

Force the above ingredients through a food grinder and mix thoroughly. No water other than that contained in the canned horse meat, carrots, and eggs is required.

Nestling birds, during their period of rapid body development, need a diet that is especially rich in protein. This we provide conveniently by adding gelatin. Initially we experimented with the gel form, which also served as a binder for other ingredients. But when we discovered that very young birds experience some difficulty in swallowing food in this form, we turned to powdered gelatin.

TABLE 1

Ingredients Used in Dietary Mixtures for Rearing Passerine Birds

Ingredients	*Symbols*
Bulk ingredients	
Honey bee pupae: taken from capped cells after metamorphosis from the larval stage but before pigmentation of thoracic and abdominal segments; fed whole or cut up, as specified.	P
Turkey starter mash: a medicated poultry feed, consisting of not less than 28 per cent crude protein; *sifted* to eliminate coarser particles.	TS
Soft bill mix: a general mix, similar to that given to insectivorous birds by aviculturists and zoological parks; made up in bulk and frozen; see text for recipe.	SBM
Supplementary ingredients	
Calcium: powdered di-calcium phosphate and calcium gluconate to supplement calcium in turkey starter mash.	C
Gelatin: unflavored powder made by Knox.	G
Cereal: rice or wheat cereal, as prepared for human babies; to supplement cereals contained in turkey starter mash and to serve as a binder.	RC or WC
Molasses and water: a solution consisting of one-half teaspoon of black molasses in one-quarter cup of water; an iron and moisture supplement.	MW
Carrot: commercial preparation for human babies, "Junior" grade.	Car
Blueberry: crushed pulp and skin; a laxative supplement.	B
Vitamins: a multiple-vitamin and mineral powder, such as Vionate by Squibb.	V

We do not know how essential is the inclusion of carrots in a diet for passerines in general. That it may be necessary for normal deposition of carotenoid pigments was dramatically demonstrated when we hand-reared Eastern Meadowlarks from the egg. We did not include carrot in the diet when these birds were acquiring their juvenal plumage and we were impressed with the abnormally pallid, almost white, breast feathers that developed. We then placed them on a diet of soft bill mix, including carrot, for several weeks prior to the first prebasic (postjuvenal) molt. The first basic ("winter") plumage that developed in these birds had the rich yellow areas typical for the species. We also noted that Blue-winged Warblers, hand-reared on our revised soft bill mix—i.e., with carrot—had a characteristically yellow plumage.

Feeding

The amount of food that a nestling passerine can take safely at any one feeding, particularly during the first few days of age, is quite limited. The problem is to provide immediately for a balanced diet when the feeding capacity is so restrictive. Some workers have met this challenge by homogenizing their dietary ingredients in a kitchen blender and feeding the resulting "soup" through a syringe. Our experience with homogenized mixtures and syringes led us to reject this solution: first, because of our inability to "trigger" the normal swallowing response of the nestling when using a syringe and, second, because of the real hazard of inadvertently "flooding" the mouth and getting food into the trachea. The alternative approach is to supply the necessary ingredients in a series of different mixtures which are fed independently and in a prescribed sequence. Each mixture is made up fresh before feeding. Since one handles the food with forceps (Figure 4), the consistency should be moist but not runny. Table 1 presents the ingredients of these mixtures and Table 2 the dietary mixtures and recommended feeding schedules. Only a few additional comments need be made here.

The first quarter of the nestling period is the most critical from the standpoint of stress on the nestling and the chances of its survival, for it is during this period that the nestling changes from the yolk to an artificial diet. It is also the time for the conditioning of a vigorous type of response to an offer of food. This response may develop slowly and at different times in the members of the same brood. Consequently, one may find it necessary at first to offer food as often as every 15 minutes. Once all the nestlings are gaping well, however, a feeding for the entire brood every 30 minutes is sufficient (Figure 4). The quantity of food, prepared for a single feeding, depends on the number in the brood and the size of the young, and is quickly determined through one's experience. For a brood of six Black-capped Chickadees during the first quarter of the nestling period, for example, a single feeding would consist of 6 honey bee pupae (cut up), 3 forcep pinches of calcium powder, and 2 forcep pinches of powdered gelatin.

There are three signs that indicate the health of nestlings. The first is the behavioral response that they continue to show to an offer of food, assuming that they developed initially a strong conditioned response. The second is the color of the membranes lining the inside of the mouth. One should note the color and the moistened appearance of these membranes immediately following hatching. Any suggestion of a drying of the mouth or a paling of its color—i.e., anemia—is a warning that all is not well. The third useful index to health is the frequency and appearance of the fecal sacs. Each sac should be gelatinous—i.e., not too loose—with a prominent white portion, showing that the

TABLE 2

Dietary Mixtures and Feeding Schedules for Rearing Passerine Birds[1]

Nestling period, first quarter: alternate feedings of four different mixtures
1. P (cut up) + C + G
2. P (cut up) + WC *or* RC (see text)
3. TS + MW + Car + G
4. B + C

Plus V three times per day

Nestling period, second and third quarters: alternate feedings of three different mixtures
1. P (cut up) + C + WC (but see text)
2. SBM + MW + Car
3. SBM + G + P (cut up) + B

Plus V twice per day

Nestling period, fourth quarter: alternate feedings of three different mixtures
1. P (whole) + C (+ RC if needed; see text)
2. SBM + Car + MW
3. SBM + G + B + V

Young fledglings, not yet feeding from dish or drinking: one mixture for all feedings
1. SBM + Car + MW + G + C + V

Plus P (whole) as part of training to feed for themselves (see text)

Older fledglings, drinking but not yet feeding from dish: one mixture for all feedings
1. SBM + C + V

Plus P (whole) as part of training to feed for themselves, and G once per day when birds are molting (see text)

Juveniles, feeding for themselves: one mixture for all feedings
1. SBM + V

P (whole) or other live food can be provided as a supplement, but only sparingly and then late in the day (see text)

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[1] See Table 1 for meaning of symbols

ingredients of the artificial diet are being digested thoroughly. Wheat is the cereal normally used to help bind the juices released when the bee pupae are cut up to proper size for feeding. If the fecal sacs are too loose and runny, substitute rice for the wheat, and return to the wheat when the symptoms disappear. If there is reason to suspect constipation, increase the gelatin content of the diet.

During the first quarter of the nestling period, add one forcep pinch of the multiple-vitamin and mineral powder to each of three feedings per day. Too heavy a dose of vitamins may cause diarrhea. During the second and third quarters, limit the vitamin supplement to two feedings per day, and decrease the frequency of feedings of mix to one every 45 minutes, giving the nestlings more time for preening and exercise. It is during this period that we introduce the nestlings to the soft bill mix. During the fourth quarter of the nestling period, we include the bee pupae whole in only one of every three feedings.

Remember that our ultimate objective is to eliminate the pupae from the diet in favor of the soft bill mix. We drop cereal from the diet during this period, unless the appearance of the fecal sacs suggests a need for rice, and limit the feedings to one per hour. The nestlings now are consuming a greater quantity of food per feeding and should have ample opportunity for exercise and grooming.

By the time the young birds are ready to fledge, their capacity for ingesting food is great enough to warrant a single bulk mixture of all ingredients that can be used for each feeding. We make this mixture up fresh several times each day. They no longer need the blueberry laxative, because they now are getting plenty of exercise. At this stage the bee pupae are strictly a supplement and not included in the preparation of the bulk mixture. We offer the pupae only when we are training the fledglings to feed themselves—e.g., as an inducement for them to take food from the forceps (Figure 5) or from a dish. As soon as the fledglings are drinking water, we drop the molasses and water from the bulk mixture. We give the gelatin powder as a supplement only when the birds are in active molt and then only once per day.

Older juveniles, capable of feeding for themselves, are given a dish of mix, with a very light "dusting" of the multiple-vitamin and mineral powder, at the beginning of each day. On very warm summer days it may be necessary to change the mix at mid-day to prevent spoilage. We provide bee pupae or other live food supplements only sparingly, because the birds show a preference for such items and ignore the soft bill mix. For this reason, live supplements should be given in small quantity and preferably toward the end of the day.

We cannot stress too strongly the importance of a careful vigil of feeding behavior during that transitional period in which fledglings become less dependent upon taking food from the forceps and more reliant on taking food from a dish. There is an understandable tendency for the laboratory technician, who has labored long and diligently throughout the seemingly endless period from hatching to fledging, to be impatient and prematurely assume complete independence of his charges. Not all individuals of a brood mature at the same rate nor become independent feeders at the same time. One generally can judge how much food a particular fledgling has been getting on its own by the strength of its begging response when offered food on the forceps. When a number of fledglings are housed together, one must give particular attention to possible instances of competitive exclusion at the food dish, whereby the more aggressive individuals prohibit the less aggressive from feeding regularly. The task of hand-rearing passerines from the egg is far too demanding and rigorous for the investigator to be deprived of his reward when just at the threshold of success.

Summary

The difficulties encountered in raising passerine birds from the egg often prevent research workers from even trying to study such young in the laboratory. The authors have successfully reared Great Crested Flycatchers (*Myiarchus crinitus*), Blue Jays (*Cyanocitta cristata*), House Wrens (*Troglodytes aedon*), Eastern Meadowlarks (*Sturnella magna*), and House Finches (*Carpodacus mexicanus*) from the egg. They are confident enough of their techniques to share them with others. In this article they give detailed directions for incubating the eggs, brooding the young, and feeding the nestlings until they are ready to fledge. Table 1 gives the foods included in the diets and Table 2

the proportions of each during the four different stages until the young bird is ready to feed itself.

Acknowledgments

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Peregrine Falcon, *Falco peregrinus*. Drawing by N. W. Cusa.

STUDIES OF A NESTING COLONY OF GREEN HERONS AT SAN BLAS, NAYARIT, MEXICO

Robert W. Dickerman and Gonzalo Gavino T.

The Green Heron *(Butorides virescens)*, an abundant and well-known species, nests in suitable habitat over much of North America and southward through Central America to Panama. There it meets and may intergrade with the Striated Heron, *B. striatus* (Bock, 1956; Parkes, 1955; Wetmore, 1965), and the two may be considered a superspecies.

The literature on the nesting biology of the northern population is extensive, culminating in the excellent study of its breeding behavior by Meyerriecks (1960). Bent (1926) and more recently Palmer (1962) summarized earlier studies. Palmer's summary includes a considerable contribution of original information by Meyerriecks which we cite as "Meyerriecks *in* Palmer, 1962." As far as we know there is virtually no information on the nesting biology of the populations of Green Herons in Mexico and Central America.

In 1961, Dickerman, while carrying out ecological studies of viruses transmitted by mosquitoes in Mexico, began making annual collections of blood from nestlings in a large colony of herons and associated water birds at San Blas, State of Nayarit, on the west coast of Mexico (Figure 1). Gavino assisted him in 1962 and 1963 and, together with Carlos Juarez L., made plans to study the physical and social structure of the nesting colony in 1964. In May 1964, the authors made a preliminary trip to the colony to lay out study quadrats and outline field operations. However, with the coming of the nesting season all of the species, with the exception of the Green Heron, moved to an area about three kilometers away. We cannot explain this but believe that a late beginning of the rainy season at San Blas and an early flooding of the new area may have attracted the other species which normally nest slightly earlier than the Green Heron. With only the Green Heron nesting in the traditional colony, Gavino changed his plans and took advantage of the excellent opportunity to make an intensive study of this species.

The subspecies of the Green Heron occurring at San Blas is the nominate form *B. v. virescens* which ranges from northern conterminous United States and southeastern Canada south to Chiapas in southern Mexico.

This report is based on data in a thesis which Gavino T. submitted to the Facultad de Ciencias of the Universidad Nacional Autonoma de Mexico in 1966 as partial requirement for the title of Biologist. The senior author provided the basic plan of the project, assisted in a limited amount of field work, translated the manuscript into English, and augmented the references to literature and the discussions. Unless noted, all measurements are in the metric system.

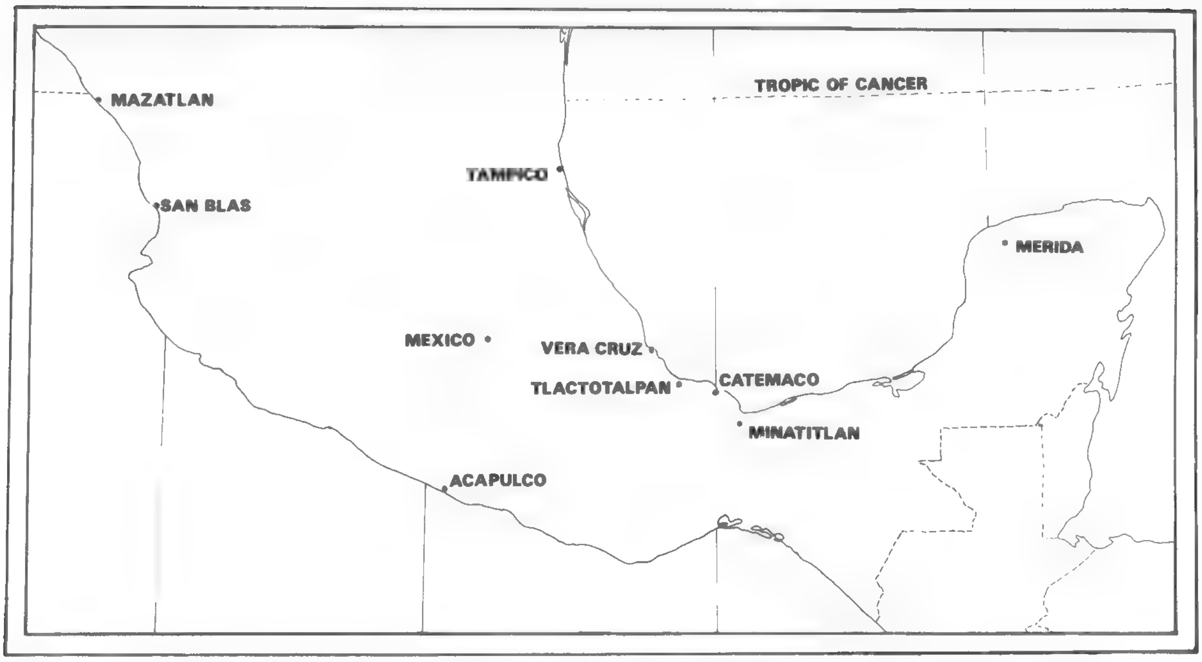

Figure 1. Map showing the location of the San Blas and other Mexican heron colonies.

Study Area

San Blas, a village on the Pacific Coast of Mexico at 21° 33′ N Lat. and 105° 17′ W Long., is in the tropical dry forest life zone, described by Holdridge (1962). The Rio del Rey borders San Blas on the north and the Rio Zauta enters the Pacific just south of the village. Mangroves edge these rivers and their estuaries which, during the rainy season, flood large areas around San Blas with brackish water forming extensive lagoons where the dominant vegetation is also mangrove. The study area, about 2.4 kilometers east-northeast of San Blas, lies along the highway to Tepic, near the junction of the road to Matanchen.

The red mangrove, *Rhizophora mangle,* dominates the river margins and the most deeply flooded inlets and is scattered through the more open areas of the shallow, seasonally flooded lagoons (Figure 2). Two other species of mangrove, *Avicennia nitida* and *Laguncularia racemosa,* are more common in the lagoons with *Laguncularia* forming dense groves. *Avicennia* grows around the edges of these thick stands or in isolated bushes in more open associations. The height of the mangroves ranged from four to eight meters with *Avicennia* being the tallest.

Based on experience in the colony in September 1961, October 1962, and October 1963, we outlined in May 1964 three quadrats, each 50 by 125 meters and each selected to cover a different ecological situation or a different nesting density of the various species of herons. The original purpose was to study the social and physical structure of the entire colony. Two of the quadrats, located in the heart of the area occupied in 1963, were essentially unoccupied in 1964. The third quadrat, fortuitously, fell in the very center of that portion occupied by Green Herons in 1964. This quadrat was mapped in detail (Figure 3).

The climate at San Blas is divided into two principal seasons, a warm, partially rainy season from April to November and a cool dry season from November to March. An intensive rainy season begins precipitously anytime from late June to mid-July and ends nearly as quickly in late September or early October. In 1964 the months from November to June received less than 25 millimeters of rainfall, a decided contrast to a rainfall of nearly 450 mm in

Figure 2. The aspect of mangroves at San Blas, Nayarit, during a dry season. *Top: Laguncularia racemosa. Middle: Rhizophora mangle. Bottom: Avicennia nitida.* Nests of Green Herons from the previous season are visible in the top left photograph. Photographs taken 18 May 1964.

September. The mean temperature seldom drops below 20° C in the coldest month—February. During the dry season—November to June—the flooded lowlands surrounding San Blas gradually become completely dry (compare Figures 2 and 6). The annual flooding during the early part of the rainy season in June or early July is rapid, due not only to the local rainfall, but also to the rising of the adjacent rivers which carry waters from the central plateau and the Sierra Madre Occidental.

Nine species of herons and associated water birds nest regularly in the colony at San Blas. In addition to the Green Heron, there are the Snowy Egret (*Egretta thula*), Little Blue Heron (*E. caerulea*), Louisiana Heron (*E. tricolor*), and Common Egret (*E. alba*)—see Dickerman and Parkes (1968) for our use of *Egretta* instead of the generic names in current usage; the Black-crowned Night Heron (*Nycticorax nycticorax*), Yellow-crowned Night Heron (*N. violacea*), and Boat-billed Heron (*Cochlearius cochlearius*); and the Olivaceous Cormorant (*Phalacrocorax olivaceus*) and Anhinga (*Anhinga anhinga*). In 1964, a pair of White Ibises (*Eudocimus albus*) hatched young that died before fledging. Although this species is present throughout the year at San Blas and along the coast of Nayarit, this nesting was, to our knowledge, the first record for this colony. The regularly nesting species are found along coastal Nayarit throughout the year. However, nothing is known of the movements of individual birds or nesting populations. A Snowy Egret, which was banded as an ambulatory young bird in the colony on 3 October 1964, was shot at Tecoman, State of Colima, about 320 kilometers to the south-southeast of San Blas on 20 March 1965.

The nesting activity at San Blas is directly associated with the rainy season and the flooding of the mangrove flats. In 1964, the first major rains of the season fell on 6 July; the first flooding of the general area of the colony was on 11 July; and the first Green Heron nest with one egg was found on 13 July. The birds may have laid this egg on 12 July. By 20 July the entire area was flooded to a minimum depth of 10 centimeters and on 23 July there were 18 nests with from one to four eggs. The following day, 24 July, there were 10 more nests with eggs and, by 25 July, 32 additional nests contained their first eggs.

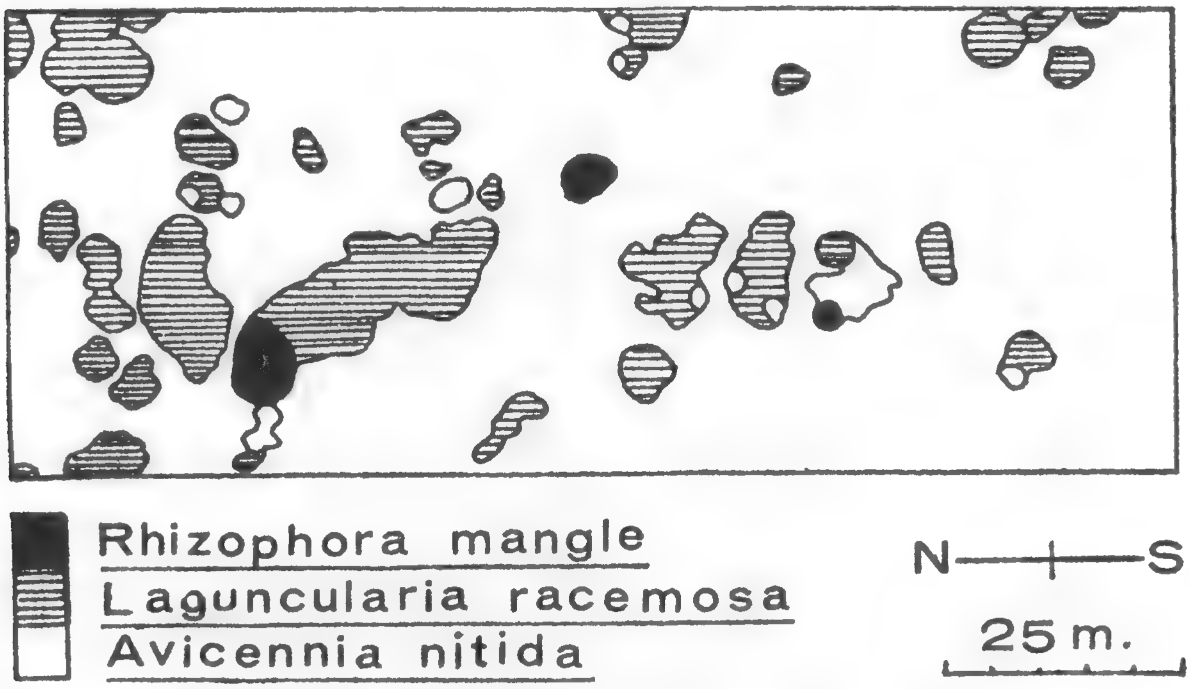

Figure 3. The distribution of mangroves in Study Quadrat A, San Blas, Nayarit.

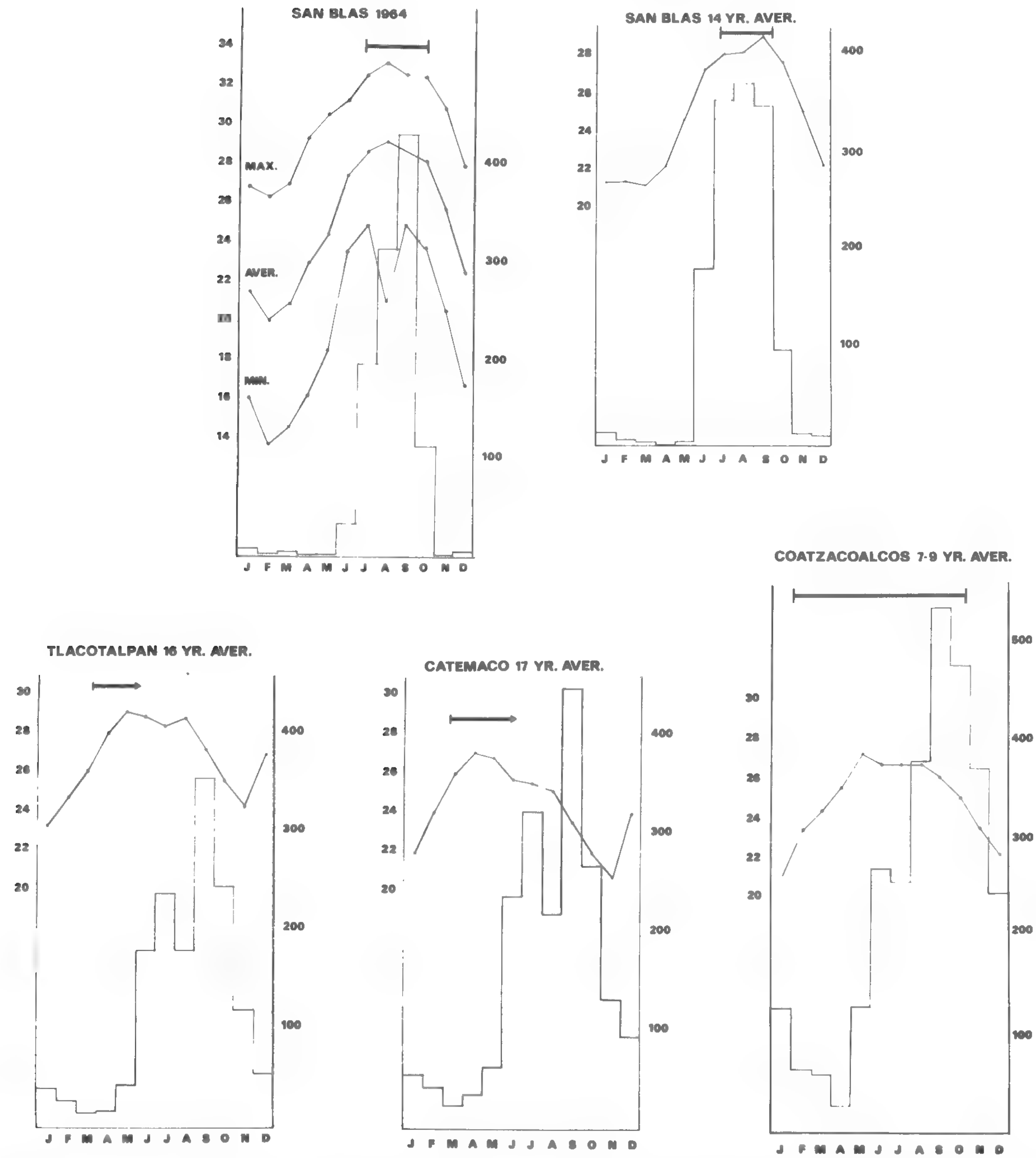

Figure 4. The bar graphs show the rainfall in millimeters; the curves show the temperature in degrees Centigrade; and the horizontal bar at the top of each graph indicates the nesting period of the Green Heron at San Blas and three other localities in Mexico.

The close association of the beginning of nesting at San Blas with the start of the rainy season and the flooding of the colony area contrasts sharply with the situation at three areas in the State of Veracruz. In these colonies — all located in permanent aquatic environments—along the Rio Papaloapan near Tlacotalpan, at Lago Catemaco, and at Minatitlan, the inception of nesting seems to be related to increasing temperatures at the beginning of the warm season which occurs usually in March but sometimes in February, as in 1965 (Figure 4). The correlation between increasing temperatures and the start of the nesting season is a common phenomenon according to Nice (1937). And graphs by Allen (1942:75) indicate the correlation between increasing temperatures and the laying periods of various species of herons and their allies.

Unfortunately we do not have dates of the beginning of laying at San Blas in 1961, 1962, 1963, or 1965. However, when we visited the colony in September and October of these years, we found conditions similar to those in 1964. Thus, we assume that the nesting season is regularly restricted to the months of July through October, the period also of maximum rainfall and flooding. While there is an extensive network of permanent rivers and estuaries in the vicinity of San Blas throughout the year, the reduced wet areas in the dry season may not produce the enormous quantity of food required by over a thousand adults and several thousand young. Nesting begins when flooding in July puts additional areas into production.

Nest Construction

Before the nesting began, a number of old nests were selected at random and sprayed with red, green, or yellow paint.

The first nests were in areas of thick mangroves. Possibly until the area was fully flooded, the herons sought denser cover. Later they placed their nests anywhere throughout the area, even in dead mangroves that offered no cover. Although they nested in all three species of mangroves, the greatest number of nests were in *Laguncularia*. Probably the characteristic branching of this species offered more suitable sites.

At San Blas, as in New York (Meyerriecks, 1960), most of the Green Herons that began to nest first built upon the remains of nests from the previous year, removing accumulated dead leaves and adding new material. Early in the season the sticks used in nest-building came mostly from other old nests. There were new nests with as many as a dozen painted sticks, generally from the closest painted nest. In some cases where several old nests in the same vicinity had been painted different colors, the birds used sticks of all three colors in the new nests. They worked the sticks into the nests by shaking movements, intertwining them several times.

In five or six cases the herons built their nest in the four to six days prior to the laying of the first egg. During the periods of egg-laying and incubation, and especially during the development of the chicks, the adults continued to add new sticks. On several occasions Gavino saw an adult help itself to sticks from a neighboring nest when the owner was absent.

The nests were moderately bulky affairs made of dry mangrove sticks up to 25 cm in length. Nests built on a base provided by a nest of the previous year were considerably more solid than the new ones (Figure 5). Generally, the only lining was a concentric arrangement of coarse sticks forming a slight cavity where the eggs were laid.

The shape of the nests varied from more or less circular to elliptical and even triangular. Measuring only the well-defined, solid portion, the average diameter of 119 nests was 23 cm. Of those not circular the maximum and minimum measurements were 39 cm for length and 14 cm for width. The depth of the nest cup varied from almost nothing to 10 cm with an average of 4.5 cm for 145 nests. The average total thickness for 72 nests was 11 cm, with one nest measuring only 2 cm. Nests with a maximum measurement of depth, 21 and 24 cm, were those that had been used several years, possibly by several different species, with repeated addition of new nesting material.

Within the study quadrat, where the mangrove trees did not reach full height, the average height of 181 nests was 68 cm above the water which, at that time, was 50 cm deep. Very few nests were above 150 cm and only two were at a maximum height of 190 cm. On the other hand, water virtually covered two nests when it rose slightly (Figure 6), and less than 50 cm separated 177 nests from the surface of the water. In places outside the quadrat, where mangroves were taller, the seven highest nests measured 260, 242, 220, 185, 170, and 160 cm above the water's surface. The nest height of the Green Heron throughout its range is apparently directly related to the height of the vegetation and may range from ground level to several tens of feet.

Figure 5. A well-built nest of the Green Heron in *Avicennia nitida* at San Blas, Nayarit. Photographed 9 September 1967.

One nest (Number 102) was very close to the water. As the level rose the adult added sticks until the nest was 25 cm deep. Another nest collapsed with its sticks falling upon the mangrove roots. One of the three chicks in the nest survived by clinging to the remains of the nest and was fed by the adult which immediately started to build a new nest on the original site. The adult continued to feed the chick for the three or four days required for construction. The young bird fledged successfully. A mangrove, supporting a nest with two young only a few days old, tipped over. Both young managed to cling to the sticks while the adults repaired the nest.

Nest Density and Spacing

The Green Heron is a solitary nester or one that nests in small colonies of up to 20 or 30 pairs (Bent, 1926). At San Blas, between 17 July and 13 August, 157 active nests were in the quadrat, 50 by 125 meters, within a colony where the estimated population was over 300 pairs.

Howell (1932) reported nesting colonies of 100 and 400 pairs of Green Herons in Florida but gave no further information on the area covered by these colonies or the breeding biology of the birds. In 1955, Meyerriecks (*in* Palmer, 1962) found 136 pairs nesting in four areas covering a total of 82,353

Figure 6. An abandoned, flooded nest of the Green Heron at San Blas, Nayarit. Photographed 9 September 1964.

square meters on Long Island, New York. And in the area of greatest density there was an average of 479 square meters for each nest. In the study quadrat at San Blas in 1964 there was an average of only 46 square meters for each nest.

In the study quadrat, which had by coincidence the densest nesting population of Green Herons, the distances between 137 nests were measured on 12 August. Of these, 45 were closer than one meter, 75 were between one and two meters apart, and 21 were more than two meters apart. The five minimal distances from nest-edge to nest-edge were 15, 15, 20, 20, and 40 cm; the five maximal distances were 840, 320, 300, 295, and 270 cm. In part, this degree of sociability was due to near optimal nesting cover. However, this same type of vegetation covered many acres outside the study quadrat and there was no obvious reason for the concentration. The spacing at San Blas contrasts sharply with that in a 10-nest colony in Tennessee where, according to Coffee (1966), nine nests averaged 790 cm apart with the closest 548 cm and the farthest apart 1,036 cm.

Egg-laying

Seasonal Rhythm

The period of egg-laying at San Blas is apparently related directly to the rainy season. The first major rains of 1964 fell on 11 July; the first egg was

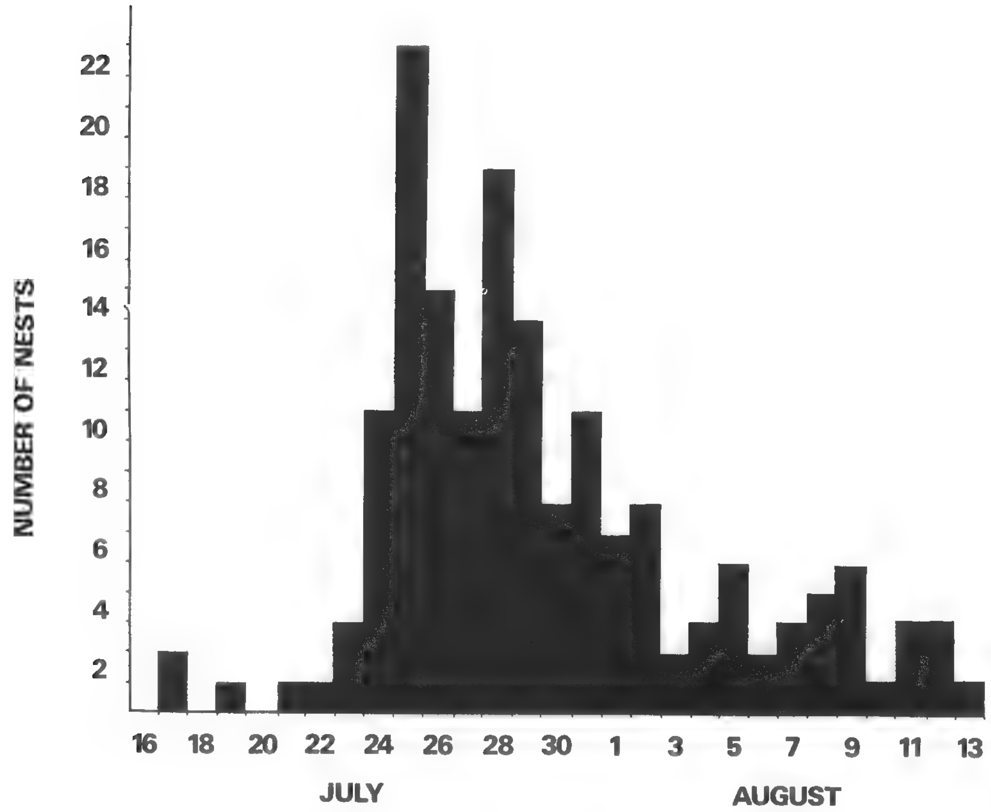

Figure 7. The numbers of Green Heron nests in Study Quadrat A at San Blas, Nayarit, that contained their first eggs during the period 17 July to 13 August 1964.

observed on 13 July; and the majority of clutches started within the following two weeks (Figure 7). On 25 July, the first egg was laid in the largest number of nests — 54, 22 within the quadrat, 32 outside. The laying of the last egg observed in the colony occurred between 9 and 11 September. Thus the egg-laying period was about 60 days in 1964.

The dates of egg-laying in other areas do not conform to those at San Blas. Near Tlactotalpan, Veracruz, in 1964, Green Herons started laying eggs the last week of March; at Lago Catemaco, in 1965 and 1966, in the second and third weeks of March. Egg dates from Georgia and Florida are 29 March to 9 July; for Louisiana and Texas, 4 April to 26 June (Bent, 1926:194). At Rulers Bar Hassock in Jamaica Bay, New York, Meyerriecks (1960) found the first egg in 1955 on 30 April and the last on 4 August. In 1957, the first egg was laid on 29 April. The length of the egg-laying period at San Blas was shorter by about 35 days than in New York—60 days versus about 95 days.

Egg Color and Measurements

There was little variation in the size and shape of the eggs except for minor departure from elliptical or subelliptical shapes. Freshly laid eggs ranged from the Lichen Green to the pale Niagara Green of Ridgway (1912). The eggs changed in color during incubation, becoming much paler, some nearly white. Four three-egg clutches were pale Olive Buff. Apparently these are the first known eggs of the species not of the usual green coloration. They were normal in size, shape, and development.

The eggs were measured with vernier calipers reading to 0.1 mm, and weighed with an Ohaus triple beam balance reading to 0.1 gram. One hundred ninety-seven eggs, weighed within two days after laying, averaged 17.1 gm with a range of from 13.5 to 20.5 gm (Table 1). The average of the 10 heaviest was 19.7 gm; of the 10 lightest, 14.3 gm. In New York, 74 eggs averaged 17.4 gm with a range of from 14.0 to 18.5 gm (Meyerriecks *in* Palmer, 1962). The eggs in 20 nests at San Blas were weighed every other day for 10 to 17 days. Minor fluctuations appeared in the resulting data due to inaccuracies in weighing; however, the combined results indicate a mean decrease of about one gram.

Table 1 records the measurements of 232 eggs from the San Blas colony, and gives a summary of comparable data on the eggs of the Green Heron reported in the literature. The figures show exceedingly little variation over a large geographical area.

Clutch Size

The size of the clutches at San Blas for 197 nests ranged from two to four eggs. Fifty-three nests (26.9 per cent) had two eggs; 125 (63.5 per cent) had three eggs; and seven (3.5 per cent) had four eggs (Figure 8). Twelve other nests, where the eggs were broken or the nest damaged before the full set was laid, contained only one egg. The average number of eggs in the normal clutch, discounting nests with one egg, was 2.75. In New York, 76 complete first clutches averaged 3.7 eggs with 50 per cent of the nests containing four eggs (Meyerriecks *in* Palmer, 1962). Wood (1951) reported nine clutches from Michigan ranging from three to six eggs with an average of 4.5. Since these Michigan records were either specimens or references from the literature, they may have attracted attention, or been collected, because of their large size and therefore may represent a more biased series than the samples from San Blas and New York. Jewett *et al.* (1953) reported that, in the State of Washington, the western subspecies *B. v. anthonyi* lays from three to six eggs in a clutch, usually four or five. These limited data might represent a north-south cline in clutch size except that Mengel (1966) reported an average of 4.3 eggs or young in 13 nests in Kentucky, an intermediate area. In the Penard collection of *B. striatus* eggs from Surinam, there were 16 clutches with one egg, 26 with two, 39 with three, two with four, and one with five eggs (Hellebrekers, 1942). Discounting the single eggs, as in the San Blas sample, the average clutch size is 2.67. If one is justified in discounting the single eggs as we have done, then there appears to be little variation in size of clutches within the *virescens-striatus* superspecies in the neotropical zone.

Daily Rhythm

The laying times observed for six eggs were between 11:00 AM and 2:00 PM. Meyerriecks (*in* Palmer, 1962) reported the laying time in New York as early morning between 6:05 and 10:14.

At San Blas, the exact time between the laying of two eggs was not precisely determined since the nests were visited daily between 8:00 AM and 4:00 PM—usually between 9:00 AM and 1:00 PM—and there may have been a one-day variation in some observations. See a discussion by Moreau and Moreau (1940: 315) of variations due to single daily visits to nests.

In the 113 nests, for which the laying dates are known (Figure 8), the second egg was laid two days after the first in 72 cases; the second egg was laid the following day in 28 cases; the second egg was laid on the fourth day in 12 cases; and on the fifth day in one case.

Of the 78 nests with three eggs, the third egg was laid two days after the second in 49 nests; the third egg was laid the following day in 25 nests. In the two nests with four eggs, the last egg was laid the day after the third egg. The maximum time in the laying of three-egg clutches was six (or five) days and for the two-egg clutches five (or four) days, compared to five or six days in

TABLE 1

Summary of Published Data on Size and Weights of Eggs of the Green Heron and Striated Heron[1]

Locality and/or reference	*Taxa*	*Number of eggs*	*Average*		*Length*		*Width*		*Weight*		
			Length	*Width*	*Maximum*	*Minimum*	*Maximum*	*Minimum*	*Average*	*Maximum*	*Minimum*
San Blas, Nayarit	*B. v. virescens*	232	37.5	29.2	40.8	34.0	31.4	27.0	17.0	20.5	13.5
Catemaco, Veracruz	*B. v. virescens*	28	37.3	28.6	40.1	36.2	31.6	27.0			
No locality (Bent, 1926)	*B. v. virescens*	43	38.0	29.5	41.0	36.0	30.5	27.5			
Eastern United States (Preston *in* Palmer, 1962)	*B. v. virescens*	20	38.3	29.1							
New York (Meyerriecks *in* Palmer, 1962)	*B. v. virescens*	74	38.8	29.6	43.3	35.7	34.8	27.0	17.4	18.5	15.9
No locality (Bancroft, 1930)	*B. v. virescens*	39	37.7	28.4							
Central Baja, California (Bancroft, 1930)	*B. v. frazari*	7	36.0	27.6							
No locality (Bancroft, 1930)	*B. v. anthonyi*	39	38.5	29.7							
San Diego, California (Huey, 1926)	*B. v. anthonyi*	17	38.9	29.5	42.0	37.0	30.0	28.2			
Dominican Republic and Haiti (Wetmore and Swales, 1931)	*B. v. maculatus*	4	39.7	29.7	40.1	38.6	29.8	29.5			
Surinam (Hellebrekers, 1942)	*B. striatus*	50	37.6	27.8	41.1	32.2	30.1	23.8			

[1] For additional data on the two subspecies of Green Heron, *B. v. anthonyi* and *B. v. frazari*, see Bent (1926).

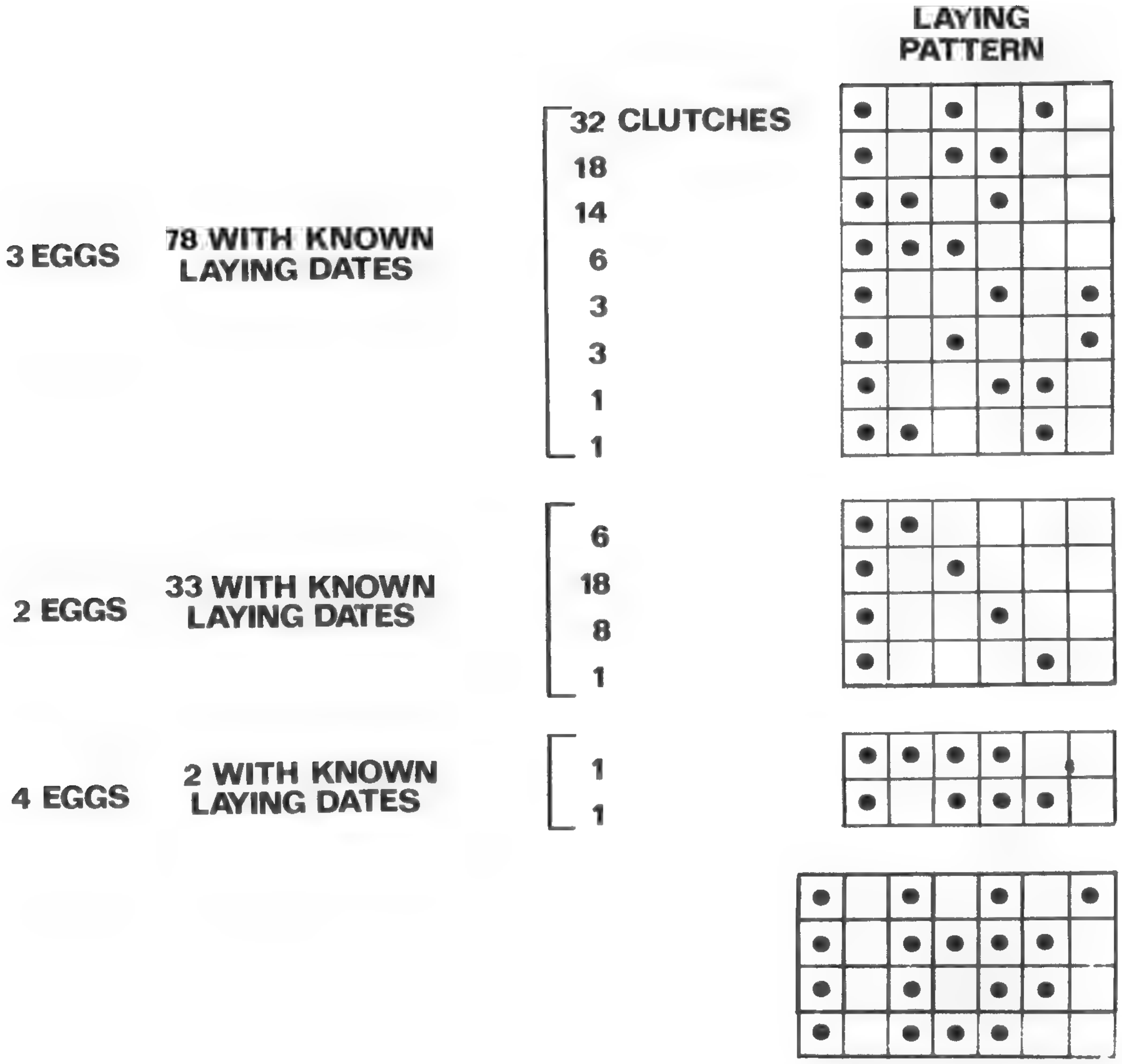

Figure 8. Summary of the laying patterns of Green Herons at San Blas, Nayarit, and on Long Island, New York (the Long Island data are from Meyerriecks, 1960).

laying a four-egg clutch in New York, reported by Meyerriecks (1960:82). He concluded: "The first and second eggs were always laid at two day intervals in the nests studied in detail, but the other intervals varied with different pairs. In the majority of nests, the third egg was laid two days after the second and the rest of the eggs followed at one day intervals." Meanley (1955) found that the Little Blue Heron laid an egg on an average of every other day with five to eight days required to complete a clutch of from three to five eggs.

The Second Clutch and Re-use of the Same Nest

Herons, after raising their first brood, often begin a second laying. This was not studied at San Blas, but the Green Herons were observed to lay new eggs in the same nest after the destruction or abandonment of the first clutch. There were seven cases of two clutches in the same nest, but there was no certainty that both clutches came from the same bird. In five nests, the first egg of the second set appeared five to eight days after the last egg of the first set.

There were only two instances where one bird may have laid twice. In one case, the three eggs of the first clutch were laid on 26, 27, and 29 July. On 2 August, the nest was empty and, on 9, 11, and 12 August, new eggs were laid, the last two of which were infertile. In the second case, eggs were laid on 25, 27, and 29 July. On 8 August, this nest was empty and, on 14, 16, and 18 August, another set was laid. Again the last two were infertile. The length of the interval between the two layings and the infertility of the last two eggs indicate that these might have been two cases of re-laying by the same females. Meyerriecks (*in* Palmer, 1962) found that the first egg of a second clutch appeared nine days after a first clutch had been removed. In this instance the bird had incubated the first clutch, from the fourth egg, for 11 days.

The Green Heron showed considerable efficiency in incubating large clutches of eggs and feeding the young under experimental conditions. Three eggs laid on 29 and 31 July and 1 August were added to a nest of three eggs, laid on 23, 25, and 27 July. The adults taking care of the nest with six eggs became more aggressive and called menacingly when Gavino approached. Although the nest was scarcely large enough to hold six eggs, and the adult was hardly large enough to cover them all, they developed normally. The original eggs hatched first, then the introduced ones as follows: two on 15 August, one each on 16, 20, 21, and 22 August.

The three young that emerged on 15 and 16 August grew normally, and since they were four or five days old when the second batch began to appear, there was a marked difference in size between the young of the two broods. For a few days all six birds remained in the nest and were fed. Before any of the six were old enough to go out on the branches, they had grown so large that the nest could no longer contain them. The three largest crowded the three smallest out of the nest.

Since all the birds grew normally as long as they remained in the nest, it appears that space was the factor that limited the survival of the nestlings. If the smallest birds had not been removed from the nest, there might have been some point at which the adults would not have been able to feed all six.

Incubation and Hatching

We determined the incubation period as the interval between the laying and hatching of the last egg in a clutch in which all eggs hatch (Nice, 1954).

The incubation started with the laying of the second egg of the clutch, which, except for one two-egg clutch, was invariably deposited on the second or third day after the first egg. Meyerriecks (*in* Palmer, 1962) reported some instances where incubation started with the first egg. Although this was not noticed at San Blas, the intervals between laying and hatching of the first eggs are the same at San Blas and New York and it may have been overlooked. Meanley (1955) found that Little Blue Herons, in Arkansas where clutches averaged four eggs, began incubating with the laying of the second egg. According to Allen (1942), the steady incubation in the Roseate Spoonbill (*Ajaia ajaja*) began only with the full clutch of from two to four eggs and even then may not have been regular for the first few days.

In 31 nests at San Blas, for which we know the dates of laying and hatching of all eggs, the incubation period of the last egg was 19 days in eight nests, 20 days in 12 nests, and 21 days in 11 nests (Figure 9). In Michigan, Cooley (1942) determined the incubation period of about 20 days for the Green Heron. Meyerriecks (*in* Palmer, 1962:425) found the incubation period in 20 nests where all eggs hatched to be 19 days in one nest, 20 days in 18 nests, and 21 days in one nest. The period from laying to hatching of the first egg in 22 clutches with three eggs was 21 days in six nests, 22 days in nine nests, and 23 days in seven nests. During the 1955 and 1957 nesting season, Meyerriecks (1960:21) found a 22-day interval between the laying of the first egg and the hatching of the first chick in the colony. The last egg in the San Blas colony was laid between 9 and 11 September 1964. It hatched 1 October.

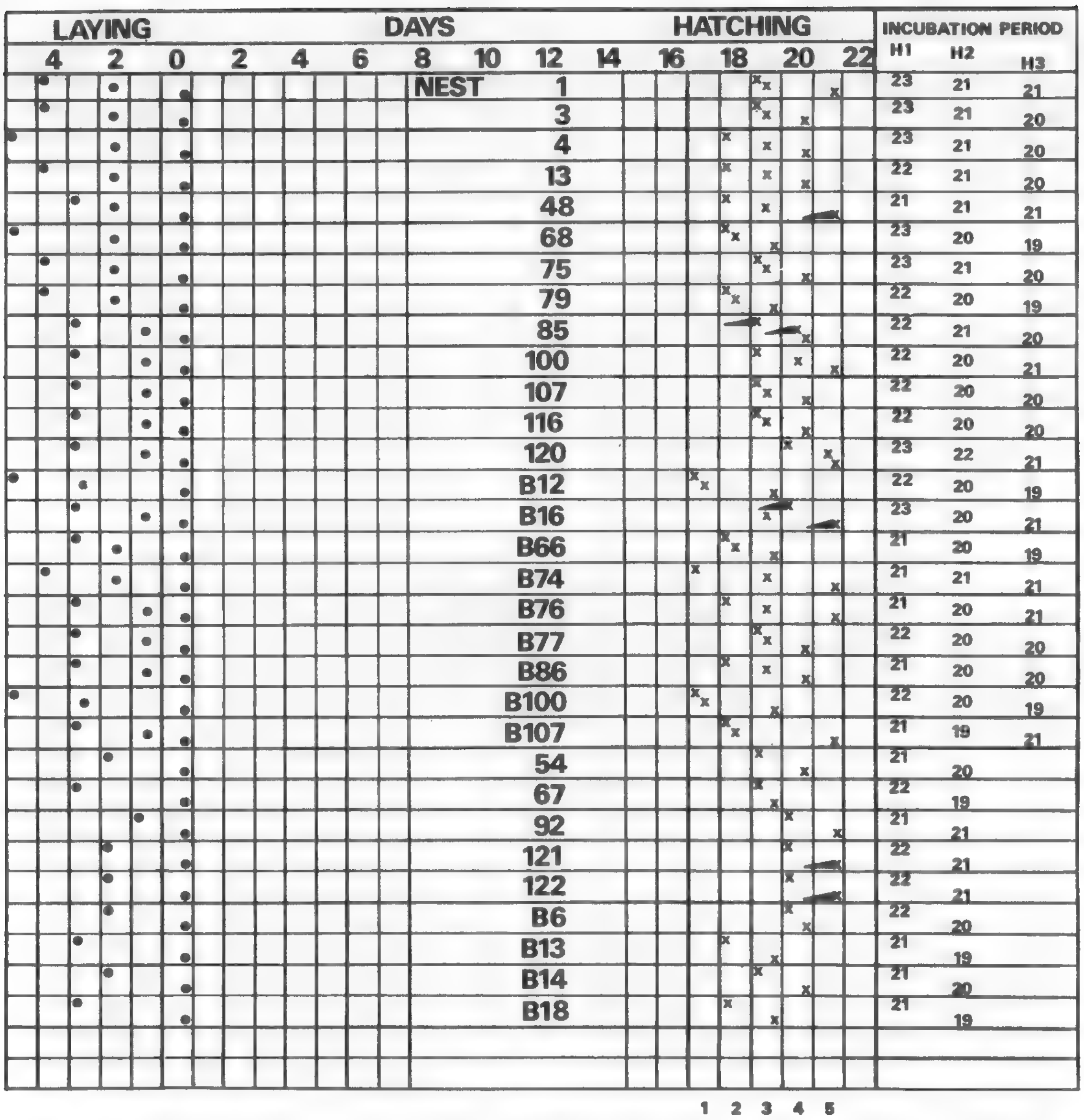

Figure 9. The schedule of laying and hatching in 31 nests of the Green Heron at San Blas, Nayarit, in which all eggs were marked and hatched. The solid dots represent days on which the eggs were laid; X represents the days of hatching; and the solid triangles represent the eggs pipped one day and hatched the next. The last column shows the incubation period of each egg of two- and three-egg clutches, and the data are aligned with the day of the last egg laid.

Eggs generally hatched in the order in which they were laid. This was true for all three-egg clutches except two in which the second and third eggs hatched on the same day even though they were laid on successive days. The first egg hatched the first chick in nine of 22 three-egg clutches and in 12 of these clutches the first and second eggs hatched on the same day. While the maximum time span for laying three-egg clutches was six (or five) days, hatching periods were usually contracted, covering the same time span as the laying period in only four of the 22 nests. More often, eggs laid over a five- or six-day period hatched in a three- or four-day period. Meyerriecks (1960) found that hatching intervals usually depended upon intervals between layings.

Shading Eggs and Young

At San Blas the mornings, even on rainy days, were usually clear and hot with intense sunshine, and the adult herons, often with wings spread, stood over the eggs or small chicks in nests not shaded by branches. The shading was most essential in the exposed nests. A number of eggs, that were weighed daily and were consequently more exposed to the sun than the others, failed to hatch. Apparently, the heat killed the embryos.

Nest Abandonment and Desertion

At the time of egg-laying, especially during the first few days, visits to the nests every other day to weigh the eggs caused some mortality. Some eggs were broken in handling; some were exposed to the hot sun for too long. Through daily checking of eggs and young, the structure of some nests was loosened and some disturbed adults trampled on their eggs and broke them.

Hostility or discontent, shown by adults and terminating in the abandonment of the nest, decreased as the laying was completed and the birds adjusted to Gavino's presence. When the eggs hatched, the adults became hostile and threatening once again, but no case of simple desertion was noted during the nestling phase. Usually the birds deserted at this time because of a number of outside influences.

From late July on, the mangroves in the nesting colony of the Green Herons were used as night roosts by increasing numbers of other species of herons, egrets, ibises, cormorants, and Anhingas. The movements of these heavy birds, particularly the Common Egrets, occasionally loosened the Green Heron nests below their perch, especially those nests at medium elevations and in thin branches. Storms caused the destruction or partial destruction of some nests. Heavy rains, accompanied by strong winds, on 6 and 29 September caused considerable destruction. A survey of the colony on 9 September indicated that a number of nests previously containing young were empty. Some had tipped over and others had completely disappeared. An estimated 50 nests were destroyed or abandoned in one section of the colony. The storm of 29 September tipped over a number of mangroves, some eight meters high, that had held nests. And, as mentioned previously, a number of nests were inundated by rising water.

Snakes were responsible for the destruction of some nests. On 12 August, a large snake was observed to devour seven eggs in a few minutes and, in moving about, to loosen several nests. Later taken, the snake proved to be an indigo snake (*Drymarchon corais*), 2.27 meters in length and a species not previously known to eat eggs. Another large snake was seen in a Boat-billed Heron's nest on 3 September near the Green Heron colony. These two snakes, living in the vicinity of the colony, could have a considerable effect on nesting success.

Raccoons (*Procyon lotor*) commonly roamed the area, their tracks appearing in the mud along the river banks. Probably, raccoons were responsible for the remains of young herons—the wings and feet—that were noticed periodically in the colony.

Nesting Success

Although we mentioned the effect of disturbance on the destruction of the eggs, we cannot evaluate its extent. Of 148 nests containing 392 eggs, 50 nests with 115 eggs were destroyed or abandoned without a single egg hatching. The bulk of this loss occurred during the first two or three weeks of the study. Gavino was directly responsible for the loss of eight nests with 22 eggs. We know, however, that the loss of another seven nests with 15 eggs was definitely not his fault but due to natural causes. Of 97 nests, in which at least one young hatched, eight per cent were abandoned or destroyed without human influence.

In 104 nests containing 290 eggs, 211 eggs or 72.7 per cent hatched — an average of two young per nest. Of the 79 eggs that did not hatch, 24, or 8.2 per cent of the total, were infertile, and 40, or 13.7 per cent, were broken or disappeared from the nests between visits. From the 211 eggs that hatched, 191 young fledged—an average of 1.8 per nest, or 65.8 per cent of the total number of eggs and 90.5 per cent of the number that hatched.

Summary

From mid-July to early October 1964, the authors studied a colony of Green Herons (*Butorides virescens*) near the Pacific coastal village of San Blas, State of Nayarit, in the tropical, dry forest zone of Mexico. Approximately 300 pairs of Green Herons nested in the colony and about 157 pairs in a study quadrat, 50 by 124 meters.

Three species of mangroves constituted the vegetation in an area that was flooded during an intensive rainy season from late June or early July to late August to early September. Nesting in the colony was directly associated with this season.

Since the nine other species of herons and associated water birds that usually nested in the same area moved to another colony in 1964, the authors had a unique opportunity to observe a concentration of Green Herons. Included in their study was nest construction, height of nests, and distance apart within the quadrat. They recorded the color, weights, and measurements of eggs, the daily rhythm of laying, the possibility of a second clutch in the same nest, the clutch size, and the ability of the Green Heron to incubate large clutches under experimental conditions. They observed incubation, periods of hatching, the care of the eggs and young, and the causes of desertion. The final section deals with nesting success in this, an almost pure colony of Green Herons.

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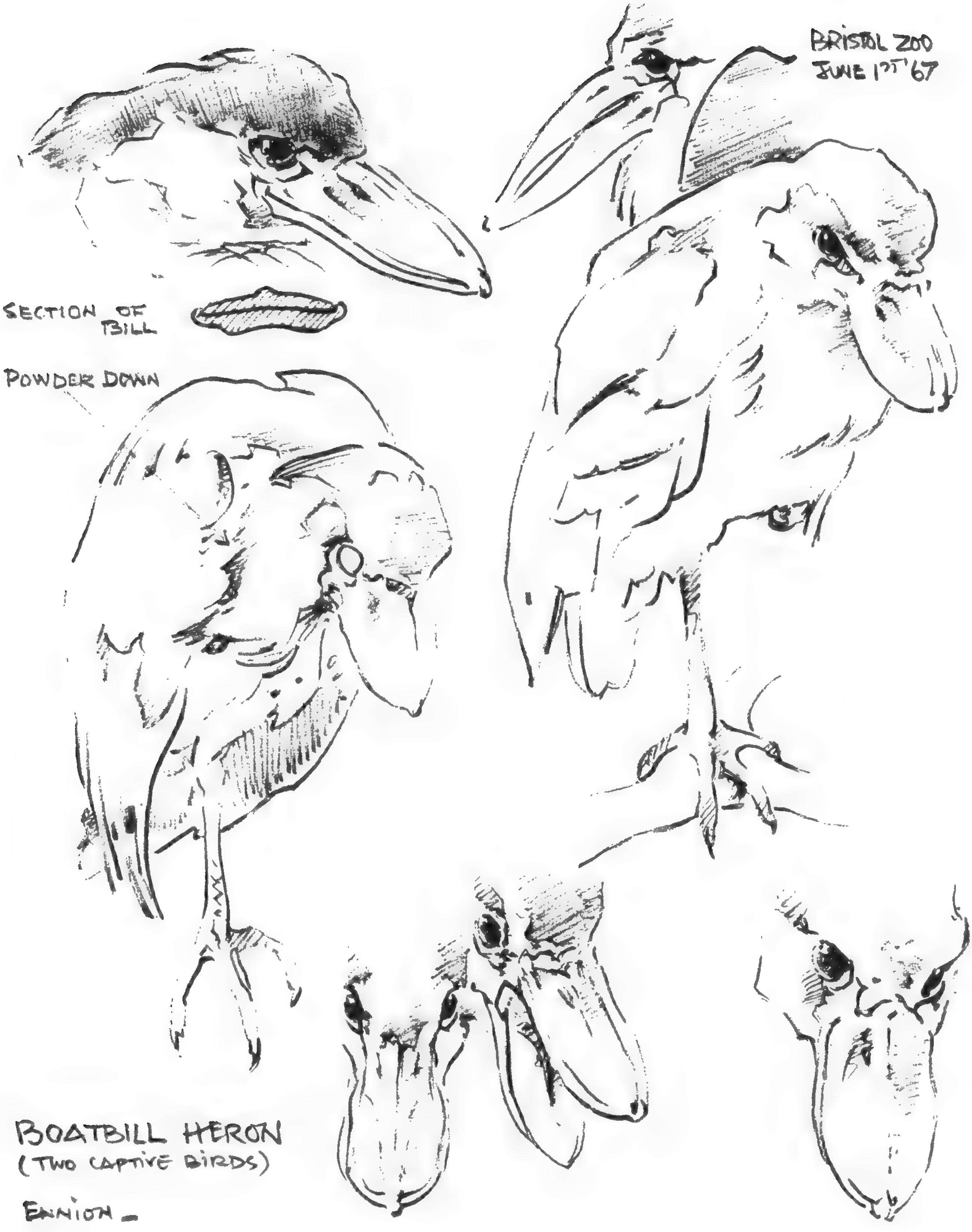

Boat-billed Heron, *Cochlearius cochlearius*. Drawing by Eric A. R. Ennion.

THE DEVELOPMENT OF MIGRATORY ORIENTATION IN YOUNG INDIGO BUNTINGS

Stephen T. Emlen

During the past decade, numerous studies have supported the view that the night sky provides at least one means of enabling migrating birds to determine the direction of their flight (Sauer, 1957, 1963; Sauer and Sauer, 1960; Hamilton, 1962; Mewaldt *et al.*, 1964; Shumakov, 1965; Emlen, 1967a). In fact, many ornithologists mistakenly believe that current hypotheses of direction finding by the stars adequately explain all the known facts of migratory orientation. This paper concerns one basic question that remains unsolved: Why do young, inexperienced birds, in the Northern Hemisphere, select a southerly direction for their first autumnal migration?

The type of directional information that birds can obtain from the stars—the stellar cues—depends on how they use such cues. Sauer (1957), for example, proposed that certain European warblers rely upon a bicoordinate grid, or a combination of information, provided by the altitude and the azimuth or declination and hour-angle positions of stars. Such a navigational system, when coupled with an accurate, internal time sense, could permit a bird to detect geographic displacement from, and to orient toward, a home area *after* it had learned the normal stellar positions and stellar motions for that locality. Similarly, a migrant could orient toward a wintering "goal" once it knew the stellar coordinate information specific for the locality in question. However, field studies involving the artificial displacement and later recapture of migrants have shown that such goals are not genetically predetermined (Rüppell, 1944; Perdeck, 1958, 1967; Bellrose, 1958). Consequently, an immature bird making its first migration trip does not possess sufficient information to rely solely upon such a bicoordinate system.

Recent experiments in stellar orientation suggest that the necessity for an internal clock, and hence for temporal compensation of celestial motion, may not be widespread among nocturnal migrants (Matthews, 1963; Hoffmann, 1965; Emlen, 1967b; Wallraff, 1968). Rather, these studies propose that migrants use additional information provided by the constant spatial relationships existing between stars—that they respond to star patterns. Such an orientation mechanism merely enables a bird to determine a specific direction and to maintain this direction through time. Without the *additional* knowledge of which direction to choose, such a system would be useless. Reliance upon a stellar compass that is dependent on star patterns could just as well send a migrant east or west as north or south. Again, we are left with the fundamental question: What factors operate in the selection of one direction over another, or what causes young, inexperienced birds to select a southerly direction for their first migration?

We usually avoid this question by consigning migratory orientation to the realm of "innate" behavior—a behavior the bird inherits. Directional tendencies, some argue, develop without any prior migratory experience and therefore must be entirely predetermined (Griffin, 1964; Schmidt-Koenig, 1965; Matthews, 1968). This argument is based primarily on the long-held belief that the young of many species make their first southward flight alone, departing from the breeding area either before or after the adults have left. (This situation holds true for many species of shorebirds but does not appear to be the rule among passerines.) What we often overlook is that even if young birds do migrate totally independent of experienced adults, there remains the possibility of some form of learning and/or imprinting of a directional tendency occurring at a stage in the bird's development before the actual migratory departure. We need research to determine the types of orientational mechanisms actually pre-programmed in young birds genetically and the sorts of experiences, if any, important for the maturing of the orientational guidance system in the adult. We can examine this accurately only through studies in which we know precisely, or can control experimentally, the early experience of the bird. I, therefore, began an investigation of the orientational abilities of hand-raised Indigo Buntings (*Passerina cyanea*).

Methods

Table 1 gives the details concerning the age, sex, and fledging date of 10 Indigo Buntings hand-reared to adulthood during the summer of 1965. These birds, taken as nestlings between the ages of three and 10 days, were brought indoors and fed on a diet of mashed liver, hard-boiled egg, baby

TABLE 1

Data Summaries for Hand-raised Indigo Buntings[1]

Bird	*Sex*	*Age at capture*	*Fledging date*	*Group*	*Eyes at capture*
w88	M	8 days	21 June 1965	A	open
w89	F	10 days	30 June 1965	A	open
w90	F	9 days	26 July 1965	C	open
w91	F	8 days	27 July 1965	C	open
w92	M	8 days	27 July 1965	C	open
w93	M	3 days	8 August 1965	A	closed
w94	F	3 days	8 August 1965	A	closed
w95	F	4 days	8 July 1965	B	closed
w96	F	4 days	8 July 1965	B	closed
w97	F	3 days	30 June 1965	B	closed

[1] In this species the eyes begin to open as narrow slits at four days of age and can be opened fully on day five or six; fledging occurs on day 10 or 11.

canary food, and live crickets. Seven buntings—w88 through w94—occupied a room with the windows covered to prevent them from viewing the sky or normal landscape. Mr. John Rice raised the remaining three individuals—w95, w96, and w97—and generously donated them for my experiments. Until mid-August these latter birds occupied a room with a south-facing window and, although covered at night, they were frequently able to observe the daytime sky and, occasionally, the sun itself.

Once the birds were self-sufficient—25 to 30 days old—they lived under one of two conditions. If kept indoors, each bird had a 2 by 2 by 2-foot cage in a windowless room with the day-length maintained equal to that outdoors. If kept outdoors, they lived in a 6 by 9 by 6-foot aviary allowing complete view of the natural sky and surroundings.

To study the possible importance of visual exposure to celestial cues during the different stages of their development, I divided the birds into three experimental groups. I held Group A—w88, w89, w93, and w94—in the windowless room until late September. Consequently, these birds never saw the daytime sky or the sun, including sunrise and sunset, after they were taken as nestlings. Similarly, I prevented them from seeing the night sky until I tested them during the migration season.

I placed Group B—w95, w96, and w97—in the aviary, allowing them full view of the sky and landscape for four weeks between 15 August and 15 September. This is late in the post-fledging period, during the postjuvenal molt, and before the beginning of normal migratory activity. At all other times this group was in the windowless room.

I kept Group C—w90, w91, and w92—indoors until the completion of the postjuvenal molt and on 15 September transferred them to the outdoor aviary where they remained throughout the migration season. They were thus exposed to potential celestial cues during the attainment and maintenance of migratory condition with its attendant nocturnal activity.

I must emphasize that at no time were these experimental birds in contact with adult Indigo Buntings. My study, therefore, tested only the effects of visual exposure to celestial cues. The role, if any, normally played by the parents or other adult birds in influencing the orientational choices of immatures remains a subject for further investigation.

Between 24 and 29 September and again from 24 to 29 October, I placed each bird outdoors under the natural night sky in its own funnel-shaped cage, recorded its migratory restlessness or *Zugunruhe* by counting its jumps and then its directional preference by the "footprint technique" (Emlen and Emlen, 1966). The funnel shape of the test cage limited the bird's visibility to a 104-degree sector of the sky, a view increasing to approximately 140 degrees as the bird jumped up the sides, yet still blocking all terrestrial objects comprising the horizon.

The results are presented in the form of individual vector diagrams. For each data distribution the null hypothesis of randomness was tested by the Rayleigh method (see Appendix 5). The mean direction, ϕ, and the mean angular deviation, s, were calculated by vector analysis (Batschelet, 1965). Values for these statistics are presented in the appendices. In addition, I computed the mean directions for each nightly experiment. The distribution of these means for each bird is shown below its composite vector diagram. In all figures, 0 degrees or 360 degrees represents north, 90 degrees is east, 180 degrees is south, and 270 degrees is west.

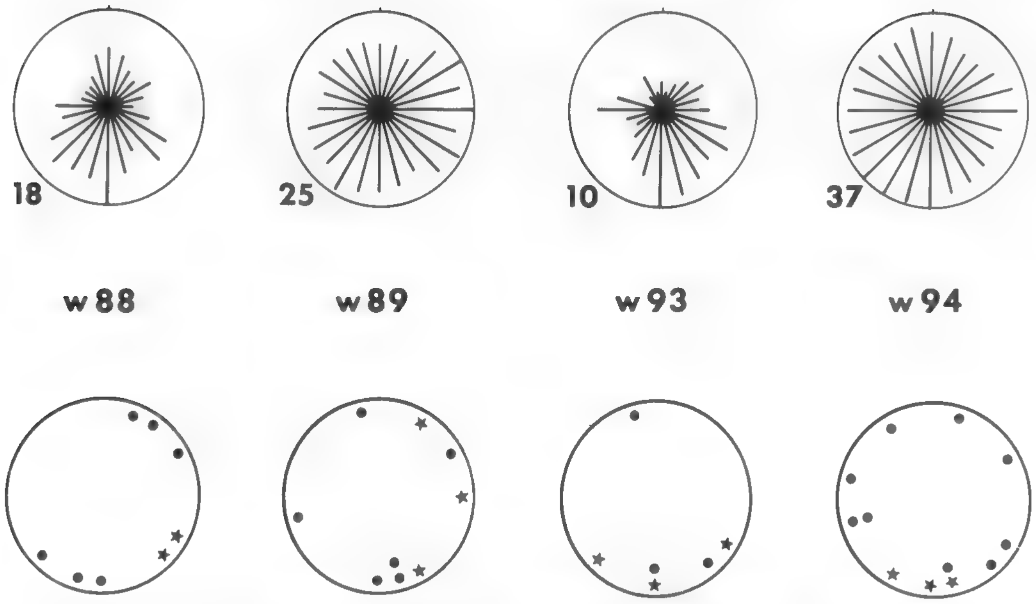

Figure 1. *Zugunruhe* orientation, or nocturnal unrest, of immature buntings, Group A.
Top: Vector diagram summaries plotted such that the radius equals the greatest number of units of activity in any one 15° sector. The number which this represents is presented at the lower left of each diagram.
Bottom: The distribution of nightly mean directions. Stars represent mean headings for the first three nights of testing; dots indicate means of later tests.

Results

The results, obtained from the birds in Group A that never saw the sky until the migration period (Figure 1; Appendices 1 and 2), indicate that one bird, w93, exhibited a significant tendency toward a southerly direction, while a second, w88, had a southerly bias ($.10 > p > .05$). The behavior of the remaining two individuals was random. Although the directional preferences of w88 and w93 were quite inconsistent from night to night, in marked contrast to the behavior of adult buntings, the preferences do suggest that a weak orientational ability had developed without the need of any social contact with experienced birds or any prolonged visual-celestial experience during their growing period.

The buntings in Group B that saw both the natural sky and outdoor surroundings from 15 August to 15 September showed a notable improvement over Group A in their directional responses. All three birds—w95, w96,

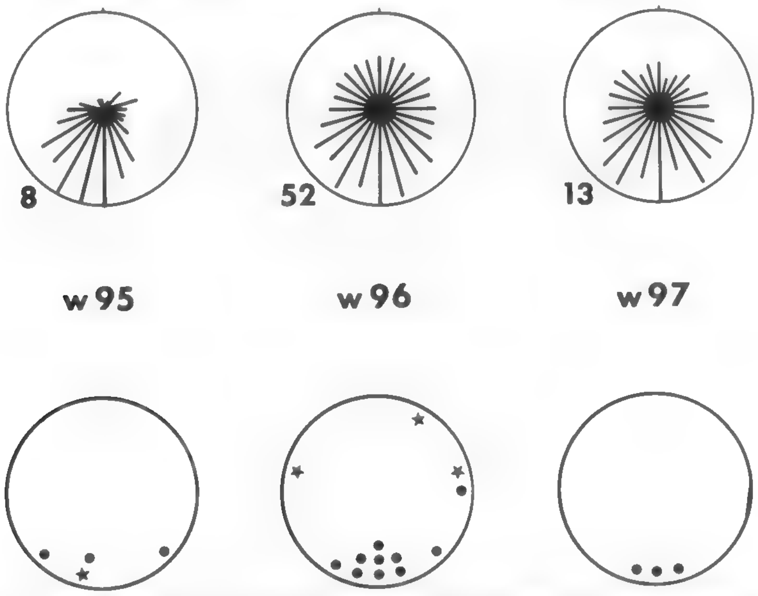

Figure 2. *Zugunruhe* orientation of immature buntings, Group B. See Figure 1 for meaning of symbols.

and w97—oriented their *Zugunruhe* southward with mean bearings of 192 degrees, 186 degrees, and 184 degrees respectively (Figure 2). The consistency of these directional responses, revealed by the nightly mean headings, also improved considerably.

One might have predicted that, if visual experience plays a role in the development of migratory direction finding, the most accurate results would occur in Group C, the birds housed outdoors when intense nocturnal activity and hence, presumably, an awareness of the starry sky first commenced. However, only one of the three birds in this group—w91—exhibited a directional response that was consistently southward (Figure 3, Appendices 1 and 2). The other two buntings in this group failed to show any significant orientational preference in either overall activity or nightly mean headings.

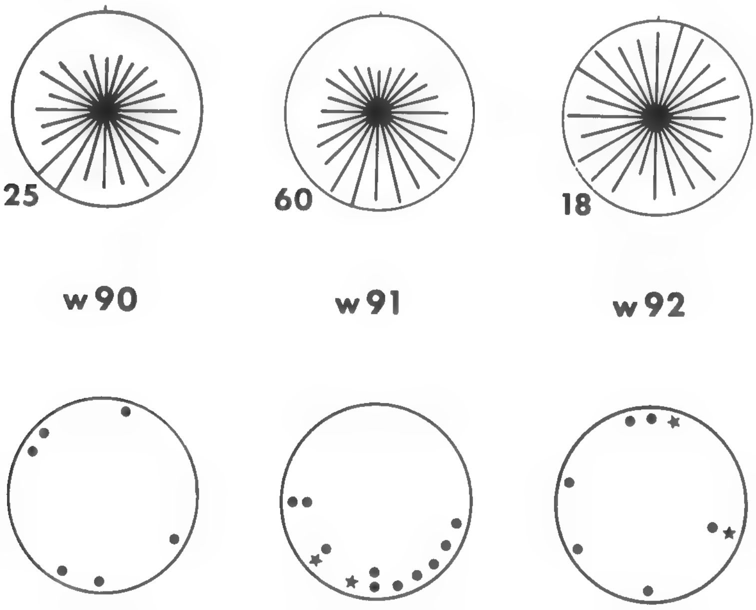

Figure 3. *Zugunruhe* orientation of immature buntings, Group C. See Figure 1 for meaning of symbols.

These findings suggest that exposure to the sky during the actual migration season does not improve orientational ability. We must, however, consider such statements highly speculative because of the small numbers of birds employed in these experiments.

It is interesting to compare the orientational capabilities of these immature birds with those of adult Indigo Buntings, mist-netted on the breeding grounds, following the completion of a normal round-trip migration. I tested 10 such adults and the immatures concurrently in identical cages, on the same nights, and at the same geographic location. The results from the experiments with these adults appear in Figures 4 and 5 and Appendices 3 and 4. Obviously, the accuracy of orientation in the adults, measured either as mean angular deviation or as consistency of response, was superior to that found in the inexperienced birds.

Taken together, these experiments suggest that some young buntings, isolated from all migratory and visual-celestial experience, exhibited a weak tendency toward a southerly direction; and that this tendency improved in both frequency and consistency when the birds had visual-celestial experience—a view of the sky—before the actual migration; but that none of the immatures, raised under the conditions of these experiments, attained the full orientational capacity exhibited by the adults.

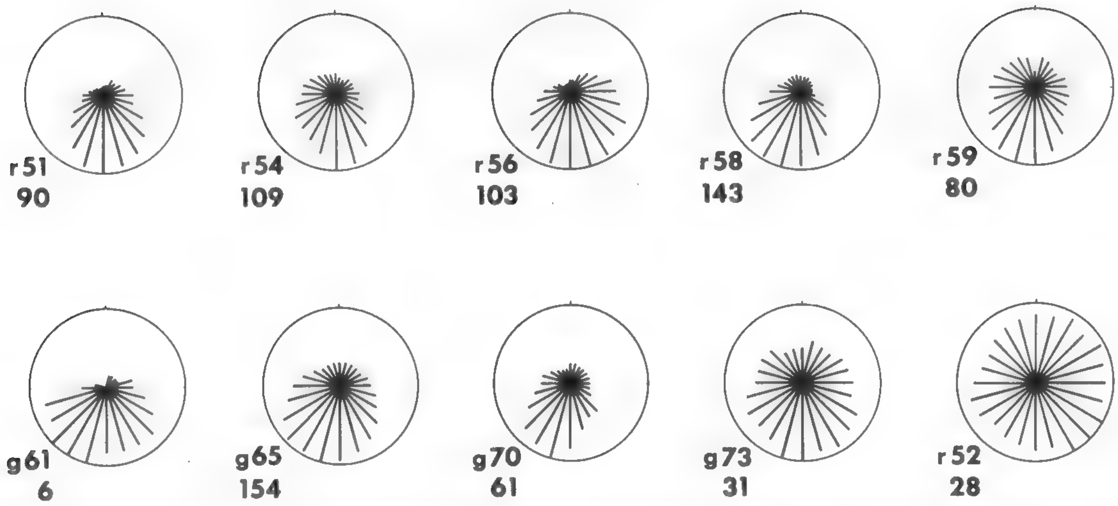

Figure 4. *Zugunruhe* vector summaries of adult Indigo Buntings. The length of each radial line indicates the number of units of activity in a given 15° sector. Compare Figures 4 and 5 with the results of the experiments with immatures, as shown in Figures 1, 2, and 3. Note the superior orientation responses in the adults.

Discussion

Additional orientation studies involving hand-raised, immature birds have been performed with European warblers, Bobolinks, and cuckoos. Sauer (1957) hand-raised 10 Garden Warblers (*Sylvia borin*) and five Blackcap Warblers (*Sylvia atricapilla*) as part of his migration study. Of the Garden Warblers, he obtained six at the age of nine days and kept them in a room with two north-facing windows, and four at the age of one day and confined them to a windowless room with no view of the sky. He obtained the five Blackcaps when they were one to nine days old and kept them in several different rooms during their development.

Although he presented data on *Zugunruhe* for only three of these birds—a Blackcap ("Blaurot") which had been housed in a room with west-facing windows, and two Garden Warblers ("Grungelb" from the windowless room and "Blau" from the room with north-facing windows)—each individual demonstrated a southerly tendency. The fact that Grungelb had never viewed the sky before the migration season suggests that visual-celestial and social experience are not essential for direction finding in this species. The results prompted Sauer (1958:46) to propose that ". . . the warblers have a remarkable hereditary mechanism for orienting themselves by the stars—a detailed image of the starry configuration of the sky coupled with a precise time sense which relates the heavenly canopy to the geography of the earth at every time and season. At their very first glimpse of the sky the birds automatically know the right direction. Without benefit of previous experience, with no cue except the stars, the birds are able to locate themselves in time and space and to find their way to their destined homes."

Hamilton (1962) hand-raised two Bobolinks (*Dolichonyx oryzivorus*) obtained as nestlings in New York State. These birds lived on a sun porch until they were able to fly, at which time they were moved to California and placed in a cage outdoors. They had considerable exposure to normal celestial cues prior to the fall migration season (W. J. Hamilton, III, pers. commun.). When tested during the autumn, "the response of these hand-reared birds alternated between north and south, with the southward trend almost due south" (1962:222). Hamilton further reports (pers. commun.) that hand-raised cuckoos (*Coccyzus americanus* and *C. erythropthalmus*) likewise showed ambivalent behavior, alternating their orientation between north and south.

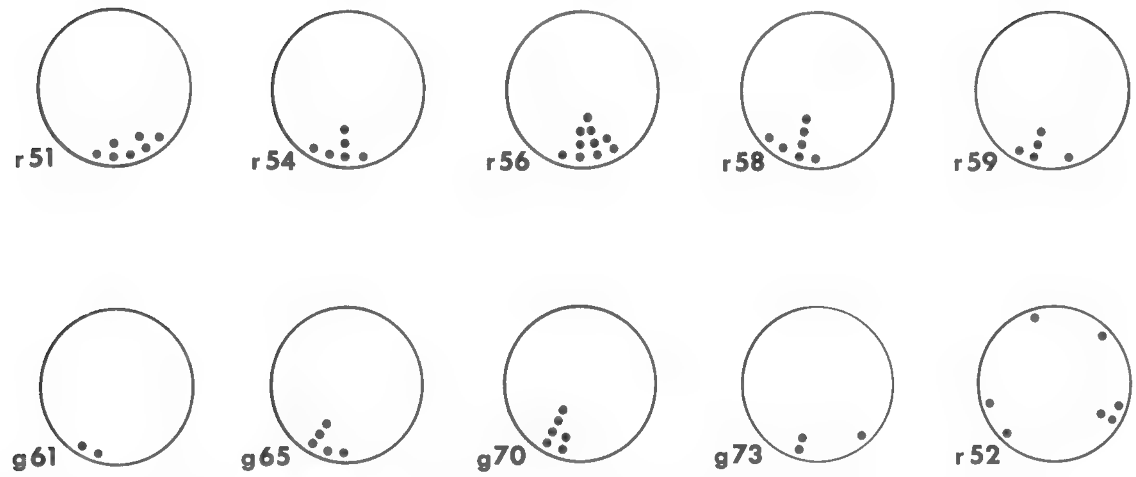

Figure 5. Nightly mean headings of adult Indigo Buntings. See Figure 4 for explanation.

The accuracy of the immature cuckoos never approached that observed in adult cuckoos. Hamilton's findings might indicate that, while a tendency to adopt a north-south axis develops in immatures with limited visual experience, the refinement of this direction-finding ability may depend on additional experience occurring during early life.

Obviously, we need additional experiments of this nature. However, in the absence of further data, I would speculate that Sauer's proposal for a genetically transferred star map is not applicable for Indigo Buntings. I base this statement not only upon the data presented above but also upon the results of experiments performed with adult birds. As part of a previous study (Emlen, 1967b) I tested the orientational abilities of adult buntings in a planetarium when various patterns of stars and portions of the artificial sky were blocked from view. My results indicated that, although most birds used the same general portion of the sky—the northern circumpolar region—for determining direction, different individuals relied upon different areas within this zone. My results, though sketchy, suggest a level of individual variation hard to reconcile with the idea of a predetermined star map, including the recognition of a goal, under rigid genetic control.

Instead, the maturing of orientation behavior appears to be a complex phenomenon involving the integration of several factors, some dependent for development on the bird's experience and others completely independent of any previous experience. Although we do not know the precise nature of these factors, several possibilities are worth mentioning.

First, the programming of a nervous system to respond selectively to a key star or star pattern would seem much simpler than demanding an innate recognition of the entire celestial sphere. For a Northern Hemisphere migrant, a star pattern close to Polaris might be optimal since circumpolar stars are visible at any time or season. Such a system could provide a simple directional reference point, and visual experience during the bird's maturing could provide additional cues to be superimposed upon this basic directional framework. The result would be an increase in directional information and, hence, more accurate orientation.

Alternately, one could propose that viewing the sun might be important for determining direction. Most nocturnal migrants are daytime animals except during the migration season, and we know that several species possess an ability to orient by the sun (St. Paul, 1953; Shumakov, 1965, 1967). The path of the sun and, in particular, the position of the sunset could serve as a reference point (Vleugel, 1953). The coupling of information from the stars with this daytime reference system might account for the improved performance of the birds in Group B that had visual experience.

(I must emphasize again that the birds in Group A never saw the sun either before or during the migration season. Consequently, while exposure to solar cues might improve a bird's orientational ability, such exposure does not appear to be essential for its occurrence.)

A third possibility involves a differential response to the apparent rate of rotation of stars located at different points on the celestial sphere. An awareness that the stars located near the celestial axis move through much smaller arcs (have a slower linear velocity) than those near the celestial equator could allow the birds to recognize a north-south directional axis. During their early development the birds might come to associate certain patterns of stars with areas of either fast or slow rotation. This type of hypothesis might best explain the north-south ambivalence displayed by immature Bobolinks and cuckoos. Once the positions of star patterns became fixed in this rotational reference system, the birds would not actually need to view the celestial motion. This last sentence is a necessary corollary to the third hypothesis because adult birds can orient normally in a planetarium under stationary skies (Sauer, 1957; Emlen, 1967a).

These hypotheses need not be mutually exclusive. Unfortunately, they remain entirely speculative. I include them in the hope of stimulating others to experiment in this area.

In discussing possible genetic bases of stellar orientation, we must consider the long-term reliability of the stellar cues themselves. As Agron (1962) points out, the positions of stars are not constant through evolutionary time. This is due, primarily, to the precession of the earth's axis. Agron likens this to the wobbling of a spinning top and states: "The angle of tilt of the earth's axis remains constant, but the direction of the axis changes. In a period of 25,800 years, the gyration, in a cone, of the earth's axis causes the celestial poles to make one circuit about a circle of 23.5 degrees radius" (1962:525-526). This motion produces marked seasonal and latitudinal changes in the apparent positions of stars, the "spring" stars of the present becoming "autumn" stars in 13,000 years, and *vice versa.* The values of declination also change; as the axis moves through its circle of 47 degrees, Vega becomes the new pole star and the declination of Polaris shifts from 90 degrees N to 43 degrees N. Similar changes occur for all stars with the result that the stellar information typical for any given latitude or season is altered markedly.

The implications of these changes for the evolution of celestial navigation are obvious. If migrants are to rely on a genetically fixed star map that they have inherited, the rate of genetic change must be rapid enough to allow for changes in celestial position of as much as 90 degrees in a 6,500-year time span.

A maturation process involving the coupling of stellar information with a secondary set of reference cues could minimize this problem. As mentioned previously, the path of the sun could provide one such cue. The axis of apparent celestial rotation could furnish another because this axis is aligned with geographic north-south regardless of what stars are located at its "poles."

Again these considerations are purely theoretical. But they suggest a possible selective advantage for a maturing of the migratory ability which blends experience-dependent factors and experience-independent factors. Determining the precise nature of these factors provides a stimulating challenge for future experimentation.

Summary

Current knowledge of stellar orientation is insufficient to explain how inexperienced, young birds in the Northern Hemisphere select a southerly direction for their first migratory flight. In an attempt to study the full development of this orientational ability, ten Indigo Buntings (*Passerina cyanea*) were hand-raised, from the nestling stage, in various conditions of isolation from view of the sky. Their orientational capabilities then were tested in circular cages under the natural night sky during their first autumn. Two of four individuals which had been isolated from all visual-celestial experience exhibited weak southerly tendencies. Directional responses improved in both frequency and consistency among birds allowed a view of the sky and natural surroundings for a one-month period prior to the migration season. Hand-raised birds never attained the accuracy of orientation typical of adult buntings.

It is proposed that the maturation of orientation behavior is a complex process involving both experience-dependent and experience-independent factors. Although the nature of these factors and of their interaction remains unknown, several possibilities involving the integration of stellar, solar, and rotational information are discussed.

APPENDIX 1

Statistical Treatment of *Zugunruhe* Vector Summaries of Immature Indigo Buntings

Bird	*Group*	*Hours active*	*Total N**	*Rayleigh statistic, z**	*Mean direction, ϕ*	*Mean angular deviation, s*
w88	A	23h 50m	70	1.69	Random	—
w89	A	29h 20m	160	0.60	Random	—
w93	A	17h 20m	40	3.14	158°	69°
w94	A	38h 40m	251	0.81	Random	—
w95	B	13h 20m	24	7.42	192°	54°
w96	B	43h 10m	273	5.14	186°	75°
w97	B	10h 0m	64	2.88	184°	73°
w90	C	16h 30m	110	0.05	Random	—
w91	C	40h 40m	339	8.80	172°	74°
w92	C	23h 20m	122	0.23	Random	—

*See Appendix 5.

APPENDIX 2

Statistical Analyses of Nightly Mean Headings of Immature Indigo Buntings

Bird	*Group*	*Number of nights tested*	*Rayleigh statistic, z*	*Mean direction, φ*	*Mean angular deviation, s*
w88	A	8	1.47	Random	—
w89	A	9	0.85	Random	—
w93	A	6	1.52	Random	—
w94	A	12	0.76	Random	—
w95	B	4		Insufficient sample size	
w96	B	13	4.07	166°	54°
w97	B	3		Insufficient sample size	
w90	C	6	0.16	Random	—
w91	C	12	4.95	182°	49°
w92	C	8	0.17	Random	—

APPENDIX 3

Statistical Treatment of *Zugunruhe* Vector Summaries of Adult Buntings Tested Concurrently with the Immatures

Bird	*Hours active*	*Total N**	*Rayleigh statistic, z*	*Mean direction, φ*	*Mean angular deviation, s*
r51	24 hr. 30 min.	303	65.67	170°	59°
r54	29 hr. 40 min.	401	46.51	197°	66°
r56	40 hr. 10 min.	424	72.5	163°	62°
r58	35 hr. 20 min.	852	152.63	206°	62°
r59	20 hr. 30 min.	358	19.20	205°	71°
g61	5 hr. 0 min.	22	19.42	185°	55°
g65	38 hr. 50 min.	695	64.54	198°	67°
g70	24 hr. 10 min.	206	26.21	207°	65°
g73	17 hr. 50 min.	170	4.76	176°	74°
r52	28 hr. 40 min.	190	0.64	Random	

*See Appendix 5.

APPENDIX 4

Statistical Analyses of Nightly Mean Headings of Adult Buntings Tested Concurrently with the Immatures

Bird	*Number of nights tested*	*Rayleigh statistic, z*	*Mean direction, φ*	*Mean angular deviation, s*
r51	7	6.25	165°	19°
r54	6	5.68	185°	13°
r56	10	9.51	169°	12°
r58	7	6.68	200°	14°
r59	5		Insufficient sample size	
g61	2		Insufficient sample size	
g65	5		Insufficient sample size	
g70	6	5.94	205°	7°
g73	3		Insufficient sample size	
r52	7	0.36	Random	

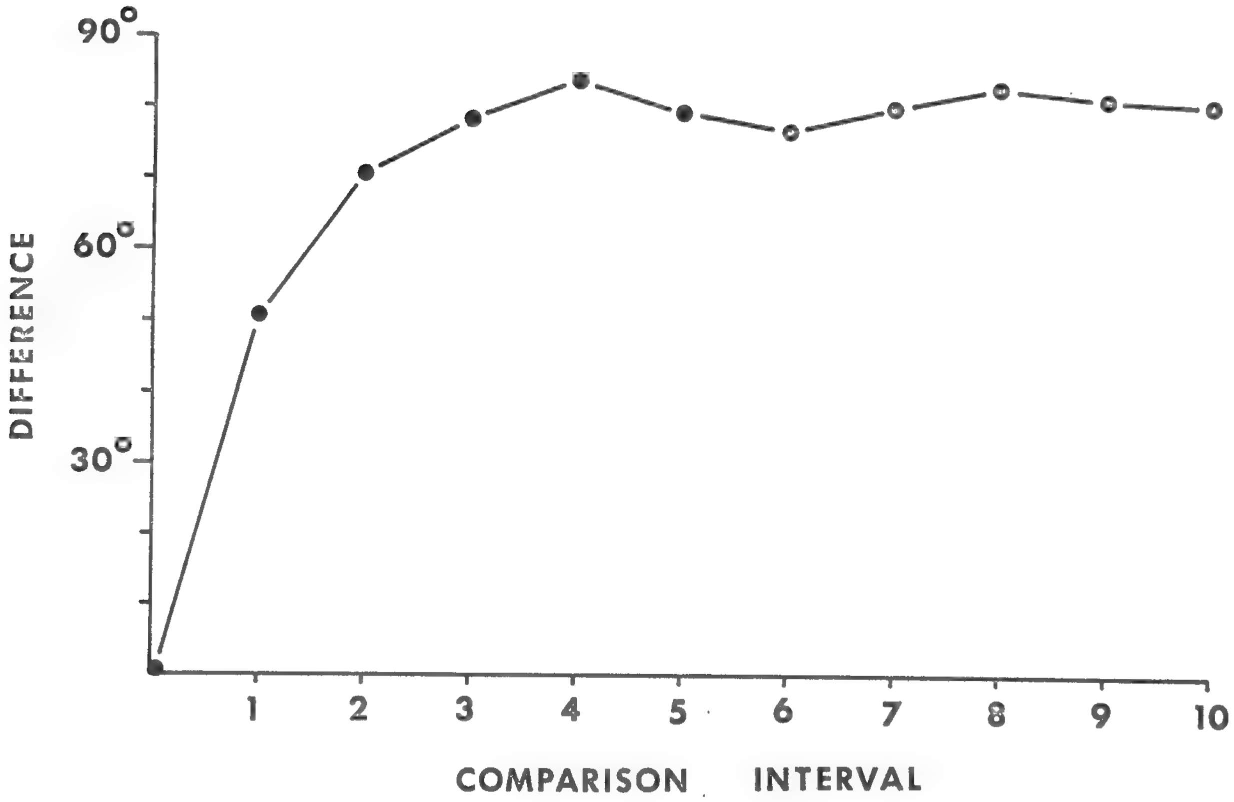

Figure 6. The mean difference (in degrees) between pairs of jumps plotted against the interval between comparisons.

APPENDIX 5

Determination of Sample Size, N, for Statistical Analyses

The analysis of behavioral data collected from repeated observations on a single individual animal presents statistical problems because of the difficulty of determining meaningful sample sizes (N). This problem is particularly acute in orientation work since the value of the Rayleigh statistic, z, used in testing randomness, is directly proportional to N.

We can overcome this situation in one of two ways: devise a statistical measure insensitive to the absolute magnitudes of directional activity (Emlen, 1967a); or determine empirically the interval at which activity measures—in this case, jumps—become independent of one another. For the experiments reported in this paper I calculated this independence interval.

I placed the birds in funnel-shaped cages covered with translucent glass that eliminated all visual cues. Under this condition activity was random. I replaced the floor of the cage with a plexiglas pan and observed the bird's behavior directly from below. I then recorded in sequence the direction of each jump taken by the bird. The mean directional distance between pairs of jumps was plotted for various orders of pairs, 0 (Figure 6). Since the birds' behavior was nondirectional, the expectation value for independence should approximate 90 degrees.

Auto-correlations were also performed on these data to determine the level at which independence occurred—where the auto-correlation coefficient becomes zero (Figure 7).

As seen in the graphs of Figures 6 and 7, this independence interval was approached at 0=4, and definitely reached at 0=8. Both techniques yielded similar results. Consequently, to obtain a *conservative* estimate of sample size for orientation data, the actual number of jumps made by each bird should be divided by 8.

However, we expressed the quantity of footprint records in "activity units," not actual jumps. By counting the number of jumps made during sample tests and then quantifying them in the normal manner, I obtained a value of 2.8 jumps per unit of activity. We can now calculate the meaningful sample size by the following formula: $N = \frac{U \times 2.8}{8}$ where U equals the total number of activity units. I used this value of N in determining all Rayleigh statistics (z) and randomness levels presented in this paper.

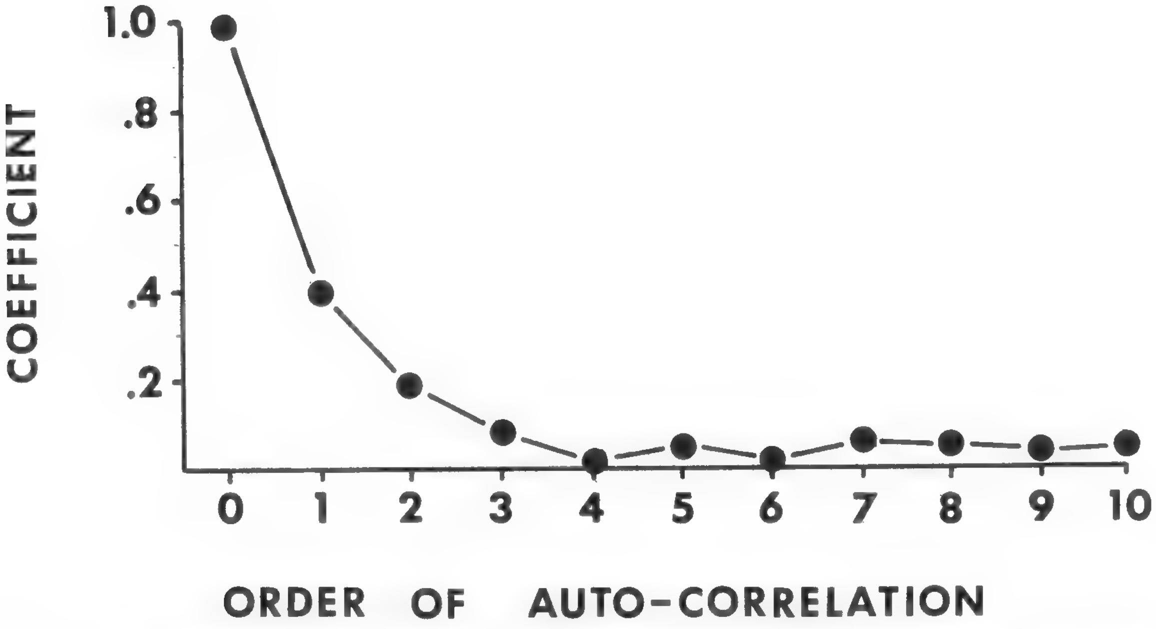

Figure 7. The auto-correlation coefficient plotted against the order of correlation (the interval between comparisons).

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ITHACA, NEW YORK

Plate I. *Above,* Red-legged Honeycreeper, *Cyanerpes cyaneus.*
Below, White-vented Euphonia, *Tanagra minuta.*

WHAT IS A TANAGER?

ROBERT W. STORER

Color photographs by JOHN S. DUNNING

In 1886, when the British ornithologist, Philip Lutley Sclater, published his list of the tanagers, he wrote: "In essential structure the Tanagers are closely allied to the Finches, and it is in many cases exceedingly difficult, if not impossible, to draw a line between the two groups .... On the other hand, some of the Tanagers have also nearly equally close relations with the *Mniotiltidae* [Parulidae] and the *Coerebidae*; and I do not think it is at present practicable to give any absolute characters which would serve to differentiate the birds of these three families in all cases." Today, Sclater's statement is as valid as it was eighty-three years ago.

Tanagers belong to the large assemblage of "nine-primaried" songbirds, so named because the outer (tenth) primary feather of the wing is minute and concealed (except in some vireos). This large group numbers over 700 species and includes the vireos, honeycreepers, wood warblers, icterids, and at least the cardinaline and emberizine finches. All, except the last group, are normally confined to the New World. Within this large and complex assemblage, the tanagers have been characterized by Sclater (1886:49) as being separable from the finches "as a general rule . . . by the possession of a notch near the end of the upper mandible .... But this notch is obsolete or scarcely apparent in certain genera . . . , while it is very strongly developed in others .... The principal food of the typical Tanagers appears to be ripe fruit . . . ; but other Tanagers feed on seeds and grain after the manner of Finches."

More recent attempts to characterize the tanagers have done little to advance our understanding of the relationships within the group or those between the tanagers and the finches or the wood warblers. For example, in his study of the jaw muscles of songbirds, Beecher (1953) commented on the variability within the tanagers and their approach in the characters he studied to some of the honeycreepers and finches. We are thus left with an unsatisfactory definition of the tanagers—"nine primaried" songbirds with more or less notched bills.

Amadon (1950) showed convincingly the great evolutionary plasticity of bill form and function among the Hawaiian honeycreepers. This is an extreme but by no means a rare type of adaptive radiation, perhaps more obvious on oceanic archipelagos but also to be found on continental areas. Through an understanding of this type of radiation, we are coming to realize that modifications of bill form, which for decades were considered important generic and familial characters, can occur quite rapidly in an evolutionary sense. Thus convergence in bill form between distantly related species and divergences between closely related ones can obscure the phylogenetic relationships within large groups. This suggests that tanagers are not a natural group and that a reappraisal of the whole nine-primaried assemblage is needed before the relationships of and within the tanagers are understood.

Where then can we look for clues to these relationships in a large group like the nine-primaried songbirds? Comparative behavior and life history are possibilities; but although much valuable information is being gathered in North America, in Latin America, where most of the species occur, the vast majority remain to be studied in spite of the many life history studies of Skutch (1954, 1962) and the valuable behavior work of Moynihan (1962a, 1962b, 1966). Biochemical studies of protein offer other possibilities, but, to date, work in this area has been more successful in providing evidence for the relationships between orders and very well-marked families than for those between members of such a closely-knit group as the nine-primaried songbirds. Pattern, color, and texture of plumage offer many clues to relationships and in some cases are more conservative than bill form. I believe that their importance has not been fully realized by systematists. If this is the case, it is obvious that any effective revision of the tanagers must be part of an overall study of the whole assemblage. I believe that such a study will show that the traditional lines between the tanagers and the finches and the tanagers and wood warblers will prove untenable, and different alignments between the genera will better show phylogenetic relationships. However, until such a large-scale study is made, it will be useful to follow the traditional arrangement.

To one familiar only with the tanagers which nest in the United States, the array of tanagers in the American tropics is bewildering. It is even more confusing to find that several groups of tanagers show convergence in structure and habits with birds of other families.

One very distinct group of tanagers is the euphonias (*Euphonia* [formerly *Tanagra*]) (Plate 1). In these, the males may be blue, black, olive, or gray above, but always with a metallic sheen; the underparts are usually yellow, as is the forehead. The females are olive variously shading into gray, yellow, or rusty. Euphonias, as far as known, feed largely on mistletoe berries. Some have rather small, weak bills whereas in others, the bill is quite stout. The reason for such variation in a group with so little apparent variation in feeding habits is unknown and would make an interesting evolutionary study.

Euphonias resemble closely the flower-peckers (Dicaeidae) of the Indo-Australian region in feeding habits, size, and bill shape; and to a lesser degree in color and nesting habits. Both build domed nests with the entrance at the side, although those of the flower-peckers are often pendent whereas those of the euphonias are not. Perhaps oddest of all, the muscular stomach has become greatly reduced in some of the flower-peckers and almost lost in the euphonias which have been investigated (Desselberger, 1931). Only the outer pulp of the berry is digested as it passes through the tubular tract. It is clear that both flower-peckers and euphonias are prime disseminators of mistletoe.

Another interesting parallel is that between the Scrub Euphonia (*Euphonia affinis*) and the Central American race of the Lesser Goldfinch (*Spinus psaltria croceus*). According to Dickey and van Rossem (1938:546), "That such a close parallel in size and color exists between two members of separate families is remarkable enough, but when the resemblance extends still further, to call-notes, general habits, and even to the occurrence of the annual molt in summer instead of fall, it seems extraordinary." The food habits are, of course, different, but one wonders what, if any, selective advantage may account for the resemblances.

Plate II. *Above,* Blue Dacnis, *Dacnis cayana.*
Below, Blue-and-black Tanager, *Tangara vassarii.*

The genus *Ramphocelus* contains some of the most common and conspicuous tropical tanagers. These birds range in color from the deep, intense red of the Silver-beaked Tanager (*R. carbo*) to the brilliant Scarlet-rumped Tanager (*R. passerinii*) beside whose velvet-black body and gleaming rump, our Scarlet Tanager looks dull. This group of tanagers is of particular interest because of the structure of the mandible (Figure 1). The bone of the lower jaw is thickened and heightened, whereas the upper jaw is not so modified. The enlarged part of the mandible is covered by the ramphotheca and extends back to and below the gape (Plate IV). Its functions remain to be demonstrated, but I believe that it evolved primarily in association with feeding on large fruit and is of advantage in being easier to clean of sticky fruit juices than if the same area were feathered. This idea is supported by examination of the skull of the oropendolas (*Psarocolius, sensu lato*), in which both jaws are similarly equipped (Figure 2). These large icterids are known to feed by inserting the closed bill into fruit, then opening the bill and feeding on the soft pulp and juices (Beecher, 1951a:425-426). In the tanagers, the lack of modification of the upper jaw and the weak development of the muscles used in gaping indicate that these birds take bites out of fruit in such a way that the juices tend to run down the sides of the mandible.

In life, the expanded portion of the mandible is bluish-white, contrasting with the black or red of the adjacent plumage. Writing of the Silver-beaked Tanager, Haverschmidt (1968:397) states: "In display the male stretches its head high and upwards, with the bill raised vertically so that the bluish-white sides of the lower mandible are presented to its opponent." Skutch (1954:125) describes a threat involving lowered head and opened bill by the Scarlet-rumped Tanager. In this genus the species can be arranged in a gradient from *R. carbo,* which has the most expanded mandible, to *R.* (*Phlogothraupis*) *sanguinolentus,* in which the mandible is "normal." In the species in which the mandible is expanded, the pale color is concentrated on the expanded part; in *sanguinolentus* the bill is nearly all pale. I think it probable that the development of the mandible arose as an adaptation for feeding on fruit and that secondarily, the display function of the (probably) originally pale bill became focussed on the expanded portion of the mandible.

Other adaptations for feeding on fruit are rarely apparent in the tanagers. The plucking and swallowing of small fruits is readily accomplished by birds with such a wide range of bill form as Myrtle Warblers and Cardinals. In many tanagers, only part of the diet consists of fruit, hence it is likely that the selection pressures acting on bill form are complex and related to more than one food source. The scarcity of apparent modifications for fruit-eating may be a result of relatively weak selection pressures for fruit-eating as compared, for example, with the more complicated and difficult processes of catching and killing insects. The complex of selective pressures has probably resulted in a bill shape which could be considered a compromise. Such a situation is an ideal starting point for adaptive radiation, and this appears to be what has happened in the tanagers.

By far the largest genus of tanagers is that of the callistes (*Tangara*) with 46 species. It is also one of the most widespread; hardly any wooded area in the American tropics is without one or more species. The callistes are somewhat larger than euphonias, the largest of them being about the size of a House Sparrow. Virtually every color of the rainbow is to be seen on at least one species in the group. Although none have a metallic sheen to the plumage, several have an opalescence, which is rare in birds. Skutch (1954:200-

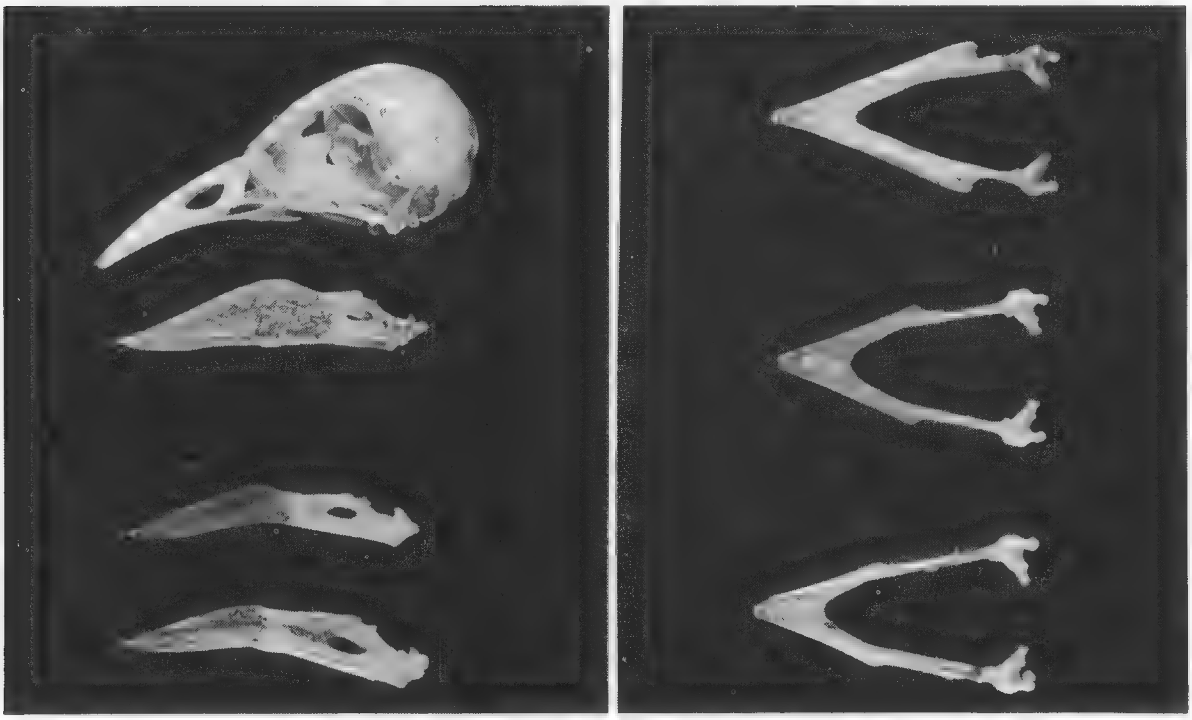

Figure 1. The expansion of the mandible in tanagers of the genus *Ramphocelus*. *Top to bottom:* Silver-beaked Tanager (*R. carbo*), Scarlet-rumped Tanager (*R. passerinii*), and Crimson-collared Tanager (*R.* [*Phlogothraupis*] *sanguinolentus*). The expanded portion is covered by the ramphotheca. Photographs by Louis P. Martonyi.

240) has published life history studies of five of the Central American callistes. According to his accounts, they feed on both fruit and insects, tending to eat more fruit as adults and to feed more insects to the young. The nest is an open cup, and the clutch normally consists of two eggs, in contrast to the euphonias, which may lay as many as five. Both parents care for the young, and in the case of a brood of Plain-colored Tanagers (*Tangara inornata*), four adults attended the young.

While the callistes' diet is quite varied, the group appears to have given rise to several lines of more specialized feeders. The most obvious case is that of the Golden-collared Honeycreeper or Honeycreeper Tanager (*Tangara pulcherrima*). This bird was first described as a member of the "honeycreeper" genus *Dacnis* and later placed in a separate genus (*Iridophanes*) by Ridgway, largely on the basis of bill shape. The slender bill of this little-known species may reflect the habit of feeding at flowers like the other honeycreepers, but in plumage it is extremely close to the Black-headed Tanager (*Tangara cyanoptera*). The females of the two species are almost identical in plumage; the male of *pulcherrima* differs from that of *cyanoptera* only in having a yellow nape, more black on the back, and more blue on the wing. The opalescent plumage of the rump and underparts of the two species is strikingly similar. If one accepts the premise that bill form is very plastic, it must be conceded that these two species are very closely allied, in fact congeneric.

Another line of "honeycreepers" appears closely related to the callistes. This is the line containing the genera *Dacnis, Chlorophanes,* and *Cyanerpes* (Plates I and II). Starting with the Blue-and-black Tanager (*Tangara vassorii*),* which has a short, but rather finely pointed bill, there is a progressive lengthening, thinning, and curvature in the bills of the Turquoise Dacnis-Tanager (*"Pseudodacnis"* [=*Dacnis*] *hartlaubi*), White-bellied Dacnis (*Dacnis albiventris*), Blue Dacnis (*D. cayana*), Green Honeycreeper (*Chlorophanes spiza*), and Red-legged Honeycreeper (*Cyanerpes cyaneus*) to the Purple Honeycreeper (*C. caeruleus*). Beecher (1951b:274-287) pointed out the resemblance

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*In Plate II the name *Tangara vassarii* should read *Tangara vassorii.*

Plate III.

Above, Swallow-tanager,
Tersina viridis.

Right, Gray-headed Tanager,
Eucometis penicillata.

in jaw muscles and horny palate between *Tangara* and *Cyanerpes*. The strong similarities in the color, pattern, and texture of the plumage which run through this group of species and most of their congeners provides additional strong support for the idea that these birds are all closely related. They are, presumably, tanagers which have become adapted for feeding on nectar. Figure 3 shows some of the stages in bill form in the series culminating in the Purple Honeycreeper.

The rationale for using a series of living species to illustrate how evolution might have occurred may need explanation. It cannot be implied that one of these living species gave rise to any of the others, rather, each may be likened to a stage in the evolution of the "end" species, in this case, *C. caeruleus*. It is significant that each of the intermediate forms is a viable species, which shows that similar intermediate forms could have survived and given rise to more "advanced" ones in the series.

The migratory Swallow Tanager (*Tersina viridis*) (Plate III) may also have been derived from a calliste-like ancestor. This species, like the tanager-honeycreepers, has diverged so far from the tanagers in its habits and structure that it is frequently placed in a separate family. Although the color pattern is not like that of any calliste, the color and texture of the feathers are like those found in some callistes, and the sexual dimorphism (blue males and green females) is like that in the Blue Dacnis. The Swallow Tanager's bill (Figure 3) is rather like that of a calliste but much broader at the gape, a reflection of its flycatching habits. Like the callistes, Swallow Tanagers may also drift through the canopy of the forest in groups, feeding on small fruits. Swallow Tanagers build an irregularly shaped open nest in a natural

Figure 2. The skull of the Chestnut-headed Oropendola (*Psarocolius* [*Zarhynchus*] *wagleri*), which is adapted for gaping in large fruit. The expanded portions of the maxilla and mandible are covered by the ramphotheca. Photograph by Louis P. Martonyi.

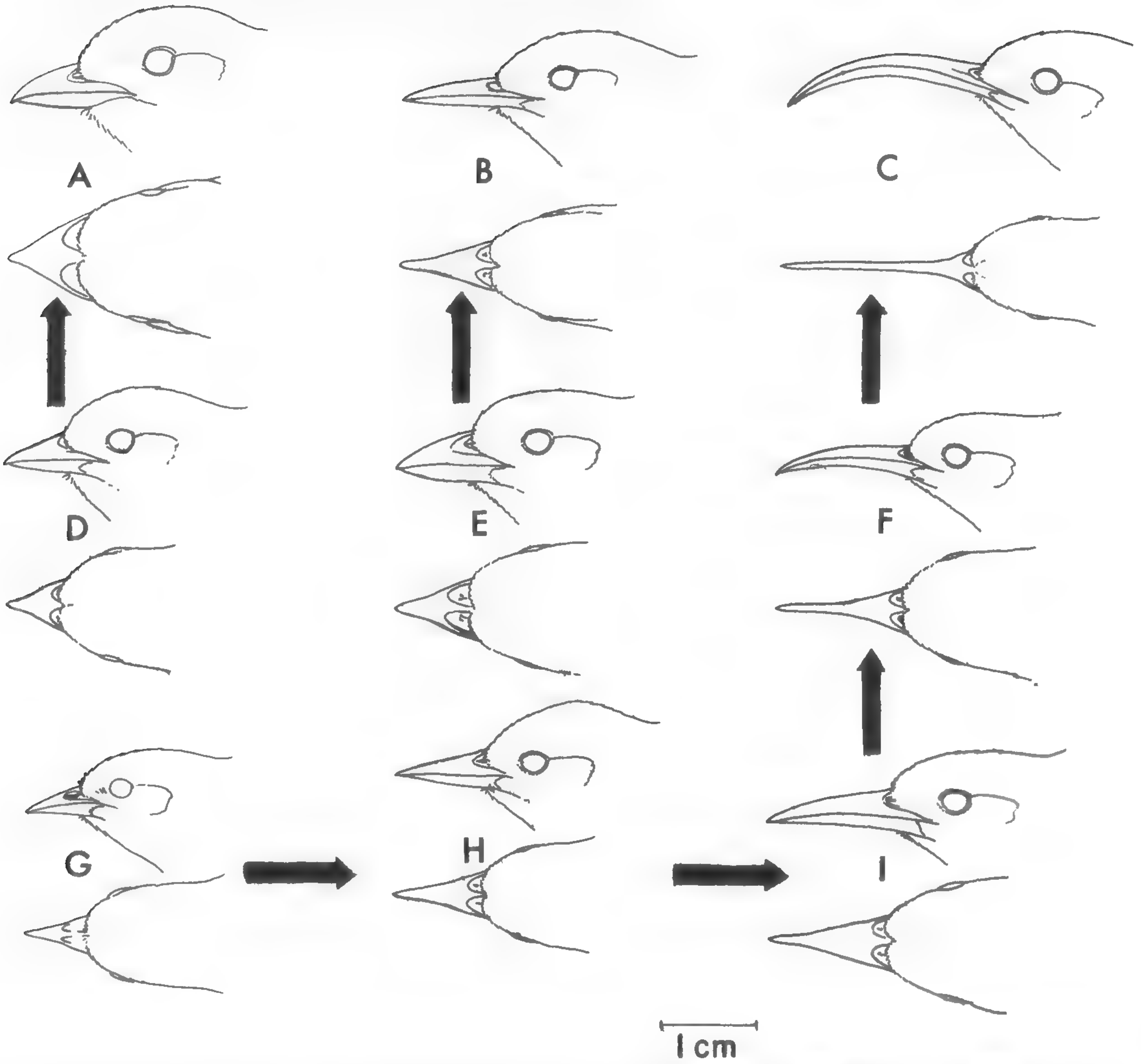

Figure 3. Probable trends in the evolution of a "honeycreeper" assemblage. These birds are probably all closely related through similarities in jaw muscles, horny palate, and the pattern, texture, and color of the plumage. They include: A, Swallow Tanager (*Tersina viridis*); B, Yellow-collared Honeycreeper (*"Iridophanes pulcherrima"*); C, Purple Honeycreeper (*Cyanerpes caeruleus*); D, Blue-and-black Tanager (*Tangara vassorii*); E, Red-necked Tanager (*Tangara cyanocephala*); F, Red-legged Honeycreeper (*Cyanerpes cyaneus*); G, White-bellied Dacnis (*Dacnis albiventris*); H, Blue Dacnis (*Dacnis cayana*); I, Green Honeycreeper (*Chlorophanes spiza*).

or man-made cavity and may even dig a burrow in a vertical bank. The clutch size is usually three. Ernst Schaefer's account (1953) of the life history of this species is probably the most thorough of any tropical tanager.

In the New World, shrikes are not found south of the Isthmus of Tehuantepec. Instead, shrike-like birds have evolved in at least five different Neotropical families: the antbirds, cotingas, tyrant flycatchers, vireos, and tanagers. The shrike-tanagers (*Lanio*) have bills very similar to those of the true shrikes except that the "tooth" is farther from the tip (Figure 4). Little is known about the feeding habits of these birds, but judging from the strong bill, they must be able to take large insects and small vertebrates. The Central American forms are conspicuous members of the mixed flocks which move noisily through the dense forests. Slud (1964:362) says of *L. aurantius*: "In addition to seeking prey in foliage and on limbs, the bird fly-catches and plucks small fruits on the wing."

A conspicuous feature of Neotropical forests is the army ants, whose columns move relentlessly through the forests routing small invertebrates from their hiding places. Among the birds which habitually follow these

Plate IV. *Above,* Multicolored Tanager, *Chlorochrysa nitidissima.*
Below, Crimson-backed Tanager, *Ramphocelus dimidiatus.*

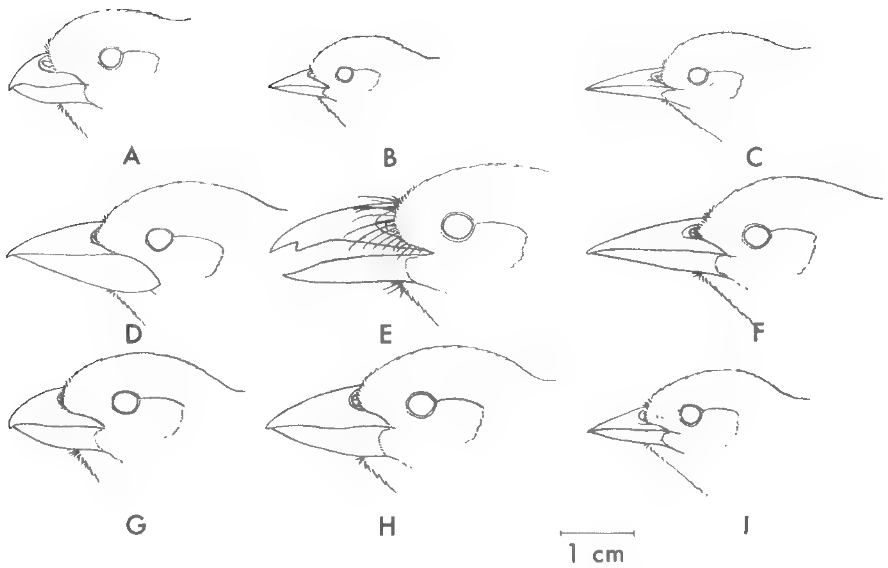

Figure 4. In addition to the "honeycreeper" assemblage, the range of bill form within the tanagers shows a variety of feeding specializations that include insectivorous and warbler-like species, finch-like seed-eaters, more typical fruit-eaters, and the shrike-like bill of *Lanio* (E), whose food, while little known, probably consists of large insects and small vertebrates. Examples shown here include: A, Green-throated Euphonia (*Euphonia* [= *Tanagra*] *chalybea*); B, White-vented Euphonia (*Euphonia* [= *Tanagra*] *minuta*); C, White-winged Ground Warbler (*Microligea montana*); D, Silver-beaked Tanager (*Ramphocelus carbo*); E, Black-throated Shrike Tanager (*Lanio aurantius*); F, Black-crowned Palm Tanager (*Phoenicophilus palmarum*); G, Diademed Tanager (*Stephanophorus diadematus*); H, Finch-tanager (*Oreothraupis arremonops*); I, Black-backed Bush-Tanager (*Urothraupis stolzmanni*).

ants and feed on the dislodged animals are at least two tanagers, the Red-throated Ant-tanager (*Habia fuscicauda*) and the Gray-headed Tanager (*Eucometis penicillata*) (Plate III). Willis (1960) has described well the foraging methods of the Red-throated Ant-tanager at army ant swarms and has pointed out that these birds are not found on the Pacific slope of Mexico north of the Isthmus of Tehuantepec, where the range of army ants stops. Oddly, the closely related Red-crowned Ant-tanager (*Habia rubica*) rarely visits army ant swarms (Willis, 1960).

If one adds to the foregoing list of "specialists" the species of tanagers which are insectivorous and warbler-like, finch-like seed-eaters, and more typical fruit-eaters, the range of bill form within the group is remarkable (Figure 4). So also is the range of plumage types. The metallic sheen of male euphonias and the opalescence and wide range of bright colors of the callistes have already been mentioned. Another unusual feather texture is found in males of such genera as *Chlorophanes* and *Chlorochrysa*. Under the microscope the waxy-textured feathers of these birds appear to have the barbs fused with the barbules in such a way that each barb looks like an enameled pine needle. Behind the ear openings, males of *Chlorochrysa* (Plate IV) have patches of feathers, the tips of which are fused into deep orange, club-shaped structures. The appearance of the waxy feathers suggests that they may be efficient in shedding rain drops; the club-tipped feathers may function in courtship or sex recognition, but virtually nothing is known about the behavior of these birds.

At the opposite pole in terms of plumage color and texture is a large group of nine-primaried oscines which are currently placed in three families. Examples of this rather large group include the wood warbler, *Basileuterus melanogenys,* the emberizine finches, *Atlapetes torquatus, Lysurus crassirostris,* and *Arremon aurantiirostris,* and the tanagers, *Chlorothraupis carmioli, Mitrospingus cassini,* and *Hemispingus atropileus.* In this group, the plumage is dull and lax and the rectrices are soft and obtusely pointed. The colors run from black and gray to olive, yellow, white, and rusty, with olive backs and paler underparts predominating. Aside from breast bands in a few species, the patterns are almost entirely confined to the head—crown stripes, ear patches, etc. Birds of this group vary widely in foraging methods and food, and also in altitudinal distribution, but most are said to inhabit dense lower vegetation in areas of moist climate. Although convergence in plumage texture, color, and pattern may have evolved in response to similarities of environment, the resemblances in plumage might well indicate a closer degree of phylogenetic relationship than is expressed in current classifications. One thing is certain: these resemblances have caused confusion. The rare *Oreothraupis arremonops* (Plate V) was considered a tanager long after several genera such as *Saltator* were transferred to the finches. This bird is so similar to several species of the finch genus *Atlapetes* that I have recommended that it be transferred into or near that genus (Storer, 1958). It is not unlikely that some were influenced against making this change much earlier by the presence of the root for tanager (*thraupis*) in the generic name. Confusion within this drab group of birds reached a peak when two authorities on South American birds redescribed a well-known species of the "tanager" genus *Hemispingus* in the "wood warbler" genus *Basileuterus*.

It should be clear that much new information, especially on the behavior of the nine-primaried oscines, is needed before we can reach a satisfactory understanding of the group. Reducing the rank of the wood warblers, tanagers, and finch groups from families to subfamilies has merit in emphasizing the rather close relationships of all the birds in these groups. On the other hand, it de-emphasizes the need for a realignment of the genera and simply transfers the problem to a subfamilial level. In the United States, where most of the students of Neotropical birds have lived, wood warblers, tanagers, and finches are, with the exception of a very few species, well defined groups. Consciously or not, these ornithologists have extended the narrow concepts of these groups based on temperate North American species to the much more complex assemblage in the tropics. A better understanding of the relationships between genera in this assemblage must be derived from collecting a large mass of new data on the tropical forms and analyzing it with an open mind.

NOTE ABOUT THE COLOR PHOTOGRAPHS

John S. Dunning

Several years ago I learned that Dr. Horace Loftin was conducting extensive bird-banding operations in Panama and having birds with some very fascinating variations in plumage show up in his nets. He felt that someone should make a photographic record of these exotic species in color. Here was an opportunity to work with birds of the Neotropical forest, birds that are difficult even to see, let alone photograph in the wild. The idea appealed to me. It was the trigger that sent my wife and me to Panama where we were soon trying to find some way to calm the birds so that we could photograph them unruffled and at ease with foliage from their native habitat.

During the next two years we worked out the details of the method we now use—a method that permits us to take close-up pictures of birds against a background of natural foliage, in adequate light, and, most important of all, under such conditions that the danger to the birds is practically zero.

Plate V. *Above,* Scarlet-and-white Tanager, *Erythrothlypis salmoni.*
Below, Finch-like Tanager, *Oreothraupis arremonops.*

We now run our own nets and tend them more often than the bird-banders do, removing the birds immediately—before the feathers become mussed. After taking the bird from the net, we place it in an enclosure about 10 feet long, large enough for allowing the bird to fly, and fitted with perches against a background of fresh foliage, collected and arranged just before we put the bird inside. Then, with the lens of the reflex camera through a zippered opening and strobe lights in position inside for illumination, we are ready.

If all is quiet, the bird usually calms down immediately and, with luck, pauses for a moment on a perch for a photograph. We retain each bird only briefly before releasing it in the same area where we caught it. We find that keeping the foliage crisp and getting the bird trim and alert in the proper position on the perch, all at the same time, is one of the most challenging phases of our project.

We photographed the *Cyanerpes, Dacnis,* and *Eucometis* in Panama; the *Tersina* in Venezuela; and all the rest in Colombia.

While working in the tropics we have become alarmed at the rapid rate at which the forests are being cut down. We feel that many of the birds of the Neotropical forest are in grave danger of extinction within a relatively short time. Our goal now is to make a photographic record of as many as possible before it is too late.—Burlington, Connecticut.

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UNIVERSITY OF MICHIGAN MUSEUM OF ZOOLOGY, ANN ARBOR

ECOLOGY AND ADAPTATIONS OF THE TREMBLER ON THE ISLAND OF DOMINICA

RICHARD L. ZUSI

The Trembler (*Cinclocerthia ruficauda*), known and named for a habit of trembling its wings, is native to the Lesser Antilles. It is plain brownish or grayish with a long black bill, moderately long tail, and a beady cream-colored eye (Figure 1). The sexes are similar except that the female has a longer bill than the male. Unlike most members of its family, the Mimidae, the Trembler is largely restricted to tropical or subtropical broad-leaved evergreen forests that receive a heavy monthly rainfall. Dominica is the last of the islands within its range to remain extensively forested and thus the last island on which the species is widespread and common. Little or nothing has been published on the Trembler's habits, on its adaptations to the forest environment, or on its niche and relations with other island species.

In the course of my studies on natural history of the land birds of Dominica, from mid-January to mid-April 1964, I gained preliminary information on some of these topics and returned to Dominica from 11 March to 4 April 1968 to obtain more precise information about the Trembler's feeding behavior. My account applies directly to the latter part of its non-breeding season and to the early phase of the breeding season, but probably has relevance to other phases of the annual cycle as well. There is no detailed account by which to compare foraging behavior of races on other islands with that of the Dominican race *ruficauda*.

Scientific nomenclature in this paper corresponds to that used by Davis and Miller (1960) for Mimidae, Bond (1956) for the West Indies, Eisenmann (1955) for Central America, and Meyer de Schauensee (1966) for birds restricted to South America.

The Environment

Dominica lies at 15° N Lat. in the Lesser Antillean chain between Guadaloupe and Martinique. It is a mountainous island of about 300 square miles, extensively covered by forest and plantations that receive moderate to very heavy monthly rainfall. The highest peaks of the central mountains are Morne Diablotin (4,700 feet) and Morne Trois Pitons (4,600 feet), both of which have low, tangled forest on their upper slopes. Only on the west coast, the leeward side, is there a marked seasonality of the vegetation in the form of a thorny forest that loses its leaves during the period January-May.

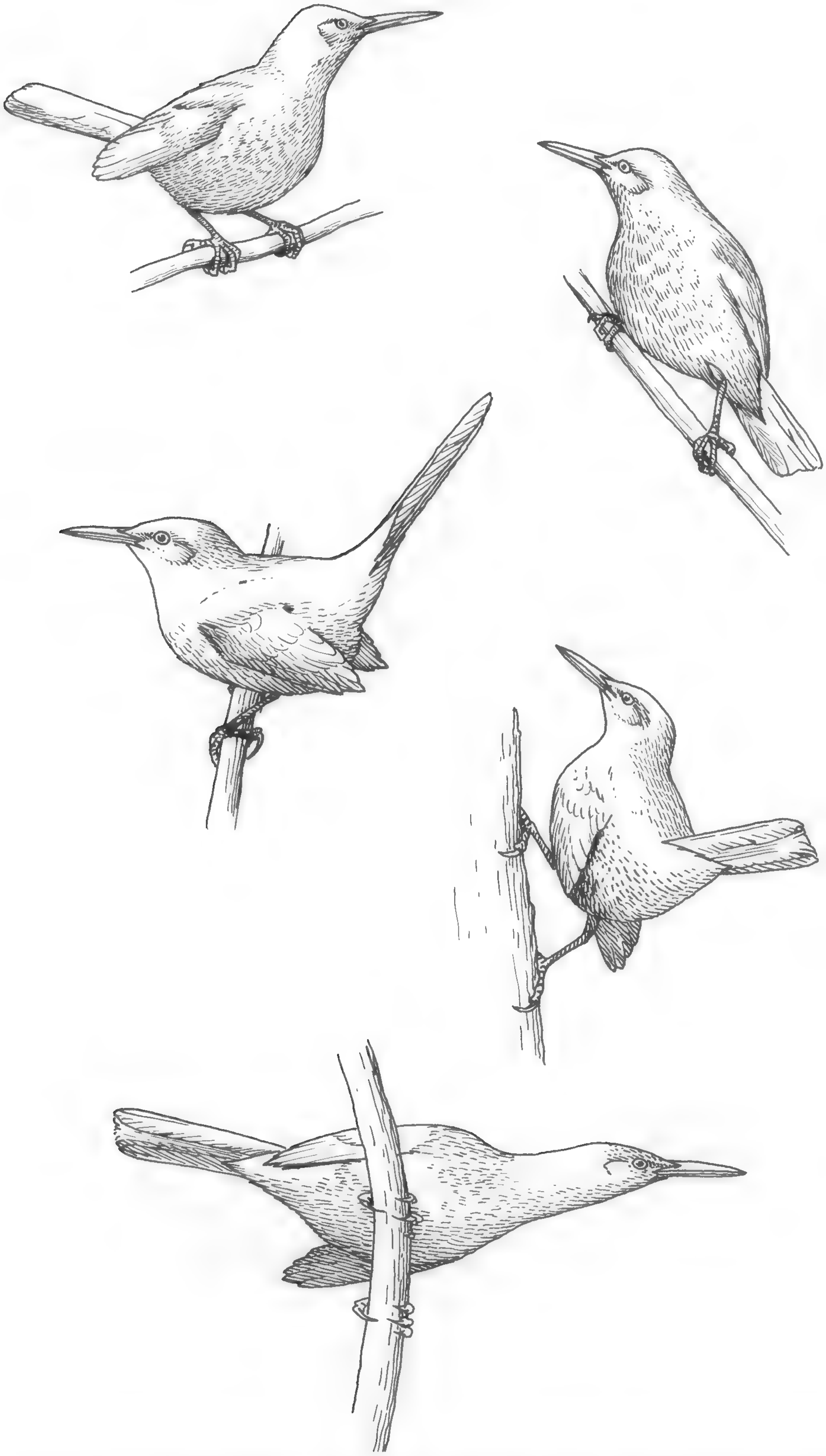

Figure 1. Attitudes of the Trembler, drawn by William C. Dilger from field sketches by the author. The Trembler, a member of the family Mimidae which also includes the Catbird, mockingbirds, and thrashers, is native to Dominica and other islands of the Lesser Antilles where it is most common in tropical or subtropical broad-leaved evergreen forests. The Trembler's curious name describes a distinctive habit—that of quivering or trembling its wings.

Most of the coastal portions of the island, the valleys of larger rivers, and much of the more level ground inland are under cultivation in coconut, bananas, citrus, cacao, or coffee, and even some of the wet, precipitous slopes have been planted in bananas. Nevertheless, in 1964 and 1968, because of the mountainous nature of the island and the lack of roads to the interior, there were still extensive tracts of relatively undisturbed timber.

Hodge (1954) described the natural vegetation of Dominica in terms of four climatic climax formations and their subdivisions: the *dry evergreen formation* consisting of littoral woodland along the windward coast; the *seasonal formations* of low elevations including a deciduous woodland of dry scrub and secondary forests of evergreen and deciduous species; the *evergreen rain-forest formation* of the interior including optimal rain forest and montane rain forest; and the *montane formation* of higher elevations—chiefly above 3,000 feet—comprised of montane thicket and elfin woodland. Transitional zones occur between the rain-forest formation and the seasonal and montane formations.

The Trembler is most abundant in the rain-forest formation. It also occurs commonly in secondary forests and less commonly in the montane formation, but I did not find it in the dry scrub woodlands during the leafless season or in the narrow band of littoral woodland of the windward coast. Plantations, especially those of citrus and cacao, also serve as foraging grounds for the Trembler. Such plantations on Dominica are small in acreage and are usually bordered by forest on ridges or along rivers. Observations on the Trembler in plantations did not help me to understand its structural adaptations because these are closely tied to its foraging behavior in the rain forest.

Rain-forest Formation

On Dominica the rain forest reaches greatest height and complexity in those portions dominated by the bois gommier, *Dacryodes excelsa,* and two species of chataignier, *Sloanea* (Figure 2). These and other trees form a forest canopy about 125 feet in height. The gommier has a straight unbuttressed trunk of about 80 feet which gives way to large spreading branches supporting its crown. The two species of chataignier are similar to gommier in general form but differ by having heavily buttressed trunks. These and almost all other trees of the rain forest have unridged bark with a slightly roughened surface. The bark of the gommier may peel off in large irregular plates, giving the trunk a somewhat mottled appearance. On the bark of certain trees anywhere in the rain forest, mosses and lichens form an encrusting mat, but bryophytes are most luxuriant on the trunk and branches in montane rain forest where the trees are smaller. In optimal rain forests, mosses are relatively inconspicuous and the main branches of larger trees are completely clothed with bromeliads, aroids, ferns, orchids, and vines. Epiphytic *Clusia* trees growing on the upper branches of large forest trees send down cable-like roots—as many as fifty from a single *Clusia*—that hang independently or sometimes run along the trunk of the host tree (Figure 3). Epiphytes, other than *Clusia,* on the dominant trees of the rain forest are found in greatest abundance on the major branches supporting the crown, in reduced abundance on higher branches and on the trunk, and sparingly in the twig and leaf zone of the crown and on the hanging roots of *Clusia.* Sub-dominant trees that help to fill in the canopy just below the crowns of the dominants have a structure similar to that of dominants. Smaller trees bear leafy branches along most of the trunk and support many epiphytes—especially bromeliads

Figure 2. Optimal rain forest where the Trembler is abundant on Dominica. On the extreme left is the trunk of a gommier tree (*Dacryodes excelsa*). Its unridged bark has a slightly roughened surface and may peel off in large irregular plates. The gommier has a straight trunk that may extend 80 feet to a crown of large spreading branches where Tremblers forage for insects and other animal life in the epiphytes.

and aroids—on their trunks from near ground level to the upper branches (Figure 4). Within optimal rain forest the bromeliads and other epiphytes are thus most concentrated in the branches of the canopy high in the dominant trees, and they occur in varying abundance from the crown to ground level on smaller trees.

Each of the bromeliads and basket-like aroids forms a trap for rain water and falling leaves. The latter decay so that the spaces between the upper green leaves become occupied with humus, usually covered by a mat of more recently fallen leaves. A mass of dead brown leaves hangs down like thatch from the base of the bromeliad, and the aroids have in addition a tangled mass of roots and humus at their base.

The largest gommier and chataignier trees are generally 40 to 100 or more feet apart with many smaller trees interspersed: these smaller species or smaller individuals of the canopy species form a more or less continuous leafy zone between the shrub layer and the canopy. A well-defined shrub layer about six feet high and a scattering of lower herbaceous plants are characteristic of optimal rain forest. The forest floor is covered with matted and usually soggy brown leaves of forest trees, prominent among which are the large, leathery, oval leaves of *Clusia* (Figure 5).

Progress through the forest is usually not difficult because the shrub layer is not dense and there are relatively few vines and other plants at ground level. The canopy is usually open enough to allow a thin patchwork of sunlight to reach the forest floor. Wherever a large tree has fallen or where a steep south-facing slope permits more sunlight to penetrate, a tangle of vegetation occurs, and successional tree species, especially members of the Melastomaceae, predominate. Dead trees, whether standing or fallen, rot rapidly and it is rare to find a dead tree with firm wood.

Figure 3. Another view of optimal rain forest and foraging area of the Trembler. The cable-like roots of a *Clusia* curtain the trunk of a dominant tree, a *Dacryodes,* in the background. The epiphytic *Clusia* grows in the upper branches of large trees, and its roots, sometimes as many as fifty from one plant, may eventually strangle the host tree.

Fruits and flowers of rain forest trees are abundant in the sunlit canopy; much less numerous are fruits of the epiphytes, smaller trees, and the shrub layer. There are numerous fruiting trees in the forest during the months January through April; I do not know whether or not this is true throughout the year. Almost all of the fruit-eating birds take the fruits of the melastomaceous trees which occur in abundance in clearings and openings in the forest.

On the forest floor, tree frogs (*Eleutherodactylus*) occurred in abundance, lizards (*Anolis*) occurred less commonly, and cockroaches, other orthopterans of various sizes, spiders, and snails hid under leaves. In bromeliads and other epiphytes I found arthropods and spiders; under loose bark and in crevices between roots and vines adhering to tree trunks were snails, centipedes, katydids, and cockroaches; in and on rotting logs were termites, ants, and beetles.

Figure 4. The understory of an optimal rain forest. The smaller trees of the rain forest often bear leafy branches along their trunks and support large epiphytes—among them bromeliads and aroids. These trees fill spaces between the columnar trunks of dominant trees such as the buttressed chataignier (*Sloanea*) shown here behind its veil of *Clusia* roots.

Figure 5. The floor of the rain forest, another foraging area of the Trembler. Walking through this rain forest is not difficult. The shrub layer, about six feet high, is not dense, and the discarded leaves of the forest trees, particularly the large oval leathery leaves of *Clusia* form a soggy brown mat on the forest floor.

Montane Formations and Secondary Forests

Montane forests, frequented by Tremblers, differed from the rain-forest formation by their species composition—for example, gommier and chataignier were absent; by their lesser stature, reduced to about 10 feet on windswept mountain ridges; by increased light penetration; and by more lush ground vegetation and the predominance of mosses among epiphytes in cloud-drenched regions. In the moss-covered elfin forest of mountain ridges and peaks I found only the occasional Trembler, but the bird was common to abundant in somewhat taller stands that merged with montane rain forest at lower elevations. These trees were enshrouded with bromeliads and other epiphytes (Figures 6 and 7).

The secondary forest of the windward coast was poor in epiphytes. It had a leaf cover on the ground, a shrub layer, and trees of varying size below the canopy. There were relatively few vines and hanging roots, and the structure of the forest was much simpler than that of rain forests.

Food and Foraging

Food

The stomachs of twenty Tremblers collected in 1964 contained the seeds, capsules, and pulp of various fruits; the remains of large insects, spiders, scorpions, and snails; and the bones of small frogs and lizards. All stomachs contained food. Thirteen contained both animal and plant food, five only animal food, and two only plant food. Eight stomachs held vertebrate remains consisting of tree frogs (*Eleutherodactylus*) and lizards (*Anolis*). Among the insects eaten by Tremblers, beetles and orthopterans, including cockroaches, were prominent. Two birds had eaten scorpions and one, snails. At least 10 different kinds of plant fruits had been taken, the largest intact specimen being a leathery capsule 17 millimeters long.

Figure 6. Montane rain forest. Mosses compete with other epiphytes for a place on the trunks and branches of trees at 2,500 feet elevation. Here the Trembler was common to abundant, but I seldom saw it in scrubby elfin woodland of the higher wind-swept mountain slopes.

Foraging

During the period January-April, the Trembler fed on fruits in the crowns of trees and in the shrub layer, and on animal life in the bromeliads and other epiphytes of the upper limbs and trunks, along trunks in crevices behind bark or vines, and on the ground. Its foraging methods might best be conveyed through extracts from my field notes.

Fruit-eating.—Montane rain forest, 15 March 1968: I saw a Trembler hopping from branch to branch in a tree bearing fruits about 0.5 inch long. The bird suddenly reached forward, plucked, and swallowed a fruit. Later it hopped among bare branches, trembling very conspicuously. The bird stopped on each perch long enough to look intently up and around, seemingly at the mossy branches or at the fruits. It plucked another fruit which was held in the bill briefly and then dropped.

In a melastomaceous tree I saw a different bird trembling; it hopped from branch to branch, eventually reaching out several times to pick berries.

Melastomaceous trees along road through optimal rain forest, 1 April 1968: One bird trembled as it perched or hopped through bare branches just below the leafy crown. It fluttered up to take one of the purple fruits, returning directly to a bare twig. Also feeding in the same trees in a similar manner (but without trembling) were a Scaly-breasted Thrasher (*Allenia fusca*) and a Pearly-eyed Thrasher (*Margarops fuscatus*). The Scaly-breasted Thrasher chased the Trembler once, and the Trembler later chased the Pearly-eyed Thrasher, but all three birds remained within the small group of trees where they were feeding.

Secondary forest, 17 Feburary 1964: I saw two Tremblers fly to the fruit-laden crown of a tree where they fed, swallowing the fruits whole, in company with Scaly-breasted Thrashers. In montane rain forest I subsequently observed similar feeding behavior in association with the Forest Thrush (*Cichlherminia lherminieri*).

When foraging for tree fruits, the Trembler and both thrashers spent much of their time hopping from one branch to another and peering about, despite an abundance of fruit in the tree. They were usually unable to perch on the fine twigs supporting the fruits, and their hopping about was probably in search for suitably ripe fruits and for a perch from which to reach the fruit. Lacking a perch they plucked fruits while fluttering upward.

On at least five occasions I saw Tremblers regurgitate what appeared to be undigested remains of fruit. They would open the bill widely, shake the head, and sometimes point it downward. Twice the birds interrupted their singing to regurgitate and once the bird swallowed the material instead of dropping it.

Ground-foraging.—Ground foraging of the Trembler is well exemplified by observations made in optimal rain forest on 14 March: A Trembler landed on a fallen log, hopped along it, trembling with the tail cocked, and then moved to the ground where it hopped in leisurely fashion from root to root or on the leaf litter (Figure 5). It stopped to pick up leaves with the bill and flick them to either side, often for a distance of two or three feet. The bird stayed in one spot until most or all leaves were removed and then peered at the exposed ground and at the surrounding leaves. Sometimes it tugged backward on very large leaves or pieces of fallen bark. From one spot the bird hopped only a short distance before it began tossing leaves again. Once, after 20 minutes of foraging in the litter it jabbed repeatedly downward, during which the bill became muddy and the throat feathers wet; then it grasped something (frog?) and flew off. The bird exhibited no trembling

Figure 7. Bromeliads on the small trees of a mountain forest. Tremblers poked between the green leaves and tore apart the hanging dead leaves of such epiphytes in their search for food.

while flicking leaves and none, or only a slight amount, while hopping on the ground. It used the bill as a forceps—never as a broom or hoe—in removing leaves. In color the Trembler was almost a perfect match for the brown fallen leaves.

Other instances of ground feeding also included the tossing of leaves. One bird ran its bill along the crevice of a long rolled leaf—a common motion in arboreal foraging as well—and another pecked repeatedly at a large leaf on the ground for about 90 seconds, hopped off with the leaf, resumed pecking, and finally secured a rounded, crab-like invertebrate. Another bird hopped along a trail where it picked up and swallowed a large insect.

Epiphytes.—Most of the Trembler's foraging consisted of a search for animal food among the epiphytes on forest trees. Optimal rain forest, 17 March 1968, 9:55 AM: Two Tremblers foraged in abundant epiphytes on chataignier and gommier trees. One worked its way up vines, perching crossways. It poked into spaces between vines and the trunk and swallowed a large katydid (?). The bird trembled as it hopped or flew upward along the trunk. It went onto a large bromeliad and threw out leaves for more than a minute. Then it flew to a gommier, perched crossways on the trunk, and poked into a mass of dead leaves in the main crotch of the tree about 50 to 60 feet up, again throwing out leaves. The bird did not tremble while on bromeliads or in the crotch of the tree. Perching crossways on the vertical trunk it poked into ferns matting the trunk. Then it flew back to the chataignier onto a bromeliad where it perched on a leaf or straddled two leaves and reached down between the bases of the green leaves of the plant, from which it tossed out dead, fallen leaves. Periodically, about six times, it flew or hopped onto a nearby twig where it sat trembling only to return each time to the bromeliad. The two birds foraged about 20 feet apart in the same tree.

Between 12:00 and 12:30 PM a group of six, possibly more, Tremblers fed in an area of forest about 300 feet in diameter. The birds were not vocal but their activities produced considerable noise in the forest—especially when dried leaves were pulled, when falling objects struck other leaves such as those of large aroids or *Heliconia,* and when birds flew short distances with a whir of wings. They foraged from the ground to the canopy in a fine stand of forest dominated by gommier and chataignier. One bird, on tangled aerial roots near the base of a large chataignier, poked among the roots and a moment later flew off with a frog (?) in its bill. Another was clinging back-down on the underside of a limb, pounding several times at the limb, and pulling off a large loose piece of bark with its bill. With the bill parallel and close to the limb it peered under other loose plates of bark. Another bird hopped on the ground, throwing leaves to either side. Nearby a bird was hopping or flying from one limb to another in the shrub layer, trembling, cocking the head, and peering about. Sometimes it sat quietly, and once it reached down to pluck and swallow a fruit from the shrub. Most birds foraged from 80 to 100 feet above ground in crowded epiphytes below the canopy and on vertical trunks where they perched on bromeliads, threw out the accumulated contents, and peered and poked into matted epiphytic tangles. One perched on a horizontal vine near a bromeliad on an understory tree and tugged backward on a dead lower leaf, finally breaking it off. It also threw out debris from between leaves. In general, the birds were leisurely about foraging, staying at one bromeliad or at one place on the ground for a minute or more. Trembling occurred most often when birds were hopping from branch to branch or perching in the open; it rarely accompanied the activity of uncovering prey on the ground, from the bark, or in an epiphyte.

Optimal rain forest, 22 March, 3:30-4:30 PM: A flock of six or more Tremblers fed, sometimes two in a tree (usually 20-30 feet apart), or singly in trees within an area about 200 feet in diameter. Feeding activity occurred primarily about 40 to 60 feet above ground in large chataignier trees on a gentle slope. The birds spent most of the time examining epiphytes, but they also investigated loose bark and rotten limbs. They often flew or hopped from an awkward perch on an epiphyte or vertical vine to a nearby branch where trembling was sometimes marked or intermittent. One bird perched on a leaning trunk and picked repeatedly at something resembling a frog. It took off little pieces, eventually swallowing the prey. At that moment another bird landed, abruptly displacing the first bird. I saw other birds tug at dead lower leaves of bromeliads, poke into dead curled leaves, perch on vertical vines and investigate crevices or scale off loose bark, lean far forward from their perches or hang straight down to reach an epiphyte, perch vertically and peck with the opened bill at a dead stub, and poke the bill into holes of stubs. One Trembler landed in a small epiphyte and fell through, fluttering downward about 15 feet before flying back up to a more secure perch.

On another occasion in rain forest, I watched a Trembler fly to a vertical vine where it perched four feet up and pecked down into the top of a large dead folded leaf. Then it reached in the opposite direction between a vine and small trunk, grasped a large katydid (?) in its bill, and immediately flew off with it. Another bird clinging to a vertical mossy trunk picked off and flung away pieces of moss, peering at the uncovered spot. Perching on a fallen rotten trunk about 2.5 inches in diameter and a foot or more from the ground, a Trembler pecked downward powerfully at the wood and with twists of the head shredded and tore off pieces of the spongy wood. It then poked its bill into tunnels that it had opened in this manner. Another bird perched on a vine along a trunk and pushed with its bill and forehead against a large loose piece of bark without succeeding in dislodging it. A bird feeding in a bromeliad fluttered downward, caught a large insect on the wing, landed on the vertical trunk to swallow the insect, and flew up to resume foraging in the same bromeliad.

In secondary forest, poor in epiphytes, a trembling bird hopped from branch to branch, stopping to peck and pull at some large, fallen, curled leaves caught in branches. It then flew toward a tree and obtained a small greenish object while seeming to bounce with its feet off the smooth trunk. Again the bird hopped or flew from branch to branch, usually trembling, yet sometimes sitting quietly. It perched and ripped at a decaying stub for about a minute before flying off.

Plantations.—Not infrequently I encountered single birds in grapefruit or cacao plantations. These birds hopped or flew from perch to perch, reaching under leaves or pecking at twigs and bark to obtain food. One bird poked into a small, vertical rotten stub, extracted and swallowed a medium-sized insect, wiped its bill several times on a branch, and flew to the outer branches of the tree. Only once did I see a Trembler in a banana plantation. That bird foraged on plants from which many dead leaves hung down, peering at the curled tips of such leaves and into crevices of the flaking banana stem, or perching on the stalks of green leaves and tossing out detritus lodged among their bases. I saw no Tremblers in coconut groves, but they often sang from royal palms planted about houses and gardens. On several occasions I saw a Trembler fly into an open banana shed and investigate the under surface of the thatched roof.

Other Behavior

Locomotion

The Trembler characteristically moves on the ground by hopping, and through trees and shrubs by hopping or by short flights. The wings may not be opened when the bird hops distances of a foot or more from one perch to another. Flight is usually direct with a steady rapid whirring of the wings. I rarely saw a bird that appeared to be flying any great distance through the forest—rather they usually flew to nearby trees. Only once did I see a bird pursue a flying insect on the wing. On the grounds of a plantation, Tremblers occasionally flew from a mango tree to the top of a taller royal palm some 150 feet away in a slow, labored, and direct fashion. By contrast Scaly-breasted Thrashers made this upward flight gracefully, rapidly, and with apparent ease.

Tremblers often perched crosswise on vertical roots or vines, or on the sides of large tree trunks. When perched crosswise the body was not adjusted to a horizontal position but remained tilted with one side toward the ground (Figure 1). Birds often hitched and hopped up vines or trunks, sometimes aided by flight. Once I saw a bird half flying and half hopping up the nearly vertical trunk of a slender coconut palm. Tremblers occasionally clung back-down on the underside of a limb or clung vertically like a woodpecker, and one bird hung straight down from its perch on a twig to reach toward an epiphyte. In large bromeliads the birds perched on a single leaf or placed the spread legs on adjacent leaves while reaching down into the recesses of the plant. Despite acrobatic foraging stances and locomotion the Trembler gave no impression of agility but, instead, seemed rather clumsy and leisurely in its motions.

Vocalizations

I heard the Trembler utter three different forms of song and two kinds of calls during the period January through April. Of the songs I regard one as full song, another as subsong, and the third as "excitement" song. The full song consisted of loud phrases uttered at approximately two-second intervals. Some of the phrases were rather harsh, others rich and warbled, still others high and squeaky. I represented phrases of the full song of three birds in Figure 8.

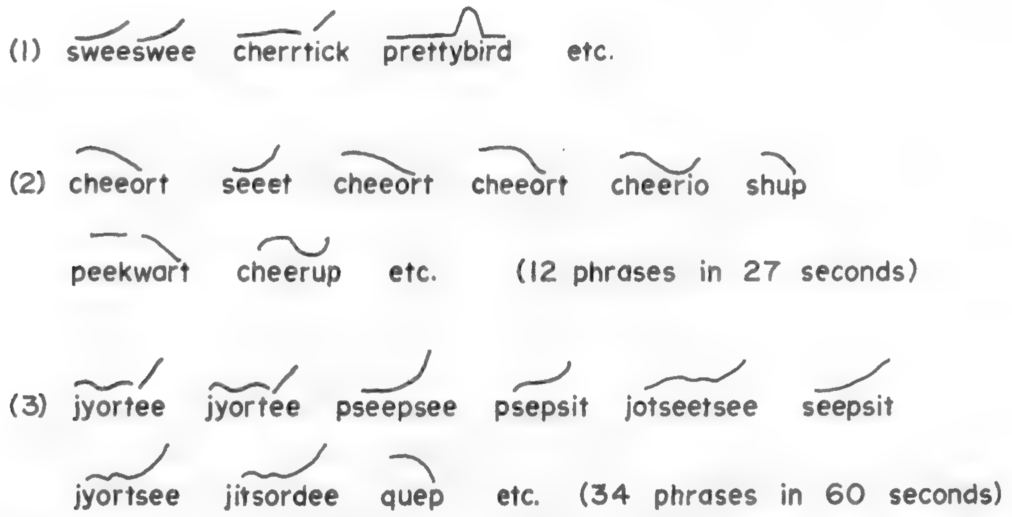

Figure 8. Verbal representation of portions of the songs of three Tremblers. Marks above the words suggest the change of pitch within each phrase, but not between phrases. Some phrases were high and squeaky, others relatively low in pitch.

One bird sang almost continuously for 20 minutes. I heard the full song delivered by lone birds from the tops of tall royal palms in the gardens of plantation houses, from a 40-foot perch in woods on a steep valley slope bordering a citrus plantation, and from the top of a tall native palm in rain forest. In March, this song was delivered at various times of the day from 6:00 AM to 5:40 PM.

I first heard the full song on 12 March 1968, the day after I arrived on the island, and I believe that this form of singing begins early in March, concurrent with the enlargement of the gonads. Because the full song coincided with the beginning of the breeding season, was loud and proclamatory in nature, and was repeatedly delivered from the same prominent perches and from palms, in which the birds nest but do not forage, I judged it to be, at least in part, territorial in function.

The subsong consisted of a quiet series of complicated phrases containing both squeaky and musical notes, each song lasting about five seconds. It reminded me of the song of the Catbird (*Dumetella carolinensis*). I first heard the subsong on 26 January 1964, well before the beginning of the nesting season. During March and early April in 1968, I heard it concurrent with the period of territorial singing. On five occasions the singer appeared to be alone, but on two occasions it was within a few feet of another bird. Unlike full song the subsong was quiet and delivered within the forest from relatively low perches and in the normal foraging habitat. In one instance, one of two birds that were foraging together gave it.

I heard the "excitement" song three times in late March and early April, each time from one or more of three birds engaged in a chase through the forest. It consisted of a loud jumble of notes, not unlike an accelerated, intensified subsong.

A common call note was a nasal, rasping *yeeeah,* often repeated many times. It preceded a subsong on one occasion and interrupted full song once. One bird in a foraging flock gave this call when another landed in the same tree, 10 feet away; on other occasions, it accompanied skirmishes or confrontations. Another call was a sharp *cht* or *chip* that sometimes preceded or followed hostile encounters in which the bird uttered the nasal call.

Social Interactions

Aggressive Situations.—I present the following observations chiefly for their value in the interpretation of trembling. Montane forest, 24 March: A bird (A) hopped and flew from branch to branch, usually trembling most actively just after landing. Across a broad trail three birds appeared and sat within six to eight feet of each other. One trembled and hopped about while the others remained still. Then another trembled and approached the other active bird, which flew off. Bird A flew across the trail, trembling violently as it approached the others, and a wild chase of the three birds ensued.

Rain forest, 27 March: A bird (A) flew, uttering the "chip" call, to feed among epiphytes about 40 feet above the ground. It flew to another tree where it had a skirmish with bird B, accompanied by nasal calls. Bird A then flew to a nearby perch where it trembled violently. Bird C flew directly at A which departed calling "chip" several times. Birds B and C then perched on branches of the same tree, trembling strongly before flying to epiphytes of the trunk where they fed within three or four feet of each other without trembling. After several minutes B flew off.

Rain forest, 28 March: Two Tremblers perched in the crown of a tall tree, trembling, with their bills pointed upward. One hopped toward the other, displacing it. Both then flew to a denser crown from which I heard several nasal calls. Several times I saw foraging birds abruptly displaced by another bird that landed nearby.

Non-aggressive Situations.—On five days in March I saw two birds foraging within a few feet of each other among epiphytes, and once I saw two foraging on the ground. Sometimes the two were alone, sometimes associated with a loose group of individuals each foraging in its own tree. Trembling rarely occurred in members of such pairs even when one flew from a bromeliad to a nearby perch. On 27 March at 5:20 PM, I heard a full song delivered in the soft tones of a subsong and found a male (?, short-billed) singing in a bush, accompanied by a female (?, long-billed). The male repeatedly flew or hopped closer to the female that remained perched or hopped away. Once both birds trembled strongly, but usually I saw no trembling. Both flew halfway up a tall tree and perched on a branch about three feet apart. The female then became aggressive, hopping at the male and causing him to fly, but he persisted in his approach to the female as both moved higher and were lost from view in the crown.

Trembling

Noble (1916:392-393) remarked of the Trembler on Guadeloupe: "When flushed from the ground where it is habitually to be found, it flits up to a low branch and begins to shake as if in the grasp of a tropical fever. At the same time it jerks the tail nervously up and down just as a Spotted Sandpiper does, accompanying these movements by a bobbing of its head in every direction."

My impression of the bird's peculiar habit was one of quivering or trembling of the wings that at high intensity caused a secondary quivering of the tail as well. I did not see tail-jerking and head-bobbing. Trembling usually occurred with the tail cocked, the wings drooping and angled away from the body, and the primaries slightly spread (Figure 1, top). The wings made rapid vertical and lateral motions.

Trembling was not associated with singing or with the activity of uncovering, dislodging, or eating animal or plant food. Birds whose attention was directed to me did not tremble. Trembling was probably not an intention movement for flight because birds often took flight without prior trembling. Similarly, as trembling was often absent during vertical clambering or moving on precarious perches, it did not appear to be an aid to locomotion. Although trembling was associated with movement to a new foraging site, it stopped when a bird actively foraged with its bill and I never saw trembling lead to the capture of prey. The quivering wings rendered the birds relatively conspicuous to me when they perched on bare branches beneath the leafy canopy or on trunks and vines. Noble (1916) remarked that "the peculiar trembling habit is probably some sort of a warning motion" and then added that a trembling bird resembles a bunch of dried leaves shaking in the wind. On the other hand, Bond (1928:536) felt that trembling made the bird more conspicuous and disagreed with the idea of a protective function through resemblance to rustling leaves.

Although trembling occurred commonly in members of loose foraging bands and in lone individuals, it was also associated with encounters among birds that were not foraging, as already described. During social encounters trembling appeared to be a signal with some aggressive content. It might have a similar meaning in foraging groups where the sight of a trembling bird could deter another from foraging in the same tree, or in the immediate vicinity.

Breeding and Molt

Of 20 specimens taken by me in January and February 1964 only three were females and all had small gonads. Males taken on 1 and 16 March showed some enlargement of the gonads; another on 16 March had large testes, as did birds taken on 25 March and 16 April. Two males from 26 and 30 March had medium-sized gonads and a female from 31 March had an ovary measuring 10 by 7 mm with follicles up to 1.5 mm. Birds taken by Albert Schwartz on St. Lucia in 1963 had "testes enlarged" on 3, 5, 10, 16, and 17 April. Bond (1941:372) records a nest and three eggs on 16 May 1936. A resident of Dominica, familiar with the native birds, told me that a pair of Tremblers fledged three young from a nestbox on the second floor porch of a wooded estate, south of Roseau, in August 1963. The Trembler thus appears to have a roughly synchronous annual breeding cycle, producing eggs in May, June, and July.

The nest, according to Bond (1941), is a cup of rootlets, lined with finer rootlets and dead leaves and placed at the base of a palm frond, in the cavity of a tree, or in the hollow stump of a tree fern. The greenish blue unspotted eggs are laid in clutches of two or three.

In 28 specimens collected from January to mid-April there was essentially no feather replacement, with the following exceptions: male, 25 January, three growing feathers on upper spinal tract; male, 8 February, molt on rump and lower back; male, 12 February, small patch of pin feathers on crown; male, 23 February, secondaries three, five, six of left wing; female, 29 February, one rectrix; male, 16 March, several feathers on upper neck; male, 16 March, two upper wing coverts, one scapular; male, 16 April, one outer tail feather.

From the irregular and restricted nature of the feather replacement and the fact that only eight of 28 specimens had growing feathers, I judge that the exceptions represent accidental loss of feathers, or, in the case of the January and early February birds, possibly the last vestiges of a post-breeding molt. The Trembler apparently has a single annual molt that follows breeding.

Ecology

Of particular importance in defining the feeding niche of a species are the kinds, quantities, and sizes of the foods taken, and the portion of the habitat from which it obtains food. Selection forces act when niches overlap and when the common food resource is in such short supply, relative to the number of individuals present, that competition results ultimately in reduced reproduction. Competition between members of a species is sometimes great because their individual niches overlap broadly or completely; between species, competition may also be great for any portion of overlapping niches. Within a species, the development of sexual dimorphism in the feeding mechanism or in body size, resulting in the taking of different foods or similar foods in different places, may reduce competition. Female Tremblers have longer bills than males on Dominica and on some other islands (Ridgway, 1907), but I gained no information in my study that would help to explain this difference in bills.

Competition between species is difficult to measure, and I have no direct evidence that competition for food caused selection forces to operate on the species under discussion. I use "competition" here to mean "potential competition."

For Dominica, I can only indicate those species that took roughly the same kinds of food in the same portion of the habitat, and support my observations with a few samples from stomach contents. Species that ate the fruits of trees in company with Tremblers, or in the same portions of the habitat, were the Scaly-breasted Thrasher, Pearly-eyed Thrasher, Forest Thrush, Red-necked Pigeon (*Columba squamosa*), Black-whiskered Vireo (*Vireo altiloquus*), and Bananaquit (*Coereba flaveola*), all in crowns of tall or understory trees; and Caribbean Elaenia (*Elaenia martinica*) and Rufous-throated Solitaire (*Myadestes genibarbis*) in understory trees and shrubs. Of these I would judge the first three to be the most important competitors. Unfortunately, stomach contents were available primarily from birds collected in or near plantations, and, in only a few cases, could I determine from what part of the habitat the fruits came. Each of seven types of fruit listed below was found in one stomach of a Trembler and also in one stomach of the following species: Fruit A, Scaly-breasted Thrasher; Fruit B, Pearly-eyed Thrasher; Fruit C, Pearly-eyed Thrasher, Black-whiskered Vireo, Caribbean Elaenia; Fruit D, Caribbean Elaenia; Fruit E, Scaly-breasted and Pearly-eyed Thrashers; Fruit F, Scaly-breasted Thrasher, Forest Thrush. Specimens containing Fruit C were taken from one locality within a three-day period; Fruit E represents the berries of melastomaceous trees in a roadside clearing in rain forest; Fruit F was taken from a single forest tree on 23 March and again on 14 April.

For arboreal invertebrates, excluding those in epiphytes, the Trembler probably competes to some degree with Scaly-breasted and Pearly-eyed Thrashers, with the Mangrove Cuckoo (*Coccyzus minor*)—rare in tall rain forest, and possibly with the Caribbean Elaenia and the Black-whiskered Vireo—taking mostly smaller prey. Invertebrates and small vertebrates on and under ground cover are taken also by the Pearly-eyed Thrasher, the Red-legged Thrush (*Mimocichla plumbea*)—not common in rain forest, the Forest Thrush, and the Broad-winged Hawk (*Buteo platypterus*). The chief competitors with the Trembler for animal food are probably the Pearly-eyed Thrasher and the Forest Thrush—both common in rain forest.

Other Islands.—The White-breasted Thrasher (*Ramphocinclus brachyurus*) occurs with the Trembler on Martinique and St. Lucia. Semper (1872) remarked of this thrasher on St. Lucia that it seemed to be strictly insectivorous and that it could be met with in pairs or in groups of four or five pairs searching among bushes near ground and in low trees. It was not seen at any great height nor did it seem to indulge in long flights. Bond (1957) considered the species to be largely terrestrial and found it only in semi-arid woodland on Martinique and St. Lucia, whereas Frederick Ober *in* Lawrence, 1879:352) claimed that it "loves deep woods and the borders of streams."

That the well-marked race of the Trembler on St. Lucia behaves like its counterpart on Dominica is suggested by Semper's description (1872) of it "constantly at work creeping about the trunks and larger limbs of trees searching for its food." Competition between the two species is probably slight because of differences in habitat and the apparent absence of foraging in epiphytes on the part of the thrasher.

TABLE 1

Distribution of Potential Competitors throughout the Range of the Trembler (*Cinclocerthia ruficauda*)

Cinclocerthia ruficauda		Bananaquit	Black-whiskered Vireo	Bare-eyed Thrush (*Turdus nudigenis*)	Cocoa Thrush (*Turdus fumigatus*)	Red-legged Thrush	Forest Thrush	Rufous-throated Solitaire	Pearly-eyed Thrasher	Scaly-breasted Thrasher	White-breasted Thrasher	Yellow-bellied Elaenia (*Elaenia flavigaster*)	Caribbean Elaenia	Mangrove Cuckoo	Red-necked Pigeon	Broad-winged Hawk
Subspecies	*Island*															
pavida	St. Eustatius	X	X						X	X			X		X	
pavida	Saba	X	X						X	X			X		X	
pavida	St. Bartholomew	X	X						X	X			X		X	
pavida	St. Christopher	X	X						X	X			X		X	
pavida	Nevis	X	X						X	X			X		X	
pavida	Montserrat	X	X				X		X	X			X	X	X	
tremula	Guadeloupe	X	X				X		X	X			X	X	X	
ruficauda	Dominica	X	X			X	X	X	X	X			X	X	X	X
gutturalis	Martinique	X	X					X	X	X	X		X	X	X	X
macrorhyncha	St. Lucia	X	X	X			X	X	X	X	X		X	X	X	X
tenebrosa	St. Vincent	X	X	X	X			X		X		X	X	X	X	X

To judge from the analyses of stomach contents of the Trembler and its competitors from various islands, made by Danforth (1926, 1937, 1938a, 1938b, 1939), Voous (1955), and myself, the Trembler, Pearly-eyed and Scaly-breasted Thrashers, and the Forest Thrush all feed on fruits of forest trees, on large invertebrates, and on small vertebrates (except the Scaly-breasted Thrasher). Of these, the Trembler takes the largest proportion of animal food and the Scaly-breasted Thrasher the smallest, with Pearly-eyed Thrasher and Forest Thrush occupying similar and intermediate positions. All but the Trembler eat fruits predominantly, and, during my period of observations, perhaps half of the Trembler's food consisted of fruits of forest trees and shrubs. Nevertheless, the Trembler spends more than half of its time foraging for animal foods simply because they are harder to find than fruits. I make no attempt here to analyze the food in detail since adequate comparative samples, taken throughout the year from natural habitats, are not available.

The geographical distribution of potential competitors within the range of the Trembler is shown in Table 1 based on data from Bond (1956). With

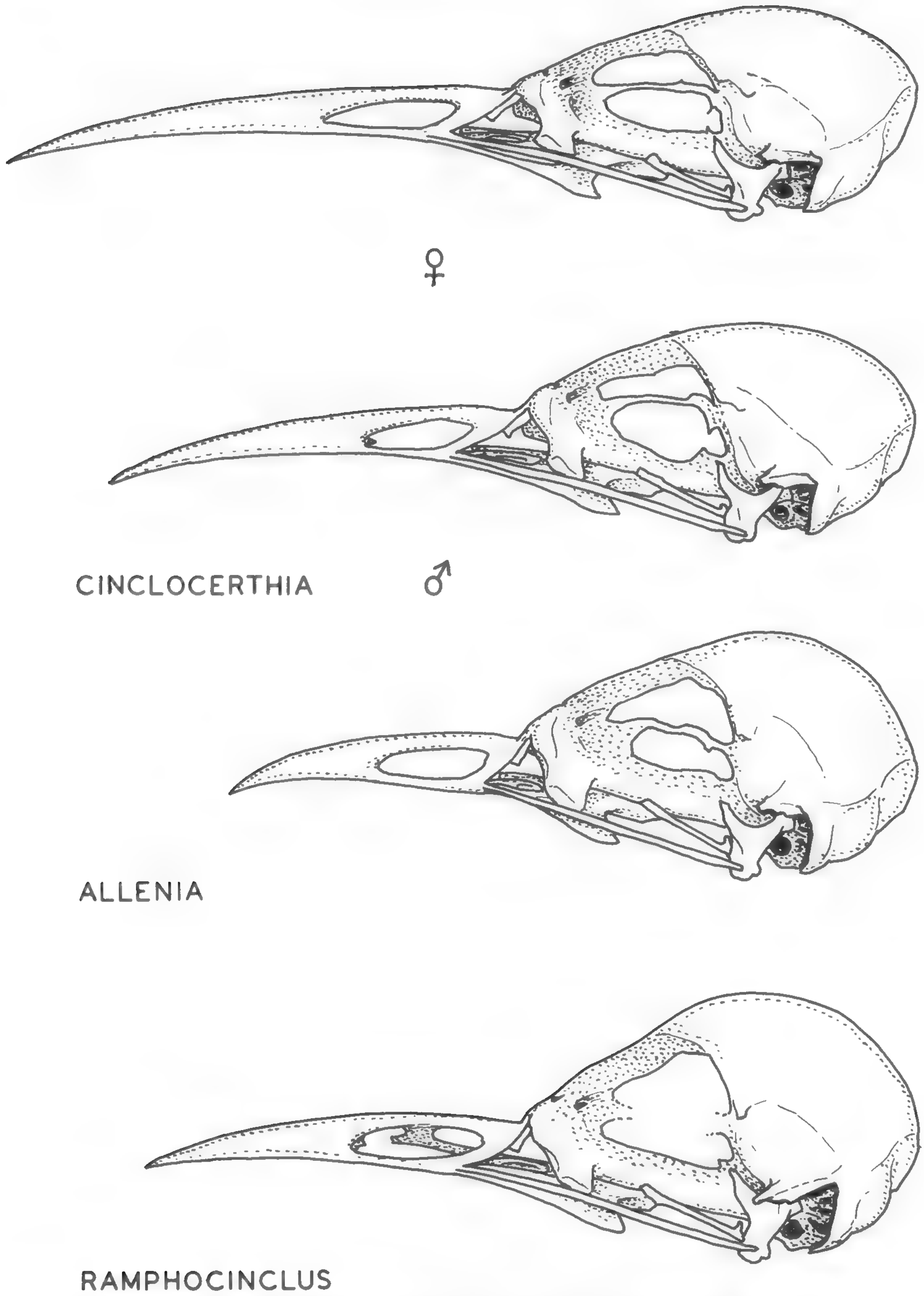

Figure 9. The skulls of *Cinclocerthia r. ruficauda* (female and male), *Allenia fusca,* and *Ramphocinclus brachyurus* drawn to the same cranial length. Note the flattened cranium of *Cinclocerthia* and the differences in the shape of the ear openings.

the exception of the Forest Thrush the fruit-eating competitors are quite evenly distributed throughout the Trembler's range. Except for Pearly-eyed and Scaly-breasted Thrashers, birds feeding on large invertebrates are generally lacking in the smaller northern islands. None of the species listed is known to feed in epiphytes.

Phylogenetic Relationships

The family Mimidae contains thirteen genera of which six are restricted to islands and seven are found primarily on the mainland. Breeding in the West Indies are *Mimus* and four endemic monotypic genera—*Margarops, Allenia, Cinclocerthia,* and *Ramphocinclus,* of which the last three are restricted to the Lesser Antilles.

The relationships of the genera of Mimidae have not been studied from the viewpoint of comprehensive comparative anatomy or bio-systematics and there has been no substantial basis for opinions on the relationships of *Cinclocerthia.* Bond (1963) regarded *Cinclocerthia* and *Ramphocinclus* as a group related to *Melanotis* (blue mockingbirds), and *Margarops* and *Allenia* as another group not closely related to any mainland genus. He pointed out that all four species of these monotypic genera have immaculate, greenish blue eggs, like those of *Melanotis, Melanoptila* (Black Catbird), and *Dumetella* but unlike those of any South American species of mimid.

Comparison of skeletons of all genera of Mimidae revealed several characters that belie a close relationship of *Cinclocerthia* and *Ramphocinclus* but suggest that, of the living mimids, *Cinclocerthia* is closest to *Margarops* and *Allenia. Ramphocinclus* is probably related to *Melanotis* but there is no compelling evidence to relate *Cinclocerthia, Margarops,* and *Allenia* to any other genus. In fact, *Cinclocerthia* is sufficiently different from *Margarops* and *Allenia* to imply that these genera were independently derived from two or three different, but related, ancestral forms.

Evidence for linking *Cinclocerthia, Margarops,* and *Allenia* comes from the morphology of the skull—in particular the ear opening and the maxillopalatines. All three species differ from other mimids in that the dorsal and posterior borders of the ear opening form a wider angle from lateral view (see Figure 9 and Table 2); in that the dorsal tympanic ridges in ventral view are roughly parallel or converge, rather than diverge, posteriorly; and in that the dorsal tympanic ridge lies medial to, and therefore independent from, the anterior edge of the tympanic cup (Figure 10). The maxillopalatine in these three genera is a slender open scoop, usually bearing a medially directed process near its posterior end. Maxillopalatines of other mimids assume various other forms. *Cinclocerthia, Margarops,* and *Allenia* also differ from other mimids in having relatively short, blunt, zygomatic processes. *Cinclocerthia* is unique in having a shallow articular portion of the lower jaw in which the ventral surface meets the posterior face in a gentle curve rather than at an abrupt angle.

Ramphocinclus differs from the three other endemic West Indian genera by the morphology of its ear opening, zygomatic process, and maxillopalatine, and differs markedly from *Cinclocerthia* in the shape of the articular portion of the lower jaw. In these features it closely resembles *Melanotis* and *Toxostoma,* and its plumage pattern is most like *Melanotis hypoleuca* in its black mask; white underparts; unpatterned dark upperparts, wings, and tail.

Donacobius (Black-capped Mockingthrush) differs from all other mimids by its small, spatulate-like maxillopalatines with broad flat stems that flare out at their attachment to the upper jaw, where each is perforated by a foramen; long, pointed transpalatine processes; horizontally flattened dorsal border of the ear opening; inflated and abruptly indented antorbital plates; and reduced ossification of the interorbital septum such that the sphenoidal rostrum is slender and strut-like. As a special offshoot of the Mimidae it need not figure in the discussion of *Cinclocerthia.*

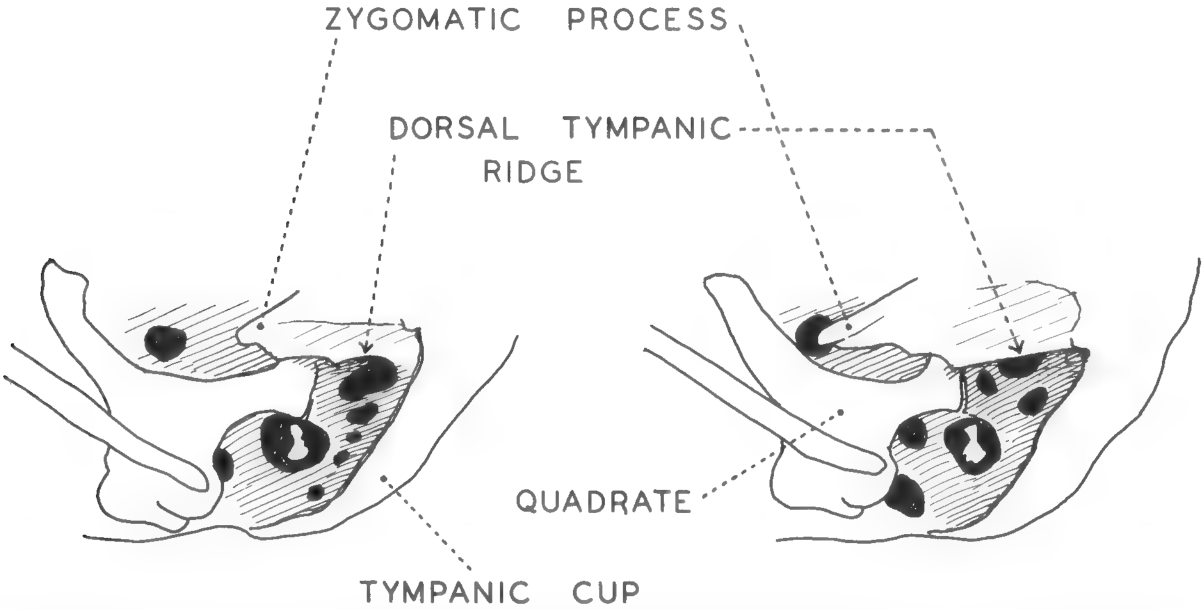

Figure 10. The quadrate and ear opening of *Cinclocerthia ruficauda* (left) and *Toxostoma curvirostre* (right), in anterodorsolateral view. Note the relationship of the dorsal tympanic ridge to the tympanic cup.

TABLE 2

Angle between Dorsal and Posterior Borders of Ear Opening of Skull in *Cinclocerthia ruficauda* (the Trembler), *Allenia fusca, Margarops fuscatus,* and Nine Other Species of Mimidae

Species	*Number of specimens*	*Angle*[1] *Mean*	*Range*
Melanoptila glabrirostris	1	52	—
Melanotis hypoleuca	1	52	—
Ramphocinclus brachyurus	1	55	—
Toxostoma curvirostre	4	56	50–61
Oreoscoptes montanus	2	57	53–61
Toxostoma rufum	5	60	56–66
Dumetella carolinensis	7	60	55–64
Melanotis caerulescens	1	61	—
Mimus polyglottos	8	61	55–68
Cinclocerthia ruficauda	12	70	65–76
Allenia fusca	10	76	69–82
Margarops fuscatus	2	83	78–88

[1] Angle measured between dorsal tympanic ridge and anterior edge of tympanic cup. Figure for each individual is average of figures for right and left sides.

Adaptations

Table 3 presents the average measurements, proportions, and intramembral ratios of *Cinclocerthia* and *Allenia.* Ratios of the lengths of various skeletal elements to thoracic length and intramembral percentages were calculated from means of the measurements. I chose the trunk length—length of last cervical and first five dorsal vertebrae—as a conservative measure of body size, and ratios to trunk length tend to show similarities or differences in proportion of skeletal elements, independent of general body size. Total length of the hindlimb and forelimb represents the sums of average lengths of the individual elements in each limb. The slight discrepancies in the figures are caused by rounding of numbers.

In order to obtain a meaningful synoptic comparison from the measurements and proportions of *Cinclocerthia* and those of other genera of Mimidae and of *Cichlherminia* (the Forest Thrush), the ratios of all measurements to trunk length for these birds were expressed as a percentage of the ratios for males of *Cinclocerthia* (Table 4). The figures provide an index to the amount by which each measurement, independent of body size, is greater or less than the figure for *Cinclocerthia*—always 100 per cent. For example, the relative depth of the sternal keel in *Mimus polyglottos* (Northern Mockingbird) is 148 compared to 100 for *Cinclocerthia*—almost half again as great. Because the samples were small, I have not attempted to evaluate slight differences, but have restricted my discussion to gross differences (20 per cent or more above or below *Cinclocerthia*) that almost certainly indicate real differences between species, and with less confidence to differences of 10 to 19 per cent, which are probably also significant.

Throughout the following discussion all terms implying size are relative to body size as represented by trunk length, or to skull size as represented by cranial length; for example, "longer" does not necessarily mean longer in actual measurement but rather, longer in proportion to the size of the bird.

Cinclocerthia.—In proportions of the hindlimb, *Cinclocerthia* does not differ widely from the other mimids, although the femur, tibia, and tarsus are somewhat shorter than those of

TABLE 3

Measurements and Ratios of the Skeleton in *Cinclocerthia* and *Allenia*

Parts of skeleton	*Cinclocerthia r. ruficauda* *Eight males*			*Allenia fusca* *Four males and four females*		
	*Mean of measurements**	*Ratio to trunk length*	*Intramembral per cent*	*Mean of measurements**	*Ratio to trunk length*	*Intramembral per cent*
Trunk	19.2			21.1		
Femur	24.6	1.28	26.0	26.1	1.24	26.3
Tibiotarsus	41.1	2.14	43.4	43.7	2.07	44.0
Tarsometatarsus	28.9	1.50	30.5	29.5	1.40	29.7
Hind limb	94.6	4.9	100.0	99.3	4.7	100.0
Pelvis (length of ilium)	24.6	1.28		25.9	1.23	
Pelvis (interacetabular)	11.0	0.57		13.2	0.63	
Sclerotic ring (diam.)†	5.5	0.28		6.0	0.28	
Sternum (length)‡	17.6	0.92		21.4	1.01	
Sternum (width)	10.8	0.56		12.3	0.58	
Depth of keel	6.8	0.35		9.3	0.44	
Coracoid	20.3	1.06		21.8	1.03	
Scapula	23.2	1.21		27.0	1.28	
Humerus	23.7	1.24	31.4	27.1	1.28	30.1
Ulna	27.9	1.45	37.0	33.7	1.60	37.5
Carpometacarpus§	13.9	0.72	31.6	17.1	0.81	32.4
Digit 2	9.9	0.51		12.0	0.57	
Wing	75.4	3.9	100	89.9	4.3	100
Bill (culmen)	29.5	1.54		20.7	0.98	
Cranium (length)	25.5	1.33		24.8	1.18	
Cranium (width)	19.1	0.99		18.3	0.87	
Cranium (depth)	13.4	0.70		14.1	0.67	
Antorbital width	9.1	0.47		11.2	0.53	
Neck	50.1	2.61		47.2	2.24	

*Measurements are of total length unless indicated otherwise in parentheses.

†Diameter of the sclerotic ring is that of the internal opening.

‡Length of sternum is from coracoidal articulation to posterior edge.

§Length of carpometacarpus is to articulation with Digit 2.

TABLE 4

Ratios of Skeletal Measurements to Trunk Length Expressed as Percentage of Measurements for *Cinclocerthia r. ruficauda*

(See below this table for explanation.)

Cinclocerthia r. ruficauda M(8)–100 per cent	*A.f. MF (8)*	*M.f. M (2)*	*M.g. (2)*	*D.c. M (5)*	*M.c. (1)*	*M.h. (1)*	*R.b. (1)*	*T.c. (3)*	*M.p. MF (3)*	*N.t. (1)*	*M.g. (1)*	*C.l. MF (2)*
Femur	97	101	101	102	103	106	*110*	105	104	101	—	*114*
Tibiotarsus	97	104	107	107	101	106	*113*	104	*113*	*115*	—	**124**
Tarsometatarsus	93	103	*111*	109	101	*113*	*117*	105	*119*	**124**	*114*	**139**
Pelvis (length of ilium)	96	105	96	98	98	101	*113*	105	99	93	—	*112*
Pelvis (interacetabular)	*110*	109	**121**	**121**	*110*	*114*	*119*	*112*	*117*	109	—	*119*
Sclerotic ring (diam.)	100	100	*114*	—	—	—	—	100	—	—	—	**128**
Sternum (length)	*110*	*118*	*115*	*119*	**131**	**126**	*117*	**123**	**125**	*112*	101	**123**
Sternum (width)	103	109	*112*	*111*	*116*	*116*	*118*	*111*	109	—	102	*118*
Depth of keel	**126**	**140**	**137**	**146**	**140**	**140**	**128**	**137**	**148**	*117*	100	**140**
Coracoid	97	107	104	105	105	107	107	104	107	95	*87*	108
Scapula	106	*114*	106	*113*	*117*	*116*	*113*	*112*	*118*	101	98	*114*
Humerus	103	*113*	105	105	*110*	108	*112*	*110*	*116*	*112*	—	*114*
Ulna	*110*	**121**	108	104	108	106	107	105	**121**	*118*	97	*119*
Carpometacarpus	*112*	**122**	103	103	104	104	*111*	104	*119*	*114*	99	*119*
Digit 2	*112*	**121**	*114*	*112*	*118*	108	*118*	*110*	**129**	**123**	102	*116*
Bill (culmen)	**64**	**76**	**77**	**70**	*82*	*83*	93	*85*	**71**	92	*69*	**76**
Cranium (length)	*89*	92	104	98	92	95	101	97	99	95	93	*110*
Cranium (width)	*88*	100	103	92	*89*	92	99	99	99	94	94	101
Cranium (depth)	96	*110*	108	104	106	104	*114*	*113*	*116*	98	103	*118*
Antorbital width	*113*	*119*	**121**	**123**	*117*	**123**	*111*	**121**	**123**	100	104	**142**
Neck	*86*	92	*87*	*88*	94	99	—	93	*90*	—	**79**	98

Italicized numbers in the above table represent a difference of 10 to 19 per cent. Numbers in bold face represent a difference of 20 per cent or more. M=male; F=female. A.f.=*Allenia fusca*; M.f.=*Margarops fuscatus*; M.g.=*Melanoptila glabrirostris*; D.c.=*Dumetella carolinensis*; M.c.=*Melanotis caerulescens*; M.h.=*Melanotis hypoleuca*; R.b.=*Ramphocinclus brachyurus*; T.c.=*Toxostma curvirostre*; M.p.=*Mimus polyglottos*; N.t.=*Nesomimus trifasciatus bauri*; M.g.=*Mimodes graysoni*; C.l.=*Cichlherminia lherminieri*. Numbers in parentheses indicate the number of specimens examined.

Ramphocinclus, Mimus polyglottos, Nesomimus trifasciatus (Three-banded Mockingbird), *Toxostoma curvirostre, Melanotis hypoleuca* (Blue-and-white Mockingbird), and the thrush, *Cichlherminia.* Comparing species in the genus *Catharus,* Dilger (1956) concluded that in arboreal forms the legs were shorter, with relatively longer femurs and shorter tarsometatarsi; conversely terrestrial forms had longer legs with shorter femurs and longer tarsometatarsi. His explanation centered on the terrestrial forms, in which long legs were said to be of advantage for moving through ground clutter, and in providing greater leverage for long, high hops. This may account for the long legs of *Cichlherminia,* but it would be dangerous to suggest a competitive advantage over *Cinclocerthia* on that basis because the Trembler's foraging method of painstaking uncovering and search does not require great agility of terrestrial locomotion. On the other hand, relatively short legs may be beneficial in arboreal foraging of the Trembler, particularly when it is perched crosswise on a vertical trunk or vine; the weight of the bird would then be most effectively supported by keeping the center of gravity close to the toes. *Allenia* is perhaps the most arboreal of the Mimidae and it has the shortest legs, but the reason is probably different because its foraging method does not require frequent perching on vertical surfaces.

The Trembler has a consistently narrower pelvis (interacetabular distance) than the other species although in length the pelvis is similar to those of the other species. The significance of the narrow pelvis is unknown.

The Trembler has a much smaller sternum than all other species except *Mimodes* (Socorro Thrasher), particularly in the depth of the keel (five of the 11 mimids exceed its depth by at least 40 per cent). This almost certainly reflects a reduced ability for sustained flight in *Cinclocerthia.* In addition, the scapula, humerus, ulna, carpometacarpus, and Digit 2 of *Cinclocerthia* are shorter than all species compared in Table 4 except *Mimodes* and possibly *Melanoptila, Melanotis,* and *Dumetella.* Reduction in the Trembler's flight mechanism could be a consequence of its foraging method of thorough search for food on the trunk and major branches, progressing slowly through the forest from tree to tree. Its broad utilization of the forest habitat also minimizes the need to fly in search of suitable feeding areas.

Proportions of the length and width of the cranium in relation to trunk length are quite uniform throughout the Mimidae. *Allenia,* however, is small-headed, and no species has as long a bill as *Cinclocerthia.* The shape of the cranium is better expressed by ratios to a standard within the skull itself, such that, for example, the overall small-headedness of *Allenia* is not reflected in the ratios. Ratios of cranial width, depth, and antorbital width to cranial length (Table 5) reveal a considerable uniformity of skull proportions in the other species and emphasize the Trembler's unique properties—narrow antorbital region and flattened cranium (reduced cranial depth—see Figure 9). The long bill and flat cranium must enable the Trembler to insert its head deeper into narrow spaces such as between leaves of bromeliads or under loose bark, and to reach farther into crevices or wood tunnels with the bill than can the other species. In comparison with *Allenia* the eyes of *Cinclocerthia* are oriented for increased forward vision, which, in combination with the narrow antorbital region, probably facilitates binocular observation of prey near the tip of the bill.

In summary, the skeletal proportions that set the Trembler apart from other mimids are either adaptations for arboreal foraging on trunks and epiphytes or indirect consequences of such foraging. I found no special adaptations for fruit-eating, tearing open rotten wood, or ground-foraging.

Margarops and *Allenia.*—*Margarops* has a well-developed sternum and relatively long wing elements in comparison with *Cinclocerthia,* and *Allenia* is intermediate between the two. Of these three genera, *Allenia* has the shortest bill and smallest cranium with respect to trunk length and *Cinclocerthia* the longest bill and a cranium about the size of that of *Margarops,* but longer and flatter. The short bill of *Allenia* may reflect a lesser ability to forage for hidden insects and a greater commitment to fruit-eating than in its relatives. *Margarops* has the greatest antorbital width and *Cinclocerthia* the least. Evidently several independent trends have occurred during the adaptive radiation of the group.

Cichlherminia lherminieri.—The Forest Thrush resembles *Margarops* in proportions of its sternum and wing but it exhibits a longer hindlimb than is found in any mimid. The relatively large legs which have already been mentioned as adaptations for locomotion on the ground do not necessarily give this species an advantage in foraging over *Cinclocerthia.* Proportions of the skull differ from *Margarops* chiefly in the relatively longer, wider, and deeper cranium, and in the much broader antorbital region. The sclerotic ring is also considerably larger in internal diameter relative to body size and in actual internal diameter than those of *Cinclocerthia, Margarops,* and *Allenia.* Eaton *et al.* (1963) suggested that a large sclerotic ring represents an adaptation for vision in reduced light on the basis of apparent correlation between relatively large sclerotic rings and darker environment in certain species of Parulidae. However, they did not determine whether the larger sclerotic ring simply reflected a larger eye or whether it reflected a dispropor-

TABLE 5

Proportions of the Cranium in *Cinclocerthia ruficauda*, Eleven Other Mimidae, and *Cichlherminia*

	Number of specimens	*Mean cranial length*	*Cranial width / length*	*Cranial depth / length*	*Antorbital width / cranial length*
Cinclocerthia ruficauda	8	25.5	0.75	0.52	0.36
Allenia fusca	8	24.8	0.74	0.57	0.45
Margarops fuscatus	2	28.0	0.75	0.57	0.46
Melanoptila glabrirostris	2	23.0	0.74	0.59	0.41
Dumetella carolinensis	5	22.3	0.74	0.61	0.43
Melanotis caerulescens	1	24.3	0.72	0.60	0.45
Melanotis hypoleuca	1	25.5	0.72	0.58	0.46
Ramphocinclus brachyurus	1	25.0	0.73	0.60	0.39
Toxostoma curvirostre	3	27.5	0.76	0.61	0.44
Mimus polyglottos	3	23.3	0.74	0.61	0.44
Nesomimus trifasciatus	1	25.0	0.74	0.55	0.38
Mimodes graysoni	1	26.4	0.75	0.57	0.40
Cichlherminia lherminieri	2	30.5	0.69	0.56	0.46

tionately large window for admitting light. Walls (1942) theorized that only a larger eye with a disproportionately large pupil and lens would provide better vision in reduced light. Measurement of pupillary openings was not feasible in preserved eyes because distortion of the cornea also distorted the iris, but I found that diameter and depth of lens in relation to diameter of the eyeball were similar in *Cinclocerthia* and *Cichlherminia,* as was the internal diameter of sclerotic ring in relation to diameter of the eyeball, suggesting that the eyes of the two species are of similar proportions though of different relative size. Thus there is no evidence at present to conclude that the large eyes of *Cichlherminia* give it a competitive advantage over *Cinclocerthia* in foraging on the dark forest floor.

Discussion and Conclusions

In forests of the mainland in Central and South America, woodcreepers (Dendrocolaptidae) and ovenbirds (Furnariidae) procure their food from surfaces or recesses of tree trunks, major branches, and their epiphytes. Accounts of foraging methods for these groups of birds are surprisingly scarce and widely scattered; here I shall mention those that brought to mind the feeding behavior or niche of the Trembler.

Of the Dendrocolaptidae, Hudson (1922:243) wrote: "Some dig like woodpeckers in decayed wood; others probe only in soft rotten wood; while the humming-bird-billed *Xiphorhynchus* [= *Campylorhamphus*], with a beak too long and slender for probing, explores the interior of deep holes in the trunks to draw out nocturnal insects, spiders, and centipedes from their concealment. *Xiphocolaptes* uses its sword-like beak as a lever, thrusting it under and forcing up the loose bark; while *Dendrornis,* with its stout corvine beak, tears the bark off."

Skutch (1945) described the foraging of the Spot-crowned Woodcreeper (*Lepidocolaptes affinis*) in mossy, epiphyte-burdened forest, where it peers and probes into crevices and fissures of the bark and into mosses and lichens, sometimes prying off loose bark or pulling moss from the trees. Insects, spiders, and other animals are extracted from their hiding places with the tip of the bill. Of the Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), Wetmore (1926:236) wrote: "Their long bills were frequently thrust into the recesses of small air plants, or under moss and loose bark, which was pried away with a quick twist of the head to expose any animal life concealed beneath."

In Venezuela, Wetmore (1939:215) observed the Olive-backed Woodcreeper (*Xiphorhynchus triangularis*) "climbing over the stems of large creepers, or the trunks of trees, probing in crevices with the bill." Slud (1964:200) wrote of the Spotted Woodcreeper (*Xiphorhynchus erythropygius*): "Its foraging habits do not differ from those normal to the family, but the bird does exhibit a special interest in epiphytes."

With reference to the Strong-billed Woodcreeper (*Xiphocolaptes promeropirhynchus*), Todd and Carriker (1922:280) stated: "It is especially fond of hunting among the bromelias, where there are always insects, salamanders, frogs and frogs' eggs to be found." Salvin and Godman (1888-1904:184) noted that a tree frog (*Hyla myotympanum*), taken by this species, had probably been extracted from a bromeliad in which these frogs take refuge during the dry season.

Wetmore (1926:240) remarked of the Red-billed Scythebill (*Campylorhamphus trochilirostris*): "From their actions I judged that the grotesque curved bill was employed to search for insects among the stiffened leaves of bromeliaceous epiphytes that grew abundantly on trees and shrubs," and Friedmann and Smith (1950:496) "often saw it using its long curved bill to probe to the bases of the pineapple-like leaves of the epiphytic plants common on the trees in the wet woods." Taczanowski (1884:181-182) quoted Jelski's description of this species using its long decurved bill to reach into holes of trees and to beat captured invertebrates against the trunk.

Certain of the Furnariidae also forage among epiphytes. Todd and Carriker (1922:284) describe the Montane Foliage-gleaner (*Anabacerthia striaticollis*) as "continually scrambling and hopping about among the branches of the trees" and "rummaging about in the bromelias for insects." The Spotted Barbtail (*Premnoplex brunnescens*) and the Buffy Tuftedcheek (*Pseudocolaptes lawrencii*) hunt for insects among the moss-covered trunks and branches of montane forests (Skutch, 1967; Slud, 1964:204-205). The Buffy Tuftedcheek "creeps along the under sides of limbs like a woodhewer, and it specializes in rummaging the masses of epiphytes that help give the montane cloud forests their fantastic appearance" (Slud, *loc. cit.*). Slud (1964) described the Red-faced Spinetail (*Cranioleuca erythrops*), the Striped Woodhaunter (*Hyloctistes subulatus*), the Buff-throated Foliage-gleaner (*Automolus ochrolaemus*), and the Streak-breasted Treehunter (*Thripadectes rufobrunneus*) as creeping or hopping on vines, trunks or twigs, rummaging noisily among trash and clusters of dead leaves and bromeliads or other epiphytes. Skutch (1952:94) wrote that the Buff-throated Foliage-gleaner hunts chiefly among curled or clustered dead leaves caught among vine-tangles or boughs of trees. It clings in various positions to probe leaf curls with the bill. In an attempt to retrieve a fallen insect from the ground one bird flicked aside leaves with its bill.

Other birds mentioned by Slud (1960:84) as feeding among epiphytes or clumps of dead leaves are the Banded Wren (*Campylorhynchus zonatus*) and the Yellow-billed Cacique (*Amblycercus holosericeus*). Slud (1964:69) also described the Blackish Crane-hawk (*Geranospiza nigra*) stepping about inside the spike-whorled leaves of bromeliads probably in search of small amphibians.

Many forest birds on the mainland eat tree fruits; others forage for invertebrates on the ground—the species of leaf-scrapers (*Sclerurus*), for example, throw leaves as does the Trembler. Thus, numerous species in Central and South America occupy niches that, together, correspond to all portions of the Trembler's niche on Dominica. Few of these mainland species or their relatives occur within the Trembler's range; indeed, the Furnariidae, Dendrocolaptidae, and most of the families that specialize in fruit-eating are absent from the Lesser Antilles. Conversely, mimids are not found in tall tropical or subtropical forests of the mainland. These facts and the absence of any close mainland relatives of the Trembler suggest that the ancestors of this mimid were less adapted to life in tall forest and evolved their adaptations to the forest environment after colonizing the islands. Competition with the ancestors of the Scaly-breasted and Pearly-eyed Thrashers and other species may then have influenced the evolution of the Trembler because its specializations now fit that portion of its niche for which there is no competition. The present reduction of the sternum in the Dominican Trembler and the existence of well-marked races on each of the larger islands suggests that the movement of birds from one island to another may now be very rare and that, to some degree, the present adaptations and habits of the insular races have evolved independently. A comparative study of the various races of the Trembler might well contribute to our understanding of ecological influences on the evolution of adaptions.

Summary

The Trembler (*Cinclocerthia ruficauda*) is a mimid endemic to the Lesser Antilles. On Dominica it is common in evergreen forests, especially optimal rain forest. Its food consists of insects and other invertebrates as well as small frogs and lizards taken from the ground or from tree trunks and limbs and their epiphytes; it also takes fruits of forest trees and shrubs. On the ground it tosses leaves to uncover prey. Most feeding is done among epiphytes and clumps of dead leaves, and food is taken from crevices such as are found on trunks or in tangled vines. Birds sometimes forage in loose bands with one or two birds foraging in a given tree at one time.

The Trembler delivers its full song beginning in March, and, in addition, gives a subsong before and during the onset of the breeding season. Breeding occurs in May-July. There is an annual post-breeding molt.

The Trembler is named for its habit of trembling the wings. Trembling makes the bird conspicuous as it hops through the trees searching for foraging sites. Trembling is not an aid for flushing prey; rather it appears to be a social signal with aggressive content that may serve to keep foraging birds distributed in different trees.

Potential competitors of the Trembler are the Scaly-breasted Thrasher (*Allenia fusca*), the Pearly-eyed Thrasher (*Margarops fuscatus*), the Forest Thrush (*Cichlherminia lherminieri*), and some other species. None of these birds feeds among epiphytes. The Trembler exhibits structural adaptations that appear to be related to its arboreal foraging methods rather than to fruit-eating or ground-foraging. Compared with other mimids, the Trembler

has short legs, probably an advantage for perching on vertical surfaces; a reduced sternum and wings, possibly correlated with the reduced need for extended flight; a long bill and flattened cranium, suitable for probing in narrow spaces; and a narrow antorbital region combined with eyes oriented for close binocular vision.

Features of the skull point to the Scaly-breasted and Pearly-eyed Thrashers as the closest relatives of the Trembler; the White-breasted Thrasher appears to be closer to the blue mockingbirds than to the Trembler.

In forests of the mainland, members of the Dendrocolaptidae and Furnariidae forage among epiphytes and leaf trash and on tree trunks. Neither family is present on the Lesser Antilles, and no mimid has a comparable foraging niche on the mainland. The Trembler's feeding adaptations probably evolved largely on the islands in the absence of species specialized for arboreal rummaging.

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THE NESTING CYCLE OF SONGBIRDS IN TROPICAL AND TEMPERATE REGIONS

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We have long been aware of differences between the faunas of temperate and tropical regions. Perhaps the most striking impression to the casual visitor in the tropics is the number and variety of both the animals and plants. For example, more species of songbirds breed in Panama than north of the Mexican border, perhaps two or three times the number as in an area of similar size in the United States.

Ornithologists, after years of studying tropical birds, have found other differences: (1) The clutch size of birds decreases as one moves south toward the equator. Songbirds in the Arctic usually raise broods of from five to seven young; through the middle latitudes, as in the United States, clutches of four or five occur most frequently. And where one enters the tropical regions, clutches of two or three eggs are the rule. (2) The length of the breeding season in most species in the tropics is greatly extended (Table 1); in fact, the nests of some species have been found every month of the year. Because of the ameliorated temperatures in the tropics the long breeding season is not surprising. (3) Largely through the careful studies of Alexander F. Skutch, we have learned that the nesting success of tropical birds is lower than that of their northern counterparts. Nice (1957), in summarizing data on nesting success for birds of temperate regions, concluded that about one out of every two eggs, laid in open nests, produces a fledgling. In Costa Rica, according to Skutch (1966), only one out of every three or four young survives the nest period (Table 2).

Stimulated by these comparisons we ask if other differences in reproductive biology have evolved between birds of the two regions. Tropical birds enjoy longer nesting seasons than birds of the temperate zone; they also have greater nesting losses and face a greater variety of nest-robbing predators — snakes, other birds, and primates (Skutch, 1966). The small clutches of tropical birds suggest that they have less available food, though some workers argue against this explanation (Skutch, 1967).

How have these differences in environment—in climate, food supply, and predators—directed the course of evolutionary adaptation? Fortunately, we now have sufficient data on nesting cycles of birds to enable us to compare many adaptations which must reflect the evolutionary interaction between the breeding biology and the environment. In this analysis we shall search for differences both between the nesting cycles of species in each region and between the diversity of adaptations among all species of each region. We shall compare "average" nesting cycles of tropical and temperate birds, just as we have compared the nesting success and length of breeding season above. To evaluate the diversity of these parameters we must use some measure of dispersion such as "variance" or "standard deviation."

I have brought together and summarized below information on the breeding of New World songbirds, based on data reported by many students, far too many to be cited here. Although the facts were not gathered by uniform field methods, we have standardized the estimation and description of many parameters of nesting cycles sufficiently to make widely gathered data of great comparative value. Perhaps the most logical starting point for our comparisons is with the nest.

Nest Construction and Location

Tropical birds build a much wider variety of nests than do temperate species. The nests of most species, especially in the temperate regions, have been described in such detail that a brief analysis will demonstrate this. Though intermediates occur, birds construct four basic types of nests—open, domed, hanging or pensile, and cavity or hole. While all four of these nest types are represented among temperate species, the domed and pensile nests are rare as shown in Table 3—six and three per cent respectively for 98 species in the New York City area. In the tropics, 25 per cent of the nests of 96 species are domed and 16 per cent are pensile. Moreover, the nests in the tropics are far more elaborate. No pendant nests in the temperate zone can compare with that of the Black-tailed Flycatcher (*Myiobius atricaudus*) with its bottom entrance (Gross, 1964) or that of the Royal Flycatcher (*Onychorhynchus mexicanus*) with its peculiar open construction. No domed nest equals the domed nests of the ovenbirds (Furnariidae).

TABLE 1

Geographical Comparisons of Nesting Seasons*

Locality	*Length of season, months***
Arctic	
Lapland	1.3
Temperate	
California	3.1
Kansas	3.8
England	4.2
Tropical	
Costa Rica	6.6
Guyana	7.7
Trinidad	9.8

*From Ricklefs (1966).

**Period during which clutches of all species of small altricial land birds are laid.

TABLE 2

Nesting Success of Temperate and Tropical Passerine Birds*

Locality	*Nest success, in per cent*	*Fledging success, in per cent*
Temperate North America		
Open nests	49.3 (24)**	45.9 (29)**
Hole nests		66.0 (33)
Costa Rica		
Open or roofed nests in clearings or second growth (23 species)	34.6 (434)***	30.4 (883)***
Open or roofed nests in forests	23.1 (52)	21.5 (107)
Hole nests	53.5 (43)	43.6 (62)

*Data from Nice (1957) and Skutch (1966). Nest and fledging success are based on broods and individuals, respectively, which survive to fledging.

**Number of studies, given in parentheses.

***Number of nests or eggs, given in parentheses.

The location of nests also appears to be more diversified in the tropics and, for many species, quite specialized. For example, several flycatchers and manakins almost always nest over water; some trogons and puffbirds nest within the nests of termites; and many flycatchers and oropendolas build close to the nests of wasps (e.g., Smith, 1968).

The forms of the nests of tropical species, unquestionably more diverse than those of the more northern birds, must reflect a greater diversity in the environment. But in which aspect? Any attempt to answer this question will only expose our ignorance; it does suggest possibilities for future study. Perhaps the increased diversity in nest form among tropical birds is related to the greater diversity of predators or a great diversity of the strategies of predators. It may also be due to the greater variety of vegetation, of "backgrounds," against which the birds may conceal their nests. Many pensile nests mimic the tangles of vines and other plant materials hanging from tropical trees. The nest form may also be related to feeding behavior. For example, the woodpecker whose bill is adapted to prying bark off tree trunks while searching for insects can also excavate a nest hole; a flycatcher cannot. Other aspects of feeding ecology may affect the choice of nest sites and the materials used in the construction of the nest. Feeding habits must set at least some limits to the type of nest and the location the bird selects.

The hypothesis that the nest form is related to predation tempts us the most since so many features of the nests in the tropics have clearly adapted to predator pressure. We can understand nests placed close to those of stinging wasps, the cryptic and inaccessible pensile nests, and the flimsy, inconspicuous nests such as those of many finches and doves. But the adaptive value of the bulky and conspicuously domed nests escapes us.

TABLE 3

Nest Construction by Temperate and Tropical Passerine Birds*

Nest construction	*Percentage of species* *New York City area*	 *Canal Zone*
Type		
Open	71	47
Domed or enclosed	6	25
Pensile	3	16
Niche or natural cavity	20	12
Special placements		
Over water	2	8
Near wasps or bees	0	9

*From Ricklefs (1968c); based on 89 species from the New York City area and 96 species from the Canal Zone, Panama.

We must also ask why a particular species has chosen one type of nest rather than another. Undoubtedly, no one nest form is equally effective in avoiding all types of predation. Each nest, specialized to avoid one or more predation strategies, becomes particularly ineffective against others. Perhaps in investigating the bird's behavior against predators we will find a second level of adaptations that are correlated with the type of nest and that compensate for the particular deficiencies of the nest form a species adopts.

Development of Young

Another feature of the nesting cycle that we can use for comparison is the development rate of the young—the length of time required to complete the various stages of the nesting cycle. The differences in the behavior of nestlings and the variations in adult care in the different species, two aspects not nearly so well documented and far more difficult to analyze, I shall defer to a later paper.

Incubation and Nestling Periods

Both the incubation and nestling periods of birds in the tropics are, on the average, about 10 per cent longer than those of birds in the temperate zone (Table 4). This is partly because about 15 per cent of the temperate-zone birds have incubation periods of only 11 days and very few tropical birds have 11-day incubation periods. And partly because many tropical birds have extended incubation periods. In the temperate zone, few passerines, except large corvids, have incubation periods longer than 16 days; in the tropics about 25 per cent exceed 16 days; some actually require up to 22 or 23 days from laying to hatching.

Unlike the incubation periods where we find the range quite different, the range of the nestling periods is quite similar for tropical and temperate songbirds—from a minimum of about eight days in many finches to 25 days in some swallows and other hole-nesting species. The main peak of the distribution among the sample of tropical species is shifted towards the longer nestling periods and results in a slightly higher mean.

Although these differences in the means of the incubation and nestling periods are not striking and may be of little consequence, they are surprising. Since the mortality rates of eggs and young are higher in the tropics, we might expect that the tropical species would compensate for it by increasing the rate of development and thus shortening the nestling period (Williams, 1966). The high mortality rates should favor shorter incubation and nestling periods. However, just the opposite occurs. Not only is the mean nestling period longer, but the rates of growth are slower (Ricklefs, 1968a).

A comparison of the diversity, or standard deviation, of the incubation and nestling periods may explain this (Table 4). The diversity of the incubation periods of the tropical sample, with a standard deviation of 2.6, is significantly greater than the 1.9 of the temperate sample. This is not true of the nestling period where the difference is slight.

I have developed a model to explain the increased diversity of incubation periods among tropical species (Ricklefs, 1968a; 1968b). Very simply, it involves the difficulty in matching the food required by the brood to the food the adult is capable of gathering. A hypothetical example will illustrate this. In Figure 1 an open bar represents the amount of food required by the brood for its greatest growth and maintenance needs and a shaded section represents the amount of food the parents are able to supply. We will first compare a brood of three with a brood of one. All the young have similar growth rates and require the same amount of food. The parents of both broods are capable of gathering more food than the brood requires. According to Figure 1, both sets of parents are wasting the same amount of energy which, if used, could increase their productivity.

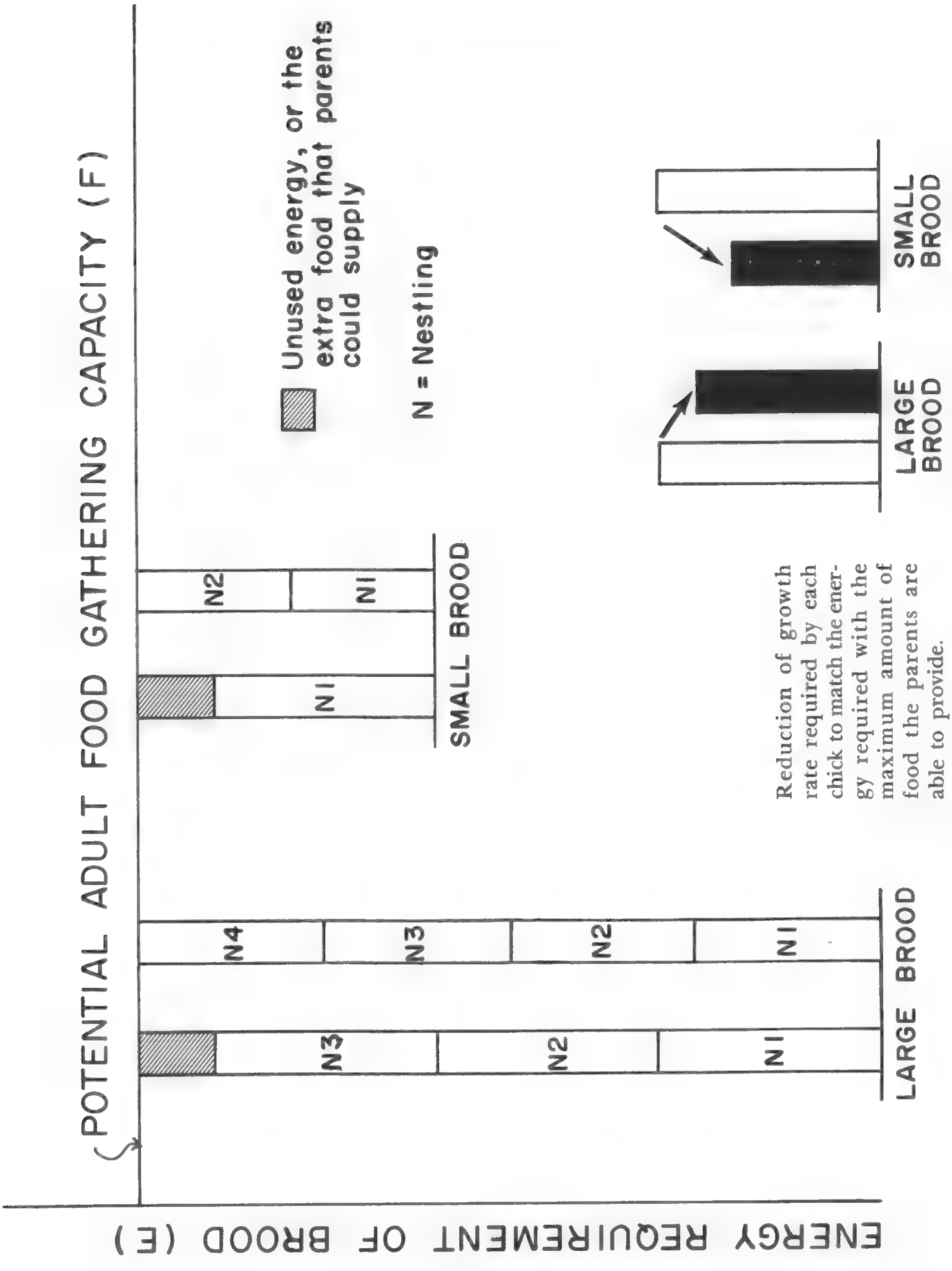
If they could increase the growth rates of their young by feeding them more, the parents could use the wasted energy, reduce the length of the nest period, and thereby increase the brood's chances of survival. However, birds in nature probably grow at physiological maximum rates (Ricklefs, 1967, in prep.) so they cannot speed up the growth rate. They can only slow it down. If the growth rate slows down and reduces the energy requirement of each young sufficiently, the difference between the requirements of the young and the parents' ability to feed will be great enough to allow the addition of

TABLE 4

Incubation and Nestling Periods of Temperate and Tropical Passerine Birds

	Percentage of species *Temperate*	*Tropical*
Incubation period (days)		
Mean (95 and 84 species)	13.6	15.3
Standard deviation	1.9*	2.6*
Nestling period (days)		
Mean (104 and 80 species)	14.3	15.9
Standard deviation	5.2	4.7

*Differ significantly (p less than .025).



Reduction of growth rate required by each chick to match the energy required with the maximum amount of food the parents are able to provide.

Figure 1. Model to explain the increased diversity of incubation periods among tropical species.

another young to the brood. If the decrease in growth rate is not too great, the addition of another offspring will more than compensate for the increased mortality due to the lengthening of the nestling period.

The diagram shows that, although the original amount of wasted energy was the same in both cases, with the addition of one young to each brood, the one young in the small brood had to lower its growth rate more than each of the young in the brood of three. Because the adjustments of growth rates in the small brood are larger, the range, or diversity of growth rates among species with small broods, is increased.

If the growth rate during the nestling period determines the growth rate of the embryo, the diversity of the length of the incubation periods in small broods will also increase. We know that nestling growth rates and incubation periods are fairly well correlated among temperate passerines ($r=0.72$ for 27 species) and we assume they are similar for tropical species. However, we must study the development rates of tropical birds more thoroughly before drawing any firm conclusions. The few data we now have indicate that, in tropical species, with small clutches, the young grow more slowly (Ricklefs, 1968a). This is consistent with our hypothesis.

Because the length of the nestling period in tropical species does not exhibit the same diversity as does the length of their incubation periods and nestling growth rates, other aspects of development must come into play. The growth rate of nestlings does not necessarily determine the pace that their survival potential develops. Functions, such as temperature regulation, do not increase at the same rate relative to body weight in all species (Ricklefs and Hainsworth, 1968), and furthermore, young birds develop behavior patterns, necessary for fledging, at different times in relation to growth. In a subsequent paper, I shall show that the speed at which the mortality rate decreases in precocial chicks is not closely correlated to their growth in weight. We may assume that, in altricial nestlings, the relationship between the ability to survive and physical growth is similarly flexible and may be modified through adaptation.

In most species the survival rate is constant throughout the nest period (Ricklefs, 1968c). Fledging should occur at that time during development when the chance of survival of the young out of the nest is greater than its chance of survival in the nest. As the nestling grows older, its physical capabilities increase, improving the possibilities of its survival as a free-living individual.

To account for the reduced variation in the length of the nestling period in relation to the incubation period in tropical species, we may suggest that the increased rate in the bird's ability to survive may be responsible for this. Alternately, the range of the rates of mortality in the nest may be narrower, or vary less, in the tropics than in temperate regions. Nest survival data are few and of questionable relevance, especially for tropical birds. An analysis of some of these data suggests that the mortality rates may vary less among tropical birds than among temperate species (Table 5)—as measured by the coefficient of variation—by about the same amount that the incubation periods vary in the other direction. The small sample is not statistically significant, however, and we should pursue the point further.

Re-nesting

Most birds, after fledging a first brood or losing a nest will lay another clutch, usually in a new nest. Tropical species require slightly longer than temperate species to replace a lost clutch or brood but the difference is not great and there is considerable overlap among species. The interval between nest failure and re-laying probably represents the minimum time required for construction of a new nest, re-activation of the gonads, and development of the eggs. Since little is known about the comparative physiology of re-nesting in birds, we can only guess at this point why tropical species should require longer. Tropical birds may mobilize reserves and accumulate additional energy for the formation of gonads and eggs more slowly. In a seemingly analogous situation, many tropical species lay on alternate days rather than daily as do most temperate songbirds.

Care of Dependent Young

Tropical species generally require much more time than temperate species to initiate a new clutch following fledging (Table 6). After a brood is successfully fledged, care of the dependent young becomes an additional factor. Observations on the parental care of young out of the nest indicate that the prolonged period of nest replacement in tropical species is related to extended periods of dependency of the young. Fledglings of most temperate species feed themselves completely when between 25 and 30 days of age and usually achieve independence between 30 and 45 days. The scattered observations on tropical species suggest that young may remain with, and be fed by, their parents to at least 50 or 60 days after hatching (Skutch, 1954; 1960). Skutch has noted antagonistic encounters between adults and their young as long as 60 to 80 days after hatching. Willis (1967), observing the Bicolored Antbird (*Gymnopithys leucaspis*) in Panama, noted that young remain hidden and their parents feed them as long as 21 to 28 days after fledging (35 to 42 days after hatching). By eight weeks, 70 days after hatching, the young "forage more or less clumsily

TABLE 5

Mortality Rates of Open and Enclosed Temperate and Tropical Bird Nests Placed above Ground*

Temperate passerine birds		*Tropical passerine birds*	
Species	*Mortality rate (per cent/day)*	*Species*	*Mortality rate (per cent/day)*
Traill's Flycatcher (*Empidonax traillii*)	0.94	White-bearded Manakin (*Manacus manacus*)	5.0
Robin (*Turdus migratorius*)	2.2	Gray-capped Flycatcher (*Myiozetetes granadensis*)	2.2
Cedar Waxwing (*Bombycilla cedrorum*)	0.9	Yellow-bellied Elaenia (*Elaenia flavogaster*)	4.7
Prothonotary Warbler (*Protonotaria citrea*)	1.4	Clay-colored Robin (*Turdus grayi*)	4.8
Yellow Warbler (*Dendroica petechia*)	2.6**	Scarlet-rumped Tanager (*Ramphocelus passerinii*)	3.3
Orchard Oriole (*Icterus spurius*)	0.8**	Blue-gray Tanager (*Thraupis episcopus*)	2.5
Brewer's Blackbird (*Euphagus cyanocephalus*)	2.4	Yellow-faced Grassquit (*Tiaris olivacea*)	4.3
American Goldfinch (*Spinus tristis*)	2.5**		
Chipping Sparrow (*Spizella passerina*)	2.0		
Average	1.7		3.8
Standard deviation	0.74		1.15
Coefficient of variation, per cent	43		30

*From Ricklefs (1968c).
**Egg mortality rate.

alongside their parents or peep and beg as they follow their parents." At about this time, young are frequently supplanted by adults and apparently are independent.

The mean interval between broods for tropical species is a conservative estimate, more so than for temperate species. A brood is completely successful only if one or more young survive to independence, but this is difficult to ascertain for most species. Thus many re-nestings following successful fledging also follow the complete loss of the brood during the dependency period. Because mortality rates of young are high and family groups are small in the tropics, the loss of broods before independence must be more frequent there than in temperate regions. Thus, differences in the duration of parental care between temperate and tropical species are greater than we can deduce from the mean intervals for re-laying after a successfully fledged brood.

TABLE 6

Interval between Broods of Temperate and Tropical Passerine Birds

	Temperate birds	*Tropical birds*
Initiation of a new brood after a nest failure (days)		
Mean (17 and 6 studies)	7.8	13.3
Range	3–11	6–24
Initiation of a new brood after a successful fledging (days)		
Mean (17 and 19 studies)	8.2	25.8
Range	1–20	8–59

These intervals are the outcome of the choice, at any one time, between whether to care for fledged young or to initiate another brood. Through natural selection and adaptation, adults will have adopted that strategy which eventually leads to the most offspring. The choice involves two factors. First, parental care must increase the survival rate of offspring during, and perhaps after, the period of dependence, but as the offspring develop physical capabilities and experience approaching that of the adult, the effect of parental care on their survival diminishes. Second, every clutch of eggs may potentially suffer losses which a fledged brood has already escaped. The probability that a new set of eggs will reach a given age after fledging is a function of nest and fledging survival rates and determines the value of a new clutch relative to a brood that has fledged. These values taken together with the effect of parental care on the survival of the eggs and fledglings determine the best strategy of parental care. The influence of parental care on the survival of fledglings is difficult to assess. We have seen that nest-mortality rates in the tropics are higher than those in temperate regions. Thus, the value of a new clutch in temperate regions, in terms of the expected number of young which will fledge, is greater there than in the tropics. Conversely, fledged young in the tropics are relatively more valuable than new clutches and are cared for at the expense of a less valuable second clutch. If the value of parental care is similar in both tropical and temperate species, this will account for the differences in the length of the dependency period and in the time required to re-nest after successful broods.

Conclusions

From this rather sketchy comparison of tropical and temperate nesting cycles I can make several generalizations. First, it appears that the great diversity of predators in the tropics has increased the diversity of strategies for reducing mortality rates. We have seen that nest construction is more diverse in tropical than in temperate regions, and we may find similar diversity in other anti-predator adaptations, especially in the behavior of adults at the nest. On the other hand, the diversity in the tropical environment apparently has had little effect on time relationships during the nesting period. These are affected more by reduced clutch sizes and increased mortality rates. We have not been able to determine from the data we now have whether an increased diversity in the tropics of the strategies against predators has in turn increased the diversity of the rates of mortality of nests and young.

It is instructive to ask why, in the face of greatly increased mortality rates, development rates of tropical birds are essentially similar to those of temperate species. Many adaptations may be altered with very little basic reorganization or adaptive cost. To make an analogy, let us consider the tremendous diversity of automobile tire treads. Each is most suitable for different driving conditions; all are equally easy to make—the machinery and the amount of rubber required for each is the same—and a change in any one would not be costly. Adaptations involving at least some color changes, differences in song, patterning on the body, and most nest construction are similar. The domed nest and the pensile nest probably require very much the same time, energy, and materials to construct, but each is a qualitatively different structure with a different value as an anti-predator strategy. On the other hand, changes in growth rate have profound effects on energy budgets and fecundity, in much the same way that the change from wooden spoked wheels to modern tires predicated the development of several new industries. Because of their high cost, we could expect to find few such changes in this direction.

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Cedar Waxwings, *Bombycilla cedrorum*. Painting by J. Fenwick Lansdowne.

A COMPARATIVE STUDY OF MOLLUSC PREDATION BY LIMPKINS, EVERGLADE KITES, AND BOAT-TAILED GRACKLES

Noel F. R. Snyder and Helen A. Snyder

In a study of the alarm responses of the large freshwater snail, *Pomacea paludosa,* we came face to face with three of its avian predators, the Everglade Kite (*Rostrhamus sociabilis*), Limpkin (*Aramus guarauna*), and Boat-tailed Grackle (*Cassidix mexicanus*). The conflicting reports in the literature on how these three birds stalk, capture, and open the molluscs, on which they all feed heavily, forced us to look for ourselves. This paper is a summary of the feeding behavior of these three birds as observed primarily in Florida in 1967 and 1968.

Food Habits

Everglade Kite

The Everglade Kite, so far as we know, feeds only on snails of the genus *Pomacea.* This exclusive food habit restricts its range to areas where these snails occur in abundance — parts of the Florida Everglades, Cuba, Isle of Pines, and Mexico south to northern Argentina. In our observations in southern Florida wild Everglade Kites ate only *Pomacea paludosa.* At the Patuxent Wildlife Research Center in Laurel, Maryland, captive kites have lived in apparent good health for over two years on horse meat and snails of the genus *Viviparus* (Ray C. Erickson, pers. commun.).

Limpkin

The Limpkin, also known as the Courlan, feeds heavily on *Pomacea* but takes other foods as well. Its range, like that of the kite, is closely correlated with the range of *Pomacea* (Harper, 1936; Sprunt, 1948), and the bird occurs from southern Georgia, Florida, and Mexico south through Cuba and Central America to northern Argentina. The northern extent corresponds closely with that of *P. paludosa.* However, Limpkins also occur on the islands of Puerto Rico and Hispaniola and have been seen on the Florida Keys and the Dry Tortugas, areas where *Pomacea* is not known to occur natively (Harper, 1936). Regarding Limpkins in Cuba, Barbour (1943:47-48) states "they seem to prefer lizards and the terrestrial molluscs which abound." In Puerto Rico, according to Wetmore (1916:37-38): "The main part of the food is said to be the common large land shells (*Pleurodonte carocalla*), and to some extent lizards."

Figure 1. Limpkin foraging on mud flats exposed by drought. The bird searches for aestivating snails by probing into the mud with its bill.

Besides *P. paludosa,* Limpkins in Florida reportedly take snails of *Campeloma* and *Viviparus,* freshwater mussels (Unionidae), and, to a lesser extent, lizards, insects, frogs, worms, and crustaceans. Stevenson (1962:323) tells of a Limpkin in Marathon, Florida, that "acquired the habit of feeding on mash put out for domestic ducks." According to Cottam (1936), *Pomacea* were found in 21 of 30 stomachs of Limpkins collected from various localities, presumably in Florida; one contained *Campeloma;* and eight, unidentifiable fleshy parts of molluscs most of which appeared to be gastropods — probably *Pomacea.* One stomach also contained traces of weeds seeds and insects. Bryant (1859:13) stated: "On the St. Johns it feeds principally on a species of Natica, which is extremely abundant, and also on the small Unios. All the specimens I killed had the stomach filled with the more or less digested remains of various molluscs—principally Unios." Harper (1941) pointed out that "Natica" is a marine genus and Bryant's snail was probably *Viviparus georgianus.* The Limpkins we watched fed extensively on freshwater mussels of the species *Anodonta cowperiana, Villosa vibex, Elliptio strigosus,* and *Uniomerus obesus,* and on snails of the species *P. paludosa* and *V. georgianus.* In some places they fed on mussels and *V. georgianus,* in others on *P. paludosa* and mussels, and in still others on mussels and both species of snails.

Their choice of molluscan food seemed to be governed by its availability and size. We have yet to see them take small snails of such genera as *Physa,* *Helisoma,* or *Tropicorbis,* even in regions where these snails abound. While size and availability may be the primary factors in food choice, individual Limpkins differ in their food preferences. On 18, 19, and 24 April 1968 at Saddle Creek Park near Lakeland, we watched a pair of Limpkins feeding close together in a small backwater where there were *P. paludosa, V. georgianus,* and mussels. Both Limpkins ate all three, but on all three days the male devoured great quantities of *V. georgianus* while the female ate mostly mussels and *P. paludosa,* both much larger than *V. georgianus.* Since the pair was building a nest, the bias of the female toward the larger molluscs may have been related to the fact that she was about to produce eggs.

Boat-tailed Grackle

The Boat-tailed Grackle is omnivorous. Sprunt (*in* Bent, 1958) mentions as items of diet: grain, crawfish, crabs, shrimp, grasshoppers, beetles, other insects, fish, frogs, spiders, berries of cabbage palm, and eggs of other birds. Skutch's list (*in* Bent, 1958) includes bananas, various berries, tadpoles, and ticks and vermin from the backs of cattle. We saw Boat-tailed Grackles eating snails of the species *V. georgianus* and *P. paludosa* and mussels of the species *A. cowperiana* and *V. vibex.* Although *P. paludosa* appears to be a favorite food for grackles in the Everglades, they are apparently not as dependent on it as are Limpkins and Everglade Kites. The Boat-tailed Grackle ranges from Delaware and Maryland south through Florida, along the gulf coast through Texas, and throughout most of Central America. Much of this range does not overlap the range of *P. paludosa* or other species of the genus *Pomacea.*

Feeding Behavior of the Limpkin

Foraging Behavior

In our observations, Limpkins used four rather distinct foraging methods: (1) visual searching on land, (2) visual searching in clear water, (3) tactile searching of surface vegetation with head above water, and (4) tactile searching of the bottom with head above or under water.

Visual Searching on Land.—On 3 December 1967, on Route 846 in Devils Gardens south of Clewiston, two Limpkins walked in a muddy field which had recently been covered by water from a roadside canal. Several times one bird probed into the mud with its bill; twice it came up with an aestivating adult *P. paludosa.* On 18 and 19 April 1968, in Saddle Creek Park near Lakeland, two other Limpkins, feeding on mud flats exposed by drought (Figure 1), took both *P. paludosa* and *V. georgianus.* The birds' behavior was similar to that described by Wetmore (*in* Howell, 1932:200): "The birds walked along with the neck bent forward and the head inclined toward the ground, but at short intervals stood quickly erect and gazed around. Most of their motions were quick and jerky, and on the whole were characteristic in nature. A large freshwater snail (*Ampullaria depressa* [=*Pomacea paludosa*]) was abundant here, lying embedded in the mud. The Limpkins searched about, occasionally probing in the mud with their long bills. When a snail was located, it was quickly drawn out and held in the bill while the bird gazed around to make sure the coast was clear." During drought, Frank Ligas (pers. commun.) saw Limpkins feeding on freshwater mussels on exposed flats, and Alexander Sprunt IV (pers. commun.) watched them eating grasshoppers on lawns in Clewiston. Several times we watched Limpkins probing in debris on the banks of canals but we were not sure they were capturing food. At Wakulla Springs on 30 March 1968,

Figure 2. Limpkin visually hunting for molluscs in clear water. The bird worked its way along the shore of a canal, sometimes wading until the water nearly covered its legs.

a Limpkin probed in cracks between the timbers of a dock for food we could not identify; it may have been spiders or insects.

Visual Searching in Clear Water.—On 29 October 1967, along the canal forming the western border of Lake Okeechobee approximately five miles northwest of Moorehaven, a Limpkin worked its way along shore, wading occasionally to depths where the water completely covered its legs and extending its neck as it peered into the water (Figure 2). Now and then it jabbed with its bill until its head was under water (Figure 3). Sometimes it came up with a mussel or *V. georgianus,* other times with nothing. The jabbing was obviously visually directed.

Tactile Searching of Surface Vegetation.—In this method the Limpkin probes with the bill partly open (photograph *in* Truslow *et al.,* 1967:544). On 5 November 1967, just south of Fisheating Creek on Lake Okeechobee, a bird fed close to shore on a dense mat of water hyacinth. It moved in a fairly systematic fashion parallel to shore, regularly jabbing its partly open bill rapidly up and down through the mat. Frequently it caught a *P. paludosa.* Apparently the Limpkin captured the snail at first touch; in only one case out of 14, in one and one-half hours, did the Limpkin seem to dislodge rather than seize a snail. The bird immediately plunged its head and neck deep into the water and retrieved it. Since the water was about two feet deep under the mat, we would have noticed other instances of this sort had they occurred. The Limpkin appears to have extremely fast reflexes, perhaps comparable to those of other tactile-foraging birds such as Wood Storks (*Mycteria americana*) described by Kahl and Peacock (1963).

Tactile Probing of the Bottom with the Head above or under Water.—This method is common in murky water with little surface vegetation. Typically, the Limpkin wades along, stops, makes a few rapid probes at the bottom, raises its head, takes another step or two, and repeats the process. When probing, it holds its bill open and often moves its head from side to side, describing an arc on the bottom. The open position of the bill and the lateral swings of the head are obvious in Limpkins foraging in shallow water (Figure 4) but are difficult to see in Limpkins working in deep water because the birds submerge their heads completely.

Individual birds practiced more than one method of finding prey. For instance, the Limpkins in Devils Gardens that probed for aestivating snails (Method 1) also foraged in highly stained water by tactile searching of the bottom (Method 4). Limpkins, observed on 12 November 1967, 12 miles east of Belle Glade, alternated between tactile searching of surface vegetation (Method 3) and the bottom (Method 4). On 7 March 1968 at Wakulla Springs, a pair of Limpkins foraged in water by tactile probing (Method 4), where the bottom aquatic vegetation was dense, and caught molluscs by visual searching (Method 2) in less vegetated areas.

Since *P. paludosa* occurs up in aquatic vegetation as well as on the bottom, while freshwater mussels and snails of the genera *Campeloma* and *Viviparus* live primarily on the bottom, we suggest that the Limpkins use tactile probing of surface vegetation (Method 3) primarily in locating *P. paludosa.* In our observations they took *V. georgianus* by visual searching on land and in clear water, and by tactile searching of the bottom; they found mussels only by visual searching in clear water and tactile searching of the bottom. However, Mr. Ligas (above) saw them take mussels by visual searching on land. *P. paludosa* was the only food we saw them take by all four methods.

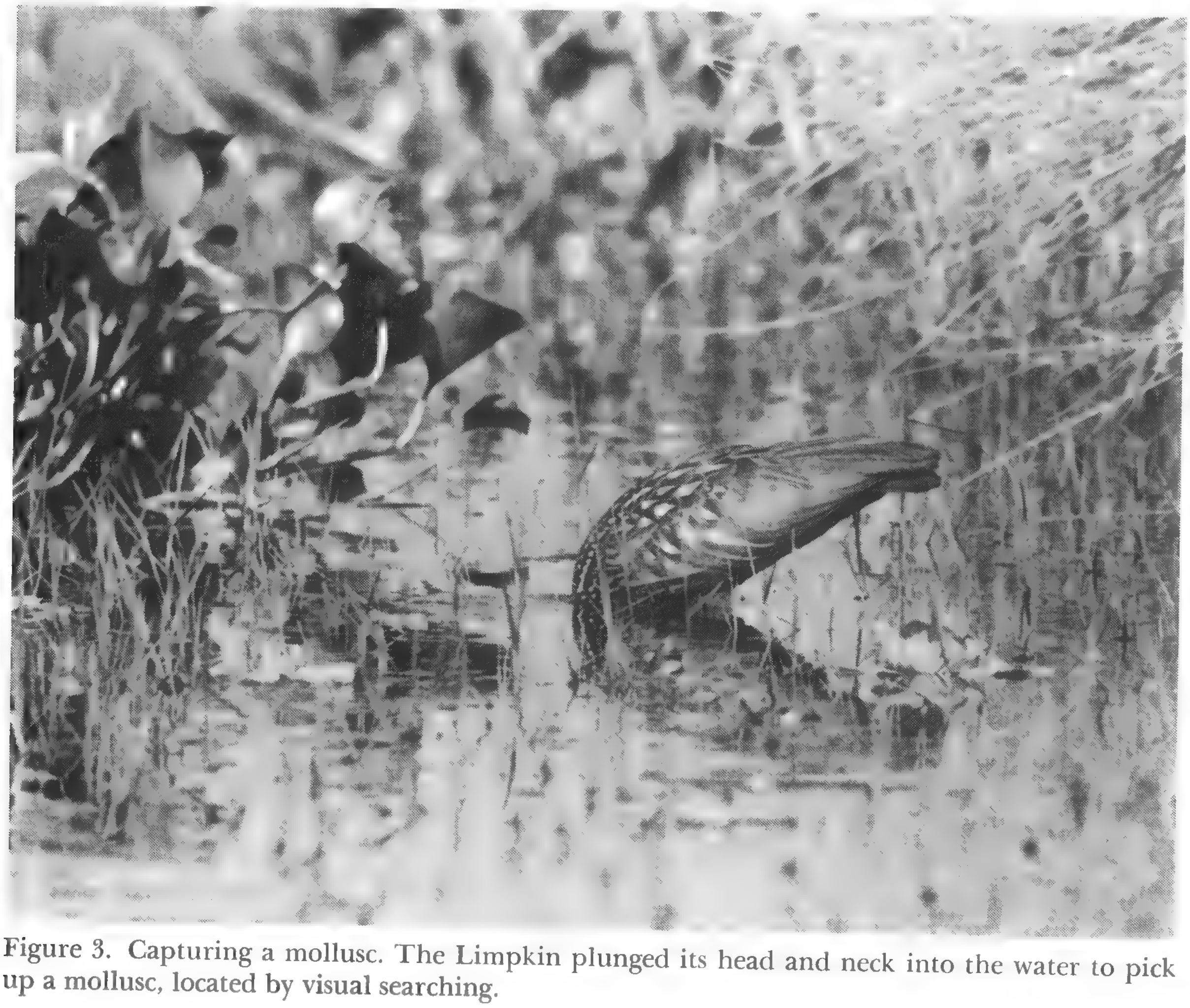


Figure 3. Capturing a mollusc. The Limpkin plunged its head and neck into the water to pick up a mollusc, located by visual searching.

Figure 4 (*above*). Limpkin searching for molluscs in muddy water. The bird walks along slowly, stopping every two or three steps to make a few quick thrusts at the muddy bottom with its bill.

Figure 5 (*below*). Carrying a mussel to shore. With the mussel held in the tip of its bill, the bird moves it to shallower water or to the shore—wherever there is a solid base—to extract the animal from the shell.

Hudson (1920) and Sprunt (1948) report extensive nocturnal feeding by Limpkins, but give no details. It is true that Limpkins are exceedingly vocal at night, but this is no proof they are feeding. Limpkins often vocalize when not feeding. Our own observations on nocturnal feeding are quite limited: On 7 March 1968 at Wakulla Springs, we observed a pair of Limpkins from 10:25 AM until 8:10 PM. Feeding during the day was fitful and interrupted by long periods of preening and bathing. At sunset, about 6:30, the birds became very active, foraging with head under water (Method 4) and catching and eating snails and mussels for about one hour. We saw them swallow the last item at 7:25 when the glow of the sunset was still barely visible and a quarter moon hung directly overhead. Then, standing close together on a stump, they began to preen. They were still on the stump when we left at 8:10.

The role of moonlight in nocturnal feeding may be important. While a Limpkin presumably can capture molluscs in the dark by tactile methods, the extraction procedures often involve accurately aimed blows which may require a certain amount of light.

When feeding in water a Limpkin often works along shore in one direction. It carries a mollusc, caught in deep water, immediately to shore or shallower water before attempting to extract it (Figure 5). The bird may extract a mollusc, caught in water up to about six inches deep, on the spot or may carry it to shallower water or dry land. Occasionally, Limpkins remove molluscs from their shells on logs or piles of floating vegetation (Figure 6). They may extract molluscs caught on land, such as aestivating *P. paludosa* or *V. georgianus,* on the spot or carry them elsewhere — sometimes to shallow water. If there is a shortage of suitably solid substrates for working on prey, the birds use certain spots over and over again, leaving large accumulations of shells (Figure 7).

Figure 6. Limpkin extracting a snail, *Viviparus georgianus,* from its shell. Occasionally, while removing molluscs or snails from their shells the Limpkins rest them on logs or, as here, on floating vegetation.

Figure 7. Feeding log of Limpkins at Wakulla Springs. When there is a shortage of firm bases on which to rest the mussels or snails for extraction, the birds often use the same one over and over again, leaving behind heaps of empty shells.

Extracting Mussels from Shells

After bringing a mussel to a substrate, the Limpkin generally rains heavy blows on it with its bill and, between blows, repositions the mussel with its bill. Since the Limpkin often extracts prey in shallow water or in thick vegetation, it was usually difficult for us to see how the bird oriented a mussel before delivering a blow. On three occasions, out of the 21 times we watched Limpkins open mussels with blows, the initial orientation of the mussel was clear: The Limpkin placed the shell hinge down, ventral edge uppermost (Figure 8), and the long axis of the shell aimed toward its feet. In one case it was clearly the anterior end of the shell that faced the Limpkin. However, damage to shells indicates that the birds do not always orient mussels in this way.

At Lake Okeechobee and 12 miles east of Belle Glade along Route 441, we collected the shells in Figure 9 immediately after seeing Limpkins open them with blows. Figure 10 shows mussel shells collected along a roadside canal south of Clewiston in Devils Gardens. We watched Limpkins open three of these with blows and then collected all the shells on the shore where the birds had been working. Limpkins had probably opened them all. On 7 March 1968, at Wakulla Springs, we took 22 mussel shells from feeding stations of Limpkins, knowing that Limpkins had opened at least six, and possibly all, with blows.

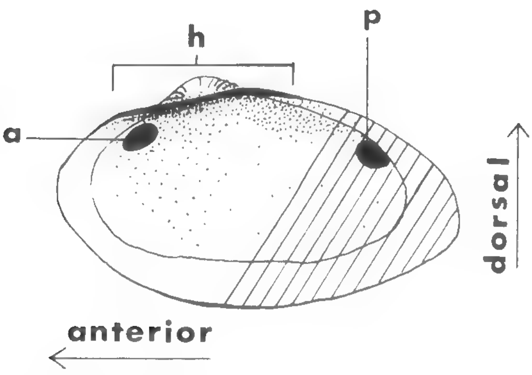
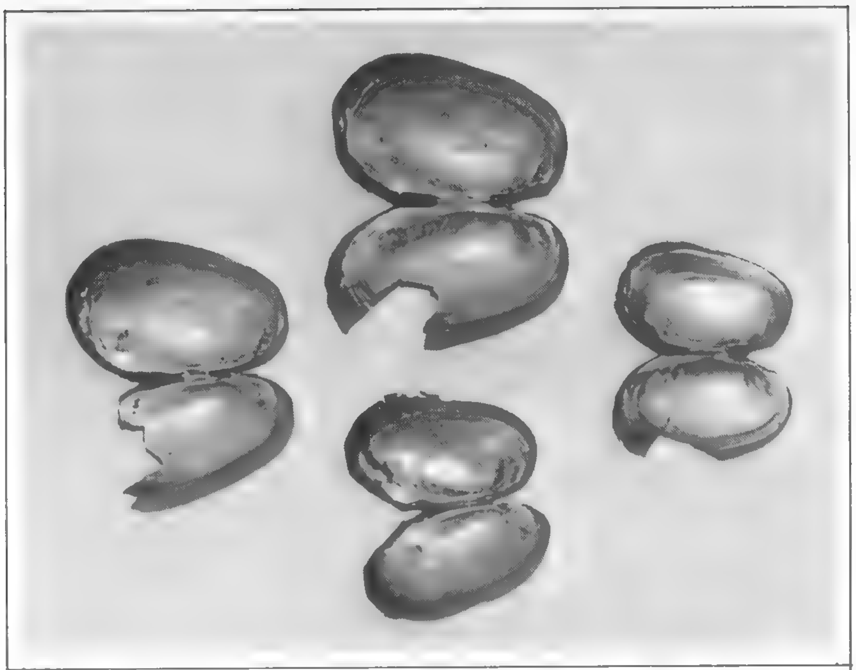
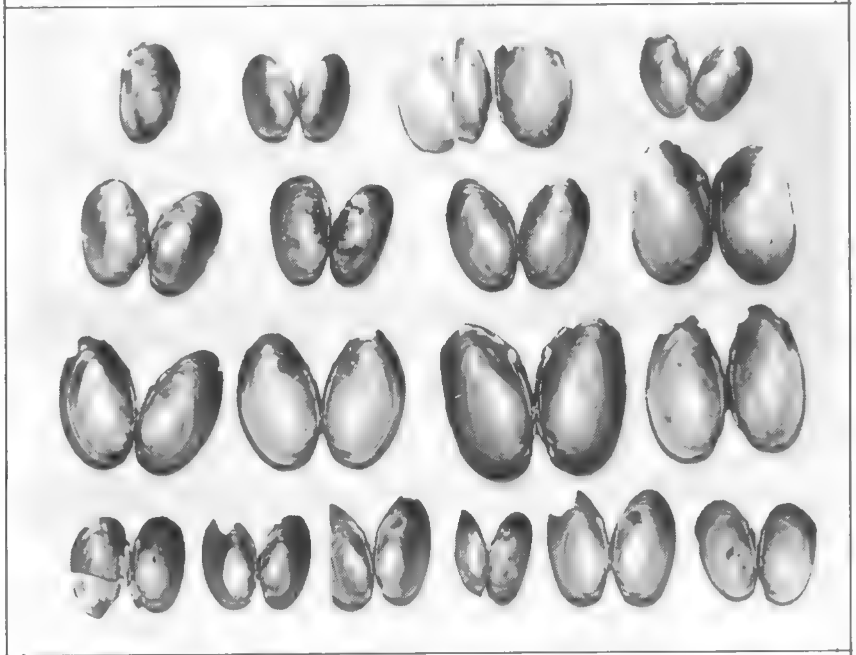


Figure 8. Typical valve of a freshwater mussel: Shaded area, the region most damaged by Limpkins; a, scar of anterior adductor muscle; p, scar of posterior adductor muscle; h, hinge of valve.

The damage to the shell is usually concentrated at the posterior ventral portion (Figure 8), the fastest growing and also the thinnest and weakest area (Norton-Griffiths, 1967). Of the 44 shells, 31 were damaged in this area alone, 11 were damaged in this area and elsewhere, and two were damaged elsewhere only. Ventral damage predominated: 23 shells were damaged in ventral areas only; 18 in ventral and dorsal areas; and three in dorsal areas alone. In 41 of the 44 shells the edges of the valves were damaged; the three others were damaged so badly we could not be certain that blows had struck the edges. Nine shells also had small holes, often paired, in the sides of the valves (Figure 11). Twenty of the 44 showed approximately equal damage to the two valves; 12 showed more damage to the left valve; eleven, more to the right; and one, since it lacked a valve, was unclassifiable. In summary, the damage indicates that mussel shells are usually placed hinge downward for blows which are usually directed at the ventral posterior end where the valves meet.

When damage is sufficient, the Limpkin jams its slender lower bill between the valves and, with its upper bill resting most commonly in the hinge region of the shell (Figure 12), cuts both muscles which hold the valves shut. When the muscles are severed, the valves spring open and the Limpkin frees the animal with a variety of manipulations, working mostly with the upper bill outside the shell and the lower bill between the valves. When the mussel is entirely free, the bird picks it up in the tip of the bill, tosses it into the air, catches it farther up in the bill, and swallows it. Sometimes, especially with large mussels, the Limpkin may eat the animal in several chunks (Figure 13). Often the bird shakes the meat vigorously before eating, sending into the air small bits of tissue which, in many cases, it never eats. The discarded valves usually show stumps of the adductor muscles and, occasionally, pieces of mantle still attached.





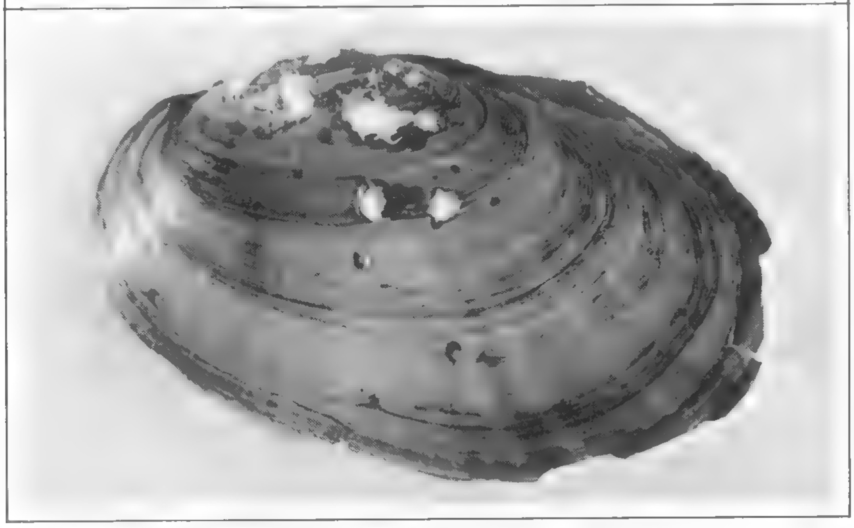


Figure 9 (*top*). Mussel shells opened by Limpkins and collected by the authors almost immediately after the birds had eaten the contents. Note the consistent damage in the posterior ventral area, the thinnest portion. For this photograph and for all other photographs of mussel shells in this paper, the authors spread the shells flat. Limpkins do not normally open mussels this far.

Figure 10 (*middle*). Mussel shells collected along a roadside canal at Devils Garden where Limpkins were feeding. The birds opened at least three and probably all of these mussels.

Figure 11 (*bottom*). A mussel shell with paired holes. There were nine shells at Devils Garden damaged in this way, presumably, by Limpkins.

Figure 12. Limpkin cutting the adductor muscles of a mussel. After the bird has damaged the shell with blows, it forces its lower bill between the valves and slices the two muscles that hold them together.

The number of blows required to gain entry to a mussel varied, in our observations, from zero to 29. In most localities Limpkins always used blows to open mussels. At Wakulla Springs, in five instances out of 17, they opened mussels without blows. Apparently the birds managed to wedge their lower bills between the valves in some other way. In one case the Limpkin already had its lower bill between the valves when it came up with the mussel. Since mussels, undisturbed in water, normally have the valves partially open at the posterior end, which faces upward, the Limpkin may have been quick enough to insert its bill before the mussel closed. The other four cases may have been similar. We were not close enough to see.

On 17, 18, 19, and 24 April 1968, at Saddle Creek Park near Lakeland, we saw a pair of Limpkins extract several dozen mussels (*Anodonta cowperiana*) without blows. Since it was clear in most cases that the birds were not getting their bills between the valves in the capturing process, we suspected there might be something peculiar about the mussels. We caught some *A. cowperiana,* by far the most common species at Saddle Creek, and found that almost all had difficulty in closing the valves tightly together even after being handled out of water for a minute or two. Apparently the Limpkins had no trouble wedging their lower bills into the space left between the valves (Figure 14). Two other less common species of mussels at Saddle Creek Park, *Villosa vibex* and *Elliptio strigosus,* did close the valves tightly, but we never saw Limpkins feeding on them at this locality.

Figure 13 (*above*). Limpkin grasping a small chunk of a large mussel, *Anodonta cowperiana*. Sometimes when the mussel is free of its shell, the bird swallows it whole; in the case of a large mussel, the Limpkin usually eats it in chunks.

Figure 14 (*below*). Opening a mussel without blows. The bird wedged its lower bill between the valves of *Anodonta cowperiana*, a species that, in this particular locality, opened slightly after being out of the water a short time.

Hudson's description of Limpkins, in Argentina, opening mussels are only speculations and do not correspond closely with our observations. He wrote (1920:173):

> Every shell has an angular piece, half an inch long, broken from the edge of one valve. Mussels and clams close their shells so tightly that it would perhaps be impossible for a bird to insert his beak, however knife-like in shape and hardness, between the valves in order to force them open; therefore I believe the Courlan [Limpkin] first feels the shell with his foot whilst wading, then with quick dexterity strikes his beak into it before it closes, and so conveys it to the shore. Otherwise it would be most difficult for the bird to lift the closed shell from the water and to carry it to land; but supposing it could do this, and afterwards succeed in drilling a hole through it with its beak, the hole thus made would have jagged edges and be irregular in shape. But the hole is, as I have said, angular and with a clean edge, showing that the bird had just thrust his beak half an inch or an inch between the valves, then forced them open, breaking the piece out during the process, and probably keeping the shell steady by pressing on it with its feet.

We have never seen Limpkins use their feet either to locate mussels or to brace them for extraction. All of the shells we have seen, opened without blows (Figure 15), had extremely little damage, only slight chips to the edges of the valves; and the shell damage Hudson described is the kind we observed in shells opened by blows. However, shells opened by blows do not always show extensive damage. For instance, in Figure 9, the bottom shell which received 29 vigorous blows is only slightly damaged at the lips of the valves.

We found evidence only once of a Limpkin failing to open a mussel. On 28 February 1968, at a Limpkin feeding station along the Tamiami Trail near Coopertown, we picked up a massive unopened specimen of *Uniomerus obesus* which showed typical but slight Limpkin damage to the posterior end.

Extracting Snails from Shells

A Limpkin carries a snail to shore gripped in a variety of ways (Figures 16 and 17). It positions the snail on a substrate with the aperture facing upward and the spire pointing toward its feet (Figure 18). With the bill the bird either immediately sets to work removing the snail from its shell or it first drives one or more, sometimes as many as eight, blows into the aperture (Figure 19,a). After a blow the Limpkin often raises its head with the snail impaled on the tip of the bill with the spire pointing down (Figure 19,b). This spire-down position of the snail was invariable in over 25 observations of nine or 10 different birds in five localities. The Limpkin then replaces the snail in the substrate and extracts the soft parts.

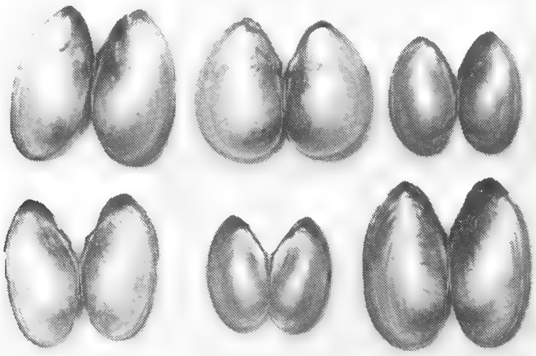


Figure 15. Shells of the mussel, *Anodonta cowperiana,* opened by Limpkins without blows. Note that the damage, if any, is very slight—merely small chips on the edges of the valves. Saddle Creek Park.

Figure 16. Limpkin carrying a snail, *Pomacea paludosa,* to shore. Note that the bird holds the snail in the space behind the tip of the mandibles.

With *P. paludosa* the blow was common, but not invariable. Though it is difficult to prove, we strongly suspect that the Limpkin only delivers blows to individuals that have pulled themselves tightly into the shell with the operculum—the doorway— sealed shut. In the Lake Okeechobee region, Limpkins opened *P. paludosa* with blows in 15 out of 18 cases. Adult *P. paludosa* collected from this region were timed for closing abilities in the laboratory. Twenty-nine of 32 specimens closed themselves into their shells more or less completely within five seconds after being picked out of an aquarium. Two of the three that did not took much longer, 45 and 57 seconds, and the third was still partly extended several minutes after removal. Thus the proportion of snails showing prompt closure was very close to the proportion of cases in which Limpkins used blows to gain entry.

At Wakulla Springs, blows to *P. paludosa* were much less common. Only eight out of 23 extractions of this snail, on 7 March 1968, were initiated with blows. An examination of living *P. paludosa* in the springs showed that many were exceedingly fat and quite unable to close the operculum completely. Of 10 snails, timed for closure on 30 March 1968, only four took less than 15 seconds and three never closed at all.

We saw a Limpkin deliver a blow to *V. georgianus* only once out of over 100 observations of five or six different birds in three localities. Figure 17 shows that snails of this species often do not close themselves tightly in their shells when removed from the water. Even when they do, moderate pressure with a probe on the face of the operculum next to the spire will cause it to pivot and permit access to the soft parts. Presumably the Limpkin can do as well with its bill.

Figure 17. Limpkin carrying the snail, *Viviparus georgianus,* to shore in the tip of the mandibles. The light spot on the snail is sunlight reflecting on the operculum that was not withdrawn into the aperture. The spire of the shell points to the upper left corner.

It appears from damaged opercula of *P. paludosa* that the Limpkin aims its blows at the shoulder of the inner edge of the operculum along the columella (Figure 20). For example, of 22 opercula collected at a Limpkin feeding station 12 miles east of Belle Glade along Route 441, 14 were damaged, all in the shoulder region. The pattern of concentric rings on the operculum (Figure 20) almost resembles a "bull's eye" for a strike. However, since the blow from the Limpkin's bill does not always damage the operculum, the bird may actually direct its blows at the seam between the columella and the operculum and sometimes avoid damaging the operculum by simply turning it aside.

Once past the operculum the Limpkin sets to work attacking the columellar muscle, which attaches the snail to its shell, and removing the operculum. In the cases we observed clearly, the shell was oriented as for blows with the spire pointing toward the Limpkin's feet. The upper bill was braced on the outside of the shell opposite the spire and the lower bill worked against it on the inside of the shell between the columella and the operculum (Figure 19,c). The lower bill tip of the Limpkin curves to the bird's right, enabling it to round the bend inside the aperture of the shell and reach the muscle attachment (Figure 21). The bird either separates the muscle cleanly from its attachment or cuts it, leaving chunks attached to the shell. Once the attachment is destroyed, the Limpkin usually shakes and pulls the snail from the shell in one piece.

We were generally unable to see how the Limpkin removed the operculum and we are still unsure as to whether this process ever precedes the cutting of the columellar muscle. A female that we watched, on 19 and 24 April 1968 at Saddle Creek Park, most certainly cut the muscle before she removed the operculum. In five extractions she did not remove the operculum until the snail was, in one case, partially pulled from the shell (Figure 19,d), and, in four cases, entirely out of the shell. For removal she oriented the operculum just to the right of her bill tips and quickly snipped at its attachment to the soft parts. The discarded operculum was entirely free of soft parts in several cases and almost free in the others. Most Limpkins, however, appear to cut the operculum free before pulling and shaking the animal from its shell. Usually no special effort is made to toss the operculum aside.

Our observations of the removal of the operculum are similar to those of others. Hall (1950:310) states that the Limpkin "draws forth the snail's operculum after a peck or two." Wetmore (*in* Howell, 1932:200): "The snail was then seated firmly on the mud with the opening pointing upward, after which the Limpkin worked the mandibles down on either side of the operculum and with a quick twitch pulled it off." And Peterson and Fisher (1955:92): "Wedging the shell firmly among the cypress roots it would work at it with the tweezer-like tip of its bill until the door of the shell, the operculum, was torn away and the soft animal extracted."

Apparently the Limpkin in Florida always, or nearly always, removes the operculum before ingesting a snail. Beside almost every discarded shell lies the operculum. Wetmore (*in* Howell, 1932:200) stated: "All through these open glades, at intervals of 10 to 50 feet, the remains of these meals were scattered. In each case the shell lay in position, undisturbed with the opening up, a few inches from the hole in the mud from which it had been taken, while the operculum lay a few inches away where it had fallen." Occasionally we did not find an operculum near a discarded shell. Whether, in these cases, the Limpkins had ingested the opercula or whether they were lost from view in vegetation or blown away by the wind was unclear. Concerning stomach contents, Cottam (1936:12) wrote: "Some of them contained small bits of the mollusk opercula." Figure 20 illustrates how the blows of a Limpkin may break an operculum into several pieces. Cottam's "bits" may represent fragments produced by blows.

In contrast, an analysis of the stomach contents of Limpkins from Argentina (Aravena, 1928) reveals that some Limpkins there regularly swallow the opercula of *Pomacea*. One stomach contained 12 opercula of *P. canaliculata*. Wetmore (1926:127) in "Observations on the Birds of Argentina, Paraguay, Uruguay, and Chile" states: "Their food consisted mainly of large freshwater snails (*Ampullaria* [=*Pomacea*] *insularum* d'Orbigny). Empty shells of these molluscs were found in abundance resting on the mud, with the opening upward and the thin corneus operculum lying a few inches away, where it had dropped after it had been pulled away." Apparently there is a variation in the Limpkin's treatment of opercula, at least in South America.

It takes the Limpkin about 10 or 20 seconds, sometimes longer, to extract a snail from its shell. Then the snail is often shaken vigorously and manipulated with the bill. Often the Limpkin removes or shakes off small chunks of flesh. These scraps and the bits of mussels, left on the ground, attract the followers one sometimes sees around feeding Limpkins (Figure 22). At different times we saw Common Gallinules (*Gallinula chloropus*), American Coots (*Fulica americana*), and Boat-tailed Grackles, all scrounging.

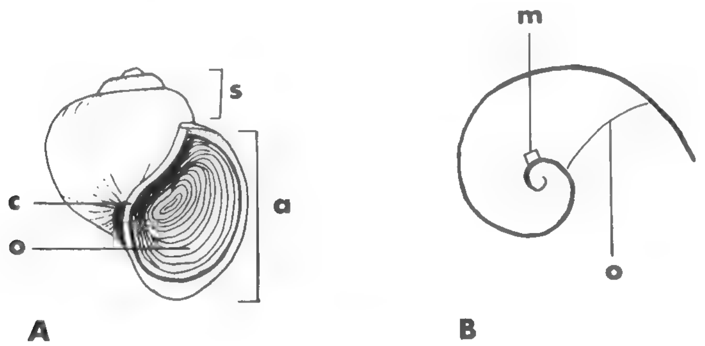


Figure 18. The shell of *Pomacea paludosa*. A, external view: a, aperture; s, spire; c, columella; o, operculum. B, transverse section: o, operculum; m, point of attachment of columellar muscle.

One organ routinely rejected by both the Limpkin and its followers is the orange-colored yolk gland of female P. *paludosa*. Rejection of yolk glands is reasonable, considering the distasteful nature of the conspicuous eggs of this snail. Guyana kites also routinely rejected the yolk glands of female *Pomacea*. We have no direct observations on the Florida kites.

The Limpkin ingests snails as it does mussels either whole or in chunks, tossing each chunk into the air, catching it farther up in the bill, and finally swallowing it.

Usually Limpkins do not damage the shells except on the lip opposite the columella where the marks, though frequent, are slight. We did find several *Pomacea* with a tiny hole, apparently produced when the blow past the operculum was strong enough to drive through the soft parts and into the shell beyond. The breakage in one shell (Figure 23,a) could only have been produced by a blow through the aperture. On 5 November 1967, on Lake Okeechobee south of Fisheating Creek, we saw a Limpkin work on a *Pomacea*, remove some of the soft parts in the standard fashion, and then pound its bill directly through the back of the shell (Figure 23,b). Apparently some part of the body remaining in the shell was inaccessible from the aperture, and the solution was to put a hole farther along. When we collected the shell, it was empty. On 7 March 1968 at Wakulla Springs, we twice watched a Limpkin pounding a hole in the spire of a previously discarded shell. Each time it extracted and consumed a small hunk of meat. An illustration in Austin (1961: 106) shows a Limpkin holding in the bill a *Pomacea* which has a large portion of the body whorl broken away. We have never seen such damage by a Limpkin, yet it does occur. According to Mrs. R. T. Peterson (pers. commun.) a Limpkin from Wakulla Springs, in Peterson and Fisher's film "Wild America," drives a blow into a large snail (presumably a *Pomacea*), smashing the shell in the process: "It then held the meat with bits of shell attached in the air and vigorously shook its head, thus getting rid of shell fragments." D'Orbigny (1846) remarks that Limpkins in South America smash shells of *P. spixii* and *P. roissyi*, but attack *P. insularum* by driving blows at the operculum. Thus the standard method of removing a snail from its shell, as described above, is not always used though it applies to nearly all the cases we saw.

There is some evidence that Limpkins occasionally swallow a snail, shell and all. Several natives of Guyana, with whom we talked in 1968, claimed that the stomachs of Limpkins they shot for food sometimes contained small snail shells.

We have never seen a Limpkin use its feet as Bryant (1859:13) describes: "Its manner of feeding is to hold the shell in one of its feet, and then with a few blows of its powerful bill to detach the animal, which it immediately swallows." Sprunt's (1948:42) description is similar: "The snail is held by one of the feet while a few strokes of the powerful bill extract the morsel which is promptly swallowed." Hall (1950:310) states: "Seizing a 3-inch snail shell in its beak, the Limpkin flies to a stump or cypress knee, places one of its feet upon it, and draws forth the snail's operculum after a peck or two. Then the Limpkin pulls out the snail and swallows it, twitching its head about as it does so." Perhaps, if there is no stable substrate available, a Limpkin may use its feet to brace the shell. We believe this is at best unusual. We have, like Hall, seen a Limpkin fly with a *P. paludosa* in its bill.

Truslow (1958), in his article on Wakulla Limpkins, observed an individual locating snails by "shuffling" its feet; extracting a snail after waiting patiently for it to "relax" its operculum; and holding an extracted snail for

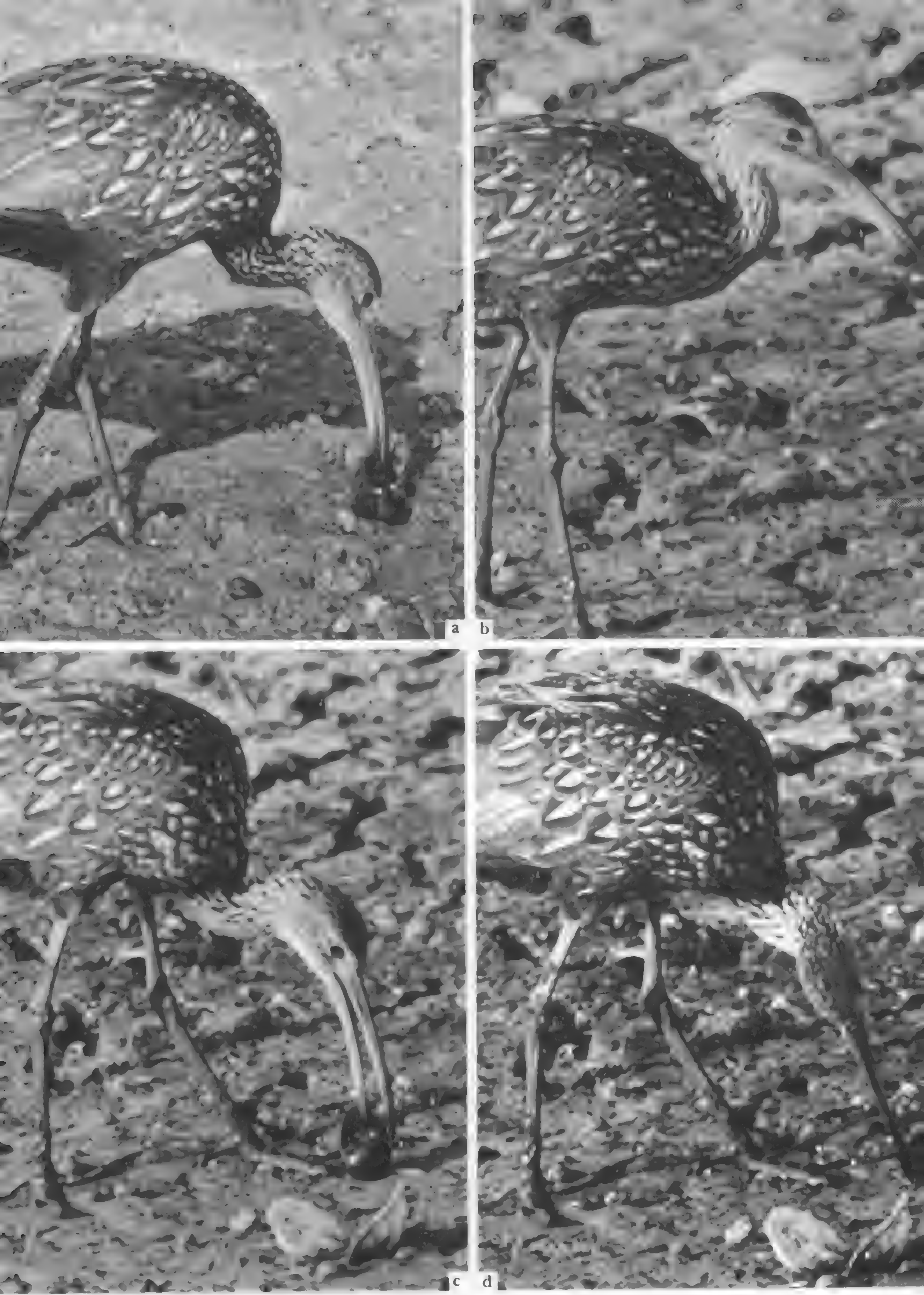


Figure 19. Limpkin extracting a snail, *Pomacea paludosa:* a, the bird strikes a blow at the aperture near the shoulder of the operculum; b, raises the shell in a characteristic position with the spire down; c, inserts the tip of its sharp lower bill through the aperture and cuts the columellar muscle; and d, removes the operculum.

Figure 20. Opercula of the snail, *Pomacea paludosa:* a, an undamaged operculum; b, an operculum damaged by a blow or blows from a Limpkin's bill. Note that the damage occurs on the inner edge of the shoulder along the columella.

a "minute or two" before swallowing it. In our observations, Limpkins at Wakulla, as elsewhere, used their feet only for walking, scratching, and standing; immediately extracted snails once they were positioned on substrates; and immediately ingested extracted snails. Truslow may have observed a frightened bird. Later observations by Truslow *et al.* (1967:544) coincide closely with our own: "Stalking shallows, the Limpkin finds an apple snail. Taking it ashore, he uses one mandible to hold the shell while the lower one deftly cuts out the meat. Jerking his head upward, *Aramus guarauna* drops the meat in mid-air, then strikes swiftly downward to catch it high in his beak."

The Limpkin's Asymmetric Bill

Hudson (1876:102) described the tip of the Limpkin's bill as "slightly bent to one side, the lower mandible somewhat more than the upper." Many authors have since called attention to this peculiarity, but its significance has remained obscure.

In the spring of 1968 we examined 252 Limpkin skins and nine skulls in the Museum of Comparative Zoology in Cambridge, the American Museum of Natural History in New York, the Academy of Natural Sciences in Philadelphia, the National Museum in Washington, and in the collections of the University of Florida, the Archbold Biological Station in Florida, and the University of South Florida. In all 252 skins, representing localities from the United States to Argentina, the bill tip is curved to the bird's right, except in one — a newly hatched chick. As Hudson (1876) observed, the curvature is

Figure 21. Lower, or ventral, view of a Limpkin's bill. Observe how the tip of the lower bill curves to the bird's right. This curvature enables the bird to reach into the aperture of the snail and around the bend to cut the columellar muscle.

usually stronger in the lower bill than in the upper (215 skins), and in 72 skins we detected no curvature in the upper bill. The degree of curvature of the lower bill varies from barely detectable to quite distinct (Figure 21), and this range of variability occurs throughout the range of the species. Of the nine skulls, the underlying bones of the bill are curved in only one, a skull from Bolivia in which the lower bill tip is very slightly curved to the right. The curvature then is primarily in the horny sheath of the bill—a rhamphothecal phenomenon.

At least one function of the curvature is obvious to anyone who has tried to remove a *Pomacea* from its shell. Even using a hook or pliers it takes considerable brute force to pull a snail free, and one frequently rips the animal to shreds. Since the Limpkin does not, in our observations, brace the shell with its feet, it cannot be using this method. If one jabs a scalpel into the shell between the operculum and the columella and cuts the columellar muscle, which holds the snail in its shell, one can sometimes remove the snail in one piece, except for large chunks of muscle left attached to the columella. Limpkins do a cleaner and quicker job. For example, six of 11 shells of *P. paludosa* collected at Saddle Creek Park immediately after Limpkins had discarded them, were entirely free of columellar muscle; five still had small chunks attached. Finally, if one uses a blunt probe, curved at the tip to resemble a Limpkin's lower bill, and aims at the columellar muscle, one can remove the soft parts of the snail fairly simply. However, even this method generally leaves some muscle in the shell. Since the columellar muscle attaches to the shell "around the bend" as one looks into the aperture (Figure 18), it is impossible to cut it cleanly with a straight scalpel without first breaking back the lip of the shell. The utility of the curved bill tip in cutting the muscle is clear. Since the Limpkin is faced with essentially nothing but right-handed snails in its range, and since, so far as we know, it always positions snails in the same way, the curve follows appropriately into the shell and part way around the bend to the attachment of the muscle.

It is one thing to say the asymmetrically curved lower bill is useful in extracting snails and quite another to say that the curvature is an adaptation for this function. Perhaps it is merely fortuitous that the curvature is useful in extracting snails. In some Limpkins the curve is so extremely slight (barely detectable in 15 of 252 skins), it could hardly be much help in cutting the columellar muscle. If the primary function of curvature is extraction of snails, why the great variability in the amount of curvature?

Barrows (1884) suggested that the asymmetry may result from the process of entering shells. Perhaps the blow a Limpkin commonly delivers to the inner edge of the operculum tends to enforce a pattern of asymmetric growth (Figure 19,a). One can argue that the Limpkin consistently positions the snail for blows as it does because a blow to be effective must presumably transmit appreciable force to the object struck—a glancing blow is a wasted blow. If a Limpkin were to position a snail with the spire pointing away from the bird's feet, there would probably be a tendency, considering the arc described by the strike, the shape of the shell, and its position, for blows directed at the inner edge of the operculum to glance off. With the spire pointing *toward* the Limpkin's feet the bulk of the snail backs up the point of contact and blows can be consistently effective. If a consistent orientation of the shell for blows is reasonable, a consistent asymmetric resistance to blows is possible. Should asymmetry be produced in the bill tip, there is only one sensible orientation of the snail for attacking the columellar muscle.

Figure 22. Boat-tailed Grackle standing beside a Limpkin. While the Limpkin extracts a snail, the Boat-tailed Grackle waits, watching for any scraps that the Limpkin might discard. The grackle is but one of several species that often follow Limpkins.

As mentioned earlier, *Pomacea* does not occur natively on the islands of Puerto Rico and Hispaniola. The large land snails of these islands, on which the Limpkins may feed, are all right-handed and lack opercula. If bill asymmetry is the result of striking blows to the opercula, we might expect to find that Limpkins from these islands have straight bills. The 19 specimens of Limpkins from Puerto Rico and Hispaniola, that we have seen, all have asymmetric bills though the curvature is generally slight.

In 1968 we examined many species of living land snails in Puerto Rico, but found no Limpkins. These birds are now possibly extinct there. The large land snails generally attach far in the interior of their shells and are able to withdraw out of sight from the aperture when disturbed. It is doubtful that the Limpkin's asymmetric bill could have been of much help in extracting these snails. If Limpkins did eat them, they probably smashed the shells in the process. One large snail, as yet unidentified, has a relatively small shell and, instead of withdrawing when disturbed, secretes slime. Possibly, an asymmetric bill could help in removing most of the meat from the shell of this species though one wonders about its palatability.

In general, the properties of the large land snails of Puerto Rico do not give obvious support to either the adaptive or developmental hypothesis for the Limpkin's asymmetric bill. Since we did not examine snails in streams, we do not know whether or not the features of aquatic snails could account for bill asymmetry here.

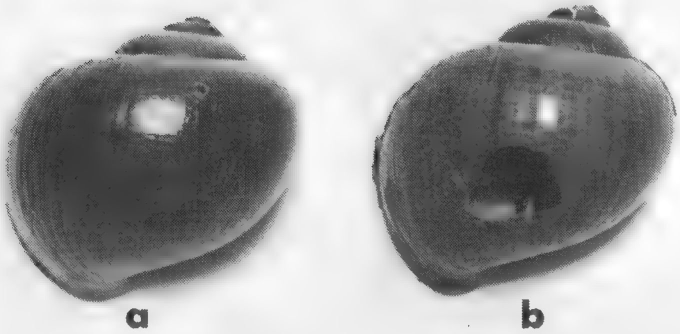


Figure 23. Shells of *Pomacea paludosa* damaged by Limpkins: a, probably by a penetrating blow into the aperture, past the operculum, and through the soft parts to the shell underneath; b, by a direct blow after the Limpkin had removed some of the soft parts of the snail in the usual way.

Perhaps the many cases of curvature in the Limpkin's upper bill are evidence for the developmental hypothesis. Although both upper and lower bills are driven into the aperture, only the lower bill is used to work on the columellar muscle (Figure 19,c). Very likely, from the paired holes in mussel shells (Figure 11), the upper and lower bills are often separated at the moment of contact with a shell. If both bills were subjected to an asymmetric resistance during blows, we might expect the lower to be bent more because it is a weaker structure. However, one could argue, from an adaptation standpoint, that curvature in the lower bill leads to curvature in the upper so that the bird may seize objects in the bill tip.

One question is, why not asymmetry to the left? The developmental hypothesis automatically dictates right-handed asymmetry because of the way right-handed snails are best oriented for blows. A straight adaptation hypothesis has more difficulty with this question. Two thoughts come to mind. First, assuming the same orientation of the shell for blows, a right-handed bill may be an advantage when driving a blow to the inner edge of the operculum, and second, it may be easier to cut the columellar muscle by proceeding away from the spire than toward it. Experiments with a curved probe have not given strong evidence either way.

Is curvature related to mussel-feeding? It seems unlikely that a curved bill is useful for damaging the valves or cutting adductor muscles, but, because a curved bill can nestle along the curves of a valve, it might help in scraping the

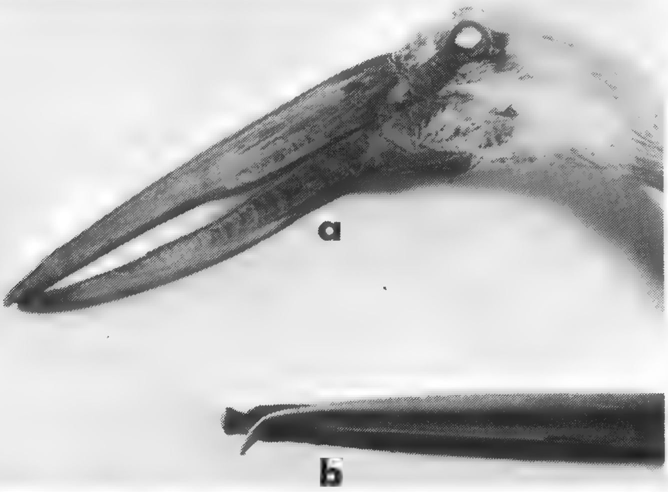


Figure 24. Bill of the Asian Open-billed Stork: a, side view showing the opening behind the bill tip; b, lower, or ventral, view. Note how the tip of the lower mandible bends to the right.

Figure 25. Profile of the Limpkin showing the space between the mandibles back from the tip of the bill. This space may be useful in grasping snails in floating vegetation as well as carrying them to shore, as shown in Figure 16.

Figure 26 (*above*). Everglade Kite foraging for snails, *Pomacea paludosa*. The kite flies low above the marsh, into or across the wind. When it sees a snail, it brakes quickly and descends into the wind to the surface of the water.

Figure 27 (*below*). Rising from the water with a snail in its right foot. When seizing a snail, the kite touches the surface of the water only and may use either foot.

animal out of the shell. Could asymmetric wear in such scraping result in an asymmetric bill? Again we face a development or adaptation dilemma.

In connection with mussel-feeding we might consider the bills of oystercatchers (*Haematopus*) which feed heavily on marine bivalves. We examined seven skins in the University of Florida collection—four of *H. palliatus*, two of *H. ostralegus*, and one of *H. bachmani*—all from Florida or South Carolina except one of *H. bachmani* from Alaska and one of *H. ostralegus* from Manchuria. In this small sampling, the bill tip, both upper and lower, is asymmetric to the bird's right in two skins, to the left in three skins, and straight in one skin. The bill tip of one was broken. Four of the specimens have a concavity at the base of the upper bill on the bird's right. Though Stresemann (1929:438-439) and Webster (1941:177) note asymmetry in the bills of oystercatchers, and many authors discuss the feeding behavior of oystercatchers, the significance of asymmetry is obscure. Since mussels themselves are bilaterally symmetrical, it seems reasonable for the bill tips of oystercatchers to lack a consistent asymmetry to one side or the other. Oystercatchers use a variety of methods in attacking mussels—often prying open shells with the bill—something we did not see Limpkins do. Perhaps the prying movements, if they are biased to one side, develop an asymmetry of the bill tips. However, since the asymmetry of the bill tips in the specimens we examined bears no consistent relationship to asymmetry at the base of the bill, and since oystercatchers also feed on snails occasionally (Dewar, 1910), the question is too complicated for armchair speculation. That the bill tip of the Limpkin, unlike that of the oystercatcher, always bends to the right may be one argument against mussel-feeding as a primary cause of asymmetry. If asymmetry in Limpkins is unrelated to mussel-feeding and is developmentally produced by snail opercula, the specimens we examined with barely detectable asymmetry may have fed primarily on mussels.

In the Far East, the Asian Open-billed Stork (*Anastomus oscitans*) feeds extensively on right-handed, freshwater snails of the genus *Pila*, closely related to *Pomacea*. The lower bill tip in 17 of the 19 specimens of this stork species in the Museum of Comparative Zoology, the American Museum of Natural History, and the University of Michigan is asymmetric to the right (Figure 24). The other two specimens have straight lower bills and none of the 19 specimens has asymmetry in the upper mandible.

Although the African Open-billed Stork (*Anastomus lamelligerus*) reputedly feeds on snails and mussels as heavily as does the Asian Open-bill, not one of 41 specimens we examined has an asymmetric bill. Dr. M. Philip Kahl (pers. commun.) has seen one skin of this species with slight asymmetry to the right in the lower bill. Unlike the Limpkin and Asian Open-bill, the African Open-bill Stork faces large left-handed as well as right-handed snails in its range: the snail genus *Lanistes*, closely related to *Pomacea* and *Pila* and common in Africa, is left-handed; right-handed snails of the genus *Pila* and family Viviparidae also abound. The lack of asymmetry in the bill of the African Open-bill may be due to the impossibility of adapting one curve to both right and left-handed shells. Or, developmentally, the lack of consistent resistance by shells to either one side or the other of the bill tip may give no impetus to asymmetric growth. Since both Open-bills feed on mussels, we can use the presence of asymmetry in the Asian form and the lack of asymmetry in the African as an additional argument against a relationship between the asymmetry of the Limpkin's bill and mussel-feeding.

Huxley (1960) summarized most of the published information on the feeding behavior of open-billed storks. He speculates primarily on the function of the space between the mandibles, favoring the idea that the storks crush snails under water in this space, and does not mention the asymmetry of the bill tip. Although observers agree that these storks often extract snails under water, there is no evidence of anyone ever finding any crushed shells.

Dr. Kahl has made extensive observations on the feeding behavior of both open-bills, has watched them extract many molluscs, and has examined the discarded shells. He reports (pers. commun.) that the methods, used to extract molluscs, are apparently very similar to those of the Limpkin. With snails, the lower mandible cuts the soft parts free from the shell while the upper mandible remains braced on the outside. Though he is not certain of the exact orientation of the snails, Dr. Kahl feels that very likely the storks attack the columellar muscle by forcing the lower mandible between the operculum and the columella. Shells are not crushed and usually have no more than minor damage. The lip of the shell is sometimes broken back for a few millimeters, possibly making it easier, especially for the African Open-bill with its straight lower mandible, to attack the columellar muscle. Like Limpkins, open-bills usually, but not always, snip off the operculum prior to ingestion of the soft parts. Dr. Kahl saw the storks extract mussels by forcing the slender lower mandibles between the valves, a method similar to that used by Limpkins at Saddle Creek Park on *A. cowperiana.*

In contrast to Limpkins, open-billed storks rarely deliver blows to shells. We know of only one report — that of an Asian Open-bill striking mussels (Henry, 1955:383-384). Dr. Kahl has never seen either species of open-bill use blows on either mussels or snails.

That Asian Open-bills usually have asymmetric lower bills yet rarely, if ever, drive blows to snails might be an argument against the hypothesis that the resistance to blows by opercula of snails develops a curve in the Limpkin's lower bill. However, as Dr. Kahl suggests, the process of wedging the bill past a tightly closed operculum might bend the bill of the stork just as the driving of blows may bend the bill of the Limpkin.

In any event, we cannot explain the consistent right-handedness of the lower bill of the Asian Open-bill, as we can the Limpkin's, by the orientation of snails for blows. It must be related to more subtle features of the extraction procedure. Perhaps Asian Open-bills orient snails for extraction, as do Limpkins, with the spire aimed toward their feet and perhaps it is easier to wedge the lower bill past the operculum in this position than in any other. On the other hand, the important thing may be the direction of attack on the columellar muscle.

In summary, with the Limpkin and the Asian Open-billed Stork the question as to whether the asymmetry of the bill is produced genetically or developmentally may best be answered in the laboratory with birds raised from eggs and fed controlled diets: either mussels alone, right-handed snails alone, left-handed snails alone, or molluscs lacking shells.

Another peculiarity of the Limpkin's bill is the frequent presence of a slight space behind the tips of the mandibles (Figure 25). Of the 252 specimens, 194 had a clear space and there was no correlation between the presence of the space and the locality of collection. Wetmore (*in* Howell, 1932:200-201) stated: "The two halves of the bill were separated by a slight aperture behind the point, giving the tips of the mandibles a tweezer-like arrangement that was probably of assistance in the manner of feeding followed by these birds." Huxley (1960) suggested that the space in the bills of open-billed storks and Limpkins may help these species in grasping shells. This is a good hypothesis when we consider a Limpkin probing for *Pomacea* in floating vegetation with the bill partially open. According to Dr. Kahl, open-billed storks also commonly forage this way. For the Limpkin there is presumably a great advantage in being able to grasp the snail on contact because a *Pomacea* reacts to a mechanical disturbance by dropping quickly to the bottom and, if the water is deep, out of reach. The snails that open-bills feed upon may drop in the same way. The space in the bills of all of these birds may be useful in grasping instantly the smooth rounded shells. Whether the birds grip the snails in the tips of the mandibles (Figure 17), apparently the usual case in all three species, or in the space itself (Figure 16), the mere presence of the space changes the angle of closure of the bill tips and probably reduces the chance of the mollusc slipping away. The rough ridges that line the lower surface of the upper mandible of the open-billed storks may also help in grasping shells.

Dr. Kahl suggests that the space between the mandibles may be important in orienting the bill tips for extracting molluscs. Of course, there is no reason why the space cannot be useful both for capturing prey and extracting them from their shells. Curiously, the space is more developed in open-billed storks than in Limpkins, yet, so far as we know, the three species feed on molluscs of about the same shape and size.

In both the Limpkin and the open-billed storks, the tip of the lower bill is very slender, a feature that may help in slipping it past the operculum of a snail and between the valves of a mussel.

And finally, we should note the ossification of the tendons of the jaw muscles in the Limpkin, concerning which Allen (1962:326) wrote: "This characteristic is most pronounced in the jaw musculature, where the ossification may aid in maintaining proper direction of pull for proper leverage in operation of the long bill. Otherwise the specializations in the feeding habits of *Aramus* do not seem to be associated with significant modifications of the jaw musculature."

Feeding Behavior of the Everglade Kite

Foraging Behavior

The foraging behavior of the Everglade Kite is relatively non-controversial. The kites generally fly leisurely at a height of from five to 30 feet over marshes containing *Pomacea.* They flap more or less continually with only brief moments of sailing and little of the tilting so characteristic of Marsh Hawks (*Circus cyaneus*) in flight. They fly generally into the wind or across it with the head inclined downward, watching the marsh below (Figure 26). At intervals they sail back downwind. On sighting a snail a kite stalls quickly, descends into the wind, grabs the snail in one foot, and flies (Figure 27).

The bird does not plunge into the water like an Osprey (*Pandion haliaetus*), but descends to the surface only. It may grab the snail with either foot, but often transfers it to the bill during flight (Figures 28 and 29). Several times we saw a kite drop a snail after transferring it to the bill. We suspect that it was rejecting a dead snail or an empty shell rather than being clumsy, but we could not find any of the rejected shells. Nicholson (1926:66) states: "I have seen Kites extracting a snail while flying, and also while perched." Howell (1932:169): "The snails are sometimes shifted from the foot to the bill and occasionally are eaten by the Kite while flying." Most authors do not report kites extracting snails in flight. Possibly a kite transferring a snail and then dropping it while in flight might give the impression, from a distance, of feeding on the wing.

Figure 28 (*above*). Everglade Kite just after landing on a feeding perch. The bird transfers the snail from the foot to bill and, in this instance, grasps it by the operculum.

Figure 29 (*below*). Finishing the removal of the operculum. The kite holds the snail against the feeding perch with its foot and removes the operculum of the snail with its bill. Note the operculum dangling from the shell—almost ready to drop to the ground.

Holgerson (1967) in an unpublished report, Bureau of Sport Fisheries and Wildlife, and Nicholson (1926:66) described another type of foraging behavior in the kite, that Holgerson terms "still-hunting." In Holgerson's description: "Still-hunting is most commonly performed from a low stub perch, 1-4 feet high, on the edge of a slough. Occasionally the bird perches on sawgrass or uses stubs 8-10 feet high. Low stubs out in the sloughs are also utilized at times. A kite that is still-hunting perches quietly and erectly and keeps an intent watch on the marsh about its perch. Captures of snails are made within a radius of 5-10 feet and this may extend to 20 feet when the higher perches are used. The captured snail is carried back to the same perch or to another one nearby." Paul Sykes was with us the one time we saw a kite still-hunting. The bird, in brown plumage, made an unsuccessful pass at a snail a few feet from its perch on a low stub in the middle of a slough in the eastern Everglades.

In Guyana we saw many Everglade Kites still-hunting from fence posts along canals and rice fields. Probably there is no intrinsic difference between the foraging methods of these two kite populations. The Guyana birds still-hunt more frequently because they have many more suitable perches. Once we saw a kite capture a *Pomacea dolioides* by still-hunting from the ground in a partly flooded pasture. According to Haverschmidt (1959), the Slender-billed Kite (*Helicolestes hamatus*), a bird in Surinam that is quite closely related to the Everglade Kite, tends to feed along heavily wooded streams and pools and uses still-hunting in capturing *Pomacea.*

Everglade Kites capture *Pomacea* close to the surface only; Limpkins may pluck snails from a depth of two or more feet. Surface-feeding may be the primary cause of the specificity of the kite's diet. As mentioned before, other large snails in Florida, of the genera *Viviparus* and *Campeloma,* are bottom dwellers rarely venturing up on surface vegetation. Lang (1924) makes a similar point about the food selection of the Everglade Kites in coastal Guyana where they feed heavily on *P. dolioides,* which occurs near the surface, and only occasionally on the abundant *P. glauca,* which is generally found deeper in the water. Our observations on food selection by Guyana kites accord with those of Lang. Among 2,000 empty *Pomacea* shells dropped by kites Lang found only two of *P. glauca.* Pain (1950) reports kites feeding extensively on *P. dolioides* in coastal Guyana and on *P. papyracea* in the interior. Haverschmidt (1962) has a photograph of 246 *P. dolioides* shells under a kite feeding perch in Surinam.

Lang (1924) states that Everglade Kites in Guyana restrict their foraging to late afternoon. In Florida and Guyana the kites forage more or less continuously during the daylight hours.

Extracting Snails from Their Shells

How Everglade Kites extract snails from their shells has been debated for many years. Lang (1924:76-77) describes kites feeding on *P. dolioides* in Guyana:

> It is absolutely necessary for them to have an opportunity to perch to remove the mollusk from the shell. Time and patience are then given full play, and as many as ten may be seen in the branches at once awaiting the opportune moment. Every new arrival is greeted with the oft-repeated harsh call 'Kor-ee-ee-a—Koree-a'.
>
> The hawks then perch on one foot and with the other quietly hold the snail in such a manner that it can emerge from the shell. The birds make no attempt whatever to extract it by force, but watch for the voluntary extension of the animal beyond the aperture of the shell. With that propitious moment comes the next step in the drama. Quick as a flash the hawk's bill pierces the snail apparently back of the operculum. It happens so rapidly that one is not able to clearly follow the operation. As a further

> step the snail, now spiked upon the beak, is instantly pushed up to the middle of the upper bill from which it stands off like a bump as big as a large walnut. Then begins a second wait. Gradually the mollusk's muscles relax. A few minutes later the Snail-hawk vigorously shakes its head and before even the light, empty shell has reached the grassy ground *Rostrhamus* has swallowed its victim, operculum and all. It would be necessary to shoot a few of these birds just after the snail is spiked or swallowed to ascertain at what point it is actually pierced. It is certainly always done in the same fashion, for the fragile shell is never injured, not even the tender edges of the aperture. As the mollusk of course exerts its full power of muscular contraction, the bill, evidently inserted behind the operculum, is caught between the operculum and the wall of the whorl about opposite the middle of the edge of the aperture.

Murphy (1955), writing of Everglade Kites in Argentina, essentially echoes Lang's description but adds a twist of his own by suggesting that the mechanism of removal of the snail involves the piercing of a "nerve plexus" by the bill of the kite. In his words (1955:205): "The long, slender bill is used not as a hook but as a lancet or poinard. It is a feat of instinctive correlation as exact as that of the spider-paralyzing wasps." Murphy and Amadon (1953:32): "It feeds exclusively on certain fresh-water snails of the genus *Ampullaria* [= *Pomacea*]; with its slender, curved upper mandible it pierces these in a nerve plexus, and the snail, soon rendered numb, virtually falls out of its shell." Pain (1950:67) quotes, but does not cite, Lang's description of the kite and adds: "In the vicinity of Georgetown [Guyana] I have watched these hawks treating *P. dolioides* (Reeve) in a like manner. As many as 2,000 shells have been counted beneath one of the trees on which these birds habitually perch. The shell is usually uninjured, but the operculum is always missing." It is not clear whether "the operculum is always missing" refers to Pain's own observations. In Haverschmidt's (1962) photograph of a pile of *Pomacea* shells under a kite's feeding perch in Surinam there are no opercula visible. However, the scale is so small that the opercula might not show even if they were present.

Stieglitz and Thompson (1967:17), regarding kites in Florida, apparently agree in general with the Lang-Murphy description: "Our observations indicate that adult kites swallow snail bodies whole after they have extracted them from the shells which are discarded. Some observers have reported seeing kites extract the snails while in flight, but the extraction process that we observed has been confined to perched birds. Usually a kite will sit on its perch for several minutes after capturing a snail before attempting extraction, but sometimes it will extract it immediately."

Howell's (1932:169) report of kites in Florida contrasts to the above: "Upon seizing a snail in its sharp talons, it carries it to a nearby bush or little mound, where the mollusk is extracted from its shell with the sharp, hooked bill of the bird and swallowed in pieces about a half or three-quarters of an inch in length." Sprunt (1905:384): "The snail is neatly extracted by the kite's specialized beak, torn apart and swallowed." And Peterson and Fisher (1955: 117): "Our snail kite had found its snail; holding on to a cluster of reeds with one foot and grasping the snail in the other, it carefully picked the animal bit by bit out of its shell by means of its curious slender hooked beak." According to Steffee (1966:42), kites in Surinam "tear the snail out of the shell," a description closer to Howell's than to Lang's.

Holgerson (1967) gives detailed observations on kites extracting snails in Florida:

> After catching a snail the kite flies to a perch, usually a dead tree stub or snag. The snail is carried in the foot or the bill, to which it may be transferred in flight soon after capture. Upon perching the kite usually begins working at the snail with its bill immediately, holding the snail in one foot against the perch. When the snail is carried

> to the perch in the bill it is usually taken in the foot immediately after perching. Sometimes the kite pulls the snail meat from the shell in pieces, swallows them and drops the shell at the completion of feeding. Other times the snail meat is extracted whole, the shell is dropped, and the kite then pulls off and swallows pieces of the meat which is held against the perch in a foot. Individual kites will use both methods, eg., a kite observed on June 20, 1966 ate two snails by the first method and two by the second method. The extraction of the snail meat in one piece is performed quickly and efficiently, in from .5-2 minutes after perching. Regardless of the method, the entire extraction and feeding is completed in a maximum of 3-4 minutes. No kite was observed swallowing the snail meat entire.
>
> During some extractions the kite will hold the whole snail in its bill for one or more intervals of 5-15 seconds. This may be done right after perching or after extraction has commenced, eg., on July 15, 1966 an adult female flew to a perch with a snail in her foot. The snail was taken in the bill, transferred back to the foot, taken in the bill again and transferred to the foot again. These movements may serve to position the shell properly for extraction.
>
> * * *
>
> The fate of the operculum during the extraction process is difficult to observe. I never definitely saw it swallowed. Twice I saw kites discard something during extraction and it was probably the operculum each time. On one occasion a sub-adult male was clearly seen to pull the operculum loose and flip it aside with his bill. A kite feeding perch inspected December 29, 1966 had nearly as many opercula beneath it as there were discarded snail shells.
>
> I have yet to see a kite perched on one foot while holding a snail raised in its other foot. I have also not observed any kite with a snail speared on its maxilla. The Everglade kites I have observed have extracted snails more in the manner described by Howell (1932) and Peterson and Fisher (1955) than in the manner originally described by Lang (1924) and reiterated by Murphy (1955).

Although our observations agree with those of Holgerson in almost all details, he did not describe a mechanism by which kites free snails from their shells. As far as we know the only author who has recognized the crux of the extraction problem is Lopes (1956:535). In an anatomical study of a Brazilian snail (*Pomacea canaliculata*), he recommends a method for removing snails intact from their shells, imitating the Everglade Kite which in Brazil, he says, enters the snail with its beak between the operculum and the columella, and then frees the snail whole by destroying the columellar muscle. He suggests a metal tool, bent to resemble a kite's upper bill, which can quickly and cleanly remove the snail from its shell. At the Patuxent Wildlife Research Center, Bruce Williams and others in charge of feeding Everglade Kite nestlings devised this same method independently.

Thus the Everglade Kite, like the Limpkin, must contend with the columellar muscle which attaches a *Pomacea* to its shell. In laboratory experiments with *P. paludosa* we found no evidence to support the ideas of Lang and Murphy that a snail can be detached from its shell by simple relaxation of the snail's muscles or by piercing of a nerve plexus. Though Lang and Murphy observed extractions of species other than *P. paludosa,* we know of no *Pomacea* lacking a columellar muscle. *P. dolioides* has a muscle attachment similar to that of *P. paludosa.*

We observed wild Everglade Kites extracting *P. paludosa* in several localities in Florida, wild kites extracting *P. dolioides* in Guyana, and captive kites from Argentina extracting *P. paludosa* at Patuxent, Maryland. The birds from Argentina, captured as nestlings, were raised first on snails (*Viviparus*) lacking both shells and opercula, later on snails lacking shells but possessing opercula, and finally on unmodified snails. The methods of extractions they used were the methods of captive birds and may not reflect the feeding behavior of wild adult kites in Argentina. Nevertheless, as far as we could determine, these captive birds extracted snails in the same way as did wild birds in Florida and Guyana.

In our observations the Argentine birds, housed in long indoor flights, were fed on *P. paludosa* placed in pans on the floor beneath their perches. Most birds, uneasy in our presence, interspersed their feeding with periods of vocalization and staring. We witnessed seven extractions from distances of from two to three feet up to 10 to 15 feet. In each case the bird flew down, grabbed a snail in one foot, and returned to its perch. In working on the snail, a kite held it against the perch with the left foot or with both feet. Usually, it positioned the snail with the spire pointing down and the aperture facing away from the perch. The kite worked to get the tip of its upper mandible hooked around an edge of the operculum, often the edge closest to the spire. The lower mandible rested outside the shell while the upper extended across the face of the operculum and probed for a crack between the operculum and the lip. We often heard the grating sound of the upper mandible scraping across the face of the operculum on unsuccessful tries. Once the bird got the tip of its upper mandible around the edge of the operculum, it removed the operculum by pulling at it with both mandibles and apparently cutting its attachment with the upper mandible. It flipped the detached operculum aside and repositioned the shell so that the aperture faced upward and the spire pointed to the bird's left. Holding the snail in this position with its feet, and with the lower mandible outside the shell, the bird thrust its long curved upper mandible into the aperture and around the bend to the attachment of the columellar muscle which it cut with a few strokes. With both mandibles it pulled the freed snail from its shell. In most cases, the bird ate the snail in several chunks, starting with small chunks of viscera and finishing with the bulk of the animal including the foot. In one case it ate the snail whole. As in Mr. Holgerson's report, the bird dropped the shell either immediately after the snail was free or after eating part or all of the snail. Like Mr. Holgerson, we sometimes saw a kite hold a snail in the bill for a variable length of time and then replace it under the feet. Unlike him, we did see a kite occasionally clutch a snail in one foot and lift it somewhat off the perch.

We examined the shells and opercula, worked on by the Patuxent kites, for damage (Figure 30). In all the shells, except one, small hunks of attached columellar muscle were visible from the aperture. Similarly, all opercula had very small hunks of muscle still attached. The only damage to the shells was at the lip of the aperture where small chips had been broken off. The damage to the opercula was more extensive: four were damaged primarily at the end closest to the spire, two were essentially undamaged, and one was damaged near the shoulder, the same region damaged by Limpkins. Four of the seven opercula were scratched presumably by the upper mandible attempting to hook over the edge.

Our observations on wild Everglade Kites are very similar to those at Patuxent and to the observations of Mr. Holgerson though most of the several dozen extractions we witnessed in the field were seen from such a distance it was impossible to make out fine details. We could see kites gripping the snails in their feet and repeatedly raising and lowering their heads in working on them. Occasionally, we saw a kite lift a whole snail in its bill for a few seconds. They dropped shells either before or after ingestion of the soft parts. We never saw kites waiting for snails to extend themselves beyond the aperture although, if one takes a *P. paludosa* out of the water and places it on shore in the sun, it will often extend after a delay of several minutes. In our observations, as in

Figure 30. Shells and opercula (lower row) of the snail, *Pomacea paludosa,* worked on by captive Everglade Kites at the Patuxent Wildlife Research Center. The birds removed the snails from their shells, damaging the shells only slightly at the lip of the aperture and scratching and breaking the opercula at the end closest to the spire.

Holgerson's, kites began extraction procedures immediately after they reached feeding perches. On 2 December 1967 along the Tamiami Trail, timing of eight extractions are comparable with those of Mr. Holgerson—seven between one and one and three-quarters minutes, and one, where possibly the removal of the operculum was difficult, from 11 to 12 minutes. We were close enough to observe the removal of the operculum and the orientation of the shell for the severing of the columellar muscle just four times — on 7 April and 2 November 1968 in a slough in the eastern Everglades. The procedure was identical to that of the birds at Patuxent (Figure 29).

On 17 March 1968, with Mr. Sykes, we collected in a kite nest (Figure 31) from which the young had just fledged a total of 66 shells, four opercula, and four whole unextracted snails—one decayed and three still alive. Twenty-seven of the 66 shells had essentially no damage; 39 had minor chips in the lip of the aperture, and in 14 of these the chips were concentrated adjacent to the spire. Forty shells still had hunks of columellar muscle visible from the aperture with a mirror; 22 were clean; three contained snails lacking opercula; and one contained about half a snail. Of the four opercula, two were essentially undamaged and two had small nicks at both ends. Scratch marks, generally parallel to the long axis of the operculum and concentrated on both ends, were visible on the faces of two opercula. Three of the unextracted snails also had scratch marks on the opercula; in two of these, the marks were similar to those described above; in the third, the marks were distributed quite generally over the surface, but usually perpendicular to the edges. Shells and opercula, collected from another kite nest and from beneath several kite feeding perches, showed similar damage.

Considering the number of shells in this nest, four opercula seems a very small number. Perhaps kites in Florida do sometimes ingest opercula. How-

Figure 31 (*above*). Nest of an Everglade Kite. The young have just fledged, leaving behind the shells of 66 snails, four opercula, and four whole, unextracted snails.

Figure 32 (*below*). Male, identified by the black plumage, landing near his nest. Dangling from the kite's bill is a snail lacking both shell and operculum.

ever, two other explanations could account for the dearth of opercula in the nest: first, the nest was high in a dead stub fully exposed to the wind, and the light opercula might easily have been blown or been flipped into the water below. Second, the adult kites may sometimes remove opercula before bringing in otherwise intact snails to the nest. At two other kite nests, on 7 and 27 April 1968, we photographed many instances of adults bringing in *Pomacea* to feed their young (Figure 32). As best we could determine from observations and photographs, the adults at these nests always brought in fully extracted snails lacking shells and opercula. Thus the stage of extraction at which snails are brought to nests is variable.

Cottam and Knappen (1939) report only "fleshy remains" of 20 *Pomacea* in the stomachs of four Everglade Kites from Florida. Presumably, had opercula been present they would have mentioned the fact because Cottam (1936) earlier reported "bits" of opercula in Limpkin stomach analyses.

We observed at close range many Everglade Kites feeding on *P. dolioides* in several localities of coastal Guyana, the country where Lang (1924) made his observations. The birds were indistinguishable from Florida Everglade Kites in appearance and feeding behavior. Briefly, our observations differ from Lang's as follows: (1) Kites did not wait for voluntary extension of snails. They began extraction procedures as soon as they reached the feeding perches. (2) Kites removed opercula from snails before ingesting the soft parts. (3) After removing the opercula, kites detached snails from their shells by destroying the attachment of the columellar muscle with strokes of the upper mandible. (4) Kites generally ingested snails in several chunks. (5) Discarded shells were often damaged slightly to moderately on the lip of the aperture. The shell of *P. dolioides* is very fragile. (6) Kites in Guyana, as in Florida, gave no vocalizations remotely resembling Lang's "Kor-ee-ee-a—Koree-a."

In heavy vegetation it was difficult to find opercula under feeding perches. They filtered down between the plant stems while the shells caught further up. A superficial examination of such feeding perches could easily have led Lang to believe that kites swallow opercula. However, even careful examinations of debris under perches never yielded as many opercula as shells. We believe this is due largely, if not entirely, to the moderate to brisk northeast wind that blows almost continuously in coastal Guyana. We often saw the opercula being blown many yards from perches where kites were extracting snails. Shells rarely land far from the base of a feeding perch. We are unable to explain other differences between our observations and those of Lang (1924), Pain (1950), or Murphy (1955).

Though it appears that ingestion of opercula is at best infrequent, we should note that the digestive tract of a captive Argentine kite that died at Patuxent contained opercula in quantity (Erickson, pers. commun.). This may have been the result of feeding on snails lacking shells but possessing opercula, and may have caused its death.

Of 221 bills of Everglade Kites that we examined at the museums mentioned earlier, all appeared to be perfectly symmetrical except four which had some lateral twist to the upper bill. The twist, not consistently oriented to the left or right, probably represents no more than a normal variation in bill shape that might be present in any species of bird. Since kites orient snails for extraction in a way that is entirely different from that of the Limpkin, the lack of asymmetry is not surprising. It seems likely that the long, slender, hooked nature of the upper bill of the Everglade Kite is an adaptation for severing the columellar muscles of snails.

Regarding the Everglade Kite in Florida, Maynard (1881:289) states: "Its long, abruptly curved upper mandible is peculiarly fitted for removing the animal and it is not uncommon to find specimens of the shell with a hole punched in the side by this hook." In our experience, kites never produced such damage to shells. Limpkins did (Figure 23,a).

Feeding Behavior of the Boat-tailed Grackle

Foraging Behavior

In our observations, Boat-tailed Grackles used two foraging methods for molluscs: foraging on shore and foraging on floating vegetation. In shore-foraging the bird walks at the water's edge or in very shallow water. Though it frequently probes with the bill, foraging appears to be entirely or almost entirely visually-directed. The bird often thrusts its closed bill into debris and then opens it wide, creating a space into which it peers. In Figure 33 a shore-foraging grackle probes in the mud for a mussel stranded by receding waters at Saddle Creek Park. Often grackles turn over rocks, plants, and other objects with the bill and examine the undersides (Figure 34). At other times they stretch out over the water, peering downward (Figure 35), locating a variety of foods—aquatic insects, snails, and mussels. Reluctant to wade very deep, they stretch out to reach their prey. However, when a grackle sees a snail or mussel in the water beyond reach, it flutters from shore and plunges part way in. Grackles regularly investigate mussel and snail shells lying on shore for scraps, and occasionally eat flesh that has been long dead. We have seen grackles capture live snails, *V. georgianus,* and mussels, A. *cowperiana, Elliptio strigosus,* and *Villosa vibex* by shore-foraging, but not live *P. paludosa.*

In our observations grackles took live *P. paludosa* only when foraging on lily pads. In the Everglades, one often sees a grackle standing on a lily pad, lifting the edge of an adjacent pad by thrusting its bill underneath and raising its head. Seeing nothing of interest, it drops the pad and lifts another. Though the undersides of lily pads are usually laden with insects and small snails, it is common to see a grackle inspecting dozens of pads in quick succession, apparently eating nothing off their undersides until it at last finds a *Pomacea.* It either stretches or flutters part way into the water and under the pad to grab the lip of the shell with its bill and then flies off to extract the soft parts in a more convenient spot.

Grackles often forage on other floating aquatic plants, such as water lettuce or water hyacinth, using somewhat different techniques. Moving from plant to plant and probing in the vegetation they pick up entire plants and turn them over, exposing the roots. Though we saw grackles take aquatic insects such as *Belostoma* bugs in water hyacinths and water lettuce, we did not see them take *Pomacea, Viviparus,* or mussels, and could not tell whether or not they took smaller molluscs such as *Physa, Helisoma,* or *Lymnaea.* One would be surprised to find a *Viviparus* or a mussel attached to floating hyacinth or lettuce, but not a *Pomacea.* Perhaps the mechanical disturbance produced by the grackle in lifting the plant is enough to cause the *Pomacea* to drop to the bottom.

The grackles may eat aestivating snails or stranded mussels on the spot or carry them elsewhere, sometimes to the water's edge. Molluscs, caught in the water, are brought to shore or to floating vegetation or carried elsewhere in the bill (Figure 36). In the eastern Everglades we were frustrated in our attempts to observe grackles extracting *P. paludosa* because the birds routinely carried

Figure 33. Boat-tailed Grackle probing the mud for stranded mussels. The bird thrusts its bill into the mud, forcing open a space within which it looks for the prey.

them into the dense sawgrass, a behavior which reflects the aggressive, prey-stealing habits of other grackles in the vicinity. Even when we put live *Pomacea* on shore, hoping to glimpse an extraction, the birds carried each one away. We saw one partial extraction of a *Pomacea* on the edge of a canal and one complete extraction on a distant lily pad. At Saddle Creek Park we had many views of grackles extracting snails and mussels. Here, probably because of the abundance of food concentrated by dropping water levels, there was little competitive interaction between grackles, and the birds usually extracted their prey either on shore close to where they found it or on the limb of a nearby tree.

Extracting Mussels from Shells

We made all our observations of mussel extractions by grackles — an extremely variable process — at Saddle Creek Park. In working on a mussel, a grackle generally gripped the shell with the feet: left foot, right foot, or both feet. The amount of shifting around gave the impression that the bird was unsure of how to proceed. Once, on 18 April 1968, a grackle tried to open a mussel which it held under one foot on the limb of a tree. Clumsily, it dropped and retrieved the mussel several times; finally it gave up. Grackles search for a crack between the valves into which they can force the bill (Figure 37). They were most successful with *A. cowperiana,* a mussel that has difficulty closing the valves tightly together. In one case, we saw a grackle catch and eat a live *V. vibex,* a mussel that closes tightly. It appeared that the grackle thrust the bill between the valves during capture. Since mussels under water normally have the posterior end of the shell open, they are vulnerable to a well-placed thrust.

In our observations, if a grackle was able to find a crack between the valves, it thrust the whole bill, or sometimes just the upper bill, inside. In this process the grackles differed from Limpkins which characteristically thrust only the lower bill inside. With the whole bill inside, the grackle often oriented its head crosswise to the shell, opened the bill, spread the valves apart, and the adductor muscles simply gave way. In some cases, however, the appearance of adductor muscle stubs left in discarded shells suggested that they were cut. Experiments in which we opened live *A. cowperiana,* using only bare hands, showed clearly that the adductor muscles of this species, at least at this locality, were very weak, possibly a result of unhealthiness under crowded conditions and dropping water levels. With the valves spread apart the grackle ate the mussel in one piece or in several small chunks usually picked one by one from between the valves (Figure 38). On several occasions we saw a grackle fly to the water's edge with the body of a small mussel it had just extracted on shore. The bird dropped the meat in the water for a few seconds, then picked it up and ate it.

We have not observed grackles hammering at mussel shells with the bill though we did see them drive blows into *P. paludosa* at one locality in the Everglades. Grackle damage to mussel shells (Figure 39) was limited to minor chips in the edges of the valves.

Figure 34. Turning over vegetation in search of food. Boat-tailed Grackles customarily walk along the edge of the water, turning over rocks, plants, or debris, searching for scraps of food.

Not infrequently, grackles, unable to open mussels, abandon them on shore. Given time and sunshine these mussels gradually weaken, die, and open, perhaps to be found later by the same grackle or other grackles. In this context we quote Root's (1963:399) report on Open-billed Storks of Africa feeding on mussels: "If the Openbill was unable to open the shell, it would stalk off to one of a large number of 'stores' or 'dumps,' untidy heaps of anything up to a hundred mussels, situated from 2-40 yards from water's edge. Any mussel that could not be opened was brought here by the bird and dropped, presumably so that they would be weakened by the heat of the sun. Every now and then an Openbill would detach itself from the feeding flocks and stalk slowly over to one of these 'stores.' There it would test anything up to a dozen shells, picking them up and squeezing them to see if they had become any easier to open." In the case of Boat-tailed Grackles, the leaving of unopened mussels on shore was not systematic. Although we often saw them finding and eating dead and nearly dead mussels on shore, the fact that they sometimes left unopened mussels in shallow water argues against there being any foresight in their abandonment of live mussels.

Extracting Snails from Shells

The process of extracting *V. georgianus* from its shell, like that of extracting mussels, was variable in the grackles at Saddle Creek Park. Frequently birds failed to get past the operculum, and most birds usually failed to get the whole animal out of the shell. Like the Everglade Kites, the grackles often gripped the snails in their feet — one foot or the other, occasionally both, sometimes neither. There did not seem to be any standard method for removing the operculum though the birds we watched always removed it in successful extractions. The birds probed into the aperture with the bill in various contorted positions, either the whole bill, the upper bill alone, or the lower bill alone. The means by which a grackle got a hold on the operculum was variable and difficult to observe. Sometimes it was pulled off clean, other times it was cut and torn free with various amounts of attached flesh. One abandoned *V. georgianus* had half of the operculum torn off. With the operculum removed, a bird probed, cut, and pulled out as much flesh as it could, usually leaving all the meat from the columellar muscle up into the spire untouched. Sometimes it cut the columellar muscle in a ragged fashion and removed the whole animal.

In Saddle Creek Park we never saw grackles capture any *P. paludosa* which, though common, tended to remain in deep water. When we put live *P. paludosa* on the shore where grackles often fed, the birds appeared bewildered. Clearly attracted to them they probed into the apertures briefly, moved the shells about, and then losing interest moved on to eat mussels and *V. georgianus.* We saw one grackle extract a very small *Pomacea,* about the size of a *Viviparus,* in the same way that it extracted *Viviparus.* The discarded operculum was damaged at the end closest to the spire, and there was a large hunk of muscle attached to it. The columellar muscle was cut and the shell was empty except for some columellar muscle.

In the Everglades, grackles are hardly bewildered by *P. paludosa.* Judging from the frequency with which grackles fly by carrying *Pomacea,* and the frequency with which they attempt to rob Everglade Kites and other grackles, it appears that *Pomacea* is a very important item in their diet. Alexander Sprunt IV, Frank Ligas, and Paul Sykes, all familiar with the Everglades, commented on this.

Figure 35 (*above*). Boat-tailed Grackle foraging. Typically, the bird stands at the edge of the water and stretches its neck over it, looking for molluscs, insects, snails, or any other bits it might find palatable.

Figure 36 (*below*). Holding a snail, *Viviparus georgianus*. The grackle has removed the operculum but not, as yet, the soft parts.

Figure 37 (*above*). Boat-tailed Grackle working on a mussel. The bird searches for a crack between the valves into which it can push its bill.

Figure 38 (*below*). Feasting on a mussel, *Anodonta cowperiana*. The grackles were most successful with this species of mussel, apparently because it does not close its valves tightly together.

On 1 March 1968, on the bank of a canal near Coopertown, we watched a grackle orient a *P. paludosa* for extraction. With the aperture facing upward it gripped the shell with both feet—the left hooked into the aperture in the spire region and the right hooked into the aperture at the opposite end. With its bill the bird drove about eight blows to the face of the operculum, mostly to the two ends near the feet. Then the bird thrust its upper bill between the operculum and the columella—the same spot where the Limpkin strikes. The upper bill was thrust in as far as it would go, with the head pushed into the aperture and the lower bill resting on the outside of the shell. The grackle repeated this process several times, sometimes with both upper and lower bill pushed into the aperture. The orientation of the shell and the movements of the head were similar to those observed in the Everglade Kite during the process of cutting the columellar muscle. Unfortunately, at this point, the grackle flew away with the snail. Alexander Sprunt IV (pers. commun.) has also seen Boat-tailed Grackles drive blows to *Pomacea.*

We saw a grackle extract a *Pomacea,* on 27 April 1968, on a lily pad in the eastern Everglades. Unfortunately, the bird was distant and the vegetation obscured many details. The bird did not drive blows into the aperture and we could see it raising and lowering its head while working on the snail which was held in the feet. The discarded shell, like all other snail shells we observed grackles work on, was essentially undamaged with fairly large hunks of columellar muscle left within. Although we found clean *P. paludosa* opercula under the lily pad, we could not tell which, if any, belonged to the shell.

The bill of the Boat-tailed Grackle, in the few specimens we examined, does not show any anatomical peculiarities that correlate specifically with snail or mussel predation. There is a slight, yet distinct, downward curve to the tip of the upper bill which may be of some use in cutting the columellar muscles of snails. Since this same curve occurs in other icterids that are not known to eat snails, we cannot identify it as an adaptation for snail predation.

Discussion

Of the three species of birds the Boat-tailed Grackle is the least specialized for feeding on molluscs. Frequent failure in extracting molluscs, at least in some areas; variability in response to *P. paludosa;* and lack of anatomical peculiarities, like those in the bill structures of Limpkins and Everglade Kites, all testify to a more or less opportunistic relationship with molluscs. Nevertheless, in certain areas, specifically in parts of the Everglades, Boat-tailed Grackles seem quite dependent on *P. paludosa.* Limpkins in these same areas often concentrate on *P. paludosa,* as, of course, do the Everglade Kites. Thus, in some localities, all three birds feed very heavily on one food—*P. paludosa.* How much do they interact and how do they divide the habitat?

We have often seen interactions between grackles and Limpkins and between grackles and kites, but never any contacts between Limpkins and kites. Between grackles and kites the grackle is often the aggressor, and a kite on a perch with a *Pomacea* is a common target. A grackle will often so harass a kite, engaged in extracting a snail, that the kite will fly with its snail to a new perch. We have never seen a grackle succeed in stealing a snail from a kite. On 27 April 1968, a male Boat-tailed Grackle flew twice to a dead stub about 10 to 20 feet from a kite nest containing three nearly grown young. Each time, as the grackle began to sing, a kite flew in and drove him off. Cahalane *et al.* (1964) mention an apparent case of predation by Boat-tailed Grackles on the eggs of an Everglade Kite.

Occasionally feeding Limpkins attract grackles. Limpkins often discard portions of the molluscs they extract, and the leavings bring in a variety of birds. We have never seen grackles steal molluscs from Limpkins though we have seen these two species threaten and chase each other on the banks of canals.

The above observations, casual though they are, suggest a measure of interspecific competition. That we saw no interactions between Limpkins and Everglade Kites may be our failure, or it may reflect slight competition between the two. While we have little concrete data to support it, we feel that Limpkins and Everglade Kites in the Everglades generally feed in different habitats. Kites forage in open sloughs with a minimum of sawgrass and other emergent vegetation, and a fair amount of open water, usually too deep for Limpkins. Limpkins in the same general areas forage in denser vegetation. Since in other regions we have seen Limpkins foraging in open, but shallow, waterways, we believe it is the depth of the water and not the openness that controls their distribution. In droughts, as water levels drop, Limpkins may move to many open areas formerly occupied only by kites and grackles. Grackles occur just about everywhere in the Everglades—from the densest sawgrass to the lily pads out in the sloughs; but we saw them capturing *Pomacea* only in open areas on lily pads.

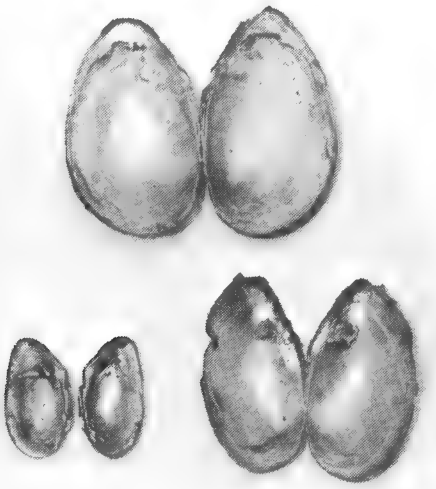


Figure 39. Mussel shells opened by Boat-tailed Grackles. The damage to the shells was slight—only a few chips on the edge of each shell.

Pomacea, one of the few operculate snails with a lung, often comes to the surface to breathe. While grackles and kites take this snail near the surface only, Limpkins capture it at depths up to two or three feet. Because Limpkins also take it near the surface and because the snails move up and down in depth, it is doubtful that these birds might effectively minimize competition for food by capturing snails at different depths.

Clearly there are, between these species, antagonistic interactions — antagonisms that we may consider a common consequence of competition. However, before we conclude from the antagonisms we saw that the three species are true ecological competitors, we should have some evidence that the presence of one species decreases the chances of the others obtaining some resource—in this case presumably *P. paludosa.* For instance, if they defended feeding territories against one another, we would have strong evidence of competition. Though our data are fragmentary, the three species do not appear to defend feeding territories from one another. Indeed, the only interaction of territorial defense that we saw was a kite driving a grackle from the vicinity of its nest. Since grackles are known predators on eggs, kites may generally benefit in such nest defense—even though there were grown young in this nest—irrespective of any competition for food.

Almost all the interspecific interactions we saw were started by grackles attracted to prey caught by kites and Limpkins. Grackles do sometimes succeed in stealing snails from other grackles, and their success may lead to attempts to rob other species even though there appears to be little chance of snatching a snail held by a kite or Limpkin. As such, interactions may reflect only the expectations of grackles—that they can obtain food more easily by theft than by foraging. While in a direct sense the grackles are "competing" for the snails held by the other species, it is not clear that true ecological competition for a limited resource is involved. From our present data we cannot say that the chances of grackles finding *Pomacea* are significantly affected by the presence of kites and Limpkins, and *vice versa.* The question of interspecific competition is best left open.

In a study of the alarm behavior of *P. paludosa* (Snyder, 1967), the snail exhibited two forms of alarm response relevant to avian predation. In one response, a *P. paludosa,* perceiving the odor of an injured or crushed snail of the same species, even in very low concentrations, commonly drops to the bottom and burrows in the mud. A snail that responds to this odor probably decreases its chances of being the next victim of the predator that caused the release of the odor (alarm substance).

Very likely this alarm response is no help against Everglade Kite predation. Even if the snail releases alarm substance when captured, which would be difficult to determine, the predator rarely returns to the same spot for its next victim. A *Pomacea* responding to alarm substance of another snail is probably wasting its time. The same might apply to grackles but not to Limpkins which often work over a small area thoroughly. A snail perceiving alarm substance near a Limpkin often *is* a snail in great danger. However, it is questionable how much value a burial response would have against a Limpkin feeding by tactile probing of the bottom (Method 4). It might be of great value against Methods 2 and 3. We have no idea how much, if any, alarm substance is released by snails captured by Limpkins, grackles, and kites. Limpkins must spread alarm substance about when they extract snails under water, scatter bits of snail tissue in the water, and rinse their bills after extractions.

In the second alarm response, *Pomacea paludosa* drops to the bottom and sometimes burrows when mechanically disturbed. Although this response is probably too slow to help snails avoid capture by kites, it may be useful against Limpkins and grackles feeding on floating vegetation. A grackle hunting in lily pads wastes no time in capturing a *Pomacea* once it sees it, but in hyacinth or water lettuce the laborious process of lifting plants to expose roots may usually give the snail enough time to respond, and escape. A Limpkin feeding on floating vegetation is a prime suspect for the value of this response, though we must add that Limpkins seem to have no difficulty in capturing snails in floating vegetation.

Summary

A study of the alarm responses of the snail, *Pomacea paludosa,* led to observations on the food habits of three species of birds that prey on this snail

in Florida: the Everglade Kite (*Rostrhamus sociabilis*), Limpkin (*Aramus guarauna*), and Boat-tailed Grackle (*Cassidix mexicanus*).

After discussing the diet of each species, the authors describe foraging behaviors and the methods by which the birds deal with their food: how they open mussels and how they get past the opercula and shells of snails.

They describe the asymmetry in the bills of Limpkins, consider the question of its development and use in dealing with molluscs, and compare it with asymmetry in the bills of other mollusc-eating species such as the Asian Open-billed Stork (*Anastomus oscitans*) and the oystercatchers (*Haematopus*).

Since in some regions Limpkins, Everglade Kites, and Boat-tailed Grackles all prey heavily on *Pomacea paludosa*, the authors consider interactions between these species and the position of each in the habitat.

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American Redstart, *Setophaga ruticilla*. Drawing by Louis Agassiz Fuertes.

A STUDY OF THE FERRUGINOUS HAWK: ADULT AND BROOD BEHAVIOR

Tony Angell

East of the Washington Cascades one descends rapidly onto the vast expanse of eroded moraine and basalt that comprises the Columbia Plateau. In Franklyn County, Washington, ancient tributaries of the Columbia River slashed coulees, leaving cliffs fronted by slopes of loose talus. On either side of the coulees the rolling sage-covered lands are broken only by an occasional farmhouse and adjoining fields of alfalfa. In the south central portion of the county the elevation averages 700 feet above sea level and, except where irrigated, the land is quite dry with few trees.

In this area the Ferruginous Hawk (*Buteo regalis*)—"rare" and "uncommon" according to *Audubon Field Notes* for October 1960, August 1961, 1964, and 1965—nested successfully in 1968.

Method of Study

Although we, William Goben and myself, first saw the nest and the hawks in late March and early April, our observations, at weekly intervals, were consistent only from 4 May to 20 July. The pattern, developed over 18 days of formal observation, involved up to three hours in a hide above the nest each morning and two hours at the nest itself each afternoon, checking the development of the brood and/or watching the adult hawks in the adjacent hunting area. Sometimes we both were present; usually one of us worked alone. In this paper I have combined the observations that we made during nearly 70 hours divided equally between us. (See the appendix for a summary of our combined field notes.)

We used two hides. From one, placed in the rocks 60 feet south and 15 feet above the eyrie, we could look down into the nest itself. From the other, on a rise directly across from the nesting cliff at a distance of 180 feet, we could see the parent birds approaching the eyrie from both the north and south. We stretched the canvas of the hides across rocks, forming a hollow from which we could watch activities of the hawk family undetected. The birds became accustomed to the hides and, after three weeks, a single observer could enter the blind just opposite the nest during the daylight without disturbing them.

From the hide a 7 by 50-power binocular was indispensible. We also observed much of the time through the lens of a tripod-mounted camera, generally with a 300 mm Takumar lens with the 35 mm Honeywell Pentax Spotmatic. Occasionally we used tele-converters which gave the telephoto

Ferruginous Hawk
Buteo regalis
Tony Angell
1968

lens capabilities up to 1800 mm. We photographed the brood on the nest with a 50 mm lens and took motion pictures with an 8 mm Bolex. Always we made field notes and sketches.

Often we entered the blind above the eyrie before daylight. If, by chance, the observer of the day was late, he needed a second person to approach with him and, after he was secure in the hide, to return to the car beyond the canyon to the east. This gesture was usually enough to "convince" the hawks that the hide was now empty and therefore nothing to fear. Following a morning session we sometimes unlimbered by climbing down to the nest to check brood development and the assortment of prey brought by the parent birds. After lunch we retired to the hide opposite the nest or walked east to the favorite hunting area of the adults. At times, however, we reversed this procedure. The morning hours of observation ranged from 4:00 to as late as 11:00 with no more than three hours spent in the blind during any one session. The afternoon and evening observations ranged from 1:00 to as late as 9:30 and averaged about two hours each.

Observations

We first encountered the adult hawks in late March and again in early April. Although we had no blinds at the time, the birds did not seem to be unduly shy and permitted us to watch from a hill crest opposite the eyrie and to walk to within 80 yards of them. Our first visits were brief, about two hours each, yet we recorded some information on copulation and nest building.

Copulation and Nest Construction

On the morning of 31 March, both adults alighted on the cliff rim 150 feet north of the nest site. They turned to face east and appeared to scan the shallow valley below. Less than two minutes later and without apparent ceremony the female bent forward and the male gingerly mounted her, keeping himself slightly aloft for a moment with the stroking of his wings. The hen appeared to squat low over the ground and perhaps 15 seconds later the male jumped to the ground. This was the only act of coition we observed.

The nest appeared as a massive pile of compressed sage branches, three feet high and three and one-half feet in diameter, perched on an outcrop opposite the cliff face (Figure 1). Leading to the outcrop were path-like ledges that extended north and south along the face of the cliff. An examination of the structure on this early date indicated that the birds had as yet added no fresh material. On 6 April the diameter extended to over four feet. On and off, for more than an hour, we watched both adults bring material to the nest. They carried the smaller sticks of sage, under 16 inches, in the beak, and brought larger branches, up to 24 inches, and sizeable chunks of cattle dung in the foot. All the nest material came from the sage-covered area immediately below and between 50 and 100 yards north of the eyrie.

The female quite deliberately repaired the nest. She held a branch slightly aloft in her beak before thrusting one end into the side of the structure. Often she paused, examined the stick's position, removed it, and inserted it in another part of the nest. She wedged a larger branch into the side of the nest by twisting it slightly from one end while at the same time pushing it forward.

Figure 1. The site. The nest rested on the fractured basalt palisade. The cave is on the right. Natural paths led to the nest from both the north and south. The top of the path, to the left of the picture, is the point the coyote had reached when the adult female struck him, turned him about slightly, and forced him to take a path above the nest.

Later on this same day, both adults brought strips of soft inner sage bark and placed them in the center of the structure, after which the female molded the inner bowl to the shape of her body contours by treading into the bark and turning slightly from side to side as she settled into a position suitable for incubation. Conditions now seemed suitable for laying; unfortunately we could not return to the site until 4 May, 28 days later. We found the female incubating three eggs that were mantled with soft down.

The nest, during our observations, underwent what we might refer to as a "functional evolution." Because of the activities of the developing brood the surface changed from the original inner bowl to a deep dish form and finally to that of a platform. The first two weeks after hatching, the bowl, some three inches deep and eight inches in diameter, facilitated brooding, provided some shade for the young when the adults were briefly absent, and encouraged reciprocal warmth at night and on cool days. By the end of the third week the active young, moving freely about, wore down the edges of the bowl (Figure 2). The now dish-like form of the inner nest still made it nearly impossible for the awkward youngsters to crest the top edge of the nest. This was fortunate, for to do so would have meant a fall of 20 feet to the talus slope below. By the fourth week the activities of the brood had turned the bowl into a nearly flat platform, permitting the young to move from the nest itself for exercise.

Incubation and Brooding

On 4 and 14 May, the female spent the mornings and early afternoons on the eggs and the male relieved her in midafternoon. Both birds were at the nest in the evening. After hatching, this sequence was generally reversed. The male did most of the brooding up through the middle of June.

During the latter stage of incubation the female stayed on the nest when the observer left the hide, opposite the eyrie, and approached the nest, holding her position until he was within 75 feet of her. The male likewise held his position during the early stages of brooding. By 1 June, however, both adults flushed when approached. Once the observer retired back across the narrow arroyo, the male circled briefly for about five minutes and then returned to the young. During the hot afternoons of 1 and 2 June the male intermittently spread his wings over the young, providing a parasol effect and held this position for up to five minutes at a time.

Feeding the Brood and Catching Prey

In seven days of observation, from 14 May to 2 June, small birds and rodents were predominant in the diet of the young hawks. Following 2 June, jackrabbits (*Lepus alleni*) were the featured prey. The adults brought the food to the nest following a morning hunt. We could usually depend on one adult, the female in all cases observed, arriving with game before 7:00 AM. By midday several carcasses lay at the edge of the nest and hunting ceased. Twice, the morning supply must have been sufficient to feed both the adults and young for the rest of the day because we did not see the adults do any more hunting. Usually, however, they brought prey to the nest again in the late afternoon.

In the first two weeks following hatching the adult hawks thoroughly plucked all birds and sectioned the small mammals before feeding them to the young. Often the adults ate the heads of the different species before bringing them to the eyrie; sometimes they consumed them at the nest. After 15 June we never saw either adult feed a young bird. The hawk merely alighted on the edge of the nest platform with, for instance, a portion of jackrabbit gripped in one foot, put it down, and, after a pause of perhaps 15 seconds, flew back to the cliff face or the hunting range. Before noon the young had all fed on separate or shared carcasses. Twice, on 15 and 22 June, the female left the nest in the afternoon with the remains of the lower leg and thigh of a jackrabbit.

On 15 and 29 June, we noticed the adult male fly from a cluster of sage 350 yards north of the nest. On the second flight from this area the hawk brought part of a jackrabbit to the nest. When I examined the spot in the sage from which the hawk had flown, I discovered what appeared to be a cache for prey. This was a passage 16 inches high by eight inches wide that tunneled two and a half feet back through straw grass and thin branches into the sage. At the end of the passage lay the lower portions of two jackrabbits, fresh enough to have been taken that morning and sectioned in the same way as the portions found on the nest edge. Because the young hawks left the nest the following day, our attempts to follow the scattered family kept us from checking the cache again until late afternoon when we found it empty.

The Hunting Behavior of Adults

Three-quarters of a mile east of the eyrie, in low rolling hills dotted with sage clusters and laced with gullies, the adult hawks did all of the hunting that we observed. The area had a sizeable rabbit population—perhaps six or eight per acre. In late May and through June the rabbits fed in the open until about 10:00 AM and then retreated to the shadowed coolness of the burrow or the thick sage at the gully's edge. In their hunting the hawks ranged over perhaps two square miles of this land.

Surprisingly, several writers (Fisher, 1893; Cameron, 1914; May, 1935; Sprunt, 1955) refer to the Ferruginous Hawk's flight as heavy, labored, or slow. Our observations on this range revealed that the Ferruginous is a versatile flier. Although both adults occasionally soar when seeking prey, most of their hunting is done from a height of from 40 to 60 feet. On the morning of 8 June, we watched the adult female take a half-grown jackrabbit thus:

At 8:00 AM the hawk approached from the north, flying at an altitude of about 60 feet with an almost accipitrine style—three or four wing beats interspersed with a glide. A minute later her flight pattern suddenly changed to a series of very fast and deep beats and then a rapid glide toward the ground. We soon learned to associate this change in manner of flight with the sighting of prey. A jackrabbit, previously unnoticed by us, broke from the sparse grass in the open ground. The hawk entered the clearing at an angle permitting her to intercept the rabbit and make the kill before it could reach the cover of sage. Cameron (1914) also noted such "intercepting" techniques when the hawk preyed on prairie dogs (*Cynomys ludovicianus*).

On 5 July, we again saw the female flying hard and then gliding to a position between the clear field and the cover that the prey might seek. The

Figure 2. June 8. The hawks were now more vigorous in their movements over the nest surface. They used their wings for balance as they waddled about. All fed themselves some although they still depended on the adults to feed them the bulk of their meal. In response to the presence of a human on the nest, they turned to face the intruder, opened their mouths, and backed to the distant edge of the nest.

Figure 3. Through the months of our study the adults spent many afternoon hours simply sitting on the rocks north of the eyrie. Their position provided a view of the entire valley and the opportunity for quick reaction to all intrusions—particularly those of a neighboring Red-tailed Hawk. The Ferruginous Hawk pictured here is the female.

chase that ensued was away from the closest cover. In this instance the hawk did not catch the rabbit before the animal reached cover. The bird pulled up short at the edge of the brush and entered on foot. Her persistence was successful. She flushed the rabbit back down the slope and into the open where she seized it after a short flight. We watched both captures through binoculars at a distance of 300 feet before approaching more closely.

The hawk seized the rabbit and killed it in a matter of 10 seconds by a series of rapid strikes with the feet, driving the talon of the hind toe presumably into the heart and lungs. Astride the rabbit she bit deeply into the side of the animal at the neck and below the shoulder. After feeding briefly she flew back toward the eyrie. On the second occasion she alighted on the crest of the hill 60 yards south of the nest, fed for perhaps 15 minutes, and then took the remaining portion of the prey to one of the young perched in the rocks below the eyrie.

On the Aggressiveness of the Adults

Only occasionally did the male make a perfunctory swoop at us as we approached the eyrie, and then only when our eyes were diverted toward the ground away from the flying bird. Indeed the passivity of these hawks in defense of the nest so moved Dawson (1909) that he labeled them "arrant cowards." The same lack of aggressiveness in the species may have impressed Taverner (1943) when he wondered how these ground-nesting birds escaped the predation of the coyote (*Canis latrans*). On 28 June we made the following observations on the aggressive behavior of this species when defending its brood:

At 4:30 AM when it was still so dark that a flashlight was necessary to safely traverse the rocky coulee, I walked to the hide in the rocks above the eyrie. The adult hawks saw me and flushed from the nest. The male hovered momentarily, gave its wavering cry of alarm, and then circled back to the rocks north of the nest. I retired to the hillside across from the nest. As mentioned earlier, at this stage in the study it was possible to observe freely from the blind without disturbing the activities of the hawks. The wind rushed up the valley casting a white dust from the crest of the hill behind the canvas hide. Perhaps 20 minutes after entering the hide, I heard a coyote call from the south and up wind. His thin wail grew to a stacatto bark. Another coyote replied to the call from somewhere far to the east. I looked hard into the tangle of sage below and saw nothing.

An hour passed. The cliff face sharpened as the shadows were cut cleanly by the sun. The brood stretched and preened. I was facing the young hawks when a motion 50 yards south of the eyrie caused me to turn. A coyote trotted along a worn trail towards the nest, its nose to the ground. Probably it was following the human scent left from our visits. But I had no time to wonder if we were to be in part responsible for the destruction of the brood.

The adult hawks had been calling for perhaps a minute before I saw the animal. The male's cry was longer and more intense than the breathy notes heard earlier in the morning. The female answered from the hunting range to the east. When the coyote was perhaps 60 feet from the young hawks, both adults came in over my head with the wind, pumping rapidly with their wings before flexing them close to the body for the last one hundred feet. The female came first and, catching the coyote, still trotting with its eyes and nose to the ground, by surprise, struck it nearly full in the face. The strength of the blow from a bird weighing nearly four pounds and the

Figure 4. May 31. The young hawks moved more freely over the nest surface. Their activities wore the inner nest into the form of a dish some 16 inches in diameter with the bottom one and one-half inches below the still extant nest rim. The oldest bird, center, was 17 days old and was feeding by itself on a pocket gopher. The second oldest, on the right, fed by itself the following day. The tips of their primaries were just beginning to show.

coyote's reaction spun it around to a path above the eyrie. A second later the male raked its right rear flank. Both hawks, still screaming, banked to the right, turned to climb into the wind, and stooped again. Alerted now, the coyote jumped to meet the attacks, but it was in vain. By stooping together, at least one of the two birds delivered a glancing blow with each dive. The coyote threaded its hurried way through the brush above and north of the nesting cliff, and, after six vigorous dives, the intensity of the hawks' attacks began to abate. They resorted more to harassing flights that persisted for another three minutes—until the intruder crested the hill and vanished from my sight.

Both birds circled the point of the coyote's exit for another 30 seconds and then drifted back into the valley. With a series of choppy wing beats the female flew to the hunting area. The male glided down to the cliff face and perched in the shade of an overhanging rock a short distance from the nest (Figure 3).

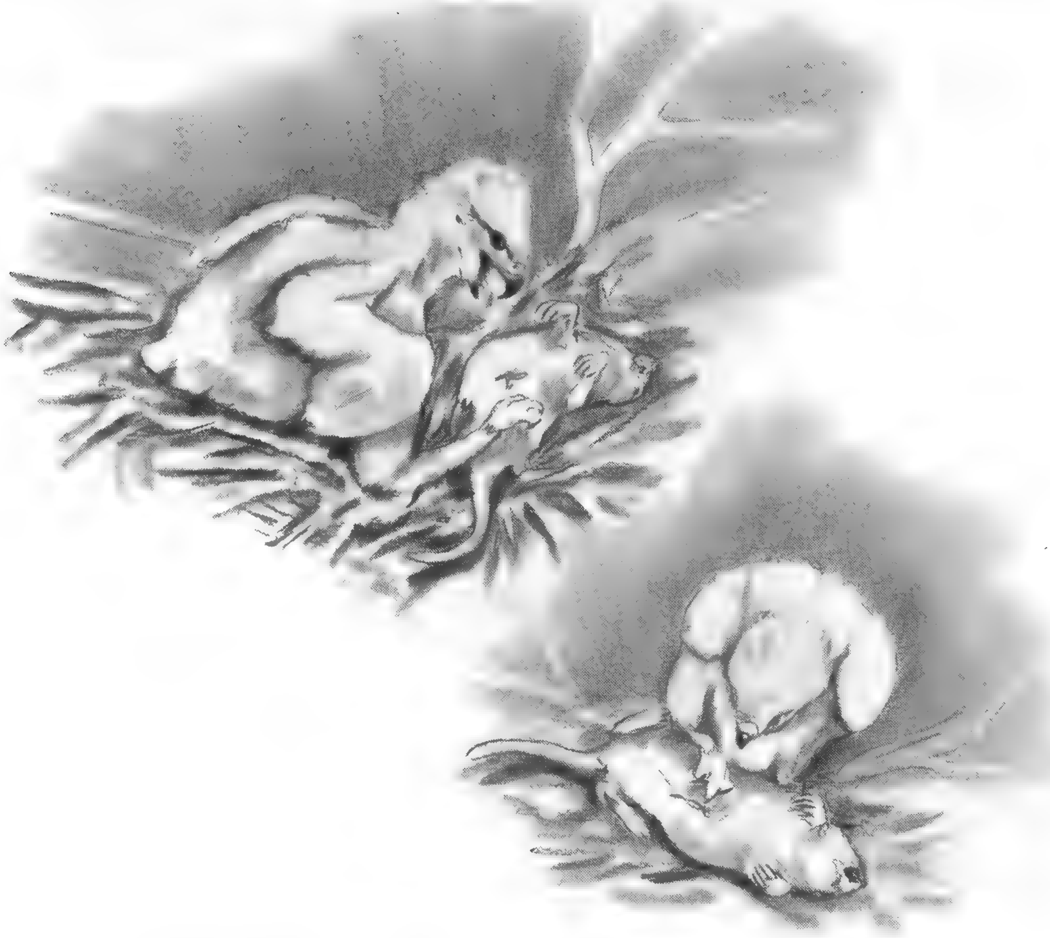

Figure 5. By the seventeenth day the oldest and largest young hawk, which we believed to be the female, was doing some self-feeding. Sitting at the nest edge she steadied the morsel, a pocket gopher, with her feet and fed from a puncture wound in the animal's abdomen. The active young hawks had so worn down the sides of the inner nest that its surface was now dish-like in form.

The Ferruginous Hawks were equally vigorous in attacking a Red-tailed Hawk (*Buteo jamaicensis*) that nested a mile away to the north and occasionally ventured into the valley. On the afternoon of 31 May, as I approached their nest, the Ferruginous Hawks circled at a distance and uttered cries of protest. Their cries were suddenly punctuated by those of the Red-tailed Hawk, which, apparently attracted by the sound, flew directly toward me. The female Ferruginous stooped just in front of the intruder's head, ending its flight abruptly. The Red-tailed turned quickly and flew just as rapidly back to its own territory. Cameron (1914) and Weigand (1967) both noted intense Ferruginous aggressiveness toward Great Horned Owls (*Bubo virginianus*).

Hatching

At 1:00 PM on 14 May, when we climbed to the eyrie and flushed the female hawk from the nest, one of the eggs was hatching. On the morning of 18 May the third egg hatched. Sometime between 14 and 18 May the second egg hatched.

Feeding

Our observations and the inspection of castings during the first three weeks following hatching—14 May-1 June—indicated that the young hawks' diet consisted largely of birds and smaller rodents. We often found the carcasses of young Chukar Partridges (*Alectoris graeca*), Ring-necked Pheasants (*Phasianus colchicus*), and Western Meadowlarks (*Sturnella neglecta*) at the nest edge. Never did we find remains of adult birds. Among the rodents the northern pocket gopher (*Thomomys talpoides*), rock pocket mouse (*Perognathus intermedius*, and Ord kangaroo rat (*Dipodomys ordi*) were eaten. Jackrabbits did not play a large part in the young hawks' diet until after the third week, when these mammals became the most important food.

On the afternoon of 31 May, I observed the largest and oldest of the brood, probably a female, feeding by itself on a pocket gopher (Figures 4 and 5). Resting on her heels she steadied the morsel with her foot as she fed from a puncture wound in the abdomen of the animal. The wound appeared to be the result of the animal's capture by the adult rather than any tear made by the young. This bird had hatched just over 17 days before. On the following day the two oldest hawks both displayed the same self-feeding activity on a kangaroo rat. This behavior in the Ferruginous Hawks seems somewhat precocious when compared with the development of the Red-tailed Hawk, discussed in a study by Austing (1964). The Red-tailed brood began self-feeding at 20 days of age.

Movement of the Brood

At 1:00 PM on 15 June, when we approached the hide opposite the eyrie to begin observations, we paused, as was our custom, about 200 yards away and, using the binoculars, checked on the activity of the brood. To our surprise we saw no birds on the nest platform. Fearing the worst we climbed the slope and found the three young hawks out of the eyrie and nestled in the shade of the rocks on the cliff ledge some five feet from the nest. Thirty-two days had passed since the first egg had completely hatched; the youngest hawk was but 28 days old. Apparently the intense afternoon heat, 95°F, had stimulated them to move from the nest to the face of the cliff. On 21 June the birds sat open-mouthed on the platform enduring the 90° heat of the afternoon. The largest bird grew restless and pivoted around to walk over the nest toward the cliff; the others followed. Within a minute they had traveled 20 feet over the rocky outcrop along the cliff ledge and into a cave that cuts some 15 feet back into the basalt. An hour later when we climbed to the site, all three birds were nestled in the cool loose dirt of the cave floor some four feet back from the entrance. As I moved closer, they rose up one by one and faced me. When I was five feet away, they broke and scuttled crab fashion, backs against the cave wall, until they turned and ran to the nest platform.

In the cave on the afternoon of 22 June the largest of the brood demonstrated marked aggressiveness. Stepping into the cave I inadvertently cut the hawks off from their path back to the nest. Rather than retreat farther back into the cave, the largest bird bolted at me. With feathers erect, mouth agape and hissing, and wings partially open, it ran forward. On reaching my boot it braced with its tail and delivered a series of sharp thrusts with the feet. When I moved aside, it hurried along the path to the nest platform and the other two followed. I could clearly see how this young bird, by doubling its size (Figure 6) and taking the offensive, would discourage any predator. By the last week in June, the brood spent most of their afternoons near the mouth of the cave (Figure 7).

Leaving the Nest

The morning of 1 July was cool and cloudy. The young hawk stood on the platform and, as had been their habit for the past two weeks, stretched, preened, and occasionally broke into a session of violent wing flapping.

Figure 6. July 1. The youngest hawk nestled beneath a sage bush and, when I approached, rose and assumed the typical defense posture—wings spread, contour feathers erect, and mouth agape—and prepared to brace on the tail in order to thrust forward with both feet.

Figure 7. By the last week of June, the brood spent most of their afternoons near the mouth of the cave some 20 feet north of the eyrie. This cool, dark retreat offered relief from the often intense afternoon heat. The open mouths at this age and in these circumstances are a signal of protest at our intrusion. Once, when the largest of the brood was cut off from her retreat back to the nest, she took the offensive and, rushing at the observer, lashed out with her feet at his boots.

Anchored by feet that gripped the matted nest platform, they stroked the air slowly at first and then accelerated sometimes to the point of letting go on the nest and rising into the air to a height of three feet. The oldest bird was now 48 days from hatching and the youngest 44. We could only estimate the age of the third as 46 days. From the hide above the eyrie the young hawks appeared almost identical to their parents in plumage, lacking only the cinnamon and brown barring of the pantaloons and the ivory base on the tails. Since the feathers of both wings and tail were not yet fully developed, they still looked smaller than the adults.

A quarter of a mile north of the eyrie both adults drifted easily above the sage and then sailed vertically to perch above the cliff edge. It was now nearly 10:00 AM and they had fed the brood only once. The three young hawks stood closely grouped at the edge of the platform and appeared to scan the horizon in the direction of the adults. Then, without any hesitation, the largest bird leaped from the platform and the two others followed. Although the wind was steady out of the southeast, the action of the oldest hawk seemed to be one of choice rather than circumstance. The wind did not seem to force the hawk to take flight. The younger hawks, however, appeared to be caught up in the excitement generated by the wing flapping; most certainly the smallest hawk was actually knocked from the nest.

For an instant it seemed as if the three birds were entangled in each other's thrashing wings and would fall to the slope below, but they quickly separated and caught the support of the breeze. Legs dangling and, at first, canting from left to right, they turned awkwardly and flew up the valley toward the adults. Within two hundred yards of the nest the two younger hawks plummeted into the sage brush nearly 90 feet below. The largest of the brood stayed aloft another 150 yards and gained the face of the cliff near the parents. Their life at the nest platform had now ended.

After Leaving the Nest

We never saw the brood together again. Our observations of individual birds indicated that after the first day out of the nest all the young birds were successful in reaching the cliff face and climbing to an elevated position among the rocks. Before this we found one hawk nestled in the sand beneath a sagebush where it remained motionless when approached and would have been very difficult to spot had I not known exactly where it had landed.

On the afternoon of 5 July, I saw the largest of the immature hawks make a simple kill of a bull snake (*Pituophis catenifer*). The bird, perched close to the ground 200 yards north of the nest, merely made a shallow dive to an open spot in the sage 20 feet distant, ran three feet, and seized the two-foot-long snake. After feeding for 20 minutes at the point of the kill, the hawk returned to perch on the cliff ten feet above the ground. This was the only kill by the young hawk that we saw.

Visiting the area on 15 July we observed two immature hawks flying three-quarters of a mile east of the eyrie. They disappeared over a distant rise. At the nest site we saw the smallest of the brood near the ground. On 20 July we scanned the site and the adjacent lands for an hour without seeing a sign of either the adults or immatures.

Summary

The Ferruginous Hawk (*Buteo regalis*), known to breed in the upper Sonoran and Transition Zones of Washington State, displays behavioral patterns

well suited to life here. The ground nesting situation of this hawk made the brood accessible to the predation of the coyote, yet all of the young hawks fledged. Although the adults were rather indifferent to the presence of humans, the success of this eyrie was largely a result of what might be termed the hawk's "selective aggressiveness." Both birds roosted with the brood at night, and the male consistently held a sentinelling position during day. They displayed the ability to vigorously defend the nest against a predator as large as the adult male coyote. One of the young hawks, 33 days old, likewise was capable of taking the offensive and attacking a human intruder who stood between it and the nest. The two adult Ferruginous Hawks would not tolerate the presence of neighboring Red-tailed Hawks south of a large hill, a prominent point three-quarters of a mile north of the eyrie, that seemed to mark the residents' northern territorial boundary.

The young hawks appeared somewhat precocious in their ability to feed themselves when compared with the Red-tailed Hawks of the same age. At 17 and 18 days two of the brood fed from fresh prey brought by the adults. Later in the study we saw the oldest bird, 52 days after hatching and but four days out of the nest, take live prey. These hawks moved about and out of the nest somewhat early. The youngest bird left the nest to travel a short distance to the shade of the rock when only 28 days old.

As a hunter, the Ferruginous Hawk is far from a sluggish and labored flier. The adult female hunted with a style that gave her a positional advantage when approaching a field or arroyo where she might find game. As she closed on a jackrabbit, the hawk accelerated with an almost accipterine quickness and pursued with persistence. On one occasion she entered brush on foot and chased the prey into the open where she seized it after a short flight.

Some of the prey appeared to be cached about one-quarter of a mile north of the nest site. The adult used this cache at least once to retrieve part of a prey carcass and bring it to the young.

For the first three weeks the adults brought small mammals and young birds to the young; after that time the jackrabbit was the staple food.

APPENDIX

The following is a résumé of the field notes, giving the date, time, and observer; the development of the young; activities of the adults; condition of the nest; and prey taken:

31 March, 1:00 PM, Goben.

Ferruginous Hawks mating 150 feet north of nest site. No evidence of rebuilding nest; no fresh sticks on flat surface, 3.5 feet in diameter. No hunting.

6 April, 10:30 AM, Goben.

Both hawks carrying sticks, dung, and—later in the day—bark to nest in both feet and bill; female forms inner bowl. Nest seems to be in final stages of rebuilding; inner bowl lined with sage bark; diameter extended to 4 feet.

4 May, 1:00 PM through afternoon, Goben.

Three cream-colored eggs, one with cinnamon splotch. Female incubating eggs, reluctant to flush, and allows approach to within 75 feet. Inner bowl of nest 8 inches in diameter, 3 inches deep, and lined with sage bark and feather down. No prey carcasses at nest.

14 May, 1:00 PM into afternoon, Goben.

Two eggs, the third hatching; hatching not complete at end of day. Male spends all afternoon as sentinel, gives alarm call when observers are 0.5 mile away; female incubates. Fresh down added to nest bowl, more pieces of cattle dung on nest edge. Pocket gopher and kangaroo rat on edge of nest.

18 May, all day, Angell and Goben.
Two young hawks and one egg; birds covered with down; eyes slightly open. Morning, male incubates, female hunts; afternoon, roles reversed; male dives at observer. Inner nest is still a bowl. Three one-week-old pheasants, one meadowlark, one kangaroo rat, one pocket gopher, and one-half small jackrabbit on nest edge.

19 May, all day, Angell and Goben.
Two young hawks, third egg hatching; oldest hawk lifts head when observer makes noise on nest; all gape. Male brooding, female hunting; same in afternoon; female brings prey at 8:00 AM; both adults feed young. Bowl form of nest retained. Two one-week-old pheasants, with heads partially eaten, at nest edge.

25 May, all day, Angell.
Three young hawks; never any egg shells; search found none. Male broods; female delivers all prey observed; both adults feed; male shades young by standing above them. Bowl form of nest retained but edges worn. Two gophers and two immature meadowlarks, with heads eaten, at nest edge.

31 May, all day, Angell.
Three young moving about somewhat; oldest feeds self on pocket gopher. Female delivers prey in morning; both adults feed young; male shades young by spreading wings above them; female chases Red-tailed Hawk. Bowl of nest worn to dish form, 16 inches in diameter and 1.5 inches below rim of nest. Three pocket gophers and one-half small jackrabbit at, or in, nest.

1 June, all day, Angell.
Two oldest young show tips of primary feathers in sheaths; both do limited self-feeding. Female does all hunting observed; male serves as sentinel; both feed young. Nest bowl in dish form. Two lower portions of jackrabbits on nest.

2 June, all day, Angell.
All young hawks move more freely on nest; all self-feeding. Female hunts; male stays close to nest. Nest bowl still dish form. Three jackrabbits and one gopher at nest.

8 June, all day, Goben.
All young feeding themselves some. Male feeds them; female hunts and later chases Red-tailed Hawk. Nest bowl still dish form. Female catches jackrabbit in range east of nest.

15 June, all day, Goben.
More self-feeding; oldest birds out of nest and onto rocks at cliff edge. Female hunts in morning; both adults at nest briefly to feed young. Nest now only a platform, 36 inches in diameter and slightly concave in center. Two jackrabbits brought to nest. Both adults protest presence of observer.

21 June, all day, Angell and Goben.
Young out of nest and in cave behind eyrie; all self-feed without help of adults. Both adults bring jackrabbits in morning and afternoon and leave after delivery; four visits. Edges of platform used for feeding by young. Three jackrabbits, partially eaten.

22 June, all day, Angell and Goben.
All young hawks in cave; largest strikes at feet of observer as it hurries to nest. Both adults bring prey; male flies from nest with rabbit bones and apparently leaves them on hill, 0.25 mile south. Nest a platform. Two jackrabbits on nest.

28 June, all day, Angell.
Young feed in morning and move to cave in early afternoon; exercise frequently. Female hunts; male hunts and acts as sentinel. Nest a platform. Female delivers one jackrabbit to nest.

29 June, all day, Angell.
Young on nest platform all morning, cave in afternoon; exercising very much. Coyote intrudes; male calls alarm, female flies from hunting range; both birds drive animal from vicinity. Nest only a platform. One jackrabbit, one pocket gopher. and one kangaroo rat. Cache found with halves of rabbit.

1 July, all day. Angell.
Young exercise, the oldest deliberately flies from nest and others follow. Male flies to cliff, female delivers prey to young, and then both adults perch on cliff north of nest. Nest only a platform.

5 July, all day, Angell.
One young on cliff side; oldest young kills bull snake. Adults bring prey to young and protest presence of observer. Nest abandoned. Female killed jackrabbit one mile east of eyrie.

15 July, all afternoon, Goben.
Two young flying east of eyrie. Adult male protests briefly from soaring position.

20 July, afternoon, Goben.
No hawks in sight.

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Black-crowned Night Herons, *Nycticorax nycticorax*. Drawing by N. W. Cusa.

DISCOVERY OF THE NEST OF THE HAWAIIAN THRUSH

Andrew J. Berger

One endemic genus of the thrush family (Turdidae) occurs in the Hawaiian Islands. Of the four main islands—Kauai, Oahu, Molokai, and Hawaii—that once supported populations of the Hawaiian Thrush (*Phaeornis obscura*), only Kauai and Hawaii claim this species today. Its status on Oahu and Molokai is now unknown. A second species, the small Kauai Thrush (*P. palmeri*) that has always been confined to the island of Kauai, exists there now in the Alakai Swamp area in unknown numbers. We consider it rare.

In writing of the Hawaiian Thrush, Henshaw (1901:79-80) stated that "practically nothing is known of its nesting habits. The author feels assured that the bird nests far up in the tall forest trees, and that only by the merest accident will its nest be found."

Bryan (1908:86) wrote as follows about the Molokai race: "On May 1 I took from thirty feet up in an Ohia tree growing in the dense woods on the summit of Puualu, a nest which I have no hesitancy in referring to this species. In the locality was a pair of resident Olomao, evidently the owners of the nest . . . . Externally it is over 6.00 inches in diameter by 3.50 inches deep. Small dead Ohia twigs form the foundation of the structure. Into this is placed a generous lining of moss and fine rootlets neatly woven together to form a substantial thrush-like nest. The hollow of the nest is 3.50 inches across by 1.50 inches in depth. The nest has evidently been used and deserted, though unmistakably of recent construction. It is singular that as yet nothing is known of the eggs of any of the species of the genus, save the reference by Henshaw (Birds of the Hawaiian Islands, p. 31) to the finding of a small fragment of an egg shell in the stomach of a Hawaiian Hawk (*Buteo solitarius*) which he suggests might be a portion of an egg of *Phaeornis obscura* of Hawaii."

The above quotations appear to be the only early statements in the literature about the nest of any race of the Hawaiian Thrush, and there is, of course, considerable doubt that the deserted empty nest found by Bryan was, indeed, a thrush nest.

Munro (1944:73, 76) wrote that "one female had a well developed egg in her eggduct," but added that "no eggs or chicks in the down have ever been found of which we have any record."

The following brief statement by Ord (1967) most certainly was based on Bryan's uncritical comments: "Nesting habits little known; builds a nest of twigs and leaves high in the treetops."

I observed my first Hawaiian Thrush on 20 December 1965, and made casual observations on the species thereafter when in suitable habitats. Because of my preoccupation with the Hawaiian honeycreepers (family Drepanididae), however, I did not make a concerted effort to learn more about the thrush until December of 1967. There appeared to be no reliable information in the literature on which one could base even a remote guess as to the breeding season of the thrush. I decided, therefore, to visit the study areas periodically and attempt to discover when the birds nested. I worked in the Saddle Road areas on the island of Hawaii at least twice a month during the following five months.

Very little is known about the season of song, and especially the relationship between singing and the breeding season, for endemic Hawaiian land birds; they definitely do not follow the pattern of North American passerines.

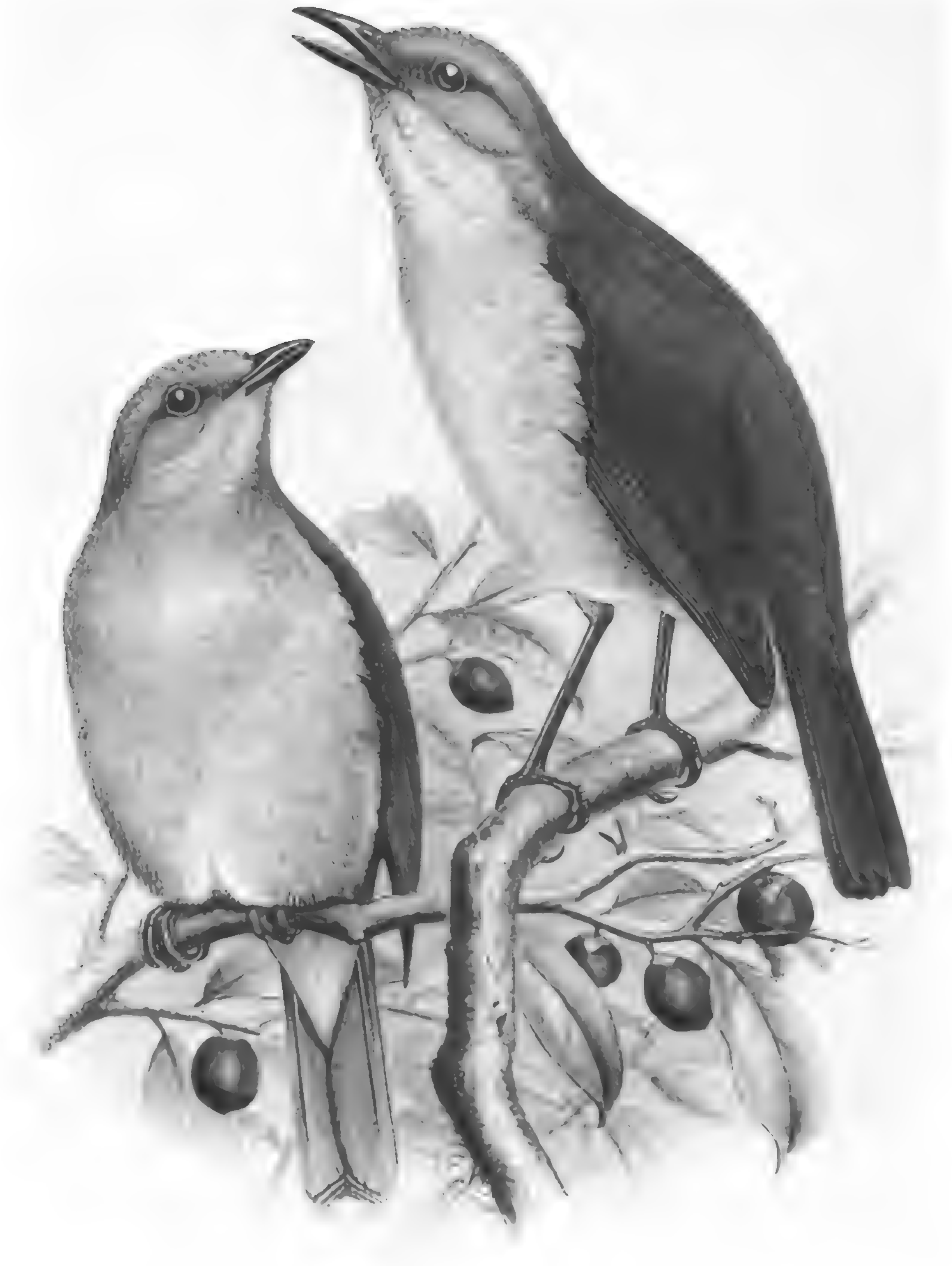
The thrushes on Hawaii begin to call and sing at least by October. The songs at this time often are whisper songs, given from a concealed perch in the interior of a shrub, thicket, or tree. Later the birds typically sing from exposed perches, often from the top of a tall dead tree. They also have a flight song. For the latter, a bird may fly from a dead branch 40 or 50 feet above ground, singing during its slightly arched upward flight. At the end of the upswing, the bird stops singing and dives quickly downward into the forest.

The Hawaii race (*P. o. obscura*) of the Hawaiian Thrush may be considered a fairly common bird in suitable habitat on Hawaii, the "Big Island." I have found it most common along the eastern part of the Saddle Road, which ascends from Hilo into the high "saddle" land between Mauna Kea and Mauna Loa; along the Kulani Prison Road on the eastern slope of Mauna Loa; and at the Thurston Lava Tube in Volcanoes National Park, as well as in similar rain forests adjacent to the Park. In addition, there are vast tracts of land on the island of Hawaii which have not been visited by an ornithologist for many years, and where the thrush probably still exists.

The areas where I have studied the Hawaiian Thrush are regions of high rainfall—for instance, 100 inches annually at Volcanoes National Park headquarters. The region of the Saddle Road, lying between elevations of about 2,000 and 4,000 feet, boasts the highest rainfall, 300 inches, the results of the combination of prevailing northeast trade winds and the two large mountains of Hawaii, both of which tower more than 13,000 feet above sea level. This is the rain forest. The rainfall decreases above 4,000 feet elevation but is still ample for some distance—about 100 inches annually at 6,000 feet—to encourage the re-vegetation of lava flows and the growth of tree ferns and other moisture-loving plants.

A number of eruptions from the north flank of Mauna Loa have poured lava across the region of the present Saddle Road during the past 125 years. The amount of vegetation on these several lava flows varies primarily with the amount of rainfall in the area, which is in turn directly related to the elevation as discussed previously. Where the rainfall is adequate, the re-vegetation of lava flows by lichens, ferns—including tree ferns—and ohia trees (*Metrosideros collina*) takes place in a relatively short time, and a passable native forest may develop in less than 100 years.

Molten lava flows like water, seeking the lowest level. It flows around hills and, sometimes, around mounds of older lava, thus leaving islands, "kipukas," which may be heavily forested (Figure 1). Because of a succession of eruptions from different vents in a rift zone, therefore, kipukas may be bounded by lava flows of different ages and in different stages of re-vegetation.



Hawaiian Thrush, *Phaeornis obscura*. Reproduced from Wilson and Evans "The Birds of the Sandwich Islands" (1890-1899).

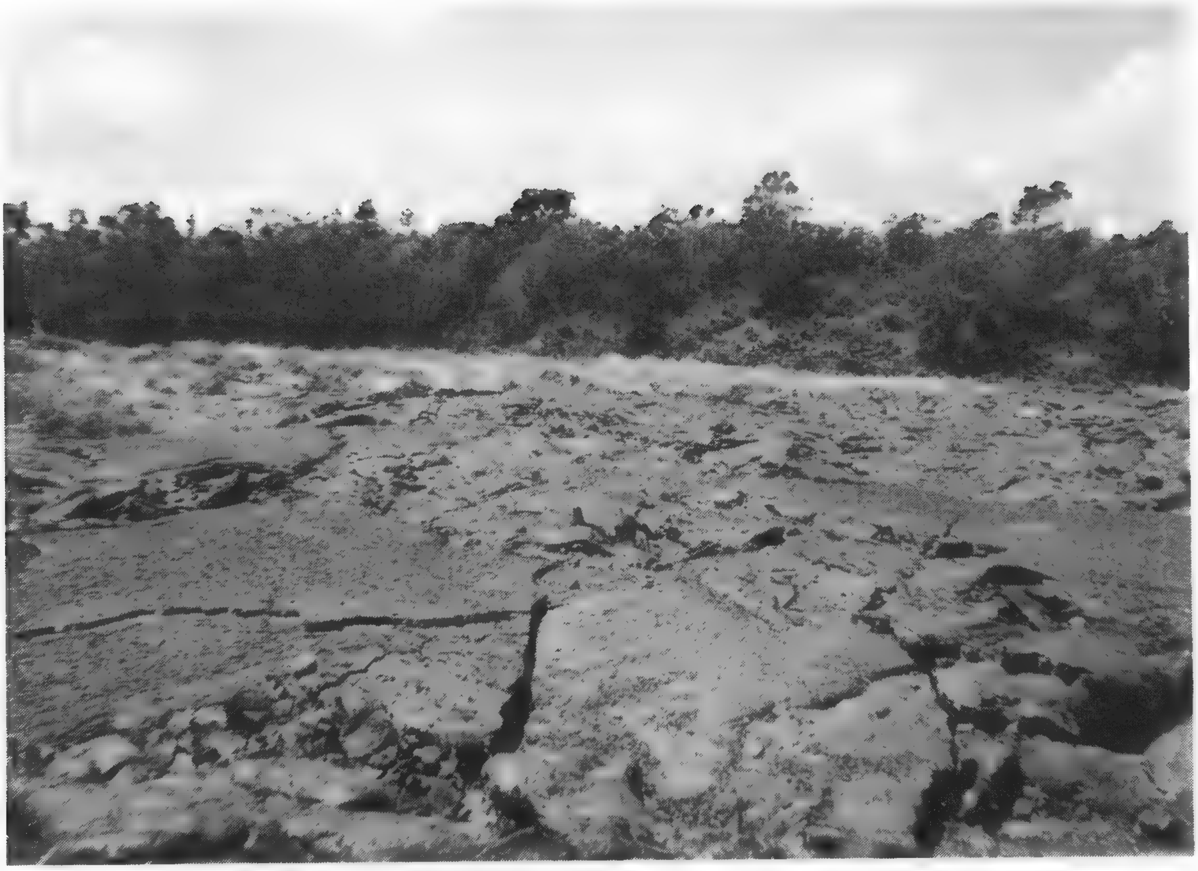


Figure 1. One side of a kipuka and 1935 pahoehoe lava which covers an 1843 flow. Kipukas such as this provide ideal habitats for the Hawaiian Thrush and other endemic animals as well as plants. Photographed 15 July 1967.

Kipukas also may exist at the leading edge of a lava flow that stopped because the eruption came to an end. The kipukas are, in any event, good places to search for endemic plants and animals.

During the winter months, I discovered that singing thrushes were fairly well scattered over the very rough but relatively open lava flows where the ohia trees were only 15 to 25 feet tall. I thought that if the thrushes did, in fact, build their nests in ohia trees, the finding of one in these low trees would be an easy matter. Although I spent many hours, often rainy hours, climbing slowly over lava flows with a series of ravines, 20 or 30 feet deep, where one had to test each lichen-covered block of *aa* lava in order to make sure that it would not roll or tip, I found no nests; and, as the season progressed, I could not even find females or pairs of birds. And, to be sure, when I found the first thrush nest, it was not on a lava flow at all but in the depths of a dense kipuka.

The kipuka was, in part, an elevated area bounded on the western, or upslope, side by a lava flow probably less than 100 years old, on which the scattered ohia trees were of moderate height. On its eastern, or downslope, side, the land fell away steeply into a crater-like depression. Both the crater and the elevated portion of the kipuka supported a dense tropical vegetation, of which ohia was the dominant tree. In addition to a variety of mosses, liverworts, and ferns, other plants included kolea (*Myrsine* sp.), pukiawe (*Styphelia tameiameiae*), lapalapa (*Cheirodendron* sp.), kanawao (*Brussaisia arguta*), pilo (*Hedyotis* sp.), ohelo (*Vaccinium calycinum* and *V. reticulatum*), pioi (*Smilax sandwicensis*), and tree ferns (*Cibotium* sp.).

After some six months of searching in difficult terrain, I found the first thrush nest on 11 May 1968. I was working in a difficult place where mosses, other low ground vegetation, and tree ferns so concealed the gaping holes and crevices in the lava substrate that it was necessary to watch every step taken. The thrushes often led me into the luxuriant tropical vegetation and I had to move slowly and carefully along slippery and rotting, prostrate tree trunks that lay in profusion across the deep lava ravines. I kept returning to such areas because of their intrinsic beauty, as well as because I always entertained the hope that I would find the nest on the next trip.

I had searched unsuccessfully in two areas on 11 May and tried a third area, a kipuka, at noon after hearing a thrush giving its single, hoarse meow-like call note. Shortly after entering the kipuka, I saw a thrush fly up and alight on a branch some fifty feet away. As is characteristic of the species, the bird began to "quiver" its wings, repeating the single call note, which proved to be, in part at least, an alarm note. A second thrush flew up almost immediately. I sat on the ground at the side of a small tree fern and watched as the birds flew from tree to tree, giving their alarm notes. The birds followed one another in flight, and I got the distinct impression that the first bird wanted to return to its nest although I did not know where to look for the nest in the dense vegetation. I did feel that the nest probably would not be "high in a tree," as Henshaw had predicted. It occurred to me that the nest might be among the rich growth of roots along a nearby eight-foot-high bank. As I searched the bank, the first bird perched on a branch about thirty feet above the ground and preened its feathers, occasionally gathering what

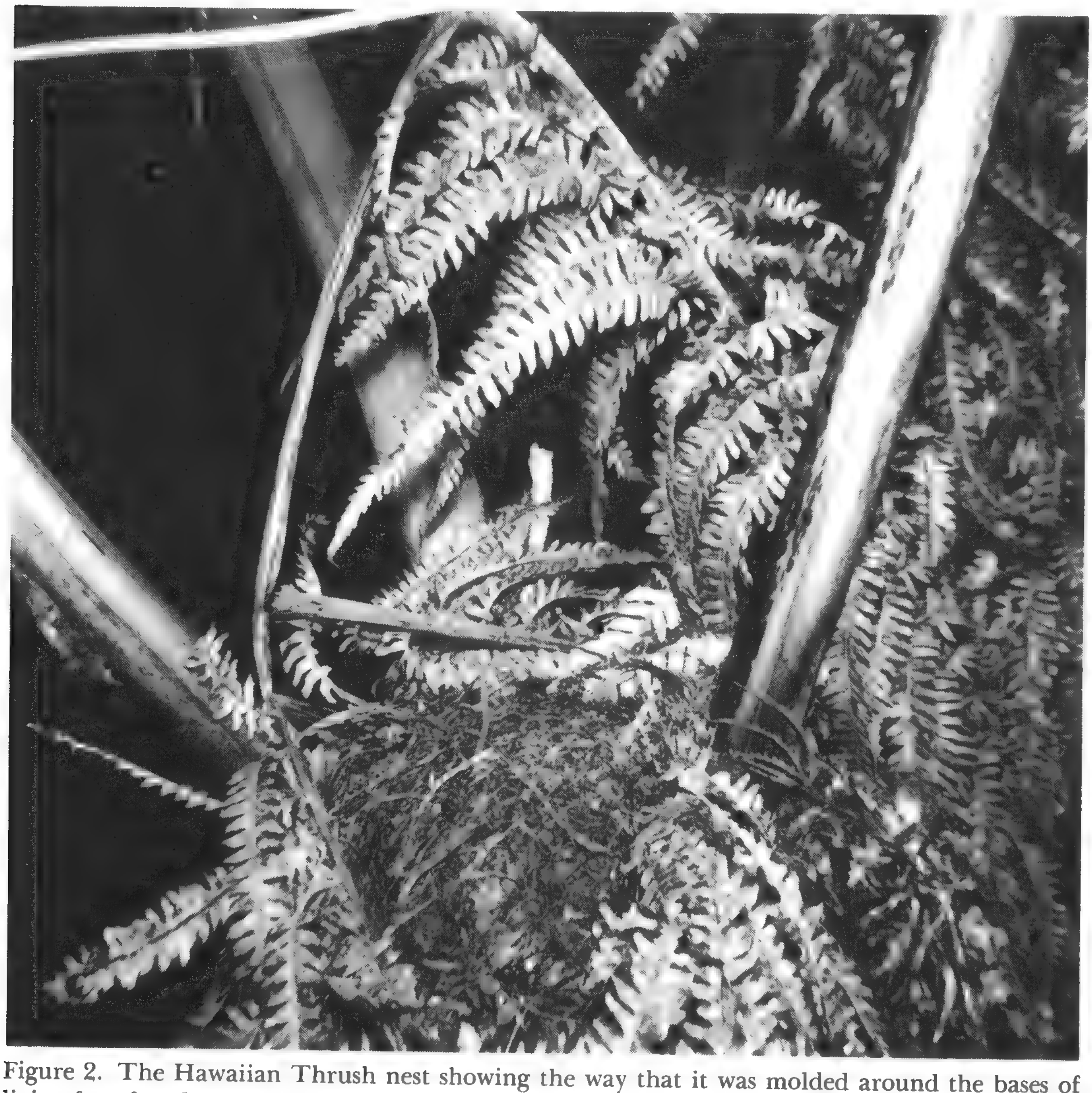


Figure 2. The Hawaiian Thrush nest showing the way that it was molded around the bases of living fern fronds.

Figure 3. A front view of the Hawaiian Thrush nest, showing the triangular shape and the way dead fern fronds are molded around the exterior of the nest.

Figure 4. A close-up of the nest cup of the Hawaiian Thrush nest with its single egg. After taking this picture, I picked up the egg and discovered that it was pipped. Photographed 11 May 1968.

I presumed to be insects or larvae from both leaves and branches. Slowly the birds moved northward and out of my sight. I changed my position again and stood behind a large tree. Within three minutes the birds returned and began to utter their alarm notes. One bird, presumably the male, then flew off to another part of the kipuka; the other bird continued to give intermittent alarm notes. I decided to make a brief search for the nest and then leave the area so that the bird would come back to its nest. By returning later, I thought, there was a good chance that I might flush the bird from its nest. I had taken only a few steps, however, when I saw what I presumed to be the nest. It was.

The nest was 4.3 feet from the ground near the top of the trunk of a tree fern and was supported, in part, by the bases of both dead and living fronds (Figure 2). The dead leaflets of at least one dried frond had been molded around the exterior, thus serving to camouflage the nest.

The back of the nest, built against the trunk of the tree fern, was very flat and triangular in shape. It measured 7.5 inches from top to bottom, approximately 6.5 inches across the top, and tapered to a width of about 1.5 inches at the bottom.

The nest was also triangular in shape when viewed from the side. In front, the distance from the top of the nest rim to the tapering bottom was 5.5 inches (Figure 3). The back rim of the nest extended about 3.25 inches above the front rim.

The rim of the nest had a maximum thickness of one inch; the outside diameter at the rim was 4 inches; the inside diameters of the nest cup were 2.75 inches from side to side and 2.25 inches from front to back. The nest cup was 3 inches deep in back and only one inch deep in front.

The bulk of the nest, both the body and the lining, was constructed of unidentified rootlets and strips of bark. Woven primarily into the outer wall of the nest were a variety of mosses (*Taxithelium mundulum, Leucobryum solfatare* var. *hawaiiense, Pseudosymblepharis mauiensis*), liverworts (*Lophocolea* sp., *Bazzania* sp., *Herberta* sp.), and ferns (*Xiphopteris saffordii, Sphaerocionium obtusum, Grammitis hookeri, Cibotium glaucum*), as well as one ohelo (*Vaccinium reticulatum*) seedling, one pukiawe seedling, and several parts of leaves of an unidentified grass or sedge.

When I found the nest, at 12:45 PM, it contained one pipped egg (Figure 4). Through a hole, about 0.25 inch in diameter, the bill of the young bird protruded. The adult thrush, presumably the female, had been incubating the egg. At 10:30 AM the following day, the young bird, though active and calling faintly, still had not hatched. An adult was on the nest again at 11:30 AM when I had to leave.

I did not visit the nest again until 25 May. It was empty and I found no evidence of adults feeding a fledgling in the vicinity. Although I visited the kipuka several times during the following two months, I was unable to find another nest of this pair of thrushes.

Summary

The Hawaiian Thrush is a common permanent resident in the rain forests of the island of Hawaii. During much of the year, the birds are widely distributed over very rough lava flows where low (15 to 25 feet high) ohia trees are widely dispersed. The first nest, containing a single egg, of the Hawaiian Thrush was found in a kipuka on 11 May 1968.

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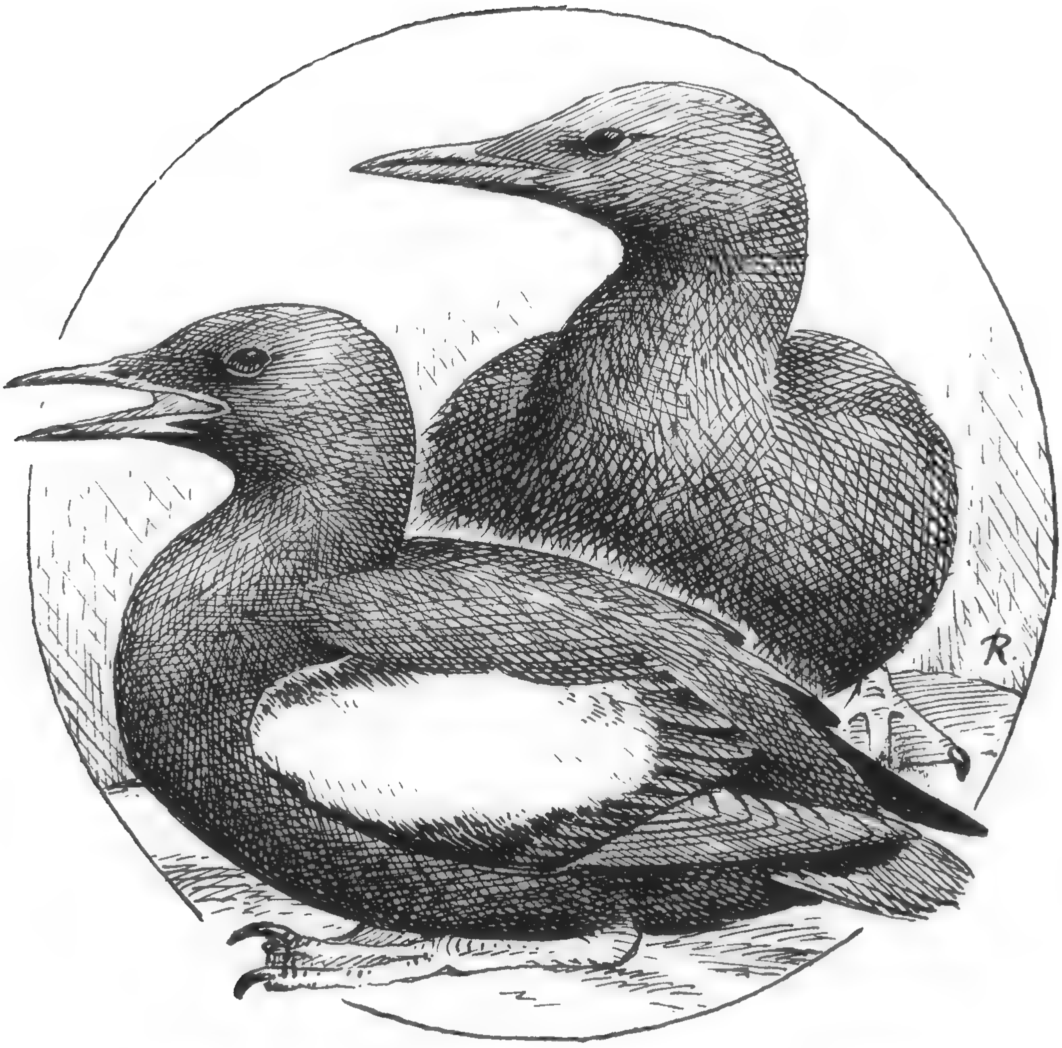
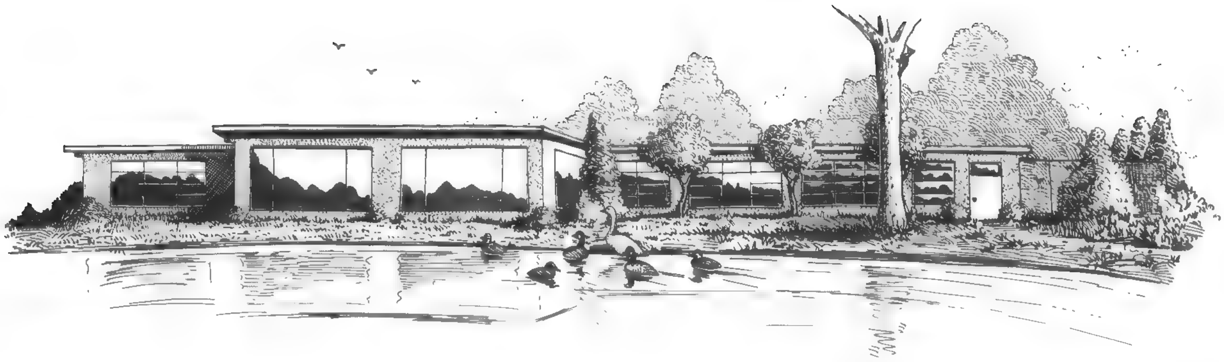


Black Guillemot, *Cepphus grylle*. Drawing by R. A. Richardson.



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