THE CONDOR

VOLUME 47 SEPTEMBER-OCTOBER, 1945 NUMBER 5

A STUDY OF CAPTIVE GALAPAGOS FINCHES OF THE GENUS GEOSPIZA

By ROBERT T. ORR

INTRODUCTION

The Galapagos Islands, because of their isolation and peculiar fauna and flora, have been of keen interest to naturalists since they were visited by Charles Darwin in 1831 during the voyage of H. M. S. Beagle. Among the many biological problems which these oceanic islands have presented none has proven more difficult than those concerning the origin and development of that group of native passerine birds commonly known as ground finches. Certain species of these birds are superficially so divergent that until recent years forms now known to be closely related were placed in widely separated families of the Passeriformes. This avian group, now considered by some to represent a separate fringillid subfamily, known as the Geospizinae, was first thoroughly monographed by Swarth (1931) who greatly contributed to our knowledge of its relationships. In his estimation it merited recognition as a separate family for which he proposed the name Geospizidae (Swarth, 1929). The justification for such separation has been denied by most taxonomists subsequently.

The study of systematic allocation and relationships of the various geospizids was carried to a further stage of development by David Lack (1945) who published a detailed account of variation occurring within the group. This monograph contributed considerably toward clarifying the relationship and origin of certain forms, and also it presented an analysis of observations made in the field upon geospizid behavior and ecology. It was the expedition to gather information pertaining to the latter part of Lack's work that made the present study possible.

On leaving the Galapagos Archipelago in April, 1939, after five months of intensive field work, Mr. Lack brought with him thirty-one live finches. He had originally planned to transport these birds to England but their condition upon reaching Panamá and the imminence of war in Europe made it advisable to bring them to the United States. Accordingly, Mr. Lack approached the California Academy of Sciences and arrangements were made for the Academy to take care of them. Later the writer agreed to undertake a behavior study of these captive birds, although it must frankly be admitted not without some misgiving and considerable skepticism at first as would be natural to one primarily interested in field observation. These sentiments were soon lost, however, when it was found that the behavior pattern appeared essentially the same in captivity as in the wild, allowing of course for the artificial environment. Furthermore, it was soon discovered that experimental methods, which would be impractical or impossible in the field, often shed new light on certain phases of behavior.

Grateful acknowledgment is here made, both personally and on behalf of the California Academy of Sciences, to Mr. David Lack for this generous gift, and also to those organizations that sponsored Mr. Lack's expedition, the Royal and Zoological societies of London and the Elmgrant Trustees, Dartington Hall, Totnes, South Devon, England.

To Mr. Eric C. Kinsey of Manor, Marin County, California, the writer is deeply grateful. Mr. Kinsey generously kept these birds in his own aviaries for several months after their arrival in San Francisco and contributed valuable advice in the planning of new aviaries on the roof of the North American Hall of the California Academy of Sciences in Golden Gate Park where the birds were later kept. For many helpful suggestions and criticisms the author wishes to thank Dr. Robert C. Miller, Director of the California Academy of Sciences and the late Mr. James Moffitt, Curator of Birds and Mammals in the same institution. Many contributed to the care and feeding of these birds, especially Miss Grace Irene Crowe who also assisted greatly in the final preparation of the manuscript.

SPECIES

Thirty of the thirty-one live birds secured on the Galapagos Islands survived the trip to San Francisco. Four of the fourteen species of geospizids recognized by Lack were represented. There were three *Geospiza magnirostris*, four *Geospiza fortis*, twelve *Geospiza fuliginosa* and eleven *Geospiza scandens*. All except two *fortis* and one *fuliginosa* were secured at Academy Bay on Indefatigable Island. These three birds were captured at Progreso on Chatham Island.

The four species represented are identical as regards color of plumage, the adult males being entirely black except for the under tail coverts which are margined with pale buff. The immature males vary from a female-like plumage through various partially black stages. The females are streaked grayish brown. The principal differences among the four species involved are in body size and in the shape and proportions of the bill. *Geospiza magnirostris* is the largest, its body about equaling that of a large Crossbill (*Loxia curvirostra*) but its bill is enormous, being even larger than that of an Evening Grosbeak (*Hesperiphona vespertina*). *Geospiza fortis* is slightly smaller, more nearly approaching a Purple Finch (*Carpodacus purpureus*) in size and with a bill averaging proportionately smaller than in *magnirostris*. *Geospiza scandens* is about the same size as *fortis* but, instead of possessing a heavy coccothraustine-like bill, its bill is long and starling-like in character. The smallest of the four species involved is *Geospiza fuliginosa* which is not much larger than a Pine Siskin (*Spinus pinus*); whereas its bill is relatively heavy, it is more nearly of normal finch-like proportions. All the species involved possess the usual geospizid characteristics, that is, a relatively stocky body, short tail, rounded wing poorly adapted for long sustained flight, and long, dense feathers of the rump and lower back. For a detailed description of the individual species the reader is referred to Swarth (1931).

The mortality was relatively high for the captive birds in the year 1939, undoubtedly due to several factors. Among these may be mentioned the climatic change the birds were subjected to in coming from the Galapagos region to the San Francisco Bay area, the fact that they were not used to confinement, and, lastly, the incompatibility of certain birds which resulted in severe fighting with fatal injuries occasionally inflicted.

Eight birds were lost by the end of the first year. These included three *Geospiza fuliginosa*, two *Geospiza scandens*, and three *Geospiza fortis* which left only one male of this species represented. During 1940 and 1941 only two losses occurred. These were both *Geospiza scandens*. The heavy losses in 1939, however, were compensated for by exceptional success in the rearing of young during the following year. Unfortunately, with only one *fortis* remaining it was impossible to increase the numbers of this species. This was very much regretted as it had been planned to attempt to hybridize both *magnirostris* and *fuliginosa* with *fortis* which is intermediate in size. The surviving male *fortis* was exceedingly wild and refused to mate with females of either of the two pre-

viously mentioned species. Nine of the original stock, including six *juliginosa,* two *scandens* and one *magnirostris* were sent to the New York Zoological Society on February 10, 1942. It is not known what the survival rate among this group has been. Two of the eleven remaining birds of the original stock kept in San Francisco died during 1942. These were both *G. juliginosa.* One loss of an individual of this same species occurred in 1943. No losses occurred during 1944. Thus at the close of the latter year, five years and eight months after their arrival in San Francisco, thirteen of the original thirty geospizids received were known to have died, nine were sent to New York and their fate is unknown and eight were still living in San Francisco. The latter comprised two *magnirostris,* one *fortis* and five *scandens.*

CAGES

An adequate aviary was constructed with the assistance of labor provided by the Work Projects Administration during the summer of 1939. Cages were made sufficiently large to accommodate large brush and tree cuttings so as to facilitate breeding on the part of the birds. The aviary was placed on the roof of the North American Hall of the Academy's buildings and was so situated as to be protected from wind on the north and west sides and exposed to the southward in order to receive the maximum amount of available sunlight and warmth.

This aviary was forty feet in length, seven feet in height and ten feet in depth and was divided into ten separate cages by means of wood and wire mesh partitions spaced four feet apart. The framework was made of two by three inch and two by four inch redwood lumber and was covered with one-quarter inch wire mesh. Doors five feet in height and two feet in width were present at the front of each cage. The back of the aviary was against a concrete wall and both the roof and sides of the cages were boarded for a distance of four feet from the back of the aviary. This afforded protection from rain and wind as well as secluded nesting sites. The roof was covered with mineral surfaced Malthoid roofing. Additional protection was given the birds by extending boarding down from the front end of the four-foot boarded roof a distance of two feet. The remainder of the roof was of wire mesh. Both the floor and the roof of the cages sloped to the south at about a 7° angle, to allow for drainage. The floor of the cages was covered with an additional two-inch layer of small gravel. Perches were placed both in the protected and open parts. A feeding box with a waterproof roof was placed inside of the cage just to the left of the door.

FOOD

According to Lack (1945:39) the native diet of the species considered here is composed principally of fruit, berries, flowers, flower nectar, young green leaves, buds, seeds, occasional caterpillars and other small insects. Aware of the rather varied type of food normally eaten by these birds, a diet was suggested by Mr. Eric C. Kinsey which proved very successful. This consisted principally of bird seed mixture, a substitute nectar food and either berries or greens. The nectar food was concocted of honey, Mellin's baby food, evaporated milk and water. Pyrocantha and cotoneaster berries of several varieties commonly used in horticulture were relished by the birds. These were available principally during the winter months. In the spring, summer and early autumn sow thistle (*Sonchus oleraceus* and *S. asper*) proved highly satisfactory as food. The flowers, green seeds and leaves were all consumed and as sow thistle is often heavily infested with aphids this additional insect food was eaten. When neither berries nor sow thistle were obtainable, dandelion flowers or lettuce leaves were used as substitutes. An abundance of fine gravel and a piece of cuttle bone was furnished to each cage.

Berries or greens were either eaten on the ground or carried to a perch and eaten. It was quite characteristic of the caged birds to let the wings droop slightly when foraging over the ground in search of food. At such times, likewise, the tail was regularly bobbed up and down and frequently fanned. On several occasions members of the species *Geospiza fuliginosa* were noted attempting to capture on the wing small insects that flew into the cages.

Considerable care had to be used with certain birds to prevent them from becoming excessively fat. Some individuals became so overweight that their wings failed to lift them off the ground. This was found to result from the excessive eating of seed, almost to the exclusion of other items of food, and was remedied only by the elimination of seed from the diet for varying periods of time.

GENERAL BEHAVIOR

There have been many accounts written describing the tameness of Galapagos birds but, as indicated by Lack (1945), geospizids show more fear of man than do most of the other native land birds of that region, seldom allowing a human to approach closer than six feet. Many individual differences in this regard were exhibited by captive birds, both those secured in the wilds and those hatched and reared in captivity. Among the former, certain individuals were moderately tame when they first arrived in San Francisco while others were quite wild. These wild individuals never became tame, even after several years in captivity, although they did finally cease beating themselves against the cages whenever approached, as they had done at first. Young, upon leaving the nest, were usually quite wild but as a rule were readily tamed. A few, however, always exhibited a great deal of wariness.

Members of all the species studied showed a considerable degree of inquisitiveness. *Geospiza scandens* seemed to excel in this character and the young of all species after they were several months old showed greater curiosity in their surroundings than did adults. When a new bird was placed in a cage with subadults, the latter would evince great interest in it, following it closely as it moved about the cage often to the obvious annoyance of the newcomer. Any new objects placed in their cages were carefully examined and pecked at with the bill. The tamer individuals would often perch on the author and other persons with whom they became familiar and gently grasp at buttons, eye glasses, pencils, coat lapels, fingers and even ear lobes. In this regard mention may here be made of the manner in which *G. scandens* diverged somewhat from the other species in the use of the bill. Tame individuals when perched on the writer's hand frequently used their bills to pry his fingers apart. By opening the mandibles after the bill was inserted between two fingers considerable pressure was exerted, sufficient at least to force relaxed fingers apart. Sometimes individuals would peck violently in woodpecker fashion. Members of this species invariably peeled all the bark off the branches and twigs of brush and tree cuttings in their cages. Perhaps in the native state many insects are secured as a result of this habit of peeling bark.

In general somewhat fewer conflicts appeared to occur between members of different species when kept in the same cage than was true where individuals of the same species were confined together. One instance occurred wherein a pair of *G. magnirostris,* confined in the same cage with an adult male *G. scandens,* built a nest, laid eggs, incubated, and hatched young without any serious conflict taking place. The male *magnirostris* would occasionally fly at the male *scandens* and attack but the latter would usually attempt to keep out of the way. Most of the chasing occurred during the earlier

stages of the breeding cycle at which times the male *magnirostris* was principally concerned with chasing his own mate.

Aggressiveness seemed to vary a great deal with individuals. Some males would constantly try to make violent attacks on males in adjoining cages, irrespective of the species. Other males were only mildly aggressive, their attack consisting principally in flying toward other males perched on the wire screen of adjacent cages, no attempt being made to use the bill. In other instances breeding males showed nearly complete indifference to adjacent males even of the same species. For the most part, however, males of the same species were incompatible during the period of breeding activity.

On several occasions Oregon Juncos (*Junco oreganus*) and Allen Hummingbirds (*Selasphorus sasin*) were released in the same cages with geospizids. The only reaction on the part of the latter to juncos was a normal curiosity such as would be exhibited upon the release of a new individual of their own species in the cage. When hummingbirds were released, however, the reaction was quite different. Galapagos finches would pursue a hummingbird and one gained the impression that they were trying to catch a moth.

The flight of captive members of the genus *Geospiza* is relatively weak as would be expected of species possessing relatively short, rounded wings, a stocky body and a proportionately short tail. Perhaps more noticeable, however, is their inability to maneuver in the air. This lack of agility, as it may be termed, was especially conspicuous when local species such as Song Sparrows (*Melospiza melodia*) and Oregon Juncos (*Junco oreganus*) were placed in the same cage with Galapagos finches. The former species could hover and wheel about in the flyways, while the finches would normally fly in an approximately straight line from one point to another and if alighting on the screen sides would hit with considerable force. *Geospiza scandens* appeared to have the strongest and most rapid flight as well as the greatest agility of any of the species studied. *Geospiza fuliginosa* on the other hand showed the weakest type of flight.

PAIR FORMATION IN CAPTIVITY

The normal breeding period for members of this group in the Galapagos Islands extends from mid-December to April. This is correlated with the rainy season. Some years when there is an exceptionally prolonged rainy season nesting may continue until June and there are indications that breeding, to a limited extent, may take place in almost every month in the year. Unusual climatic conditions may be responsible for this latter fact.

Birds maintained in captivity bred from March to November, inclusive, and there were evidences of some nesting activity on the part of a few individuals during every month in the year. In general, however, the nesting period for most of the captive birds was confined to spring and summer, in this regard conforming to the habits of most North American species.

In late winter and early spring the males were first to show an increase in sexual activity. This was indicated either by an increase in song in those individuals which sang to some extent throughout the year, or by the beginning of song on the part of those that had ceased singing by the end of the previous summer. The instigation of song appeared correlated with increased activity on the part of the males. They flew about their cages considerably more and occasionally attempted to attack other males in adjoining cages. This stage was followed by the chasing of the female by the male. Sometimes the male would begin to pursue the female within a week after the incep-

tion of song or it might be a month before the chasing began. This sexual flight was accompanied or in some instances preceded by the carrying of nesting material by the male. Often this was carried about the cage in a vague sort of way for some weeks before any nest was constructed. The chasing of the female and the carrying of nesting material by the male was usually continued until such time as the female was ready to participate in the nesting activities. There were instances, of course, in which the female became sexually active before the male. Under these circumstances she generally became the aggressor and did the chasing.

Experiments involving the switching of members of pairs so as to change mates during the peak of the breeding season brought some interesting results. On several occasions pair formation between individuals from different cages, where they already had mates, took place instantly when they were placed together. Copulation sometimes followed within a few seconds after which both individuals would jointly participate in the construction of a new nest in which eggs would be deposited within several days. This, of course, was not the usual thing, occurring only when two birds of opposite sexes in the same advanced sexual condition were placed together. Many individual differences were noted, certain males being much more responsive than others and certain females being more aggressive than others, the behavior of the latter, of course, depending to a large extent upon the dominance of the males.

This matter of dominance or of aggressiveness was quite striking among the caged pairs. Certain males were so aggressive that if confined with a docile female that was known to be ready to mate the male would chase and harass her so violently it would be necessary to remove the female to prevent her death.

To cite an example of this, at 4 p.m. on June 24, 1940, an aggressive male *scandens* was placed in a cage with a female which had been seen carrying nesting material. The male had shown so many signs of sexual activity, as evidenced by song, the carrying of nesting material, extreme aggressiveness toward other males and an inclination to chase females, that it had been found necessary previously to place him in solitary confinement. When the two birds were placed in a new cage together, both looked it over for a few minutes, then the male picked up nesting material that had been deposited there and shortly afterward began carrying it to a selected site, apparently starting a nest. Within one-half hour he was seen to chase the female. The following morning at 9 a.m. the female showed signs of having been severely chased and was cowering in a corner of the cage. She was immediately removed. A female from a near-by cage was then placed with the male. This female had already paired with a male, built a nest and was very aggressive, in fact so much so that she had regularly chased the male with whom she had been mated. When she was released, she flew down to the gravel on the floor of the cage. The male immediately flew down beside her and sang. He then fluttered his wings, raised his bill upward, emitted a shrill drawn out note and circled her closely, posturing as he did so. The female then postured and copulation immediately followed. As soon as the act was completed the male threw his head back and, with mouth open, shrilled and fluttered in circles about her for almost one minute. After this he flew about the cage a bit, singing whenever he perched, vibrating his wings as he did so. Later he chased the female a bit and worked on the nest which had been started the previous day. This was half built on this morning and was three-fourths complete by noon. In the ensuing few days the male chased the female a bit but she did not seem very much afraid of him, although she did attempt to avoid him. The female during the following few months only showed sporadic interest in nesting. The male continued in song, occasionally built nests, and maintained his generally aggressive behavior. As a general rule

it was found that birds of either sex tended to be aggressive if they became sexually active before their mate. Females obviously in a sexually active condition were noted chasing males which failed to respond. This did not occur frequently, however, as the male usually was first to show signs of sexual activity and instigate sexual flight.

In the summer of 1941 a wild-taken adult female *G. magnirostris* that had hatched four broods of young in 1940 lost her left foot. This was the result of her biting a leg band so that circulation was cut off at the base of the tarsometatarsus. No attempt was made to remove the band at the time the injury was discovered for fear of infection. Ultimately the foot was amputated and by autumn of that year the stump was completely healed. It was feared that this would seriously interfere with breeding activities on her part. The following summer and autumn, however, she successfully reared one brood and hatched another, all of which unfortunately died due to a severe storm. Again in 1943 she successfully reared young and in 1944 laid again, although the eggs were destroyed, possibly by house mice. The behavior of this one-legged female and her mate was perfectly normal. In only one respect did they differ from other pairs and this was in the location of the nest. It was placed inside the food shelter rather than in brush cuttings in the cage. This may have been accidental as certain birds constructed nests on ledges in their cages. On the other hand it appeared that the problem of constructing a nest by a female so handicapped was greatly simplified by the selection of the box-like food shelter as the site.

SONG

A rather complete account of song in the geospizids has been given by Lack (1945). It is felt unnecessary, therefore, to give any detailed account of this subject here. As generally understood song serves two primary purposes. First it is a means of announcing territory by a male to other males of the same species and second it is used as a means of advertisement to females of the same species on the part of an unmated male desirous of a mate. Its function, therefore, is two-fold, but its action normally is confined to other members of the same species. Furthermore, among most birds, even those closely related, each species has its own characteristic song which is distinguishable from that of other species.

This specific distinctness of song, as has long been known, does not hold true among the Galapagos finches. In the four species studied in captivity individual differences between the songs of males of the same species were often much greater than between males of different species. In fact no two males of the same species had songs that even closely resembled each other, whereas, in several instances, males of different species had nearly identical songs.

Lack (*op. cit.*:33) states that "all of the species watched were, at times, seen to attack individuals of most of the other species of Geospizinae." He goes on to say, however, that such attacks are sporadic in occurrence and usually of short duration. Furthermore, bill recognition in a frontal attack usually causes a complete collapse of such aggressive behavior when an alien species is encountered. In captivity certain males exhibited an extremely aggressive attitude to neighboring males of different species. Wire screen partitions prevented actual contact and may likewise have interfered with recognition.

If it were not for Lack's implication to the contrary, one might almost suspect that territorial conflicts would easily occur among those closely related geospizids that are essentially alike in their general behavior, food habits, and nesting habits, and which even flock together outside of the breeding season. If such similarity in habits exists, there must be interspecific competition for food and nesting sites during the reproduc-

tive period. The unusual overlapping in song, therefore, may possibly serve a very definite purpose. Where such song is common to several species it might readily serve as warning to males of any of those species against encroaching upon an occupied territory and thus tend to reduce overcrowding among competing species. This method would often fail of course in the case of an aggressive intruding male of a different but closely related species. Under such circumstances one would expect bill recognition to cause a cessation of aggressive behavior as soon as the established male and the intruder came to grasping bills. A less aggressive male, however, might be deterred from attempting to establish territory close to males of a different species but which possessed the same song. Further observations in the field would be necessary to determine this.

While song in general was quite variable in the group of captives, it consisted for the most part of from one to five syllables, joined together and repeated either slowly or rapidly without much musical quality. The only striking variation from this generalized song pattern was exhibited by a wild-taken male *magnirostris* which had a song very reminiscent of the liquid *ookaleee* characteristic of North American blackbirds of the genus *Agelaius*. This blackbird-like song is mentioned by Lack (*op. cit.*:29).

Song in all four of the species studied is often preceded or succeeded by a rather shrill, descending whistle. This is most marked during the peak of the sexual period and is of the same type as that uttered when posturing.

Very few of the young males hatched and reared in captivity ever developed much of a song. In most instances it consisted of a single note accompanied by the whistle. This, however, did not in any way deter them from mating.

It was noted during the first fall, winter and succeeding spring, after the birds were received from the Islands, that the males sang more when it rained. The actual falling of the rain appeared to act as a stimulus inducing song. This was thought significant in view of the fact that the breeding season in the Galapagos Islands is correlated with the rainy season. Furthermore, the noise of running water and various mechanical sounds such as those made by an air blower or radio similarly were found to stimulate song among certain males at almost any season of the year. This mechanical stimulus, of course, is well known to canary breeders. Intense rain and severe storms inhibited song and usually caused a temporary cessation of all nesting activity.

Several of the other types of call notes which were commonly used by members of this group may be mentioned here. A buzzy, wren-like *churr* was the most frequent note. This was uttered when foraging or feeding or when two birds came close together. In the latter case it would sometimes be given more harshly and appear to be a warning note. When danger was detected a sharp, high-pitched *thup* was given at varying intervals until the source of disturbance had passed. These notes were common to members of both sexes. The female, likewise, had a characteristic series of rapidly uttered notes which was given when posturing, just prior to the copulatory act.

The young males developed a juvenal type of song which was found to be essentially the same for all species, although it varied to some extent with the individual. It consisted typically of a series of warbling notes loosely connected. This song was not uttered loudly. It reminded the writer of the song of the Ruby-crowned Kinglet (*Regulus calendula*) as given softly in the early spring by wintering males prior to their return to their breeding grounds. Once this song was acquired, it was repeated almost constantly during the day and was apt to vary over a period of time with the individual.

Juvenal song usually began at the age of six to eight weeks although one young individual was heard singing when four weeks old. It rarely lasted more than a few months

and sometimes terminated as abruptly as it began. Among the young males reared in captivity the juvenal song was most frequently replaced by a harsh *churr*. This single note often comprised the only adult song ever acquired, except during the breeding period when it was supplemented by the shrill whistle previously described. One young male *Geospiza scandens* developed an adult song at four and one-half months of age. Its song resembled the blackbird-like note of an adult male *G. magnirostris* which was housed in the same cage. This song was given periodically from February to May, after which the bird became silent.

POSTURING

The males were observed to posture a great deal during the period in which both members of the pair participated in the building of the nest. This behavior became more frequent as the nest neared completion and then abruptly decreased when egg-laying commenced. It practically ceased during incubation and later when the young were being fed in the nest, although a few exceptions were noted.

Many of the postures of the geospizids are described by Lack (1945:24). One of the most typical postures of the captive birds appears, however, either to have been overlooked or not seen by that author. This was a swaying posture on or very near the nest which was often participated in by both members of a pair. Both birds would crouch facing each other with the neck slightly arched and the bill partly open and sway rhythmically from side to side. The male sometimes would utter the shrill descending whistle at such times. Usually the female or, occasionally, the male would be perched on the nest. The female rarely postured more than a foot or two away from the nest and copulation rarely took place any farther away. Any attempts on the part of the male either to copulate or to posture too close to the female when away from the immediate vicinity of the nest would cause the female to assume an aggressive posture. She would crouch in a menacing attitude and remain motionless except to follow him with her head. Sometimes, instead, the warning wren-like scold was given. Posturing and copulation sharply decreased with the laying of the first egg.

A most characteristic feature of the male when posturing was the presence of nesting material in the bill. Before posturing the male invariably picked up a token bunch of nesting material. Long before the female became sexually active the male developed this habit of carrying nesting material. Frequently he sang with this still in the bill although more often it was forgotten and dropped when singing.

Lack comments upon the same attitudes assumed for sexual and aggressive behavior in the Geospizinae. This was not exactly borne out by captive birds. In sexual behavior the wings were invariably quivered whereas in no instance in the species studied was this true where the behavior was directed against males in adjoining cages. In the latter situation the wings were raised and advanced forward but not vibrated. Sometimes when perched on the side of a cage the lower wing was advanced very far forward. The principal similarity appeared to rest in the fact that the wings were elevated and occasionally the mouth was partly opened and the head swayed from side to side.

Several experiments were carried on involving the placing of mounted specimens of various species and sexes in the cages of sexually active males and mated pairs. The results are here recorded.

On June 27, 1940, a mounted skin of a female *Geospiza scandens* was placed on the floor in a cage with a male *G. magnirostris*. The latter immediately flew down and postured with fluttering wings and open upturned bill, emitting a shrill whistle. Following this several attempts were made to copulate with the mount. The skin of the female

scandens was then removed and replaced by a skin of a female *G. fortis*. This produced the same type of behavior on the part of the male. After removing the female *fortis* skin and leaving the male alone for a few minutes both the female *scandens* and *fortis* skins were placed together in the cage with the former nearest the male. The latter, however, immediately went to the *fortis* skin which was farthest away, postured and attempted copulation. The two skins had been selected for their similarity in appearance. The only noticeable difference was in the shape of the bill, that of the *fortis* of course more nearly resembling *magnirostris*. After these two skins were removed, the skin of a female Red-winged Blackbird (*Agelaius phoeniceus*) was placed on the floor of the cage. The male postured a little before it, then made an attempt at copulation. Lastly, a skin of a female *magnirostris* was placed in the cage. This failed, however, to produce any reaction or even interest on the part of the male.

These experiments merely showed that a progressive decrease in interest in specimens occurs when they are continually placed with sexually active caged males. Discrimination of species was only indicated when a choice was offered and at such time the female of the species most nearly resembling that to which the male belonged was selected.

Another series of experiments was made with a pair of *Geospiza scandens* which had shown definite signs of sexual activity. On March 1, 1940, skins of both male and female *G. fuliginosa* were placed in the cage at different times. They aroused only casual interest on the part of either member of the pair. Similarly a mirror, placed vertically on the floor of the cage, only aroused normal curiosity. On June 27, 1940, the skin of a male *scandens* placed in the cage greatly excited both the birds, causing them to utter notes of alarm. The male then attacked the skin viciously. When it was replaced by the skin of a female *scandens*, the male displayed and attempted to copulate with it.

On this same day experiments were made with two other pairs of *Geospiza scandens*. In the first instance a female *scandens* skin was placed in the cage. This immediately caused the male to posture and attempt copulation. This was repeated six times. The male even went through the copulatory act when the skin fell on its side and then lay on its back. A male *scandens* skin placed in the cage after this was warily approached and then ignored.

This same type of reaction to a female *scandens* was observed on the part of the male of another pair of this species the same day. In this instance the female *scandens* skin was later replaced by that of a female *Geospiza fortis*. This resulted in the male posturing but not attempting copulation. When the *fortis* skin was replaced by that of the female *scandens* skin, once more the male only postured. This was removed and several hours later a skin of a female Red-winged Blackbird (*Agelaius phoeniceus*) was placed on the floor of the cage. The male then postured and tried to copulate with it. Several days later, on July 1, the male attempted copulation with skins of a Song Sparrow (*Melospiza melodia*) and an immature *Geospiza magnirostris* in first year plumage.

Numerous experiments were performed on the reaction of male geospizids to their own reflection in a mirror. Almost invariably during the breeding season they would attack their own image, fighting until so exhausted it was necessary to remove the source of trouble to avoid injury. At other times of the year, however, their image in a mirror only aroused casual interest.

NEST BUILDING

Caged pairs were kept plentifully supplied with nesting material, particularly when signs of sexual activity were manifested. Sisal hemp fiber, cut in lengths of from six

to eight inches, was found most useful for this purpose. Sometimes this was supplemented with dry grass and old nests of various icterids (both *Agelaius* and *Icterus*). Certain other extraneous materials in the cages, such as feathers and pappus from sow thistle (*Sonchus*) heads, were also used by the birds.

Among captive birds, just as in the wild, the male often built one or more nests a month or two before the female showed any sign of sexual activity. Sometimes after completing a nest the male would tear it down only to start building again immediately. Occasionally nesting material was removed from one nest and carried to another as it was required.

When a female finally became interested in building, she would either accept one of the completed nests of the male, merely modifying it a bit so as to add the finishing touches, or, irrespective of the presence or absence of a completed nest, she might begin the construction of an entirely new nest.

Although both members of a pair worked on the nest, the majority of the work was seen to be done by the female. The male carried material in his bill a great deal but more often than not it was only a token which was kept while flying around, singing and posturing. Occasionally he brought it to the nest or even passed it to the bill of the female if she were in the nest. Females were not so often seen carrying nesting material but when they did so it was solely for purposes of construction.

The male, not infrequently, would pull material out of one part of the nest and, after flying about with it for a while, bring it back and add it to another part of the nest or offer it to the female if she were there. In one instance a pair of *Geospiza scandens* was seen to work for several weeks at the end of which time they had accomplished very little. The female industriously collected nesting material and brought it to the site apparently selected for the nest. The male just as industriously took the material from the nest site and scattered it about the cage.

The nests constructed by captive birds were generally domed with an entrance on one side. Many modifications of this, however, were noted. Sometimes the nest would be cup-shaped without any dome covering it. At other times it would be but partly domed over. Occasionally nests were built with two entrances instead of the usual one. This latter type of nest has already been recorded by Gifford (1919:236).

EGGS

The eggs of all the species studied are essentially alike, differing only in size which varies in proportion to body size. They are white, lightly speckled with brown. The usual number of eggs in a clutch is 3, although among captive birds the number was found to vary from 1 to 5. For *Geospiza fuliginosa* the average number of eggs for 17 sets laid in captivity was 3.1, with extremes of 1 and 5. Thirty-two wild-taken sets in the Academy collection average 3.3, with extremes of 1 and 5. Eleven sets of *G. scandens* eggs laid in captivity averaged 2.9 eggs per set, with extremes of 1 and 4. Ten sets of *G. magnirostris* eggs laid in captivity averaged 3.0 eggs per set, with extremes of 2 and 4.

Eggs as a rule were laid on successive days and generally before 9 a.m. Incubation normally started with the laying of the last egg. In one instance, however, a female *G. scandens* did not begin incubating until four days after the last egg was laid. This appeared to be abnormal.

The incubation period was found to vary from 11 to 14 days. The average time required for hatching 16 sets of eggs was 12.3 days. The variation in the incubation period does not indicate any specific difference as the extremes were recorded for the same species.

Under captive conditions no reliable information could be obtained regarding the the normal number of sets laid annually. Certain pairs seemed to be sexually active throughout the year. One female *Geospiza fuliginosa* laid during every one of eight consecutive months, from March to October, producing 10 clutches totaling 31 eggs. Only the removal of all nesting material finally prevented further laying as it was feared the overstrain might injure the female. Other mated females never laid. Many deserted their nests after eggs were laid only to lay again after a few days or weeks. Males were frequently responsible for the destruction of eggs.

Among the sets which were fully incubated in a seemingly normal manner the percentage of fertility was very low. This was believed at first to be a result of living in captivity but perhaps this condition prevails also in the wild. Beebe (1924: 157-158) comments upon the fact that fifty per cent of the eggs of four species of geospizids examined were infertile and suggests "The absence of enemies, or the effect of some other environmental insular relaxation has apparently called forth this subtle but quick response,—a conserved correlation of offspring average." The possibility that the virtual absence of native predators might in some way be responsible for this high degree of infertility occurred to the present writer some time before he discovered the same idea expressed by Beebe. It seemed to offer a solution, at least in part, to the problem of population checks in this insular group which has very few natural enemies, although under similar circumstances other species generally attain the same end by a reduction in the number of eggs laid.

The following figures show the number of eggs incubated by members of three of the species of *Geospiza* studied over a period of several years and the number of these eggs that were fertile: *G. magnirostris,* 30 eggs, 23 fertile, *G. fuliginosa,* 53 eggs, 13 fertile, *G. scandens,* 34 eggs, 12 fertile. Eggs which were deserted or broken, either accidentally or on purpose, before fertility could be determined are not included in the above figures.

COURTSHIP FEEDING

Courtship feeding is of regular occurrence among the Galapagos finches. Perhaps in its simplest form it consists in the placing of food by the male at the feet of the female. Among the captive birds such food presented by the male usually consisted of the flowering heads of dandelions or sow thistle, either one of which was placed in the cages for food daily. Sometimes the transference was from bill to bill, especially if the birds were perched on twigs or perches. Whole berries were occasionally presented to the female in this manner by the male. The term symbolic feeding used by Tinbergen (1939:224) would adequately apply to this type of behavior.

The usual method of courtship feeding, however, was by regurgitation of food on the part of the male. Although the male might feed the female any time after she became actively interested in the construction of the nest, this generally was not observed until a few days before the eggs were laid. Feeding of the female by the male continued until some time after the young left the nest. In instances where the nesting activity of pairs was prolonged it was continued occasionally for some months.

Certain males indulged in courtship feeding very infrequently, others fed their mates regularly. As a general rule this transference of food took place away from the nest although on a number of occasions females were observed being fed while perched on the rim of the nest or even while sitting on eggs. While being fed or when begging for food the female would usually flutter her wings, behaving very much like young birds under similar circumstances. Females were noted begging most often after the young had left the nest but while they were still dependent upon the parents for food.

GROWTH AND DEVELOPMENT OF YOUNG

The following account is a summary of observations made on the growth and development of numerous broods of *Geospiza magnirostris*, *G. fuliginosa* and *G. scandens*. No significant differences, other than those imposed by size, were observed between the young of any of these three species.

At time of hatching the young were found to be essentially naked and flesh colored as previously described by Beck (1924:159). There were a few small tufts of pale, buffy colored down situated on the following parts of the body: above and slightly posterior to each orbit, on either side of the occiput or, as was sometimes the case, appearing as a band across the occiput, on each of the future humeral and femoral tracts, on the future spinal tract and in the region where the greater secondary coverts later made their appearance. The remiges were indicated by a faint bluish color at the point of growth of each feather papilla along the posterior margins of the wings. The eyes appeared bluish beneath the lids which were unopened. The bill varied from bright yellow in some individuals to almost flesh color in others, although the angle of the mouth was always yellow. An egg tooth was present. The feet and legs were flesh colored and the nails appeared transparent whitish.

The young were fed regurgitated food by the parents within several hours after hatching. At this time they feebly raised their heads and opened their mouths whenever the nest was jarred. No audible sound was made by the young on the first day.

Little change was apparent on the second day (between one and two days old) aside from the normal increase in size and strength. Toward the end of the second day the bluish areas on the wings where the remiges were forming were more conspicuous.

On the third day the outlines of the remiges were quite apparent beneath the surface of the skin on the upper and posterior parts of the wings. No other feather tracts were visible. The young at this stage could be heard calling faintly for a distance of four feet.

On the fourth day the remiges had grown so that in some individuals they protruded through the skin. The greater and middle coverts were also quite apparent. The dorsal feather tract was usually faintly visible. The young when fed could clearly be heard calling at a distance of eight feet from the cage.

The eyes were still unopened by the fifth day. The remiges definitely protruded from the skin at this stage; also the greater wing coverts on the tips of which were attached some of the down feathers which were overlying them originally. The median coverts also protruded from the skin. Most of the feather tracts of the body except those on the top of the head were at least slightly indicated. No change as yet was apparent in the color of the soft parts. An increase in voice could be noted at this time.

On the sixth day the eyelids were slightly separated and the eyes appeared as slits between them. The young still raised their heads and opened their mouths when the nest was touched. The secondaries and "tertiaries" were seen breaking through the tips of their sheaths, but the primaries had not quite reached this stage. All the principal feather tracts of the body were apparent, at least to some extent, even on the top of the head, although only the humeral tracts, aside from the remiges, protruded through the skin. Next to the humeral tracts the anterior portion of the dorsal tract was perhaps most advanced; the feathers were nearly ready to break through the skin. The voice had increased in volume considerably by this time. No color changes in the soft parts were apparent. The egg tooth was still present. The young clung tenaciously to the nest whenever an attempt was made to pick them up.

By the seventh day the eyes were opened to a greater extent, although the head was still raised and the mouth opened whenever the nest was touched. The feet, tarsi and nails showed some darkening, giving them a slightly vinaceous appearance. The primaries as well as the primary, greater and middle coverts were beginning to break through their sheaths. The secondaries were most advanced. The lesser secondary coverts were apparent. The alula quills and their coverts were seen breaking through their sheaths. The under wing coverts and axillars were not yet visible. The feathers of the capital tract were beginning to protrude through the skin and those of the femoral, humeral, ventral and spinal tracts were well through the skin. The caudal tract was well developed with the rectrices bursting through their sheaths while the crural feather tracts were still poorly developed.

On the eighth day the young still tended to open their mouths when the nest was touched. The legs and feet were more vinaceous than on the previous day. The secondaries and tertiaries showed the greatest advancement so far as feather development was concerned. In *Geospiza magnirostris* they averaged about 2 mm. beyond the ends of the sheaths. The primaries, greater and middle coverts were all breaking through their sheaths as also were the alula quills and their coverts. The primary coverts and lesser coverts were about ready to break through their sheaths. The under wing coverts and axillars were not yet in evidence even beneath the skin. The feathers of the femoral tracts were more advanced than those of other parts of the body, having already broken through their sheaths. Some of the feathers of the humeral tracts also had broken through as had those of the most anterior part of the spinal tract. Those feathers of the capital tract that had made their appearance were, for the most part, protruding through the skin. The crural tracts were very limited, each consisting of about half a dozen feathers to be seen on the lower shank. These barely protruded through the skin. The rectrices and upper tail coverts were breaking through their sheaths. No under tail coverts nor any feathers of the anal circlet were to be seen. Feathers of the ventral tracts were bursting through their sheaths at this stage.

On the ninth day the young still raised their heads when the nest was touched lightly. If it were moved much, however, they would crouch down and remain very quiet. The legs and feet still showed a progressive darkening. The primaries were all through as were the secondaries and "tertiaries." These feathers in *Geospiza magnirostris* were from 1 to 3 mm. beyond the ends of their sheaths. The primary, greater and middle coverts had all broken through their sheaths as was also true of the alula quills and their coverts. Most of the lesser coverts were breaking through. There were no signs of any under wing coverts or axillars. The feathers of the femoral tracts were still more advanced than those of any of the other body tracts, being well fluffed out at this age. Those of the humeral tracts extended far beyond the broken tips of their sheaths. All of the feathers of the spinal tract had broken through. The feathers of the capital tract all protruded through the skin; the more posterior ones were about ready to break through their sheaths. The few feathers of the crural tracts had not as yet burst through, although they protruded through the skin of the shank. All twelve rectrices were now through their sheaths and about six upper tail coverts were in evidence and nearly ready to burst through. Neither under tail coverts nor feathers of the anal circlet could yet be seen. All feathers of the ventral tracts were through their sheaths.

By the tenth day the young could be heard calling fifty feet away. They raised their heads and opened their mouths when the nest was touched lightly but remained quiet and looked slightly belligerent if it were moved very much. Measurements of young *Geospiza magninostris* at this age showed the primaries to extend from 4 to 8 mm. beyond the broken tips of the sheaths. The secondaries and "tertiaries" averaged longer in general, the longest secondary being 9 mm. beyond the tip of its broken sheath. The primary coverts were from 2 to 5 mm. beyond their sheaths. The greater coverts extended from 4 to 7 mm. beyond the tips of their sheaths while the median coverts similarly extended from 2 to 4 mm. All the lesser coverts had broken through. The alula quills were about 6 mm. beyond their sheath tips and their coverts were well developed. No under wing coverts or axillars could be seen. The most posterior feathers of the capital tract were breaking through and all the feathers of the humeral tracts were already through. This, likewise, was true of the spinal tract, although the most anterior feathers were more advanced than the others. The feathers of the femoral tracts were all fluffed out while the few crural feathers were just breaking through. The rectrices in *Geospiza magnirostris* on this day were 1 to 1.5 mm. beyond the tips of their sheaths. The upper tail coverts were about to break through and approximately four small under tail coverts could be seen protruding through the skin. No feathers of the anal circlet were yet to be seen. The ventral tracts were well advanced and the feathers were fluffing out. At this stage the young stretched their wings a great deal. The bill was essentially unchanged in color.

During the eleventh and twelfth days all the feather tracts which had broken through showed rapid progress in development. The least advanced feathers present were those of the anterior part of the capital tract which, however, had broken through. The anal circlet, axillars and under wing coverts generally had not made their appearance by this time. The feet and legs had become noticeably darker.

The young occasionally left the nest by the thirteenth day. The wings were not sufficiently strong for flight but they assisted considerably in hopping and balancing. In some individuals the under wing coverts, axillars and feathers of the anal circlet were indicated by this time, although feathers still were lacking on the under side of the head and upper neck. The bill showed some indication of darkening, just median and also anterior to the nostrils. The legs and feet were fairly dark though not yet approaching the coloration of the adults. No additional crural feathers nor under tail coverts had made their appearance.

Usually by the fourteenth day all the young were out of the nest. Those that had left on the previous day were generally able to hop about quite agilely and used their wings to some extent. In *Geospiza magnirostris* at this age the wing from the bend measured as much as 55 mm. The only remnants of down to be seen were attached to the tips of the feathers dorsal and posterior to the eyes on either side of the head. The time of appearance of the under wing coverts, axillars and feathers of the anal circlet varied considerably. In some individuals they made their appearance at about two weeks of age, in others, not until they were three weeks old. The upper mandible showed a faint darkening around the nostrils by the end of the second week.

At three weeks of age the feathers of the anal circlet, the under wing coverts and the axillars had usually appeared, at least to a limited extent. At this age feathers were also making their appearance on the underside of the head and neck, although it was several days before they broke through their sheaths. The darkened area around the nostril was more apparent. The young were still fed by the parents.

At four weeks of age the young were picking up food of their own accord and about able to feed themselves. The male at this time often attacked the young viciously, as though in effort to drive them away from the nesting territory. This probably succeeds in the wild but with cage-reared young it often resulted in severe injury to the bills of the juveniles. The young were noted bathing at this age. A few more axillars and under wing coverts were apparent and the chin and neck were well feathered. The basal portion of the upper mandible was quite black.

When five weeks old the entire basal half of the upper mandible was black, although the lower mandible was still unchanged. The legs were the color of those of the adult female. Juvenal song was sometimes heard.

The juvenal plumage, when fully acquired, was somewhat similar to the first year plumage, differing, however, in the structure of the body feathers and in the nearly complete absence of ventral streaking. The body feathers were fewer in number than in later plumages and were soft and loose due to the greater space between the barbs and barbules. This resulted in much of the basal gray showing through, thus producing a drab color in combination with the terminal buff of the feathers.

At six weeks of age the upper mandible was about two-thirds black and juvenal song was well developed. Certain individuals were even noted carrying nesting material. Postjuvenal plumage frequently made its appearance at this time and many new feathers could be seen breaking through their sheaths along the dorsal and ventral body tracts as well as the median and lesser wing covert tracts.

By seven weeks of age the basal portion of the lower mandible was black. Postjuvenal feathers were making their appearance over most of the body feather tracts. Some of these appeared in regions which were unfeathered during the juvenal phase, as on the legs, with the exception of the shank, and median to each of the juvenal ventral tracts. Only the rectrices, remiges, primary coverts, the alular quills and their coverts appeared not to be replaced during this molt.

The bills of young hatched in captivity appeared to grow until about the tenth week. In some instances slight growth was noted after this time but it was difficult to determine whether or not this was due merely to the fact that normal wear did not occur under conditions in captivity.

CARE OF THE YOUNG

Both the male and female parents participated in caring for the young while the latter were confined to the nest. By the time the young were ready to leave, however, the male was doing most of the feeding. Observations made upon geospizids in the

Galapagos by Lack (1945:28) indicate that the rôle of feeding is entirely the responsibility of the male once the young have left the nest. This did not hold true for captive birds. In many instances the male did the majority of the feeding but nevertheless the female did contribute in this work. Several times females were seen to feed young while incubating a new clutch of eggs. Sometimes this behavior would continue to within a day or so of the hatching of the succeeding brood.

Difficulties occasionally arose as a result of males attacking young when the latter had been out of the nest a week or slightly longer. Under such circumstances it was frequently necessary to confine the male to a small retaining cage within the nesting cage in order to prevent the young from being killed. Consequently the problem of feeding the fledglings rested entirely with the female. This habit of attacking the young, occasionally exhibited by the males, seemed probably to be a result of inadequate diet which may have retarded the speed of development of the offspring. Possibly when the normal time arrived at which the males would drive the young from the nest territory, under natural conditions, the captive reared young were not sufficiently advanced to care for themselves and could not, therefore, be removed.

On a number of occasions males of several species were found to kill the young or remove them from the nest and drop them on the ground as soon as they hatched. This habit, however, was generally lost after several sets of young were so destroyed.

The young invariably were fed regurgitated food. The parents at such times were kept plentifully supplied with greens and flower heads and, whenever possible, aphids. During the first breeding season (1940) preserved grasshoppers of the type sold commercially for bait fishing were also added to the diet. Owing to World War II, however, it was not found possible to secure these in succeeding years. Hard boiled egg was occasionally supplied to nesting pairs. In transferring food the bill of the parent was thrust far down the throat of the young.

The nest was maintained in a sanitary condition by the removal of all fecal sacs upon deposition. Both parents performed this duty.

MOLTS AND PLUMAGES

The sequence of molts and plumages in geospizids, the time required by the males in some genera to acquire black plumage, and the question as to whether certain males ever become fully black have been problems long puzzling students of this group. It is believed that the evidence presented in the following account will be of some assistance in arriving at a solution to certain of these problems. To settle completely all of the disputable matters involved, however, it seems likely that further study of a good many if not all the forms in their native environment or at least under semi-captive conditions in the Galapagos area is necessary.

Information derived from museum specimens aided greatly in the interpretation of facts derived from observations on living birds. So far as could be determined from the evidence presented by the very large series of study skins in the collection of the California Academy of Sciences, there is no indication that more than one molt normally occurs each year after postjuvenal plumage is acquired. This series represents the various forms of the genus *Geospiza* taken in every season of the year and it includes all ages. The occurrence of but a single molt was largely borne out by observations on captive birds although, as will be seen, some exceptions were noted. That these exceptions were due to environmental conditions in captivity and do not regularly occur in the wild seems most likely. It must be remembered that the captive birds were maintained in San Francisco which is at 38° N. latitude, in contrast to their native Galapagos Islands situated essentially on the Equator. The results obtained during the first year when the

birds were becoming acclimated to northern hemispheric conditions were obviously abnormal as later observations showed. Likewise, the molts of some of the young hatched in 1940, the year following the arrival of the parent stock in San Francisco, failed to conform with those of young hatched in succeeding years with the exception of one individual hatched in 1943.

It is readily understood that a certain period of time would be required for the physiological adjustment of birds transported from their equatorial home to 38° N. latitude before their molt periods would correspond with those of northern birds. The normal time for the annual molt in this group is from late February to early June or approximately at or near the completion of the breeding season. As noted by Lack (1945:52) and others, however, breeding possibly may occur during any month in the year. This, likewise, was found to be true in the case of certain captive individuals. Since the annual molt of adults usually follows the breeding season, it is not surprising that a certain amount of irregularity as to its time of occurrence is indicated in extensive series of study skins. This, combined with the fact that there is a great deal of individual variation in the plumages of the young males as well as adults, no doubt is responsible in part for the present confused state of knowledge on the subject of geospizid plumage.

All thirty birds received in San Francisco on April 29, 1939, directly after coming from the Galapagos Islands, either had just completed their annual molt or were still in process of doing so. Some of these were young of the year, and consequently they were undergoing their postjuvenal molt. In the latter part of August and during September of the same year all the original birds that had survived again went through a complete molt. This would indicate a relatively rapid adjustment on their part to northern conditions as this is about the time most passerine species in the United States undergo their annual molt. In succeeding years these same birds have had but a single molt during the year. This has usually taken place between the middle of August and the early part of October. Occasionally, however, a few feathers were noted coming in on the head and neck of some individuals as late as January.

Since accounts of the natal and juvenal plumages as well as the postjuvenal molt are given in the section on growth and development of young for the species studied (see p. 189), the present discussion will be confined primarily to plumage changes succeeding the assumption of postjuvenal plumage. Furthermore, no attempt is made here to describe the color of various other members of this group as this has already been done adequately by both Swarth (1931) and Lack (1945).

No unusual features regarding the arrangement of the pterylae were noted in any of the geospizid studies. Mention may be made, however, of the presence of a rudimentary tenth primary. This has been noted in other fringillids, notably in *Carpodacus mexicanus* by Michener and Michener (1940). As is usual when a distal vestigial primary occurs the corresponding primary covert is lacking. The order of feather replacement follows the general pattern of the postnuptial molt of other passerine birds starting with the loss of the first or innermost primary and ending with the replacement of the sixth or proximal secondary.

There are no apparent secondary sexual differences in color pattern in postjuvenal plumage, although males and females may at times be recognized by differences in behavior. Members of both sexes possess the brownish streaked plumage which is seemingly indistinguishable from that of the adult female. Likewise, no specific differences either in times of molting or in the color of the various plumages of the male were discernible among the species studied.

The postjuvenal plumage appears to be maintained normally for about one year or until the first complete annual molt, hence it is referred to as the first year plumage.

The phrases "first year plumage" or "postjuvenal plumage" correspond to Dwight's (1900) first winter plumage. The latter term could hardly be used to describe a plumage in birds from the Equator where there is no true winter. The term "normally" is used with some reservation because some of the young that hatched the first year the birds bred in captivity, that is during the summer and autumn of 1940, underwent what was presumed at the time to be a first prenuptial molt in the spring of 1941. A "prenuptial" molt only occurred once in but one of the young hatched in succeeding years and then took place when this individual was one and one-half years old. It was never indicated in the case of adults.

To check with certainty the possibility that a slight first-year prenuptial molt might be overlooked, two young male *Geospiza magnirostris* that had hatched in September, 1943, were partly colored with aniline dyes when in full postjuvenal plumage so that a representative group of feathers of each of the major pterylae was clearly marked. When the colors faded in the spring of 1944 the feathers were dyed again. No replacements occurred nor were there any additions to the first year plumage up to the time of the first complete annual molt in August, 1944. However, in the spring of 1945 one of these birds again underwent a complete molt. It is possible of course that a few individuals in the native state do undergo a prenuptial molt of some sort. This, however, is certainly not of general occurrence judging from the evidence presented by large numbers of study skins, in the collection of the California Academy of Sciences, representing yearlings as well as second and third year birds in worn plumage taken just prior to and during the normal breeding season.

Those few captive reared males, previously mentioned, that molted the first spring appeared to undergo a complete plumage change including even the flight feathers at this time. The resulting plumage was similar to that usually attained as a result of the first complete annual molt. These same birds again molted completely in the autumn of 1941, some of them assuming full black plumage. These two molts, occurring as they did in the spring and autumn of the year following that in which the young were hatched, seemed to correspond in all respects, aside from the time element, to the first and second complete annual molts as they appeared to occur normally in other young. It seems probable that some factor resulting from their captive environment abnormally speeded up these two molts so that the normal first year plumage was only kept for approximately six months. Following this a partial black plumage was assumed, corresponding to the normal second year plumage. This in turn was molted in about six months so that by the time they were slightly over one year of age they were in a black or nearly black plumage corresponding to that of the normal third year. Following this, however, these same birds reverted to the normal rhythm of but one complete molt a year.

In the other exception mentioned, the young hatched in September, 1943, assumed postjuvenal plumage before November of that year. This was maintained, as was proven by dyeing the feathers, until the fall of 1944 when a complete molt occurred. In the spring of 1945, however, it again molted and acquired the plumage which would not normally have been acquired until the fall of that year. Unfortunately this individual died when the molt was nearly complete.

This brings up the subject of male plumage in *Geospiza* concerning which much confusion has existed. From large series of specimens representing the genus in the Academy collection males of any of the several species, in complete fresh plumage, may be selected showing a complete gradation from the streaked first year plumage, similar to that of the adult female, to a pure black, except for the under tail coverts which always possess a certain amount of buffy edging to them. Some show black

only on the top of the head and the throat, on others it may extend down the neck to include the breast and anterior back. Certain specimens are essentially black with varying amounts of buffy margining to the more posteriorly situated body feathers. Such color gradation often makes it very difficult to segregate certain skins into definite age groups. It does, however, give indication of a large degree of individual variation, the existence of which has been borne out by following the plumage sequence of a number of captive-reared geospizids.

While individual variation is great and in any extensive series of study skins males may be selected showing the complete transition from a female-like plumage to the pure black, nevertheless, most specimens may be allocated to definite plumage stages. This was pointed out long ago by Snodgrass and Heller (1904:273-275) who described six plumage stages distinguishable in male geospizids. It is noted, however, that not all species pass through each of these stages. Members of the genus *Geospiza,* as now understood, are described by these authors as passing through Stages II to VI. These five plumage phases correspond to the juvenal, first, second, third and fourth year plumages described in the present account. The interpretation by Heller and Snodgrass of the significance of these stages, however, is quite different from that presented here. One must presume from their detailed account of *Geospiza fuliginosa* that the changes from Stage II to Stage VI occur within a few months. To quote them (*op. cit.*: 303): "During the time from December to February the males go through Stages III, IV and V, arriving at Stage VI by the first of March." From their further account it appears that their specimens, collected during the months from December to March, had by chance shown progressive plumage stages each succeeding month. It is evident, however, from their comment on the small number of feathers seen growing in at any time and the fact that the darkened feathers are described as brownish rather than black that the specimens studied were in very worn faded plumage which we now know to be normal for members of this group at that time of year on the Galapagos Islands.

As has already been indicated first year plumage is generally replaced completely the year following that in which the young are hatched. This occurred during August and September in captive birds and, judging from museum skins, it takes place between February and June in the Galapagos Islands. Just prior to its replacement the plumage presents a darker appearance, especially on the throat and breast, as a result of the wearing away of a considerable part of the buff-colored tips to the feathers of these parts. In captive birds this condition prevailed from May to July, whereas study skins from the Galapagos Islands taken between January and March often show similar wear.

In second year plumage the feathers on the head and neck of the male are black. Below this they are normally margined with buff, the margins becoming broader and the amount of black more and more reduced on the feathers situated progressively nearer the posterior end of the body. This results in a darkly mottled breast, a lightly mottled belly and an abdomen essentially like that of the first year plumage. The feathers of the back show a similar progressive increase in the extent of the deep buffy margin from anterior to posterior end of the body. There is, of course, a great deal of individual variation in this plumage. Some males show only a slight increase in the amount of black over the first year plumage, while in others it is very extensive. Needless to say it was not found possible to determine the age of females on the basis of color after they assumed first year plumage as this appears to be identical with later plumages.

The second complete annual molt occurs at approximately the same time the following year when the birds are slightly over two years of age. Prior to this molt, however, the males appear considerably darker than they were in fresh second year plumage due to the wearing away of much of the marginal buff on the body feathers. Males

in fresh third year plumage, as a result of the second complete annual molt, possess totally black feathers on the head, neck, breast and anterior back. The feathers of the lower back and rump are usually black, narrowly margined with deep buff and those of the belly and abdomen are black margined with pale buff. As in the preceding plumage the buffy margins are broader on the more posterior body feathers and with wear tend to become progressively reduced. A few individuals in captivity became totally black in third year plumage while others were but slightly darker than the average male in second year plumage. It is highly probable that this same degree of individual variation occurs under natural conditions.

The third complete annual molt in the male results in a fourth year plumage which may be pure black, except of course for the margins of the under tail coverts. Certain individuals, however, exhibited little color change in this plumage from that of the average third year male. In others the amount of buffy tipping was reduced in varying amounts.

It would have been impossible actually to follow the plumage sequence of the male beyond the third year on the basis of study skins alone. Observation of captive birds, however, showed that those individuals which were not totally black by the time they assumed fourth year plumage more nearly approached the total black condition each year thereafter. Some males received in April, 1939, nevertheless, still possessed a few buffy-tipped feathers on the lower abdomen after the completion of the annual molt in the autumn of 1944 and, as has already been explained, others hatched in captivity during the summer of 1940 assumed full black plumage by the time they were one year old, although this is believed to have been abnormal.

Numerous conflicting ideas regarding the black plumage of the male geospizid have been expressed by those who have devoted much time to careful research upon the group. These cannot all be enumerated here but perhaps some of the foremost with which the present writer must necessarily disagree, until definite proof has been shown, may be mentioned. Swarth (1931:24) says that ". . . with such an absence of streaked males as we find in the series of [*Geospiza*] *acutirostris* from Tower Island, and [*G.*] *debilirostris* from James Island, for example, it seems likely that in those forms the streaked stage is frequently, perhaps almost invariably, not passed through." Again Lack (1945:59) says "On Tower, the proportion of the male *G. magnirostris* and *G. difficilis* in fully black plumage is so high that one can be certain that a large proportion of the males must molt into fully black plumage before they are a year old."

I am of the opinion that such conclusions have been arrived at on the basis of an insufficient number of specimens or because such series as were available did not adequately represent the island populations as a whole. Too little consideration has been given to the matter of seasonal movements and the congregating of various age groups in different portions of any one island. That this occurs is shown by Lack (*op. cit.*: 56) who found that on Chatham and Indefatigable islands, where most of his observations were made, the males breeding near the coast were in streaked or partially black plumage. Those breeding in the intermediate forests were mostly black. Consequently, if collecting were carried on only along the coast or only in the intermediate forests without a knowledge of this seasonal segregation it might easily result in a series of males which would be misleading if considered as representing the male population as a whole.

This point is brought out by Lack in refuting Swarth's contention that there was an exceptionally low proportion of "full-plumaged" males for all species on Abingdon. Swarth based his conclusion on the California Academy of Sciences collection made in 1905, whereas Lack has shown that other collections made in different years have not

borne this out. On the other hand the latter writer agrees with Swarth that inter-island variation exists in the number of males in "black, partial black and in streaked plumage."

The number of streaked or first year males is bound to be far greater toward the end of the breeding season when many of the young of the year are in fresh postjuvenal plumage and the young of the previous year have not as yet lost their worn postjuvenal plumage than would be true at the beginning of the breeding season. Although it cannot be asserted with any degree of certainty, the writer is, nevertheless, of the opinion that even in the genera *Camarhynchus* and *Platyspiza* in which the male appears never to become fully black, several years normally are required before the mature plumage is attained.

That this secondary sexual character of the male to develop a black plumage was once common to the ancestral geospizid stock and is now in process of being lost seems indisputable, as both Swarth and Lack agree. Experimental evidence leads to the conclusion that the production of black plumage is at least partly under hormonal control. This was indicated by the administration of estrogenic hormone to fully black males of *G. fuliginosa* with the result that some of the new feathers that later came in possessed buffy margins, indicating a reversion, to a limited extent, to the partial black plumage.

A number of birds were experimented on with sex hormones but misfortune seemed to befall most of them. It was necessary, consequently, to discontinue this work to avoid depletion of numbers of birds which were required for other purposes. Later the writer hopes to be able to resume this line of research with the same group, including especially those genera in which the male normally becomes black only on the head, neck and upper breast, and with those groups in which the male is not known ever to possess any black plumage.

Captive-reared individuals of both *Geospiza magnirostris* and *G. fuliginosa* were subjected to intramuscular injections of sex hormones primarily in an attempt to cause a reversal in plumage. Males were injected twice weekly with small dosages of α estradiol dipropionate and one female was injected similarly with testosterone propionate. No results were obtained with the female, a two year old *magnirostris*. This individual was first injected on May 26, 1943, and twice weekly thereafter until July 6. Each dose consisted of .03 cc. of testosterone propionate dissolved in sesame oil in proportion of 1.25 mg. per cc. Feathers were plucked from parts of the occipital and nape region on May 28, from parts of the upper breast on June 8, from parts of the crown on June 21, from parts of the upper breast on June 29 and from the crown on July 2. The color pattern of the incoming feathers was readily discernible three weeks after feathers were removed. In no instance was any color change apparent.

Four two-year old males were treated with the α estradiol dipropionate twice weekly. One of these, a *G. magnirostris,* escaped due to a faulty cage ten days after the administration had begun. The other three birds were *G. fuliginosa.* Two of these escaped from the same faulty cage before the opening was detected and the third died before the experiments were completed. However, one of the birds that escaped and the one that died had both shown evidence of slight plumage reversal. Their histories therefore will be given.

Male number 2, as one was designated, was in full black plumage. Between May 28, 1943, and the date of its escape June 21, 1943, it was injected twice weekly with .05 cc. of α estradiol dipropionate in sesame oil (.05 mg. per cc.). A small patch of feathers was removed from the lower back and rump on the day of the first injection. On June 1 a small patch of feathers was plucked from the left side of the breast and another from the belly. On June 8 another patch was removed from the right side of the breast and

on June 21 feathers were again removed from the rump. New rump feathers, replacing those plucked the day of the first injection, were well through their sheaths on June 11 and were definitely black. By June 15 new feathers were quite apparent on the left side of the breast, replacing those black feathers which were removed on June 1. These new feathers, however, possessed narrow buffy margins. The effect of the female hormone on pigmentation in the concentration used was noticeable therefore in feathers replacing those plucked three days after the first administration, although it did not affect those removed the first day. By June 18 it was apparent that new feathers coming in on the right side of the breast, to replace those removed on June 8, were also margined with buffy. The escape of this bird on June 21 was indeed unfortunate.

The other full black-plumaged male in which partial reversal in plumage was effected was designated as number 4. Considerably stronger doses of hormone were given in this instance. Semi-weekly injections of .04 cc. of α estradiol dipropionate (1 mg. per cc. of sesame oil) were given this individual between June 22, 1943, and July 8, 1943, at which time it died. A patch of feathers was removed from the left side of the breast on the first day, June 22, from the right side of the breast on June 29 and from the rump on July 2. By the latter date new feathers were apparent on the left side of the breast replacing those removed the first day. In this instance these feathers showed slightly buffy tips indicating that the effect of the hormone in great concentration is almost immediately noticeable. This individual prior to June 22 had been actively carrying nesting material. At the time of its death, sixteen days later, the testes were small, measuring only 4 mm. in length as contrasted with 7 to 8 mm. for normal, sexually active males.

No attempt was made to administer testosterone to males in either juvenal or first year plumage, just prior to the period of molting, to see if one or more of the intermediate plumage stages might be omitted. Unfortunately by the time these lines of inquiry presented themselves it proved difficult to induce successful breeding and such young as were reared were required in order to follow the normal sequence of molt.

BILL COLOR

Little of a definite nature has been obtained from a study of the bill color of captive birds. Many factors such as changed diet, climate, latitude or perhaps confinement may have been responsible for interference with the normal seasonal change in bill color which is asserted by Swarth (1931:26) to occur among members of this group. Under normal circumstances adult geospizids assume a black bill color during the breeding season, whereas the bill is pinkish yellow during the remainder of the year. Males generally acquire black-colored bills in advance of females, although members of both sexes on occasions have been noted breeding with only partially dark bills. Some juveniles are reported to leave the nest with the bill a light color and others with dark areas appearing on parts of the bill. Certain young develop completely dark bills when slightly over one month in age.

Among captive birds the same variability in regard to the development of the black bill in the young was noted but no regular periodicity correlated with the breeding cycle was apparent among the adults. Most of the males of the four species received in April, 1939, possessed black bills upon their arrival. This black color remained permanently, their bills showing no seasonal change in this regard during subsequent years. A few of the younger males had flesh-colored or yellowish bills which likewise became permanently black within a few months. The majority of the females received in 1939 showed the same tendency as the males. Most of those that possessed black bills on their arrival remained permanently in this state while those that did not, for the most part, soon

acquired the black bill color. Males hatched in captivity, likewise, developed permanently black bills.

A few of the females, both wild-taken and captive-reared, however, showed some indication of a periodic change in bill color throughout the year. In some instances the bill merely changed from black in the spring and summer to horn color in the fall and winter. The bills of a few females became brownish yellow outside of the breeding season and that of one definitely turned a flesh-color except for the distal third which remained black. Several females, likewise, failed ever to acquire a pure black bill, this structure remaining always either a horn color or a brownish yellow.

If the periodic development of black bill color is associated with an increase in gonadial activity as inferred by Swarth (*op. cit.*: 26-27), this may account for the failure of most of the captive birds to show a seasonal lightening of the bill. Most of the males under observation sang throughout the year which would indicate an incomplete recrudescence of the gonads. This seemingly is not of normal occurrence among members of these same species on the Galapagos Islands where even the territorial instinct disappears outside of the breeding season and flocking occurs. Furthermore, some of the captive females also showed signs of sexual activity the year around. Those females that failed to develop a dark bill at any time similarly failed to show any sign of sexual activity throughout the year.

The bills of young birds were either yellowish or flesh colored. This color variation appeared in young of all three species hatched in captivity. It was not confined to either sex and was observed among members of the same brood. The bill sometimes started to darken as early as the fourteenth day after hatching. The change from a flesh-colored or yellow bill to a black bill was gradual, the darkening first becoming apparent just anterior and usually slightly mesial to the nostrils. It then expanded so as to include the entire proximal half of the upper mandible. When the change had progressed this far on the upper mandible, slight indication of darkening was seen at the base of each ramus of the lower mandible. The last part of the upper mandible to become dark was the tip. By the time this occurred all but the distal third of the lower mandible had become dark. The tip of the lower mandible was last to change color.

In those birds that changed from a black to a pale bill after the breeding season the lower mandible was first to lose the black. The black pigment, likewise, disappeared first at the base of the mandible, the tips being last to become pale. That this same sequence of change in color of parts of the bill occurs in the native state was borne out by the bills of wild-taken study specimens in the Academy collection.

REACTION TO DANGER

There are reportedly few natural enemies with which geospizids must contend in the Galapagos Islands. One hawk (*Buteo galapagoensis*) and two owls (*Tyto alba punctatissima* and *Asio flammeus galapagoensis*) are the only raptorial birds endemic to the region. None of these species constitutes an important menace to the smaller land bird populations. No native predatory land mammals occur in the archipelago. From these facts Lack (1945:53) therefore concludes "The Geospizinae would thus seem to have lost the normal reactions of a small bird to predators due to the absence of the latter."

Although one quite logically might assume that a group of birds developed on an isolated insular area where natural enemies are practically non-existent would lose their fear of predators, this was disproven by captive birds in San Francisco. Members of all four of the species studied exhibited alarm at the proximity of local predatory birds. The appearance of the following species was seen to produce this effect on the

caged birds: Red-tailed Hawk (*Buteo jamaicensis*), Cooper Hawk (*Accipiter cooperii*), Sharp-shinned Hawk (*Accipiter striatus*), Sparrow Hawk (*Falco sparverius*), Turkey Vulture (*Cathartes aura*) and Raven (*Corvus corax*). None of these species nor even any representatives of the family Corvidae occurs in the Galapagos Islands. This would indicate that fear of enemies is a very fundamental and deeply rooted response, capable of becoming immediately active in a group of birds in which it probably has been of little use for many hundreds if not thousands of generations.

The captive birds became nervous, ceased singing and emitted loud call notes whenever any predatory species appeared on the horizon. Frequently under these circumstances they would dart into the brushy cover provided them in their cages. So typical was their behavior in the aviary at such times that the writer, whose office was downstairs and a considerable distance away, could invariably tell by their loud call notes when a predatory bird was in the vicinity. Even fledglings would cease calling and assume a crouching attitude. Mounted specimens of hawks and owls similarly aroused considerable fear among the caged birds when placed within their view. When such were placed in their cages they would attempt to hide in brush and remain silent. This tendency to remain silent when they suspected danger to be very close was exhibited another time when a freshly killed Cooper Hawk was placed on the screen roof of the aviary. After the first alarm at the appearance of the hawk the birds remained hidden and noiseless.

CONCLUSIONS

As was stated at the beginning of this paper, the author began this study with some misgivings inasmuch as it was believed that the results would apply essentially to captive birds and have little bearing on the behavior of the same species under natural conditions. Although still firmly convinced that nature's own laboratory is the most ideal one for research in the field of avian behavior, it was revealing to find that there was surprisingly little difference between the reactions and responses of the species studied in captivity and those in the wild state where corresponding types of observations have been made. The dependability of observations made on semi-captive birds has been commented on by Ivor (1944). Birds maintained in captivity, furthermore, may be subjected to experiments which sometimes contribute greatly to an understanding of the more fundamental factors producing the normal pattern of behavior. Many such types of experimentation are impossible in the wild.

The systematic treatment of the geospizids has proven a difficult problem to all who have worked upon the group. One finds that many of the normal rules that apply to most variable groups fail here. Evolutionary development seems to have occurred along a number of divergent lines, more or less at random rather than through active selection. An analysis of geospizid behavior hardly presents fewer problems than those encountered in a systematic study.

The four species which were under observation exhibited great similarity in their actions and reactions. In fact if it were not for differences in body size and in shape of bill it would have been impossible to distinguish them so similar was their behavior. Under natural conditions at least three of these species, *Geospiza scandens* possibly being an exception, show essentially no differences in feeding habits other than those imposed by size. In captivity no distinguishable differences were apparent among any of the four species in this regard. All appeared, likewise, to be identical in courtship behavior and nesting habits. Juvenal song was essentially the same in these species and there was a definite interspecific overlapping in the pattern of adult song as well as great intraspecific variation. It seems probable that, as pointed out by Lack (1945:33) bill recognition is of prime importance in specific identity.

Plumage patterns and sequences were found to be similar in all the species studied. In captivity the males, at the completion of the postjuvenal molt, possessed a female-like plumage which normally was retained for one year. Second year plumage showed black on the head and throat of the male. In third year plumage this black coloration extended down to the breast and the anterior part of the back. Full black plumage was usually attained the fourth year. A great deal of individual variation in the amount of black present in the various male plumages after the first year resulted in some overlapping. That this occurs in the native state is borne out by museum specimens.

Despite the practical absence of native predatory species likely to prey upon small passerine birds in the Galapagos region, captive geospizids showed a definte fear of the avian enemies to which most continental birds of comparable size are usually subject. A high percentage of egg infertility was found to occur in captivity and is also recorded in the wild among geospizids. This may be correlated with the absence of natural enemies.

It would seem highly desirable that further field observations be made on those closely related species of the genus *Geospiza* which occupy nearly identical habitats to determine to what degree interspecific competition exists. It does not seem possible that two or more forms, differing somewhat in structure, but practically identical in habits and occupying the same territory, can avoid competing with each other. If this does not occur, it is probable that some slight yet nevertheless extremely important ecologic differences exist which have not as yet been recognized.

LITERATURE CITED

Beebe, W.
1924. Galapagos, World's End (G. P. Putnam's Sons, New York), xxi + 443 pp., 422 figs. in text, 8 colored pls., 1 colored frontispiece.

Dwight, J., Jr.
1900. The sequence of plumages and moults of the passerine birds of New York. Annals N. Y. Acad. Sci., 13:73-360, pls. 1-7.

Gifford, E. W.
1919. Field notes on the land birds of the Galapagos Islands and of Cocos Island, Costa Rica. Proc. Calif. Acad. Sci., 4th ser., 2:189-258.

Ivor, H. R.
1944. Bird study and semi-captive birds: the rose-breasted grosbeak. Wilson Bull., 56:91-104.

Lack, D.
1945. The Galapagos finches (Geospizinae). A study in variation. Occas. Papers, 21, Calif. Acad. Sci., viii + 159 pp., 26 figs., 4 pls., 1 map.

Michener, H., and Michener, J. R.
1940. The molts of house finches of the Pasadena region, California. Condor, 42:140-153.

Snodgrass, R. E., and Heller, E.
1904. Papers from the Hopkins-Stanford Galapagos expedition, 1898-1899, xvi, Birds. Proc. Wash. Acad. Sci., 51:231-372.

Swarth, H. S.
1929. A new bird family (Geospizidae) from the Galapagos Islands. Proc. Calif. Acad. Sci., ser. 4, 18:29-43, 1 fig. in text.
1931. The avifauna of the Galapagos Islands. Occas. Papers, 18, Calif. Acad. Sci.: 1-299, 57 figs. in text, 1 map.

Tinbergen, N.
1939. On the analysis of social organization among vertebrates, with special reference to birds. Amer. Midl. Nat., 21:210-234, 2 figs. in text.

California Academy of Sciences, San Francisco, August 15, 1945.