

BEHAVIOR OF THE INCA DOVE

By RICHARD F. JOHNSTON

INTRODUCTION

The Inca Dove (*Scardafella inca*) is a small, ground-foraging species that occurs from the southwestern United States through México to northern Costa Rica. Observations of wild Inca Doves in southern Dona Ana County, New Mexico, Travis and San Patricio counties, Texas, and southern Sonora, México, form the basis for this report. These doves are notable for their apparent preference for living in modified urban parkland. Thus it is that three of the populations referred to in this paper occurred on the campus of New Mexico State University, in the suburbs of Austin, Texas, and on the grounds of the Welder Park Zoo, Sinton, Texas. In New Mexico, in areas used by Inca Doves, vegetation other than agricultural crops consists of introduced, broad-leaved deciduous trees and exotic conifers, and in Texas such areas have as dominants the native live oaks; there is in any such area relatively little understory vegetation.

The Inca Doves in Sonora maintained a breeding population near Alamos along a small stream, the Río Cuchujaqui. The vegetation there is composed of various short-tree woodland elements, mainly legumes and figs (see Gentry, 1942), and of certain riparian dominants such as bald cypress (*Taxodium mucronatum*) and occasional sycamores (*Platanus*). Open ground and broken understory have been created along the flood plain of the stream by direct and indirect human activity and it is, characteristically, in association with such areas that Inca Doves are found.

Behavior on the periphery of the range of the species, as in New Mexico, may differ from that in non-peripheral areas. Between any two such areas, breeding and territorial behavior probably differ less than other kinds of behavior. However, behavior in autumn and winter does vary between the New Mexican and the more southerly areas. Geographic variation in behavior will thus be emphasized in the discussion when it is appropriate.

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The narrowness of total range in kinds of behavior in Inca Doves is particularly evident in the nonbreeding season, when the apparent energy output by these birds is considerably below that of other kinds of birds living nearby. At such times the activities of icterids particularly point up the general poverty of overt motor activity in Inca Doves, but most other kinds of birds also show a greater range in activities than do these doves. Likewise in the breeding season Inca Doves exhibit a restricted range of ritualized courtship behavior; relatively few stereotyped actions are necessary for effecting formation and maintenance of the pair bond.

Only in the hostile aspects of territoriality can the Inca Dove be said to show a "vigorous" set of behavioral patterns. Indeed, it is this aspect of the birds' behavior that has attracted the most attention in the past and which is responsible for the idea that Inca Doves are aggressive, hostile, and "vigorous" birds.

The matter of "restricted" behavior will not be stressed in the material to follow; it is mentioned here partly to emphasize that the following account is a fair delineation

of major aspects of behavior in these doves and partly to suggest the nature of some of the problems involved in attempting to understand the derivation of certain behavior patterns. It is never clear, of course, whether elements of a derived behavioral gestalt faithfully reflect a precursor condition or whether elements of a precursor condition have been dropped in the derived behavior.

Flight.—The beat of the wings is strong and rapid in Inca Doves, and in straight-away flight their appearance is clean and trim. Short flights of a few feet or yards are jerky; the wing beat is irregular and the long tail is fanned and contracted and swung up and down and back and forth as the birds move at slightly over stalling speed.

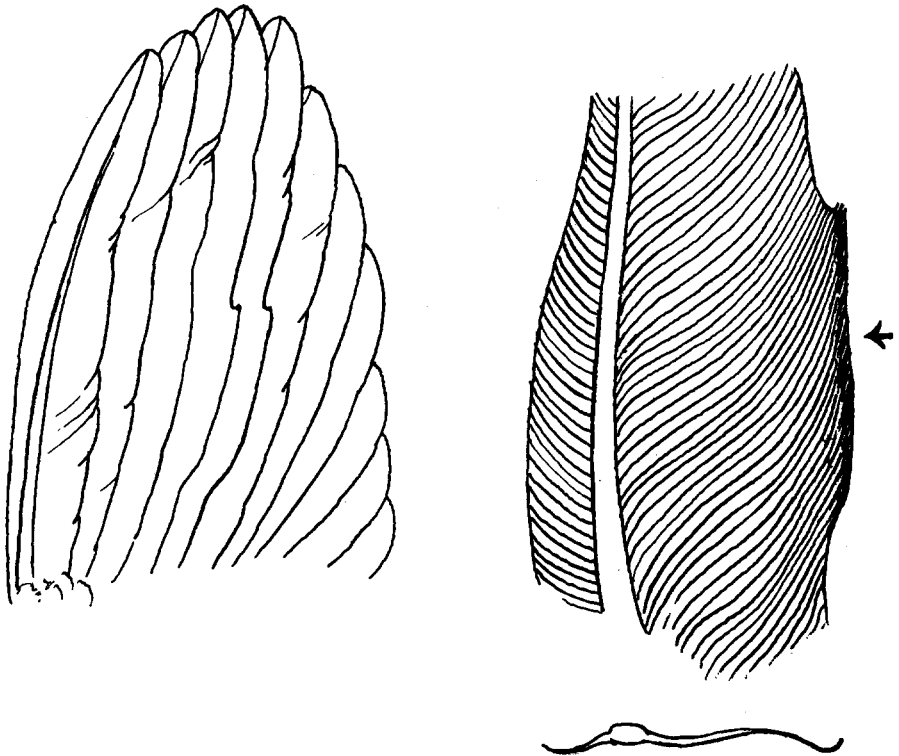


Fig. 1. Underside of wing and primary 8 of an Inca Dove (KU 34901). The diagram shows the emarginations are a function of relative spacing and differential lengths of the barbs. Drawing by R. M. Mengel.

In flight the remiges cause a characteristic sound of flat, buzzing quality. This sound is heard easily for 20 to 30 yards. In my experience only the Ground Dove (*Columbigallina passerina*) makes a sound similar to this. The quality of this wing-beat sound is probably a function of emarginated trailing edges, which both species have on certain primaries; adult Inca Doves have them on primaries 7 and 8 (fig. 1) and Ground Doves have them on primary 8 only. It is significant that the sounds differ slightly in the two species, and this indicates a reasonable functional significance of the sounds, that of species advertisement.

It seems unlikely that the flight sound functions as a "warning" signal for group

flight or other escape behavior. Juvenal Inca Doves have this emargination on primary 8 only (primary 8 only in the Ground Dove), and they make less noise than do adults. Thus, their contribution to "warning" other doves would be minimal. But also, if the sound signal is one of species advertisement, the contribution of the juveniles might reasonably be minimal, for the young birds are relatively unimportant in the sociality of adult breeding interactions. The "adult" condition of the primaries is reached by almost all juveniles in the postjuvenal molt. Similar emarginated primaries are found in the other species of *Columbigallina*, in *Claravis* and *Columbina*, and in the African *Tympanistria*.

Foraging.—Inca Doves forage on the soil surface, taking small seeds of a wide variety of plants. Wheat, cracked corn, oats, and milo are taken readily if available, but the naturally occurring seeds the doves eat are almost always much smaller than these. The doves whisk their bills in dry soil, sending up small puffs of dust at each swipe and uncovering seeds previously hidden in the soil surface. Ordinarily three or four swipes are made in succession, after which the birds pick up whatever they uncover. Rock Doves (*Columba livia*), Mourning Doves (*Zenaidura macroura*), Ground Doves, Diamond Doves (*Geopelia cuneata*), and perhaps a majority of the Columbinae also forage in a similar manner in dry soil. Foraging on moist surfaces involves no swipes of the bill.

Vocalizations.—Inca Doves produce but four kinds of vocal sounds. These are:

1. "Song" (syllabically, *coo-coo*). This call is given both in the breeding season and in the time the birds are in groups. The responses of other doves at these two periods are different, and they will be taken up under appropriate headings later.

2. Aggression call (syllabically, *cut-cut-cut-ca-dóah*). This is discussed beyond under considerations of territoriality.

3. Courtship call (syllabically, *cut-cut-ca-doah*). This is discussed under considerations of courtship behavior.

4. Alarm note (syllabically, *cut*). This note is relatively "soft" in quality. One such note is given each second or two, usually for a short time, in response to apparent stress; as far as I know this has always consisted of my presence near the birds. This kind of note is difficult to locate in the field, for it has a nearly imperceptible beginning and end; this is obviously adaptive in that the bird does not automatically reveal itself to what has alarmed it. Andrew (1957:35) thinks this kind of note in buntings (Emberizinae) expresses "strong fear"; "weak fear" in buntings seems to be expressed by a more explosive note, one that has social communication value. In Inca Doves, the alarm notes probably are an expression of "weak fear"; they seem to express "strong fear" by flying away from its source; these doves are much stronger flyers than are buntings and it is reasonable to assume that they have a different orientation to strong stress situations.

Dispersal.—Little information is available on the dispersal of Inca Doves. The species is resident wherever its populations exist and presumably the young-of-the-year undertake dispersal; such movements would therefore occur in autumn and winter. Extralimital vagrancies that seem to be instances of dispersal have been recorded in autumn (Corona, California, Audubon Field Notes, 1955, 9:56; Boulder City, Nevada, Audubon Field Notes, 1953, 7:30), spring (Mesilla Valley, New Mexico, 1935, Harry G. Williams, MS), and winter (Harvey County, Kansas, 1951–52, Tordoff, 1956; Meade County, Kansas, 1956–57, Hardy, 1958; Ponca City, Oklahoma, Audubon Field Notes, 1957, 11:48). The record for Meade County, Kansas, is supported by a specimen (KU 33241); it is a bird-of-the-year. It is probably also meaningful that the only Inca Doves I ever recorded at my house two miles north of New Mexico State University were present in late August, for only two days, and at least one of the two individuals was a juvenile.

BREEDING BEHAVIOR

COURTSHIP AND NEST BUILDING

Courtship behavior is here considered to involve those activities that lead to the formation of the pair bond and to behavior tending to maintain that bond. In New Mexico by late January vocalizations of Inca Doves increase in frequency; this is the sign of incipient breeding behavior. Clear attempts at pair formation follow. Males do not seem to recognize females at sight (the species is not sexually dimorphic) but by their responses to certain ritual behavior. Displays seen at this time are not qualitatively different from those seen later, but they are of lower intensity: they are given for short periods, they are interrupted or may be incomplete for any of several reasons (some of which may not be apparent to an observer), males frequently seem to have no organized plan of behavior toward a specific female, and females regularly ignore the occasionally strong displays of males. By early March some pairs are established, but usually it is not until the end of March that the bulk of the population is arranged in pairs. Thus, it is in March, or in April in years having heavy rains and low spring temperatures, that definitive courtship display may be seen. Following this time, that is, after sex recognition and formation of the pair bond, the full range of epigamic behavior is rarely seen. Maintenance of the pair bond is accomplished with considerably less activity and fewer displays.

In Sonora early phases of courtship probably occur somewhat later in the year, for the birds there breed primarily near the inception of the rainy season, which on the average is in late June. Courtship patterns typical of birds not yet nesting were seen on June 7, 1957, in which year the rains began in late June. But, by June 4, 1958, most Inca Doves had already built nests and no courtship behavior was noted for any of the mated birds watched; 1958 had a prolonged occurrence of light spring rains and vegetation came into leaf about one month early. Probably doves respond to the timing of the growing season in Sonora in a fashion similar to their response in New Mexico.

Head bobbing.—Shortly after the increase in calling activity male Inca Doves engage in a bobbing ritual. This display consists of birds raising heads high on moderately extended necks followed by an abrupt downward movement of the heads and necks; the bill is maintained in a nearly horizontal position, and the action is repeated many times in a single display. Males bob at females or other males early in the season. Later, by a few days or a week, females reciprocate, and this seems to be an important part of sex recognition. Males almost never bob in return to another male.

Head bobbing bears a close resemblance to a notable sign of anxiety in Inca Doves. The birds make use of what appears to be a form of rapid-peering when they are under stress. In this action the head is moved from one position to another vertically above or below the initial position; a short arc is described by the head, as the movement involves in midcourse a slight rearward shifting. The movement is initiated either when the neck is extended or shortened, but in either case the action is repeated several times over and the head is moved up and down similarly to epigamic bobbing. If males are in fact under conflicting drives, as of attack and escape, early in the season, it is reasonable to think that epigamic bobbing could be a ritualization derived from an anxiety signal.

Mutual preening.—Bobbing is usually followed by preening of head and neck feathers of females by males. Females eventually preen in return. Similar activity in Rock Doves has been termed "nibbling" or "heteropreening"; it is advisable to use "mutual preening" with Inca Doves, first to emphasize that both males and females are involved and second to distinguish it from the similar behavior of Rock Doves. It is not the

earliest expression of epigamic activity in Inca Doves, whereas it probably is the earliest in Rock Doves. Also, in the latter it is often discontinued after pair formation, but in Inca Doves it remains one of the most characteristic features of the entire period of breeding.

Mounting.—This behavior occasionally precedes any of the stereotyped activities just outlined; it involves males standing on the backs of females and, ordinarily, attempts at copulation by the males. Copulation is probably almost never effected, however, since females at this time regularly ignore the presence of males on their backs, even to the extent of continuing foraging while the males attempt to maintain balance. Two birds early in the season may associate in this manner for five to ten seconds and then spend up to two minutes preening each other; yet after this they frequently part and never again associate with one another. However, such breakups probably become less frequent as the season advances, and mounting would seem to be integral in pair formation.

Mounting is also important in sex recognition. A mounted male actively rids himself of the bird on his back, but, as has been noted, a female is ordinarily passively tolerant of the mounter, even though she may show no tendency to behave sexually.

Up to this point in New Mexico most of the displays will have taken place in winter flocks; pairs leaving the flocks do so gradually through time and come to live in the parkland areas of the campus to breed. A considerable amount of time is required for the whole of the wintering population to assort into pairs and leave the flocks. Thus, at one point in the spring, birds in "winter" flocks, birds showing early epigamic display, recently-paired individuals, early territorial pairs, and pairs with nests and eggs can be found in various places on the campus. There is a difference in the ages of the differently-behaving birds: adults pair and leave the flocks earlier, and immatures remain longer in the wintering flocks. Later breeding of immatures than of adults in the same population has been documented in other kinds of birds, and it is not especially surprising to find this in the Inca Dove. Specimens have been taken to support this conclusion in the present study, but the bulk of the observations are of birds in the field. In Inca Doves the postjuvinal molt is mostly incomplete in the remiges; the eleventh primary, and occasionally the eighth through the tenth remain. Such feathers have a buff-white leading edge, which is lacking in the adult feather. Under favorable conditions these "white" primaries can be seen, in the closed wing, for at least 20 yards with 6×30 glasses.

Vertical tail fanning.—One to two weeks after the activities just described are evident in the population, and after pairs are on breeding territories, more intensive displays appear. Vertical tail fanning by males (fig. 2) is characteristic at this time. Males assume a horizontal posture one or two feet from females and face them. Tails are then elevated to a nearly vertical position and fanned; the black-and-white markings on the outer tail feathers are given prominence by this action. Males give a characteristic call in this posture; it may be rendered, *cut-cut-ca, doah*. It is a soft, throaty call; it carries poorly and is intended clearly for the female a short distance away. The complex of behavior associated with tail fanning by males probably serves to bring females more nearly into breeding readiness. Females participate little in response to this display, although females preen males whenever they come close. But about a week subsequent to the appearance of tail fanning nest building activity is initiated.

After first nestings are begun, full courtship display wanes. The pairs become involved with low-intensity displays only. Head bobbing is a continuing activity and mutual preening occurs until the end of the breeding season. Bobbing and preening seem thus to be primarily related to the establishment and maintenance of the pair bond, and therefore only secondarily related to sexual behavior as such, but they serve as a be-



Fig. 2. Upper, courtship fanning of the tail by a male Inca Dove; center, roosting posture of an Inca Dove, from a photograph of a bird loafing in midafternoon in winter; below, aggressive tail fanning by a male Inca Dove.

havioral matrix during the season of breeding; the specific, primary breeding activity is superimposed on them.

It is pertinent here to note that at least *Scardafella*, *Zenaida asiatica*, and, under certain conditions, *Zenaidura macroura* have a tail-raising habit on alighting. In *Scardafella* about one second after alighting, and in *Zenaida* and *Zenaidura* about two or

three seconds subsequent to alighting, the tail is pumped abruptly up two or three inches. In its present form this movement probably has to do with anxiety. It is important to note that female Inca Doves raise their tails about $1\frac{1}{2}$ inches when they are put under stress—this is a signal of anxiety; however, females do not fan the raised tail. Agonistic tail raising and fanning may well have been derived from such a signal of unrest. Goodwin (1955:63) suggests the simple pump had its ultimate origin as a balancing movement; the possible derivation of a sign of psychic disquiet from one of physical unbalance certainly merits attention. It is also of interest to note that tail raising after alighting does not occur in *Columba flavirostris*, *C. livia*, *C. fasciata*, or *Columbigallina passerina*, and none of these exhibits vertical epigamic or agonistic fanning.

Nest construction.—The building of nests by Inca Doves, as in practically all other columbids, is a cooperative undertaking of members of the pair. Typically, the males gather nesting material and the females sit on nest sites or partly-built nests and arrange material brought by the males. Building by these doves in New Mexico occurs in the morning hours and ordinarily ceases by about 10 a.m. At least three times as much time is spent by males in searching for nesting material as is spent in transferring it to females. In one instance of intense building activity a male averaged 47 seconds on the ground and 13 seconds at the nest site; 12 trips to and from the nest were made in 12.2 minutes. This is as much building activity as an observer is likely to see in Inca Doves in New Mexico; such a schedule is also characteristic of *Columbigallina talpacoti* (Skutch, 1956:190), but it is of course surpassed by the more intense activity seen in some other doves, as, for instance, *Columba livia*, males of which I have observed to make five or six trips per minute for a quarter-hour. Exceptionally, females gather nesting material while males remain at the nest site in an apparent reversal of the usual roles of the sexes. I observed this to happen once; a pair tended to alternate the hunt for material for about a 20-minute period one morning. The alternation was not complete, however, and the female made about one-third of the total trips. Also, the male did not arrange nesting material at the site.

Building usually occurs on about three consecutive days. Frequently nests are partly made and then deserted or ignored. A pair can build one or two "false" nests before the final nest is made. False nests do not persist long; winds or House Sparrows (*Passer domesticus*) remove the sticks. False nests seem to have no function of themselves; it would seem that the doves engage in the building activity for its own sake, as if it were a necessary part of the rituals leading to the laying of eggs.

Building routines follow this pattern: males fly to the ground and look for sticks and other pieces of vegetation, and many are examined; when suitable pieces (possibly determined by weight, Lorenz, 1955) are found, males fly with them, one piece at a time, toward the positions of females and alight nearby, walk to the females, and climb on their backs. When the males are on the mid-scapular region of the females they pass the nesting material to or toward the sides of the females, who place or arrange it in the nests. This sequence seems to be necessary as a sequence, and it amounts to a rigid ritual. Even the routes to the females tend to be the same each trip.

This ritual is doubtless an important part of the epigamic activities of Inca Doves. Possibly it is pre-copulatory in nature, but copulation begins well before nest construction is begun, although it continues through the time of nest building and probably while the clutch is being laid. Lehrman (1955:249) has shown that stimulation by the heads of young of the outside of the crop of parental Ring Doves (*Streptopelia risoria*) plays an integral role in bringing about the complex of behavior called regurgitation feeding; by analogy, it is possible that peripheral stimulation of the dorsum of female

Inca Doves plays a part in stimulation or maintaining a tendency toward copulatory behavior.

While engaged in building, Inca Doves show a marked single-mindedness; they are nearly oblivious to activities around them. The major exception to this is intrusion of another Inca Dove into the territory of the builder. Humans can approach exceedingly close to the doves without seeming to startle or alarm them; such behavior is not wholly typical of the birds at other times of the year.

Nest sites.—Nests on the campus of New Mexico State University were located in medium- to large-sized trees, never in shrubs or on the ground. In 1957, exotic conifers contained four nests and deciduous, broad-leaved trees contained five. Heights of nests above the ground varied from eight to 20 feet and averaged about 16 feet. No *Opuntia* was used as a nest site; Anderson and Anderson (1948:152) reported *Opuntia spinosior* to be a favored nest-site plant in the vicinity of Tucson. *Opuntia spinosior* is present in abundance in the university botanic garden, which is an area suitable for nesting Inca Doves.

Nests were much harder to find along the Río Cachujaqui, and no generalization can be made from the data gathered. It is likely, however, that the behavior of doves there is similar to that of doves in New Mexico. One nest was located 25 feet up in a tall, deciduous, leguminous tree, and another was at the same height in a bald cypress. At this locality the Ground Dove (*Columbigallina passerina*) is abundant, and it nests low (average of four nests was six feet) to the ground; possibly there is a competition for nest sites between these two small doves, with the result that Inca Doves take higher nesting sites than they ordinarily do. I do not think this a likely thing, but it needs further investigation.

Persistence of nests.—Inca Doves tend to use nests for two or more consecutive nestings. This is significant as far as stability of the nest is concerned. When first constructed an Inca Dove nest is a relatively loose platform of small sticks having a shallow, although definite, cup. During the period of brooding, the nest becomes rimmed and infiltrated with feces and excrement. If the first brood fledges, enough waste will have accumulated to serve as a strong binder for the sticks and grasses of the original nest; a rigid, substantial structure with a fairly deep, broad cup results from this process. A small amount of lining is added before the second clutch is completed, and the second brood, and any subsequent brood, continues to add cement to the nest. Many nests last through the fall and winter in good condition and are available for use the following year. I was not certain that any pair I watched used a nest from a previous year, but pairs commonly seemed to do so in the Tucson area (Anderson and Anderson, 1948: 152). There, one nest was actually used for four successive years, housing 11 broods.

Spring windstorms frequently blow down first-effort nests of Inca Doves, but the short, violent storms of summer rarely damage the aged, cemented nests. The likelihood of young being fledged increases considerably if the nest has been used successfully at least once before. Such a situation reduces egg and nestling mortality as the season progresses. Mortality rates of eggs and nestlings of Inca Doves should thus be continually shifting in value in time, posing an interesting problem for further work.

Aberrant nestings of Inca Doves exceptionally may be damaged by the increase in weight of feces. One such nesting occurred at the house of Dr. A. R. Phillips in Tucson. The doves placed the nest on a wooden lattice and the cup was directly over an opening of some 2-inch by 2-inch squares in the lattice. The first brood fledged successfully, but continued use and possibly the added weight of the cement eventually worked the nest through the opening and the second clutch of eggs was destroyed when it fell down (Phillips, MS).

TERRITORIALITY

Territoriality in Inca Doves qualitatively resembles "classical" territoriality seen in passerine birds. A pair of doves during the season of major breeding is oriented toward a specific plot of ground in which mating, foraging, nesting, and parental activities take place; this plot of ground has more or less clearly defined boundaries that are known by the occupant pair and the neighboring pairs of Inca Doves; this plot of ground is defended against intrusion by any other Inca Dove. This is wholly true in Sonora, Arizona and New Mexico, but only partly true of breeding activity in winter in southern Texas, and presumably also slightly farther south.

It is important to note that the Inca Dove as a species actually breeds all the year around in the more nearly tropical parts of its range; this is emphasized by Dickey and van Rossem (1938:196) for El Salvador. In southern Texas (Sinton; San Benito, Cameron County) a few pairs of Inca Doves can be found nesting and holding "territory" in winter; young are known to have fledged in December and January. The relationships of these breeding males to their domiciles (sites of breeding activities) and to nonbreeding doves are not quantitatively typical of territorial behavior in spring and summer. At Sinton in the first two weeks of December, 1958, there were at least two pairs of Inca Doves with nests. These pairs were surrounded and their "territories" constantly infiltrated by flocking, nonbreeding doves. Aggressive, territorial defense occurred infrequently; in fact, all that I saw was intentionally provoked by me with imitated calls, and the "defense" postures and vocalizations were directed at me, not at other Inca Doves. "Driving" occurred only once in the six days that I watched the birds. Intruding birds were treated much as are juveniles during the main season of breeding; they were ignored. The significance of some of these matters will be treated where appropriate beyond.

Territories of Inca Doves vary in size and shape, presumably in relationship to the spatial configurations of important elements in the immediate environment. Certain doves tend to behave spatially in an unpredictable manner, and operation of other, possibly psychological, factors is evident. In Sonora the territories of these birds were strung out linearly along the Río Cuchujaqui. These territories were narrow and ordinarily were placed on one side of the stream bed and flood plain; they were 30 to 50 yards deep and 70 to 100 yards long. In the Mesilla Valley, territories were slightly smaller and were oriented primarily with respect to the vegetation available; they were not in a linear arrangement. Sizes ran from 30×50 yards to 70×70 yards.

Nests were sometimes placed near the peripheries of territories. Once two nests were only 30 yards apart; it is notable that the adult birds did not engage in territorial conflict any more frequently than average because of this arrangement. In fact, nest sites do not seem to be an important part of what Inca Doves apparently require in a suitable territory, beyond the fact that some kind of site must exist. The primary requisites are two: clear area, on which the doves forage, and some kind of tall vegetation, where the birds take cover, court, roost, and nest. Thus it is that the typical Inca Dove breeding territory is frequently found in man-made situations, as in urban parkland, or in the arid southwest, along streams where natural vegetation has been partly removed.

Examples of typical territorial behavior can be seen a few weeks after the beginning of epigamic displays. It is not possible exactly to describe incipience of territoriality in a population, because individual birds vary widely in expressing such tendencies early in the season. Males or pairs having nests and eggs have been seen to tolerate territorial trespass early in the season, and later they have been seen vigorously to repulse intrusion. Generally, territorial behavior occurs in low intensity two or three weeks after early courtship behavior is evident, or from one to three weeks before eggs are laid.

Driving of females by males sometimes was seen about the time of beginning of courtship displays, and occasionally this is the first form of territorial behavior to be seen. It is nevertheless possible for driving to occur without reference to an established territory, and the early occurrence of driving may not technically qualify as territoriality, in spite of probably identical neural motor paths.

Vocalizations.—A call that can be related to maintenance of a pair of birds on a specific plot of ground will be territorial in nature. In Inca Doves three calls are given that fall into this category; the first is the courtship call, the second is the "song," and the third is the aggression call. The first already has been discussed; its role in the establishment and maintenance of the pair bond is a relatively simple one and needs no further comment.

The "song" of the Inca Dove is a soft, repeated *coo-coo*. That this is song in the sense commonly associated with passerine song, and is indeed basically aggressive during the season of breeding, can be tested at practically any time in spring and summer. A simple human imitation of the call will cause males from two or three nearby territories to respond in like manner. If the human persists in calling, one or more of the doves will come close to the source, and after that time the birds will continue for some time calling by themselves, sitting near the peripheries of their territories, but not ordinarily leaving them. Males breeding in winter in southern Texas also respond in this fashion if the calls are given near the nest; otherwise calling is largely ignored. Intruding birds in winter are, for that matter, also ignored, and little territorial calling is evident in such situations. Reasons for such a turnabout in response in winter are not clear. It is, however, probably significant that flocking birds rarely call and such calls are not prolonged.

If one Inca Dove intrudes into another's territory, the "song" increases in frequency and is superseded by the aggression call. This call has been briefly described previously (p. 9); it is of throaty quality, with the last three syllables accented so that they can be heard by an observer 50 to 75 yards distant. Frequently the call becomes almost continuous, as *cut-cut-cut-ca-dóah-cut-cut-cut-ca-dóah-cut-cut*, from excited males. Each call is accompanied by an incomplete raising and fanning of the tail (fig. 2), and each series by a series of tail movements. This stage is as far as a male is likely to go if he is a winter-breeding bird; behavior of the intruder is probably important in releasing more intent aggression. Continued trespass in summer is inevitably followed by chasing, which resembles a supplanting attack, or by actual contact between two birds.

Horizontal display.—This display results from continued trespass and it is given by the resident bird; it leads to the culmination of a series of activities that eventually remove an intruding bird from a territory. The occupant male orients himself parallel to the surface on which he is standing. Approach toward the intruder follows; some approaches are direct, but most of them involve small detours along the way, so that a rough zigzag is described by the bird. Aggression calls are now almost continually given, mainly by the occupant. After ten seconds to five minutes of such display the occupant frequently goes into the wing-up and unilateral rush.

Wing-up and unilateral rush.—In most instances when the occupant male is within six to 15 inches of the intruder, the occupant rushes obliquely at the intruder, with the distal wing raised. Contact may not be made following a unilateral rush, but if the intruder does not leave, the two birds always make contact, beating vigorously with wings and pecking with bills in the usual columbid manner; they rise perhaps a foot in the air on these occasions. I have yet to see an intruder best an occupant in such combat. Likewise I have never seen the "bloody" combat between these doves that Gilman (1911) has described.

The raised wing probably indicates the readiness of Inca Doves to hit with the wing;

such wing-up displays are signs of aggressiveness in most pigeons and doves. In Inca Doves the wing-up is also used in nonterritorial situations that call for aggressive behavior, as when a male mounts another male in the early part of the breeding season. Mounted males will crouch down and push up one wing; this tends to dislodge the upper bird and also is an aggressive action tending to discourage further errors of perception. The wing-up is also used in interspecific strife (see beyond).

Probably the observations of Evenden (1954:53) on Inca Doves "courting" in Zacatecas fall into the category of aggression. Evenden reported a presumed male circling a presumed female, "dipping its head, spreading its tail, and extending its wings on [*sic*] a 'V' over the body, thus showing the chestnut of its wings . . ." Extension of one or both wings is something I have never seen in epigamic situations, and I cannot agree that Evenden's observations dealt with courtship; some aspect of aggression was probably involved. Also, the chestnut of the primaries and secondaries has never appeared to be important in epigamic display of Inca Doves I have seen. It is possibly important in *Columbigallina passerina*, males of which in courtship vibrate and flash the wing partly open and reveal chestnut color otherwise hidden.

Driving.—Driving is a type of herding of the female by the male. The usual form of driving is one in which the male appears to attempt to occupy the spot the female is on; invariably the female moves a short distance away. When the female moves one to six feet, the male follows, and three or four to a dozen such moves may be made before the male ceases to "push" the female onward. Late in the breeding season, after some pairs have ceased to breed, driving sometimes takes a more relaxed form, in which the male merely herds the female in a certain direction, by placing himself between an intruder and the female and continuously walking. No direct flights are involved in this latter behavior.

In other columbids (Goodwin, 1956:33) it seems that a mated male "drives" when another male is near the former's mate. This is true in the Inca Dove. Driving always occurs if a male encroaches either on a pair sitting or foraging together or on a temporarily unaccompanied female; driving is in fact the only expression of aggression by the territorial male under these circumstances. Straightforward aggression against the intruder sometimes follows an instance of driving, but territorial aggression may actually be terminated by the territory holder in order to drive his mate from the arena. It is thus seen that driving is a form of aggression directly related to maintaining the mated pair and is in part a direct response of a male to an intruding male. It is also in part directly related to the nearness of the female to the intruder.

Goodwin (*loc. cit.*) believes that the immediate objective of driving is removal of the female from possible sexual rivals of her mate. This hypothesis is not wholly unlikely, but it implies reasoning ability on the part of the territorial male and has additionally an overtone of anthropomorphism. Since driving is strongly stereotyped behavior, it is unlikely that reasoning or learning would play a major part in its release. Unfortunately, no alternative hypothesis concerning causation and ultimate function of driving seems much more attractive. Robert I. Smith has suggested to me that driving may be a form of redirected aggression in which the male, frustrated in outright aggression against other males, "turns back" aggressive drives onto the female; this phenomenon is relatively common in vertebrates. However, redirection occurs in no behavior I have witnessed in Inca Doves and it is unlikely to occur as a ritualization in driving.

Discussion.—Territorial behavior in Inca Doves results in the pairs being spaced through the suitable habitat available to a population. It is tempting to say that spacing is a function of territoriality in Inca Doves. Spacing seemingly "ensures" an adequate arena for effective nesting and rearing of young. All the behavior of a breeding pair

tends to be meaningful only with reference to a restricted area of suitable habitat and the aggressive elements of behavior tend to isolate the pair from other pairs. Spacing and those elements associated with spacing thus seem to be adaptive.

It must be mentioned briefly that the relationships evident in winter breeding in southern Texas do not support such a conclusion nor any heretofore reasonably acceptable hypothesis concerning the possible functions of territoriality. It is perhaps best to ignore winter breeding of this type, especially in view of the fact that such breeding is probably of little significance to the population involved. The birds breeding in winter in Texas probably are similar to doves in tropical American where breeding on a year-round schedule is not only possible but presumably adaptive. Certainly those features characteristic of "normal" territoriality in Inca Doves at higher latitudes could never have developed if there were selective advantage to the nonexclusive nature of "territoriality" seen in winter in southern Texas.

Several elements in aggressive, territorial behavior will be recognized as appearing in courtship behavior described earlier. Specifically, there is a strong relationship between the aggression call and the courtship call, between epigamic and agonistic tail fanning, and between heteropreening and aggressive pecking. In some cases the agreement in general pattern of behavior is remarkably good, and there is no reason to believe the relationships are other than real.

When such a relationship is postulated, it is useful further to inquire concerning derivation of the elements. Aggressive behavior is almost certainly more primitive in a species than are the contemporary epigamic patterns; note, for example, that Inca Doves and Rock Doves, which are not particularly closely related, share certain aggressive behavior patterns such as driving, hitting with the wing, raising the wing as a signal of intent to hit, and biting and stabbing with the bill. But they share no single epigamic behavior. It is thus reasonable to suppose that present courtship patterns have been derived from earlier, more generalized aggressive patterns.

Many ethologists (see Moynihan, 1955, and Tinbergen, 1958, for reviews) have taken the position that ritual displays have as their origins certain simple behavioral precursors; these can be classified broadly as "intention" movements, "redirection" activities, and "displacement" activities. From this point of view the elements of epigamic display discussed here would have to be classified as ritualized "intention" movements of attack or escape. It seems unlikely, as mentioned earlier, that "redirection" occurs obviously in Inca Doves, and thus far no ritualized "displacement" activity has been detected. It is possibly a matter of terminology at present whether epigamic displays of these doves should be considered as derived from the actual attack and retreat elements of general aggressive behavior, or whether they can be considered as derived from movements of intention of attacking or fleeing. The latter terminology is perhaps preferable since in these birds aggression is most often expressed as threat, that is, as *intent* to perform in a hostile manner. I doubt that the ethologists consider the matter merely as one of terminology, as is here suggested. It is instructive, however, that there is some agreement that "intention" movements comprise the great bulk of sources for ritual display; relatively few "redirection" or "displacement" sources seem to have been found in any animal species, and some of these are open to different interpretations. Certainly the latter sources seem not to be important in Inca Doves.

Certainly also the behavior of a displaying bird occurs with reference to another bird and with reference to the actions of the other bird in a precise behavioral gestalt. For instance, male Inca Doves initially tend to behave in but one way to another dove in the spring: they exhibit a generalized, low-level aggression (vocal challenge, head bob, heteropreening, charge with mounting). What happens subsequently is dependent

on the response of the second bird; if it is a male, further aggression takes place (is "suitable"), and the relationship between the two birds is transitory; if it is a female, a relationship tends to be formed (in the absence of a previous one), and behavior cannot longer be aggressive to effect this. Hence, modifications in general aggressive behavior have developed from the material immediately at hand, namely the agonistic patterns.

It is worth emphasizing differences in quality of responses of birds approached by an aggressive male; the present hypothesis deriving epigamic from agonistic behavior patterns is greatly dependent on this. A sexually-based dichotomy of behavioral response is of course evident in breeding populations, but it is perhaps more clear in the behavior of birds flocking in the territories of breeding pairs in winter. The lack of response by adults and juveniles to the territorial male effectively concludes any challenge; if an adult female is challenged and she tends to behave sexually, and this is a strongly positive response in contrast to no response at all, a pair tends to be formed or maintained. Winter breeding conditions clearly emphasize the foundation of behavioral response on hormonal condition. It is perhaps superfluous to mention that gonadal and hypophysial hormones strongly determine vertebrate sexual behavior and that at temperate latitudes hormonal levels tend to vary seasonally (for example, see Beach, 1958:89).

INCUBATION AND BROODING

The period of incubation in Inca Doves is 13 to 14 days, at least in Arizona (Anderson and Anderson, 1948:152) and in New Mexico. The birds tend to cover the eggs nearly every minute of the day, and the routine at the nest is the normal one for pigeons; males tend to sit in the middle of the day and females to sit from late afternoon to the following midmorning. The birds are for the most part unobtrusive while sitting but occasionally they give the territorial, *coo-coo*, call. Possibly both males and females give this call when incubating, although otherwise females rarely call in the breeding season. I was never able to determine the cause of such calling. It certainly is not a "nest call" in the strict sense of the term, as this ordinarily applies to a distinct note or notes used in no other context. Skutch (1956:194-195) believed that similar use of a non-specific nest call (the regular *coo*) in *Columbigallina talpacoti* was a signal that the sitting bird wanted to be relieved by its mate. This interpretation was never suggested to me by activities of Inca Doves.

They never give distraction displays when leaving the nest precipitously. The birds are exceedingly "tight" sitters and do not flush from nests until so late that any seeming value of distraction display would be mitigated. The related species of *Columbigallina* (*passerina*, in Sonora, and *talpacoti*, Skutch, 1956:196) occasionally exhibit distraction display in fairly typical fashion, simulating wing injuries, as do Mourning Doves and White-winged Doves. Inca Doves are not, in areas where I studied them, ground-nesting birds; since there is a positive correlation between ground nesting and distraction display it is reasonable that Inca Doves do not so display.

Brooding occurs for seven to nine days, and the young leave the nest 14 to 16 days after hatching. Following this time the young are attended by the parents for perhaps another week, during which time the young become progressively more independent of parental care. Resumption of nesting activities ordinarily occurs in short order; juveniles leave the parental territory and eventually take up group activities on foraging and loafing grounds with other juveniles.

Renesting.—In New Mexico many Inca Doves nest four times in one year, and some pairs probably nest five times. I have records of only six pairs nesting in 1957. Of these, three pairs nested at least twice, one pair at least three times, one pair at least four

times, and one pair probably five times. These were not all successful attempts, but the two instances of at least four attempts each saw three successful nestings in succession, followed by an unsuccessful terminal attempt. These two pairs each used one nest apiece for the entire season, emphasizing the earlier remarks concerning success of reproduction in reinforced nests. In one of the foregoing series of nestings, the second clutch was deposited on April 24, the third on May 25, and the fourth in late June or early July; in the other series, the second clutch was deposited on May 24, the third (or probably fourth) on July 27, and the fourth (probably fifth) in late August or early September. In each series the first nesting attempt by the pair occurred before I found the nests, which were aged and cemented when I found them. The earliest nest with eggs was found on March 15, in 1957; ample time was available for the presumed first nesting. In the second series outlined above I missed recording a nesting for late June, due to my absence at that time; it probably occurred and probably was successful.

INTERSPECIFIC RELATIONSHIPS

Conflicts with five other species of birds are the only items to be noted in this category. Inca Doves tend to take a passive role in the face of aggression only in winter. In the breeding season these doves are notably aggressive, and few other species act aggressively toward them.

I once saw an Inca Dove chase another from its territory, without much of a battle; the territory holder, still displaying and calling vigorously, then flew directly at a Ground Dove and forced it to take wing and leave the immediate area. It is likely that the Inca Dove misidentified the Ground Dove as one of its own species, for the Ground Dove resettled in the Inca Dove's territory after flushing, and the latter did not pursue the Ground Dove further. If misidentification is ruled out, this event could be classified as interspecific, redirected aggression.

A Black Phoebe (*Sayornis nigricans*) once foraged low over an area in which a pair of Inca Doves were working for seeds. The phoebe at one point made directly for one of the doves; the latter held up one of its wings and the phoebe veered off sharply and left the foraging ground. Perhaps the phoebe through previous conditioning had interpreted the raised wing as a signal of aggression; phoebes, however, never use their wings in this manner.

In winter, Mourning Doves, Boat-tailed Grackles (*Cassidix mexicanus*), and House Sparrows sometimes make Inca Doves remove or retreat by means of aggressive action. A short, horizontal rush is enough by each of these species to make Inca Doves move. On two occasions, however, an Inca Dove managed to best a House Sparrow in a minor squabble; each time the dove merely held up one wing and looked at the sparrow. This occurred on a foraging ground, and in neither instance was the sparrow hostile at any time toward the dove.

Boat-tailed Grackles frequently make doves move. On one notable occasion a first-year male grackle seemed purposefully aggressive, or actually predatory, toward Inca Doves. This bird strode vigorously around a barnyard foraging area, making short dashes at doves and appearing to peck them; it went so far as to pursue one dove in flight for a short distance. Twice the grackle peered intently at a dove, seeming to attempt to make certain of the dove's identity, before striking out at it. The grackle ignored House Sparrows and Brewer Blackbirds (*Euphagus cyanocephalus*) that also were foraging in numbers nearby.

AUTUMNAL SEXUALITY

In September and early October in New Mexico, Inca Doves are quiet; this period sees the height of the molt and its termination. In late October and early November

the birds again give the *coo-coo* call, associated in the spring and summer with incipient breeding behavior and territoriality; the sizes of testes of adults in October are midway between those of breeding condition and total regression. Two individuals were seen to bob in early November, and one bird fanned its tail in December. Nevertheless, no spacing of individuals was effected by these activities; "autumnal territoriality" of various authors (Nice, 1937; Johnston, 1956) as recorded for passerine birds seems of a different nature. In Inca Doves there might be gonadal recrudescence, but mostly this is reflected in abortive courtship activity rather than in the kind of aggression between males that brings about a territorial situation. It is likely that breeding behavior does not cease in populations where winter breeding occurs, but the cycle of activity of individuals is unknown. Specimens from southern Texas show no indication that timing of molt is other than that normal for populations in New Mexico.

GROUP BEHAVIOR

It is rare for an Inca Dove to do anything alone, and in the broad sense all behavior of these birds is social. The present section of this report deals with nonbreeding behavior and the emphasis is on that sociality evident in groups of Inca Doves; nearly all activity carried on outside the breeding season occurs in groups. The birds thus operate in groups (nonbreeding) under one hormonal regime and not in groups (breeding) under another. This amounts to a truism, but it must be emphasized if sense is to be made of the strikingly different modes of life evident within the two periods. The primary characteristic of group life in Inca Doves is the almost total lack of aggression on the parts of all birds. Lack of aggressive tendencies is almost without question due to the hormonal balance in males, chiefly. Stimuli evoking aggressive responses in the breeding season are frequently completely ignored by birds in groups.

FLOCKING

Where there are large foraging areas, such as livestock pens, barnyards, zoological gardens, or waste dumps near grain warehouses, fledged juveniles and nonbreeding members of populations of Inca Doves tend to gather into large, loose flocks. Most individuals in flocks in late summer and early autumn are juveniles. All breeding individuals remain territorial of course, and these birds join the flocks late in the year unless they continue breeding throughout the winter. The flocks persist until about February, when more and more birds leave to take up breeding activities.

Where there are no large foraging areas, as in the small cities of southern Texas and México, the flocks are small, and instead of consisting of 100 or more doves they may be made up of perhaps a dozen birds. The behavior of birds in the large and the small flocks tends to be remarkably similar. The cause of this lies probably in the fact that within large flocks smaller groups of 10 to 40 birds tend to maintain themselves as units, and these form nearly autochthonous foraging and loafing flocks.

The daily activity of these groups is notably uniform and notably restricted to relatively few kinds of behavior. A typical flock of ten or 20 birds will begin foraging in midmorning; the birds leave their nighttime roosting sites earlier on warm and sunny days and later on cold and overcast days. Thus, in New Mexico the doves most frequently begin to forage at about 9:30 a.m. in midwinter, but in southern Texas they start an hour or more earlier. The flock forages for perhaps an hour and then moves for perhaps another hour to sunning and loafing sites. Following this the birds forage again and then loaf, and this routine is repeated until the birds go to roost. In New Mexico in midwinter the doves move to roosting sites at about 4:00 p.m. and in Texas about a half-hour later.

In tropical areas a large proportion of doves in a population is engaged in breeding throughout the year. In such populations the majority of the birds in groups would be juveniles. There is no indication presently available as to whether the behavior of such groups differs either in general daily activities or in specific features of organization.

Sunning.—A great deal of the daily activity of Inca Doves consists of resting or loafing as has been already indicated. The most striking thing done by members of resting groups is sunning. A few to several birds, ordinarily sitting symmetrically, roll partly over on one side and slightly raise the upper wing, which is partly fanned at the carpal joint, and erect all feathers on the side toward the sun. The eye is kept open, but I cannot say that the birds stare at the sun. After ten seconds to two minutes of this the birds sit upright again and then preen body and flight feathers, occasionally working with the bill at the uropygial gland. The process of sunning and preening may be repeated two to four times in short order. Prolonged sunning (Hauser, 1957) does not seem to occur. In summer, Inca Doves do not have an obligatory behavior toward the sun, as Hauser has reported for the Mourning Dove, but not for the Ground Dove; I saw but one Inca Dove assume sunning posture in three summers of observation.

Resting, with sunning behavior, almost always occurs in strong sun, and in New Mexico on a wooden or concrete substratum or on a south-facing earthen mound, or against a wall of some type; in Texas such activity is not necessarily associated with such "sun-traps," and the birds ordinarily rest and sun on flat ground or in trees. Such variation in sunning behavior probably is a function of relative incidence of cold weather and strongly suggests that conservation of energy is the primary objective of such behavior.

Roosting.—Inca Doves roost in evergreen trees. In New Mexico these are almost exclusively exotic conifers but farther south native, broad-leaved evergreens are most frequently used. Birds leave foraging and resting areas in loose groups; the several members of a group leave in pairs or singly, rarely in trios, and the group re congregates within one or more trees. On any one perch the birds associate in units of two or more; I have never seen a single bird roosting.

The doves usually go to roost about one-half hour before the sun sets but occasionally make their way to roosts in mid-dusk. Groups frequently leave for the roosting sites one or two hours before sunset in midwinter. Under the latter circumstances the birds go through a period of intermittent shifting of positions and quiet perching; some individuals actually assume the sleeping posture and close their eyes (fig. 2). Eventually the birds become quiet as a group and spend the rest of the night wing-to-wing; occasionally one or two birds roost on the backs of other individuals. "Social roosting" of this type also occurs in *Geopelia* (Whitman, 1919), *Columbigallina passerina*, and *C. talpacoti* (Skutch, 1956:88).

Pertinent here is the fact that recently-fledged Inca Doves are attended by their parents for, ordinarily, about one week's time. In this period a family unity is maintained and the adults are accompanied by the young when roosting. The three or four birds of any one such group make their way to roosts about dusk, and the individuals typically sit wing-to-wing.

MAINTENANCE OF UNITY OF THE GROUP

It is striking that few evidences of any mechanism for maintaining groups are apparent in these doves. It is important, and probably no accident, that almost no aggression is seen in groups. It is not that aggression is out of place in groups (many other birds show aggression in groups), but in Inca Doves the only kind of aggression ever seen tends to separate individuals and thus might break up the groups. Individ-

uals in fact associate closely with one another; the concept of "individual distance" has no validity in Inca Doves. Birds frequently touch each other when resting or sunning, as well as when they roost. Additionally, in wild flocks, there is no "peck order" or any tendency for a leader to develop in any activities undertaken in flocks. Yet, to emphasize the lack of aggression in these flocks is not to explain how the groups are maintained nor how they function as units.

It is likely that at least one way in which the groups are unified is by vocalizations. However, this is by no means so clear cut as it is in other kinds of birds in groups. Infrequently—once every 10 to 30 minutes—a brief round of calling, *coo-coo*, occurs in the flock of Inca Doves. The notes are given almost offhand, one or two calls from perhaps three or four birds in a group of 10 or 15. The calling schedule is a flexible one, as I have indicated; yet, it is not possible to arouse calling from a group that has just finished calling. Ordinarily a human imitation of the call will arouse a round of calling only if perhaps 20 minutes has elapsed since the last previous round, although infrequently they can be aroused after an elapsed time of 10 or 15 minutes. The rounds of natural calling, in spite of their temporal flexibility, probably serve to orient individuals to the position of the bulk of the group.

The sound made by wings in flight perhaps also helps orient birds in groups. Movement of the group aerially simply cannot occur quietly and it is not reasonable to assume the doves are unaware of the wing sounds.

Finally, vision doubtless plays a large role in group orientation, but this is hardly susceptible even to experimental proof; a dove without sight would behave aberrantly in almost every way. It is clear that Inca Doves seek out other doves by sight in epigamic and agonistic activity, and they probably do so when in groups.

Thus in Inca Doves there is practically no evidence of strong regulation of group interaction. There is no social hierarchy (seeming lack of dominance-subordination relationships), there is no "individual distance" or "social territoriality," there is no leadership-followership behavior, with fixed roles held by individual birds. There is only a weakly-expressed group bond, manifested not by display or strong rituals but by extremely simple auditory signals, in spite of the fact that the birds are in winter markedly group-oriented.

SUMMARY

Behavior of the Inca Dove (*Scardafella inca*) was observed from 1956 to 1958 in southern New Mexico, Texas, and Sonora. Functional epigamic display occurs from February to September, but most frequently in March and April, when the pair bond is being formed. Displays of low intensity are followed by a display featuring the vertically-fanned tails of males; this ritual seems to be a powerful stimulus in bringing about primary sexual activity of both sexes, especially that of females. Nest building is a cooperative undertaking of the sexes; stages in the building process are strongly ritualized. Feces and excrement of young infiltrate and strengthen nests; subsequent use of these probably lessens egg and nestling mortality, for the strengthened nests resist destructive elements of the environment.

Inca Doves are markedly territorial; this is strikingly manifest in vocal behavior and in certain ritual displays, including tail fanning, wing raising, fighting, and driving of females by males. Spacing of pairs of doves through suitable habitat seems to be a function of territoriality.

The similarity of certain epigamic and agonistic patterns of behavior suggests that the former have been derived from the latter.

Group behavior in winter is strongly marked in foraging, resting, sunning, and roosting. Behavior of birds in winter in response to aggression of a few birds that still are

breeding indicates that the response of a bird that is challenged is as important in determining subsequent behavior as the kind of challenge received. Both actions are largely dependent on the hormonal condition of the individuals involved. There seem to be no marked mechanisms for maintenance of the group; simple auditory signals seem to be important.

LITERATURE CITED

- Anderson, A., and Anderson, A.
1948. Observations on the Inca dove at Tucson, Arizona. *Condor*, 50:152-154.
- Andrew, R. J.
1957. A comparative study of the calls of *Emberiza* spp. (buntings). *Ibis*, 99:27-42.
- Beach, F. A.
1958. Evolutionary aspects of psychoendocrinology. In *Behavior and Evolution* (Yale University Press, New Haven), pp. 81-102.
- Dickey, D. R., and van Rossem, A. J.
1938. The birds of El Salvador. *Field Mus. Nat. Hist., Zool. Ser.*, 23:1-609.
- Evenden, F.
1954. Courtship activities of the Inca dove. *Condor*, 56:53.
- Gentry, H. S.
1942. Rio Mayo plants. *Carnegie Inst. Wash.*, publ. 527.
- Gilman, M. F.
1911. Doves on the Pima Reservation. *Condor*, 13:51-56.
- Goodwin, D.
1955. Notes on European wild pigeons. *Avic. Mag.*, 61:54-85.
1956. The significance of some behavior patterns of pigeons. *Bird Study*, 3:25-37.
- Hardy, J. W.
1958. The occurrence of the Inca dove (*Scardafella inca*) in Kansas. *Bull. Kans. Ornith. Soc.*, 8:18-19.
- Hind, R. A., and Tinbergen, N.
1958. The comparative study of species-specific behavior. In *Behavior and Evolution* (Yale University Press, New Haven), pp. 251-268.
- Hauser, D. C.
1957. Some observations on sun-bathing in birds. *Wilson Bull.*, 69:78-90.
- Johnston, R. F.
1956. Population structure in salt marsh song sparrows. I. *Condor*, 58:24-44.
- Lehrman, D. S.
1955. The physiological basis of parental feeding behavior in the ring dove (*Streptopelia risoria*). *Behaviour*, 7:241-286.
- Lorenz, K.
1955. Morphology and behavior patterns in closely allied species. In *Group Processes*, Trans. 1st Conf. Ed. B. Schaffner (Josiah Macy, Jr. Foundation, New York), pp. 168-220.
- Moynihan, M.
1955. Remarks on the original sources of displays. *Auk*, 72:240-246.
- Nice, M. M.
1937. Studies in the life history of the song sparrow. I. *Trans. Linn. Soc. N. Y.*, 4:247 pp.
- Skutch, A. F.
1956. Life history of the ruddy ground dove. *Condor*, 58:188-205.
- Tordoff, H. B.
1956. Check-list of the birds of Kansas. *Univ. Kans. Publ. Mus. Nat. Hist.*, 8:307-359.
- Whitman, C. O.
1919. The behavior of pigeons. *Carnegie Inst. Wash.*, publ. 257.
- Museum of Natural History, University of Kansas, Lawrence, Kansas, June 22, 1959.*