REMARKS ON THE BEHAVIOR OF THE GROUND DOVE

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The Ground Dove (*Columbina passerina*) lives in tropical and subtropical scrub and open woodland plant formations in the Americas. The species has the largest distributional range of members of the genus *Columbina*, is generally considered to be a common bird, and tends strongly to be a permanent resident wherever it is found, but it is rather less well known than some of its relatives. This paper sets forth some descriptive material on certain aspects of the behavior of the species in the wild, suggests a reason why it is less well understood than its distribution and abundance would lead one to expect, and discusses matters pertaining to the nature of the pair bond and associated social behavior.

Observations reported here were made in the field at various places, the most important of which were in Highlands and Monroe counties, Florida (June, 1961), San Patricio County, Texas (December, 1958), near Alamos, Sonora (December, 1959), near San Blas, Nayarit (December, 1959), and near Ciudad Alemán, Veracruz (November, 1959).

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MAINTENANCE OF THE PAIR BOND

There is little ritual maintenance of the pair bond in Ground Doves. Ordinarily, members of the pair stay close to one another at all times, except when one is sitting on eggs or brooding young. The tendency to stay close to one another is extremely strong; for instance, when a pair is foraging along a dirt road, separation of the birds by more than 10 to 12 feet in distance ultimately will result in the male seeking out and coming to the side of the female, either by running or flying. Moreover, prior to rejoining the female, the male usually shows some sign of anxiety (most commonly wing-flicking). Such behavior can be seen in summer or winter.

Rituals associated with precopulatory behavior in other members of *Columbina* also occur in Ground Doves, and this behavior is probably interpretable as reinforcement, or maintenance, of the pair bond. For Ground Doves, two stereotyped actions are relatively frequently seen in summer; these are head-bobbing and the bow-coo. The latter is strongly stereotyped, as it is in most columbids. Males bow, bringing their bodies to an angle of 30° from the horizontal, flick their wings, and give a throaty call (phonetically, *broww*). They give the bow-coo while facing the females and can repeat it up to seven times in one bout. Females frequently move, afoot or on the wing, and males follow, rendering the bow-coo each time they stop.

The bow-coo is not evident in winter, and it is likely that whatever bond reinforcement is accomplished by its use is of significance chiefly when the birds are in or near primary sexual activity. Outside the breeding season, although pairs are maintained, other, aritualistic sets of behavior are characteristic. As an example, in southern Texas, in December, 1958, a threesome of two males and a female was resting and foraging

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on a dirt road. One male and the female stayed close to one another and seemed to represent a pair. This proved a reasonable assumption later when, after the birds began to ignore the presence of the observer, they resumed foraging. The route of the "mated" male took him on occasion five to six feet from the female. On each such instance the second male then moved toward the female, at which the "mated" male immediately ran or flew back to the female, interposing himself between the female and the second male. At length the birds were flushed; the "pair" flew off together, and the second male left in another direction. These observations probably do not pertain to a sexuallyactive pair, because there was neither overt aggression by the "mated" male toward the second male nor driving of the female, either of which would have occurred if the birds were sexually active in summer. The distances separating the birds were also much smaller than those normally seen when a mated male is stimulated to aggression in the breeding season. It is, of course, necessary to emphasize this last point, because Ground Doves in southern Texas are likely to breed in small numbers throughout the year.

Copulation probably never occurs outside the behavioral confines of the pair bond. This is because the ritual antecedents of copulation—solicitation for food by the female from the male and regurgitation feeding of the female by the male—seem not to take place between unmated birds. Attempted copulation involving unmated birds does occur, but such attempts are not successful, owing to the uncooperative postures of the females. Should such a female happen to be paired, the male bond-mate will drive off the intruder.

MAINTENANCE OF TERRITORY

The ecologic setting of territoriality in the Ground Dove is roughly the same as that described for the Inca Dove, *Columbina inca* (Johnston, Condor, 62, 1960:7–24). An area, used exclusively by the pair in the breeding season, and probably also outside the breeding season, is maintained inviolate by aggressive behavior of the male. Fighting is initiated by the holder of the territory and seems not to occur outside of territorial limits.

The behavioral setting of territoriality in the Ground Dove is not, however, parallel to that of the Inca Dove. Limits of the area of exclusive use are never conspicuous, and even with contiguous territories, the boundaries are vague. Considerable variation in response to territorial trespass is characteristic of these birds: aggression can be immediate, or delayed, and sometimes there is no apparent response, especially in winter.

Details of territorial aggression in Ground Doves are species-specific and have no strict parallel in other species of doves. If a territorial fight occurs, the routine is as follows: an occupant sees an intruder, stands still, holds its body parallel to the ground surface, starts flicking its wings, and gives a two-syllabled note (phonetically, *towah*). Wings are flicked two or three times per second, singly, alternately, or in unison; the call is given one note per second as the wings are flicked. Such horizontal threat postures are followed by aerial supplanting attacks. The ritual posture and attack are usually repeated, perhaps three times, following which the intruder is chased in flight, often for 100 yards. The intruder occasionally leaves after the first supplanting attack.

The attacked bird can show two responses to attack: anxiety prior to attack and/or incipient defense at time of attack. The outward signs of anxiety are wing-flicking and a downward pump of the tail. Such behavior is abandoned at time of attack, but will persist for as long as two minutes in experimental situations, as when recorded territorial calls are played near a stuffed male in the presence of an intruder.

The defense attitude just preceding attack by another bird is a horizontal posture with a raised wing. The wing farthest from the attacker is held stiffly vertical. It is here assumed that this posture is indicative of a willingness to fight by the intruder, but in fact intruders have never been seen to stand ground long enough to precipitate actual contact. The posture seems not to be a ritualized preflight movement; support for this assumption consists of observations of its use repeatedly in minor interspecific conflicts on feeding grounds, where flight by doves rarely followed raising of the wing, and by analogy with Inca Doves, in which hitting with the wing frequently follows raising of the wing. For Ground Doves, raising of both wings seems to be a stronger indication of willingness to fight; de Carvalho (Bol. Mus. Par. Emilio Goeldi, 7, 1957:1-15) and Nicholson (Wilson Bull., 49, 1937:101-114) suggest that bilateral wing-raising is a "defense" posture. Harrison (Condor, 63, 1961:450-455), speaking about Scaly Doves (*C. squammata*) and Inca Doves, suggests that raising one wing is agonistic, indicating ambivalent tendencies toward fighting and fleeing. Ambivalence is, as mentioned above, a likely concomitant of trespass or aggression, but in Ground Doves wing-flicking is its clearest expression.

It is unusual to be able artificially to induce a state of hostility in Ground Doves. A human imitation or tape recording of the territorial call given in the presence of known territorial males near their nests is almost always ignored by these birds. This is in sharp contrast to the behavior of the Inca Dove, in which readiness to engage in territorial conflict is a pronounced characteristic. On those few occasions when a male Ground Dove does respond to imitated calls, his attitude is that of a typical, aggressive territorial bird.

SOCIAL ORGANIZATION

A part of the social behavior of any species of dove, as well as of most birds, involves the relationships of the members of a pair to one another. It is unusual, however, to find nearly the entirety of social interaction in a columbid to be organized chiefly around the pair bond. It is most unexpected to find this to be true of Ground Doves, close relatives of which have a complex social life in groups wholly outside the pair bond.

The pair stands as the primary, and almost the only, social unit; no groups of other than temporary and seemingly insignificant character are formed. Associated with this is the apparent lack of signals used to communicate to members of a group. There is likewise a lack of responsiveness by Ground Doves to group signals used by Ruddy Ground Doves (*C. talpacoti*) and Inca Doves; Ground Doves tend strongly to behave as individuals or pairs and not as temporary members of a group of other kinds of doves. As an example, Ground Doves are likely to respond to a strong stimulus of danger (a passing hawk) by flight to cover, and, if they happened to have been foraging in company with a group of Ruddy Ground Doves, their path of flight almost always has no relationship to that used by the Ruddy Ground Doves.

DISCUSSION

Temporary or annually recurrent pair bonds are characteristic of most birds at midlatitudes. Such bonds are held through part or all of the season of reproduction but rarely for longer than half the annual cycle of a species. Relatively few, usually resident, species show persistent or permanent pair bonds. Such species can show special forms of social behavior dependent on or related to the permanent bond. The conspicuous examples are found in geese, in which pairs form the nuclei for familial and group activities and in which the breaking of a bond results in evident psychic stress to individuals, requiring considerable social reorientation. The present paper has indicated some evidence for persistence of pair bonds and for restricted social behavior in the Ground Dove, a member of a genus of birds otherwise characterized by formation of temporary

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pair bonds and well-developed flocking tendencies. It is the intention here to see what relationship these phenomena may have to one another.

Persistence of the pair bond.—It is prudent to note that the evidence for persistence of pair bonds is incomplete for Ground Doves. No banded or captive birds have been used in this study. The evidence is totally circumstantial and consists chiefly of repeated observations of Ground Doves in twos in all parts of the annual behavioral and seasonal cycles. When these twos are examined, the birds almost always prove to be male and female, at least by characters of plumage or of behavior. Groups of more than two Ground Doves are found occasionally, but they seem not to be permanent flocks, as has been mentioned previously.

Additional, but clearly less satisfactory, evidence for bond-persistence in Ground Doves is that no observer seems to have witnessed pair formation. This can be taken to mean that pair formation occurs less frequently than in related species, such as Inca Doves, for which the rituals have been recorded uncounted times every year. Pair formation actually would occur less often than in related species if Ground Doves had permanent pair bonds. It is not likely that observers have missed pair formation in this species because it is inconspicuous, for the available evidence shows that it probably is a conspicuous behavioral sequence. Bond-maintenance behavior in Ground Doves is of a configuration that could be called "normal" in other members of the genus. This is relevant because the rituals of maintenance in other species of *Columbina* are the same as those used in pair formation, and we may conclude that if Ground Doves show stereotyped bond-maintenance behavior then also they have such rituals for pair formation. Thus, lack of description of pair formation in Ground Doves supports the idea that they have persistent pair bonds.

Social consequences of permanent pair bonds.—Permanent pair bonds probably lead to permanent holding of territories. Individuals are thus likely to have a relatively long time to learn the configuration of territory and the behavioral peculiarities of neighboring doves. This would seem likely to result in a reduction of boundary trespass and of territorial fighting. Such, in fact, is the behavioral picture in the Ground Dove.

The enormous reduction in group activity in Ground Doves makes sense if they have persistent or permanent pair bonds. What may well be vestiges of a more robust group orientation in Ground Doves of the past can even now be found. These birds are not quite wholly oblivious to the existence of other doves of the same or related species. Ground Doves are found in or near flocks of other small doves more often than would be expected by chance. Yet, associations are transitory and all liaisons of this kind disappear when dominant stimuli in the environment demand responses other than loafing or foraging.

A seeming corollary to permanent pairing and reduction in flocking tendencies in the Ground Dove is the occurrence of precocious sexual behavior in these birds. At least some individuals at about the age of six months are capable of effective breeding (Johnston, Auk, 79, 1962:269–270). The number of such birds in any population is not known, but this is not important for present considerations because it is clear on two counts that sexually-oriented, if not sexually competent, juveniles must occur fairly often. First, as in adults, juvenal Ground Doves show no tendency to form flocks. Second, adults form social bonds only with their pair-bond members. For Ground Doves, therefore, the formation of pairs, at least one member of which is chronologically sub-adult, is favored. Two juvenal birds probably do not pair with each other, owing to gross lack of experience by either. The conclusion might thus be better phrased if emphasis is placed on regular occurrence of one inexperienced bird in a pair.

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Conclusions.—The preceding interpretations deal essentially with restricted social behavior in a species of bird that could have been expected to have shown relatively complex social or group organization and also with probably permanent pair bonds in a species close relatives of which have temporary pair bonds. The behavioral antecedents and mode of sequential evolution of persistent pair bonds and restricted social life into the behavioral repertoire of Ground Doves can only be surmised at present. It seems clear, however, that the reproductive and social characteristics represent a departure from patterns of behavior in ancestral ground doves. This can be said if we assume that the present behavioral patterns in other members of the genus *Columbina* represent something near the behavior of common ancestors of ground doves.

The critical step in the reorganization of behavior in Ground Doves probably was the development of persistent pair bonds. The other behavioral peculiarities would "logically" have followed such a step. Some of the social and reproductive behavioral characteristics of Ground Doves would seem to have had no selective advantage in the absence of a persistent pair bond; diminution of tendencies to flock is perhaps the best example of such a characteristic.

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