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SEASONAL CALLING, FORAGING, AND FLOCKING OF INCA DOVES AT GALVESTON, TEXAS

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ABSTRACT.—Inca Doves (*Scardafella inca*) were studied in Galveston, Texas, from August 1977 through March 1981, with the aim of evaluating the occurrence and nature of quantitative seasonal changes in behavior. Three such behaviors are described and analyzed: (1) number of midday-calling ("co-oh cooo") birds; (2) estival foraging in large open fields; and (3) winter flocking. The vernal increase phase of the first of these had positive and significant ($P < 0.001$) regressions with daylength during each of two consecutive years, and showed little if any relation with minutes of sun, or with temperatures, during census days. Daily timing of foraging in large open fields during summer was highly consistent for three consecutive years, with peak numbers in late afternoon. Winter flocking behavior was more variable. Although these behaviors can be seen at any season, they show significant quantitative seasonal changes or patterns in this species near the northern limit of its subtropical geographic range.

Knowledge of avian seasonal chronoethology is dominated by information and concepts obtained chiefly from studies on species in which seasonal changes are obviously great. These studies also tend to stress such major or dramatic biological aspects as sexual behavior, reproduction, growth, and migration. However, this emphasis appears to inadvertently obscure what may be the near universality of seasonal adaptations, and the mechanisms and plasticity whereby they come into being.

Inca Doves (*Scardafella inca*) in southwestern United States represent a good species for studies on the nascence and plasticity of avian seasonal behavior. Their populations are thought to be nonmigratory. They apparently vary from being reproductively active throughout the year in Central America, to having only a brief midwinter hiatus in reproduction in southwestern United States (Bent 1932, Heilfurth 1934, Johnston 1960, Oberholser 1974). Inca Doves in Galveston, Texas, are near the northeastern limit of their geographic range. Although they are now one of the most common urban birds in Galveston, their arrival here is recent (Oberholser 1974). Thus they serve as an example of a northward moving, nonmigratory, subtropical species whose environmental responses and limits are largely undefined and not yet investigated in detail. Some aspects of their water and salt balance, thermoregulation and metabolism have been described by MacMillen and Trost (1965, 1966, 1967a, b) under laboratory conditions.

The present study aimed to evaluate the occurrence of seasonal differences in observed and counted behaviors in the Inca Dove population of eastern Galveston. The longer-term objectives of this work are to provide a basis for correlative evaluation of particular meteorological and other environmental factors in avian and Inca Dove seasonal adaptation, and to provide information on aspects of the urban biology and ecology of this species.

STUDY AREAS AND METHODS

My primary data were obtained through systematic observation in two study areas within the city limits of Galveston, Galveston County, Texas. The first of these consisted of large fields at the eastern end of the city (darkened area, Fig. 1). During the first part of the study (9 August 1977 to 27 July 1978) there were four fields of 0.75, 2.76, 2.89 and 3.24 ha. By 17 January 1980, only two remained (1.28 and 2.76 ha) due to development. During most of the year the fields were mowed approximately weekly, and at all seasons vegetation was sufficiently low to permit easy detection of all birds. I counted all birds on the ground in these fields during censuses made at different times of the day from 9 August 1977 through March 1981 (censuses per year: 1977, 267; 1978, 755; 1979, 670; 1980, 619; 1981, 161; total 2,472).

The second study area was in the urbanized part of eastern Galveston, from the southwestern corner of the campus of the University of Texas Medical Branch to the center of the downtown business district. I followed a standardized course on foot (heavy line, Fig. 1) during the middle of the day (10:00 to 13:00), with consistent total times and direction of census-taking. Along this route I made two kinds of censuses simultaneously. In the first, I counted all birds on the ground in specific lots or yards and noted their activities and associations. Total area of all yards and lots

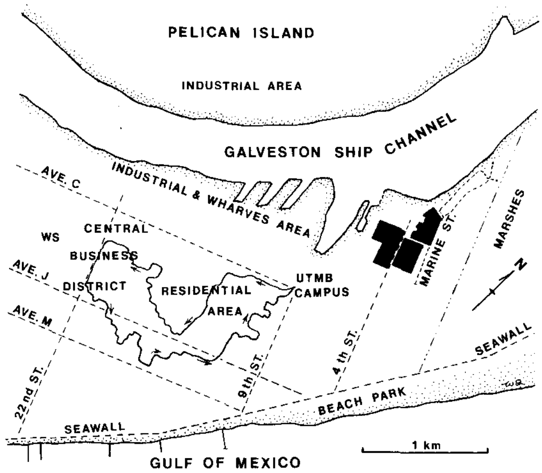

FIGURE 1. Map of eastern Galveston, Texas, showing the study areas. The large open fields comprising the first study area, in the original and maximal dimensions, are darkened on either side of the northwest end of 4th Street. The standardized census route taken through the second study area is indicated by the heavy line. Each census started and ended at the University of Texas Medical Branch (UTMB) campus and proceeded counter-clockwise, with a 20- to 40-min break near its midpoint in the central business district. The "WS" represents the Galveston weather station.

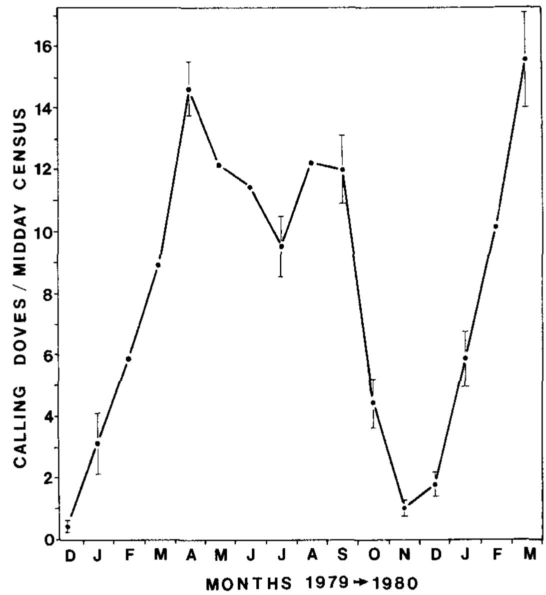

FIGURE 2. Graph of mean number of "co-oh cooo" calling doves per midday census by month, from December 1979 through March 1981. Means (±SE) are plotted. Number (n) of midday censuses per month (D = December, etc.) in sequence: D(1979) 30; J(1980) 27; F 26; M 22; A 23; M 13; J 20; J 13; A 20; S 17; O 22; N 17; D 12; J(1981) 22; F 22; M 23.

censused varied between 13,000 and 20,000 m^2 at any one time, due to either temporary disturbances or semipermanent developments (conversion to parking lots, commercial building, etc.). Thirty-six lots, ranging in size from 58 to 5,289 m^2 were usually censused, from December 1979 through March 1981 (12 to 26 censuses per month; total 305). All lots were sufficiently open to allow accurate determination of all birds on the ground.

The second kind of census was a record of all birds detected along the standard census route (heavy line, Fig. 1) with shorthand notations on activities and associations of each at the time of first detection by sight or sound. The total length of the census route was 6.09 km (3.79 mi) as measured on a detailed city map. The total time of the census averaged 80 min (range approximately 70–90).

Climatological information was obtained from the monthly summaries of "local climatological data" for Galveston, published by the Environmental Data and Information Service of the National Oceanic and Atmospheric Administration (NOAA). These were taken from the weather station on the top of the U.S. Post Office Building, 3.5 blocks southwest of the southwest limit of the census route through the business district (WS in Fig. 1).

Analysis of seasonal changes in midday-calling Inca Doves employed techniques for Model I regressions, in which published (NOAA) time in minutes from sunrise to sunset for a particular day was taken as the independent or "fixed" variable, and the number of birds engaged in the "co-oh cooo" call during the standard census was taken as the dependent variable. These and related data evaluations followed procedures as described by Sokal and Rohlf (1969).

RESULTS

Three behaviors were found to have significant seasonal patterns in the census data. They are: (1) early spring increase in number of birds engaged at midday in the "co-oh cooo" call, (2) summer use of large open fields for foraging, and (3) winter flocking. They will be considered in this order, which corresponds to their sequence in the annual cycle.

Midday censuses of Inca Doves in the urban portion of Galveston (second study area) showed an annual cycle in total numbers of individuals detected per census. Thus, when I combined data from all detection modes and avian activities, apparent numbers of Inca Doves were lowest in December. After this time, numbers increased to a peak in August–September. However, when this pattern was subdivided into its components in terms of particular avian activities at time of detection, only one activity feature was con-

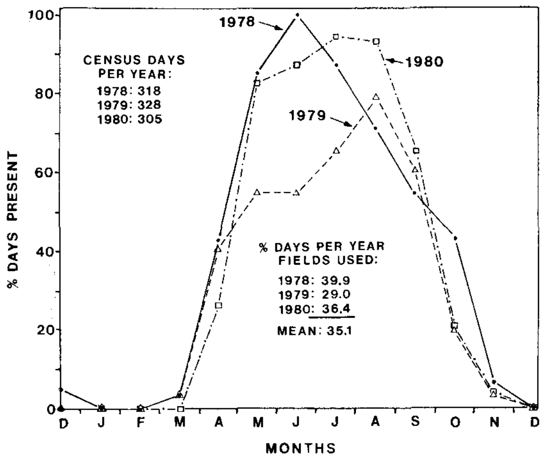

FIGURE 3. Graphs for three consecutive years of the percent of census days per month during which Inca Doves were present on the ground in the large open fields of the first study area. Marked regularity is seen in the seasonal timing of onset, and to a lesser degree of offset, of field utilization by the doves.

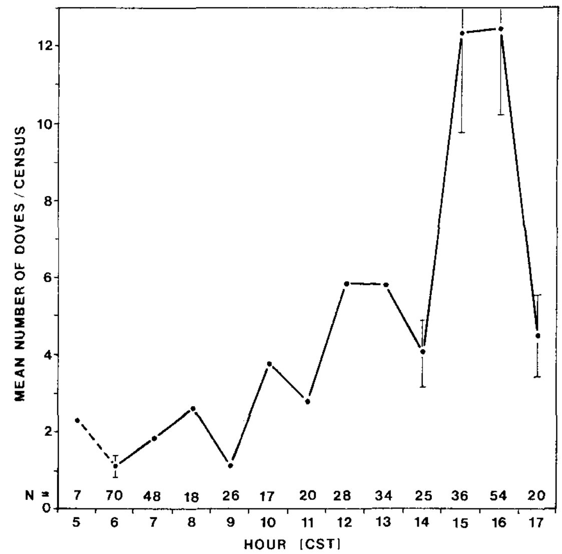

FIGURE 4. Graph of the relationship between time of day and mean number of Inca Doves on the ground in the large fields of the first study area during the summer (April–October). Means (±SE) are plotted. Values of "N" are numbers of censuses within each hour graphed (total = 403).

sistent in its seasonal pattern and high amplitude. This was number of birds at midday engaged in the "co-oh cooo" call. Quantitative analysis of birds calling at midday in urban Galveston showed high amplitude seasonal changes that were consistent from one year to the next (Fig. 2). Three major phases in this annual cycle were seen: (1) a vernal 15-fold increase from December to the first half of April; (2) an irregular estival plateau from April to September; and (3) a sharp and late autumnal drop from September to December. The most interesting of these is the vernal increase phase.

Inca Doves in eastern Galveston had a highly regular seasonal timing of foraging in large open fields, through three consecutive years (Fig. 3). This continued to be true even through spring 1981 with reduction in total area of these fields. I observed that the doves came to these fields from variable distances. Some had nesting sites and primary centers of activity in contiguous residential property, especially on the east side. Others, however, commuted by observed nonstop flight to and from residential sites at least 0.5 to 0.8 km away. Groups of foraging Inca Doves in the fields ranged from individuals and pairs to large flocks. The largest flocks (23 to 55 birds) occurred chiefly in the late afternoon and often seemed to be most active and localized at patches of favorite herb and grass species with new seed crops, and at depressions in nearly bare ground where wind-driven small seeds had accumulated. This pattern of foraging in relation to time of day is illustrated and summarized in Figure 4.

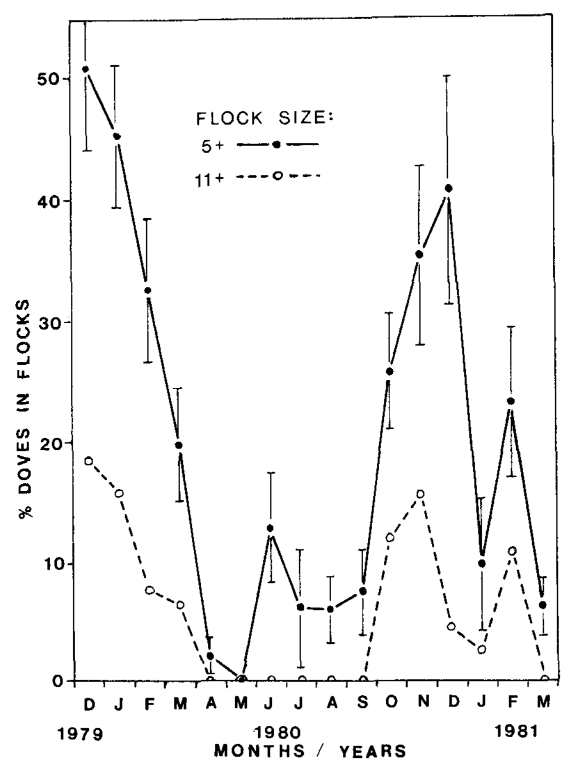

FIGURE 5. Mean percentages of birds seen in flocks during midday censuses in study area 2 in relation to month. Means (±SE) are given for data representing flocks containing five or more birds (solid lines and vertical bars), and means only for data representing flocks containing 11 or more birds (open dots). SEs for the latter, not shown, were relatively great and erratic.

The doves showed no pattern of seasonal utilization of the largest lots and school playgrounds within the central urban area (second study area). Here the monthly averages of doves on the ground were variable and had no consistent trend of seasonality, as compared with fields in the first study area (Fig. 3).

Inca Doves in the second study area showed primarily winter flocking (Fig. 5), contrasting with the estival flocking seen in the large fields in study area 1 (Fig. 3). This winter flocking was evaluated in relation to kinds of avian activities or situations at time of observation—such as, "on the ground," "perched," and "in flight." Winter flocking was typified by groups of closely spaced perched birds, huddled together, especially early and late in the day and in the absence of the sun. In the presence of the sun, group or flock basking and warming were common.

Flocking was more variable in its daily timing and amplitude in winter than in summer (Figs. 3 and 5). The larger and typical winter flocks probably contained both subadult and adult birds, on the basis of plumage (Oberholser 1974) and behavioral characteristics. They were sharply restricted to the September to April period, if 11 or a similar arbitrary number is set for the lower limit of "flock" size (Fig. 5).

DISCUSSION

Johnston (1960) and others have noted that the Inca Dove's "co-oh cooo" call (=vocalization #1 of Johnston) is given during both the breeding season and the time when birds are more commonly in groups. However, my results demonstrate that there are high amplitude seasonal changes in the number of birds calling during the standardized midday urban censuses. The biological implications of such "coo-count censuses" of Mourning Doves (*Zenaida macroura*) have been debated for many years. A review of the literature on this topic relating to Mourning Doves is available (Stone 1966), but how much of this information is applicable to populations of Inca Doves remains to be determined. Nevertheless, work on Mourning Doves provides the basis for hypotheses and models in studies on related species. Lacking information on sex ratios and quantitative reproductive success of the Galveston Inca Doves, I am at present limited in interpreting some aspects of the results of the midday censuses.

The vernal rise in calling Inca Doves was detectable by late January and coincided closely with the increase in the length of the daily photoperiod during each of the two years of the study (Fig. 6). My analysis of climatological data for Galveston from 1979 through early 1981 showed that changes on a daily basis, either in actual minutes of sunlight per day, or in temperature, had far less, if any, relation with the timing and slope of the vernal increase in calling Inca Doves. The representation of this relationship between calling doves and daily increase in photoperiod length as a positive linear regression is presented as a model. The postulated linearity of the relationship is more accurate at the lower end (late winter) than the upper end (spring), on the basis of preliminary analytical observations. The regression equations for the relation of calling doves per midday census to minutes from sunrise to sunset are: 1979–1980: $y = -56.277 + 0.09315x$; 1980–1981: $y = -44.322 + 0.08077x$. F-tests show that although the slopes (regression coefficients) of the two sampled years are not significantly different, the heights are different ($F_{[1,169]} = 11.0$; $P < 0.001$). These evaluations based on analyses of variance (ANOVA) and covariance (ANCOVA; Winer 1971) can be interpreted as supporting the hypothesis that the criterion scores (number of calling doves per midday census) were significantly increased in 1980–1981, even after statistical adjustment for the linear effect of the covariate (daily increase in length of photoperiod). This result suggests that the population of Inca Doves along the census route increased significantly during the reproductive period in 1980. There are observational reasons to doubt that the percentage of Inca Doves engaged in calling at any specific time or date was different from one year to the next. However, the possible impact of unmeasured factors, such as sex ratios and social aggregations, remains to be learned.

Winter flocking by Inca Doves has been described previously (Bent 1932, Johnston 1960), whereas summer flocking while foraging has not been noted previously as a distinctive behavior. When the lower limit of "flock" size is arbitrarily set at five birds, a small summer "shoulder" in the graphed (Fig. 5) percent of individuals in flocks is revealed. This feature in the graph probably represents chiefly family groups with recently fledged juveniles; it disappears when the arbitrary lower limit of "flock" size is raised to 11 (Fig. 5). However in this instance variance within each monthly sample is much greater. I observed summer flock foraging behavior (Figs. 3 and 4) only in the large fields outside of the business and residential areas of the city; traces of summer flocking within the latter areas (Fig. 5) probably represented smaller subgroups, possibly having a familial or extended familial composition.

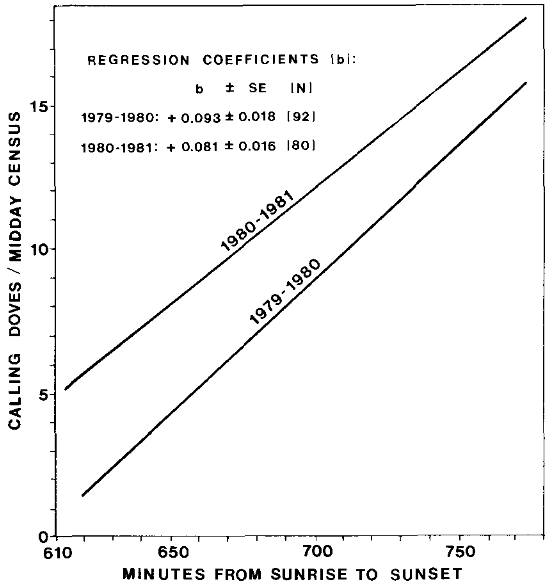

FIGURE 6. Plots of the regression of calling doves per midday census against daily minutes from sunrise to sunset. Data for the two years, 1979–1980 and 1980–1981, are plotted separately. The slopes (b) are very similar, but analysis of covariance suggests that the population levels during the two years were different ($P < 0.001$).

Winter flocking by Inca Doves has been suggested to be related to huddling for warmth (MacMillen and Trost 1967b) and to a winter increase in sociability due to release from hormonal and territorial imperatives of the breeding season (Johnston 1960). A comparison of the ambient and minimum temperatures on winter census days with and without observed flocking behavior fails to support a relationship between winter flocking and colder ambient temperature (Table 1). Nevertheless, the possibility of such a relationship occurring is not ruled out, especially for relatively inactive flocks.

The second notion also may have limited applicability. Johnston (1960) believed that Inca Dove flocks in late summer and early autumn consist of fledged juveniles and nonbreeding members of populations, and that breeding individuals remain territorial and do not join flocks until and unless they cease breeding. At least in my study areas, Inca Doves flocked throughout the year (Figs. 3 and 5). Flocking in open fields through the middle of the breeding season (Figs. 3 and 4) involved many adult pairs, as determined by plumage and behavior. Probably many of these birds were already breeding. My observations suggest that breeding and territorial behavior were probably spatially tied to particular residential sites away from the large fields where the doves congregated. Furthermore, at home feeders and

TABLE 1. Relation of winter flocking by Inca Doves in the second study area with simultaneous and early morning minimum ambient temperatures, November 1980 to February 1981.

Temperature conditions and flock size	No. census days	°C ($\bar{x} \pm$ SE)
Mean temperatures during midday censuses		
Flocks of 11+ present	10	16.44 ± 1.60
Flocks of 11+ absent	43	13.08 ± 0.75
Minimum temperature during the preceding early morning		
Flocks of 11+ present	10	9.39 ± 1.69
Flocks of 11+ absent	44	8.50 ± 0.64
Flocks of 5+ present	31	10.73 ± 1.05
Flocks of 5+ absent	36	9.72 ± 0.76

similar episodic sites of food abundance, Inca Doves flocked at all times of the year. Thus it is not yet possible to provide a simple explanation for the seasonal patterns of flocking activity by the Inca Doves, with the exception of what appears to be related to feeding at localized concentrations of particular kinds of plant food.

In Texas, movement by Inca Doves into new regions has been thought to occur mostly in winter, or during the colder months (Simmons 1925, Oberholser 1974). This view apparently stems from the circumstance that reported geographic range extensions have been based upon doves observed or collected in the winter (Lowery 1974, Oberholser 1974). This presumed winter movement and dispersal does not appear to be closely related to any of the seasonal changes in behavior that I report here. In fact, Inca Dove movement on an individual basis during cold spells in Galveston appears to be minimal. Winter flocking seems to represent a closer aggregation of resident doves within their native urban habitats rather than preparation for dispersal. The lower number of Inca Doves detected during midwinter censuses was largely due to the birds' lessened degree of observable activities at this time. Observed movements of Inca Doves to foraging areas outside of their usual breeding and nesting habitats were essentially restricted to summer (Fig. 3). Banding and other kinds of observations are therefore needed in order to tell where the doves taking part in range extensions originate.

The importance of chronoethological considerations in studies on the Inca Dove has been suggested by the results of MacMillen and Trost (1965, 1966, 1967a, b), especially in terms of circadian thermal and metabolic features under laboratory conditions. My study shows sharply timed seasonal non-reproductive behaviors in a natural population of Inca Doves. One of these behaviors, measured as the number of calling doves per midday census, was significantly positively correlated (Fig. 6) with the length of the daily photoperiod in late winter to spring. In summer, after the start of the plateau in number of calling doves (Fig. 2), I could find no relationship between calling doves per midday census and ambient temperature and certain other climatic factors. Additional kinds of observations are needed in order to elucidate the environmental and physiological factors responsible for these seasonal behavior patterns.

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