

DISTRIBUTION AND RELATIVE ABUNDANCE PATTERNS OF COLUMBIDS IN PUERTO RICO¹

FRANK F. RIVERA-MILAN

Department of Natural Resources, Scientific Research Area, Terrestrial Ecology Section,
P.O. Box 5887, Pta. de Tierra, PR 00906

Abstract. From July 1986 to January 1989 standardized call and sight counts were conducted to examine the distribution and relative abundance patterns of Plain Pigeons (*Columba inornata*), White-crowned Pigeons (*C. leucocephala*), Scaly-naped Pigeons (*C. squamosa*), Zenaïda Doves (*Zenaida aurita*), White-winged Doves (*Z. asiatica*), Mourning Doves (*Z. macroura*), Common Ground-Doves (*Columbina passerina*), Ruddy Quail-Doves (*Geotrygon montana*), Key West Quail-Doves (*G. chrysis*), and Bridled Quail-Doves (*G. mystacea*) during the different seasons of the year in the dry, moist and wet zones of Puerto Rico. The relative abundance of all columbids peaked during the spring-summer period (March-August) in the life zones. The relative abundance of Zenaïda Doves and Common Ground-Doves peaked during the spring-summer, but a second noticeable peak occurred during the fall (September-November) in the dry zone. The seasonal patterns of relative abundance were detectable at local as well as at regional scales of sampling, regardless of the observer involved and the counting technique applied. The detected patterns are not considered to be either the result of sampling error or of statistical artifacts. The seasonal patterns of relative abundance in the three major life zones probably represent the most general and repeatable aspect of the population dynamics of columbids in the island. Two components of the environment of columbids are considered of principal importance in determining their seasonal relative abundance in the life zones: (1) rainfall in the dry zone, and (2) fruiting phenology of key tree species in the moist and wet zones.

Key words: *Columbidae*; distribution; relative abundance; life zones; seasons; standardized counts; Puerto Rico.

INTRODUCTION

Of the 284 species of pigeons and doves (Columbidae) recognized world-wide (Goodwin 1983), 10 species are native to Puerto Rico: Plain Pigeon (*Columba inornata*), White-crowned Pigeon (*C. leucocephala*), Scaly-naped Pigeon (*C. squamosa*), Zenaïda Dove (*Zenaida aurita*), White-winged Dove (*Z. asiatica*), Mourning Dove (*Z. macroura*), Common Ground-Dove (*Columbina passerina*), Ruddy Quail-Dove (*Geotrygon montana*), Key West Quail-Dove (*G. chrysis*), and Bridled Quail-Dove (*G. mystacea*). The Rock Dove (*C. livia*) and the Ringed Turtle Dove (*Streptopelia risoria*) are non-native species found mainly in domestic and semi-domestic states (Raffaele 1989; Rivera-Milán, pers. observ.), and were not considered in this investigation.

Four species are legally hunted during fall (September-November): Scaly-naped Pigeons, Zenaïda Doves, White-winged Doves, and Mourning Doves. Habitat loss and illegal hunt-

ing are probably the two principal causes of endangerment of columbid populations in Puerto Rico (Pérez-Rivera and Collazo-Algarín 1976, Wiley and Wiley 1979, Raffaele 1989, Rivera-Milán 1990). Long-term studies of the population dynamics of columbids are needed to generate recommendations for an integrated management plan (Rivera-Milán et al. 1990).

In July 1985 a sampling scheme was established to determine the distribution and relative abundance of Zenaïda Doves and Scaly-naped Pigeons in the three major life zones of the island (Collazo-Algarín et al., 1985). Five principal sampling units (PSUs) 8 km long each were randomly selected per life zone to conduct standardized roadside counts; i.e., a total of 15 PSUs were established following the rationale of a stratified random design (see Cochran 1977). In July 1986 the sampling scheme was expanded to include both game and non-game columbid species, and detection distances were defined as unfixed and fixed at 60 m for call and sight counts (Rivera-Milán 1990).

Here I provide data from unfixed counts and discuss the resulting distribution and relative

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abundance patterns of columbids at different spatial (PSUs, life zones, islandwide) and temporal (seasons, years) scales of resolution. I had two specific objectives: (1) to examine the distribution and relative abundance patterns of columbids during the different seasons of the year in the three major life zones of the island, and (2) to determine how dependent are the patterns on the spatiotemporal scale under consideration. Special attention was given to the most general and repeatable patterns of aural and visual detections. The goal of this investigation is to detect real population patterns and propose testable explanations of the controlling processes involved.

STUDY AREAS AND METHODS

LIFE ZONES

Puerto Rico, the smallest (8,801.9 km²) and easternmost of the Greater Antilles (17°55'–18°35' north, 65°37'–67°17' west; Fig. 1), lies within the subtropical latitudinal region, and contains six life zones (Ewel and Whitmore 1973). The three major life zones have been classified as subtropical dry, subtropical moist, and subtropical wet, and comprise approximately 98% of the total land area. Presently, the forest area of the island encompasses about 2,790 km² (Birdsey and Weaver 1982).

The subtropical dry zone encompasses approximately 14% (1,216.4 km²) of the total land area of the island. Mean annual precipitation ranges from 600 to 1,100 mm. Rainfall normally peaks during May and from September to November. The vegetation is characteristically deciduous or semi-deciduous on most types of soil. Plant species commonly have thorns and spines. Epiphytes (e.g., bromeliads and vines) are common, but they rarely provide much cover over branches. Tree heights rarely exceed 15 m, and their crowns are usually broad and flattened with sparse foliage.

The subtropical moist zone encompasses about 60% (5,326.1 km²) of the island. Mean annual precipitation ranges from 1,100 to 2,200 mm. Rainfall usually peaks in May and from August to November. Tree heights commonly reach up to 20 m, and their crowns are usually rounded in shape. Many plant species are deciduous during the dry season (usually from January to April). Epiphytes are common and provide important cover over branches. Grasses characteristically cover the ground after deforestation. Patches of

variable sizes of successional tree species with rapid growth rates are common in disturbed areas.

The subtropical wet zone encompasses about 24% (2,124.8 km²) of the total land area of the island. Mean annual precipitation ranges from 2,200 to 4,000 mm. Rainfall usually peaks during May, and from August to November. Epiphytes are widespread, and usually provide complete cover to branches. Successional tree species have rapid growth rates, forming closed canopies at about 20 m. Most plant species are evergreen and sclerophyllous. In karstic areas, the vegetation is more xeric than expected due to water percolation and runoff of soils.

STANDARDIZED COUNTS

Five PSUs 8 km long each were established per life zone along secondary and tertiary roads that were lightly traveled during the early morning hours (Table 1). Six sampling stations, spaced at regular intervals of 1.6 km, were established per PSU. Counts were conducted for 3 min at each sampling station. During each count, the number of pigeons and doves heard calling, as well as the number seen (e.g., singles, pairs, or flocks of variable sizes), were recorded, regardless of detection distance (= unfixed). Each observation was classified as aural or visual depending on the initial form of detection. A separate record was kept of the individuals seen per species while driving between stations. Aural detections while driving were considered negligible, because of their low frequency of occurrence. Driving speed between stations normally fluctuated between 16–32 kph (10–20 mph) depending on problems such as road conditions.

Counts were conducted from 06:00 to 10:30 hours. Surveys were suspended when it was raining or the wind speed exceeded 12 mph (19.2 kph). Standard data sheets of unfixed counts were similar to those used by the U.S. Fish and Wildlife Service (USFWS) for Mourning Doves (Dolton 1985).

The PSUs were sampled at least once per month by two experienced observers. The sampling period covered from July 1985–June 1988 in the moist and wet zones; and from July 1985–January 1989 in the dry zone. Counts were not conducted in urbanized areas, although some species are well adapted to urban habitats (e.g., Common Ground-Dove and Zenaida Dove).

Some distant calls of quail-doves could have

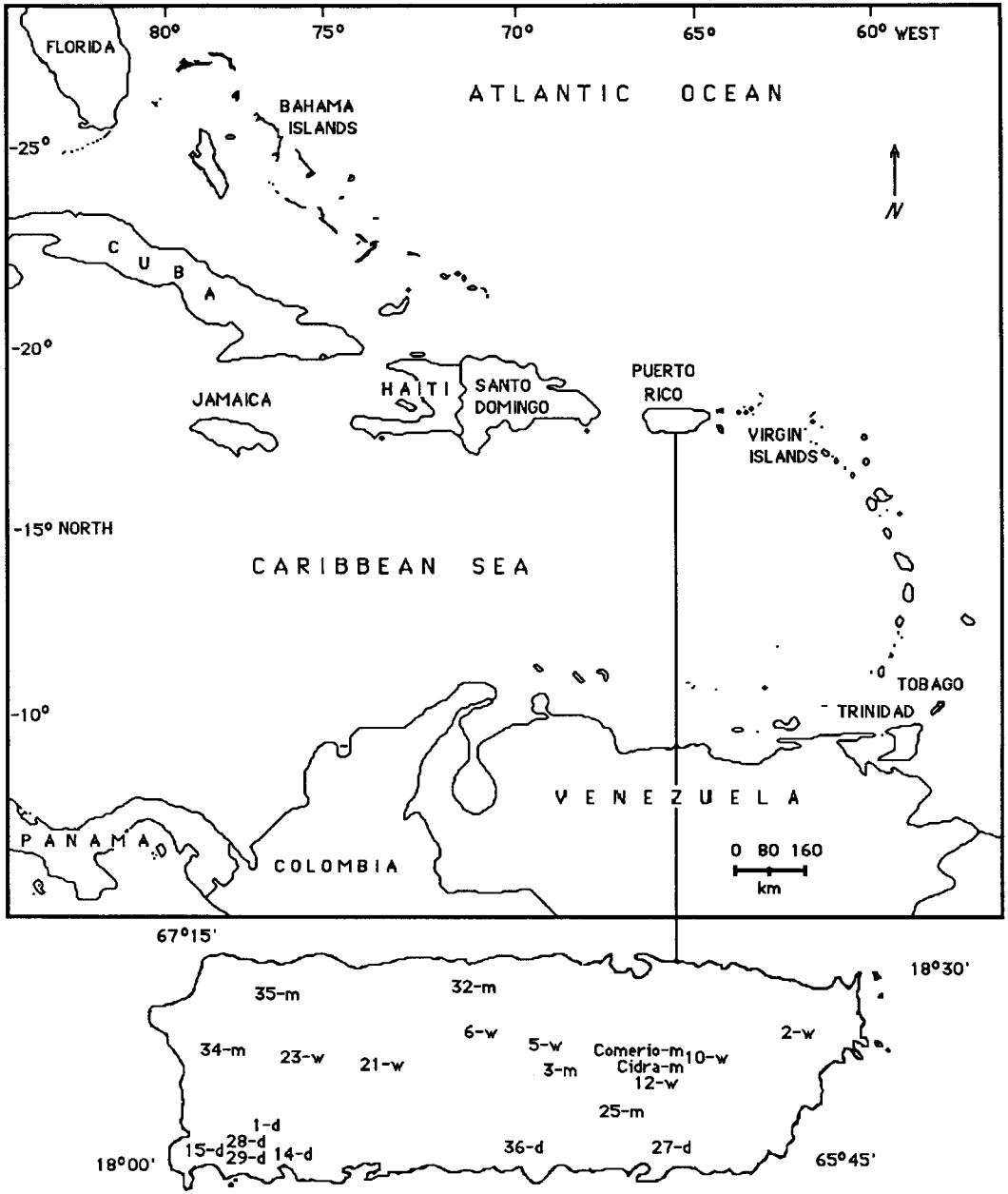


FIGURE 1. Caribbean region showing the location of Puerto Rico with respect to the rest of the Greater and Lesser Antilles, and the principal sampling units (PSUs) under study.

been confused due to the presence of background noise (e.g., near rivers). Moreover, Bridled and Key West Quail-Doves could have been confused in some instances, because of their body size and plumage characteristics (see Raffaele 1989). The problem was circumvented by pooling aural and visual detections of the quail-dove

species before conducting statistical analyses of counts (see below).

RAINFALL

Rainfall data for the dry zone were obtained from pluviometers in the xerophytic forest of Guánica (PSU 14; Canals, unpubl. data) and the dry coast-

TABLE 1. Principal sampling units (PSUs) used to estimate the seasonal relative abundance of columbids in the three major life zones of Puerto Rico.

Location	No. PSU	Habitat type ^a
Subtropical moist zone		
(1) Aibonito: roads 7718, 14, 723, & 558	PSU 3	Moist montane forest
(2) Guayama: road 708	PSU 25	Moist montane forest
(3) Barceloneta: tertiary roads	PSU 32	Wetland, agricultural, & moist limestone forest
(4) Mayagüez: road 108	PSU 34	Moist montane forest
(5) Isabela: road 112	PSU 35	Moist limestone forest
Subtropical wet zone		
(1) Río Grande: roads 191 & 9966	PSU 2 ^b	Upper & lower montane rain forest
(2) Barranquitas: road 143	PSU 5	Wet montane forest
(3) Ciales: road 143	PSU 6	Wet montane forest
(4) Cayey: tertiary road and road 184	PSU 10 ^b	Wet montane forest
(5) Cayey: road 742	PSU 12	Wet montane forest
(6) Adjuntas: road 128	PSU 21 ^c	Wet montane forest
(7) Maricao roads 120, 365 & 366	PSU 23 ^c	Wet montane forest
Subtropical dry zone		
(1) Lajas: tertiary road	PSU 1 ^c	Agricultural & dry coastal forest
(2) Guánica: tertiary road	PSU 14	Xerophytic forest
(3) Cabo Rojo: tertiary road & road 302	PSU 15	Dry coastal forest
(4) Guayama: road 706	PSU 27 ^b	Agricultural, xerophytic, & dry coastal forest
(5) Cabo Rojo: tertiary road & road 303	PSU 28	Dry coastal forest
(6) Lajas: road 324	PSU 29	Dry coastal forest
(7) Santa Isabel: tertiary road & road 545	PSU 36 ^b	Agricultural & dry coastal forest

^a Habitat types described according to rainfall and general composition of the vegetation (see Ewel and Whitmore 1973).

^b Sampling in these PSUs was initiated during February 1987.

^c These PSUs were not sampled after January 1986. Substitutes were selected at random from a pool of 36 possible choices (see b above).

al forest of Cabo Rojo (PSU 15; USFWS, Caribbean Islands National Wildlife Refuge, unpubl. data). Rainfall patterns were examined as totals and averages per month, based on five and eight years of data available from PSUs 14 and 15, respectively. Call counts of Zenaida Doves in the dry zone covered a period of 43 consecutive months. Rainfall data were divided into six month intervals to study the possibility of time lags in the responsiveness of calling Zenaida Doves during the nesting season (Rivera-Milán 1990). Time lags were studied up to two years previous to the detected calling peaks of doves in PSUs 14 and 15. Rainfall was also studied on a seasonal basis, using years as replicates ($n = 3$). Following Faaborg et al. (1984), DeSante and Geupel (1987), and Faaborg and Arendt (in press), departures from normal (DFN) were calculated as absolute values resulting from the subtraction of 'actual' from 'normal' rainfall. DFN values were used to detect negative or positive responses of calling Zenaida Doves to rainfall extremes.

FRUITING PHENOLOGY

The data gathered by Cardona et al. (1986) were used to depict the fruiting phenology patterns of key tree species in the subtropical wet forest of Río Abajo. The following tree species were considered important food sources for pigeons and doves in Río Abajo (see Cardona et al. 1986, and literature therein): Apple Rose (*Syzygium jambos*), Puerto Rican Royal Palm (*Roystonea borinquena*), India Laurel Fig (*Ficus citrifolia*), Trumpet Tree (*Cecropia schreberiana*), Night Shade (*Solanum torvum*), Martinique Prickly-Ash (*Zanthoxylum martinicense*), Mountain Immortelle (*Erythrina poeppigiana*), Rabo de Ratón (*Gonzalagunia spicata*), and False-Mastic (*Mastichodendron foetidissimum*). I studied the fruiting phenology pattern of *S. jambos* from July 1987–June 1988 in the PSUs of the wet and moist zones and Carite Lake riparian forest (Cayey). Binoculars were used to make observations from the ground in 8 0.1 ha strip-transects located in

the riparian vegetation bordering Carite Lake, and 60 circular plots (radius = 60 m) located in the PSUs of the moist and wet zones. I also conducted phenological observations of *Z. martinicensis*, *C. schreberiana*, *D. morotoni*, *R. borinquena*, *F. citrifolia*, *Erythrina poeppigiana*, *Camasey (Miconia prasina)* and *Myrcia* spp. from July 1987–June 1988 in 7 0.1 ha strip-transects in patches of secondary growth forest in Cidra and Comerío.

STATISTICAL ANALYSES

Seasonal statistics were computed by pooling counts per month per life zone ($n = 5$ PSUs) as follows: winter: December, January and February; spring: March, April and May; summer: June, July and August; and, fall: September, October and November.

Statistical analyses of counts need to account for the repeated measurements made per PSU (P. H. Geissler, K. H. Pollock, pers. comm.). The problem is that the same sampling units (PSUs) were visited month after month. Hence, positive correlations among visits were expected (see Wiener 1971; Gurevitch and Chester 1986; Beal and Khamis 1990, 1991; Quinn and Keough 1991). The counts can be expected to be more correlated (dependent) as visit intervals decrease (Gurevitch and Chester 1986). These positive correlations can be the cause of a serious underestimation of the variance associated with the counts, and of an increase in the Type I error rate (alpha) associated with the statistical analyses conducted.

Since I was interested in examining counts conducted at intervals of one month, analyses of variance (ANOVAs) with repeated measures at one factor (e.g., seasons) were conducted. Upon significance, paired *t*-tests and Student-Newman-Keuls (SNK) multiple comparisons procedures were performed as follow-up tests (Sokal and Rohlf 1981, Day and Quinn 1989). Significance was accepted at $P \leq 0.05$.

After finding several significant *F*-max and Bartlett's tests, and significant positive correlations between means and standard deviations of, for example, calling Zenaida Doves ($r = 0.931$, $df = 25$, $P < 0.001$) and Scaly-naped Pigeons ($r = 0.883$, $df = 25$, $P < 0.001$), counts were log-transformed ($\log_{10}x + 0.5$). Counts based on aural and visual detections appeared to be reasonably close to a log-normal distribution.

Dummy variables were generated from the

fruiting phenology data gathered by Cardona et al. (1986) at Río Abajo forest. Eight categories ($k - 1$) were used to define the availability of immature and mature fruits (pooled) of key tree species on a seasonal basis at Río Abajo (see Kleinbaum and Kupper 1978). The availability of immature and mature fruits of *S. jambos* in the PSUs of the wet and moist zones and Carite Lake riparian forest was categorized as: 1 = low (0–25%), 2 = moderate (25–50%), and 3 = high (> 50%); similar categories were used for the phenological observations made in Cidra and Comerío. Linear and multiple regressions were used in evaluating the relationships between dependent (e.g., calling birds) and independent (e.g., rainfall and fruit availability) variables.

RESULTS

Data for Plain Pigeons, White-crowned Pigeons, and Bridled Quail-Doves are discussed only in relation to the most general and repeatable patterns of aural and visual detections of all columbids in the life zones. In mainland Puerto Rico, these species are uncommon outside a few localities. For example, Plain Pigeons outside the municipality of Cidra (in which density estimates were in the order of 0.4–1.2 birds per km²) were detected only twice after 2,400 point counts conducted in 90 sampling stations (Rivera-Milán 1990). Bridled Quail-Doves were infrequently detected in PSUs 14 and 32, whereas White-crowned Pigeons were infrequently detected in PSUs 2, 15, 32, 34, and 35.

ZENAIDA DOVES

A significant calling peak was detected for the spring months after 3 years of data collection in the life zones ($F = 12.293$; $df = 3, 108$; $P < 0.0001$). In the wet and moist zones calling activity extended from January until at least August, whereas calling activity from September to November was negligible. In the dry zone calling activity peaked between April and June, but a second noticeable peak occurred between September and November ($F = 2.482$; $df = 3, 36$; $P = 0.076$). Visual detections in the life zones peaked during the spring–summer period (March–August: $F = 11.441$; $df = 3, 9$; $P = 0.002$).

The number of calling birds detected in the dry and moist zones was significantly different from the wet zone ($F = 9.522$; $df = 2, 36$; $P = 0.0005$). When the wet zone was excluded from the analyses, the difference in the number of call-

ing birds detected in the dry and moist zones became non-significant ($F = 0.035$; $df = 1, 24$; $P = 0.854$). Similarly, the number of visual detections in the dry and moist zones were significantly different from the wet zone ($F = 157.226$; $df = 2, 3$; $P = 0.0009$). However, the difference in the number of visual detections between the dry and moist zones was non-significant (SNK; $P > 0.05$). The seasonal patterns of aural and visual detections of Zenaida Doves in the life zones remained unchanged during the sampling period covered (aural: $F = 0.070$; $df = 1, 3$; $P = 0.808$; visual: $F = 0.031$; $df = 1, 3$; $P = 0.868$; total: $F = 0.149$; $df = 1, 3$; $P = 0.725$).

SCALY-NAPED PIGEONS

A significant peak of Scaly-naped Pigeons calling was detected during spring in the life zones for the 3 years ($F = 23.862$; $df = 3, 108$; $P < 0.0001$). In the moist and wet zones, calling activity extended from January until at least July, whereas calling activity from September to November was negligible. Visual detections in the moist and wet zones peaked between June and October ($F = 3.988$; $df = 3, 9$; $P = 0.046$). Aural and visual detections in the PSUs of the dry zone were negligible during the surveys. Scaly-naped Pigeons were detected only twice after conducting 1,080 point counts in the dry zone.

The number of calling birds detected in the wet zone was significantly different from the moist and dry zones ($F = 20.117$; $df = 2, 36$; $P < 0.0001$). Even when the dry zone was excluded from the analyses, the significant difference predominated ($F = 5.757$; $df = 1, 24$; $P = 0.024$). The calling activity in the wet zone was significantly different from the moist zone during spring ($F = 10.286$; $df = 1, 74$; $P = 0.002$), and approached significance during winter ($F = 3.532$; $df = 1, 74$; $P = 0.064$) and summer ($F = 3.138$; $df = 1, 74$; $P = 0.081$). The seasonal patterns of aural and visual detections in the moist and wet zones remained unchanged during the sampling period covered (aural: $F = 2.410$; $df = 1, 3$; $P = 0.218$; visual: $F = 0.031$; $df = 1, 3$; $P = 0.870$; total: $F = 1.636$; $df = 1, 3$; $P = 0.291$).

When the call counts of Scaly-naped Pigeons and Zenaida Doves in the moist zone were pooled, April stood as the month of peak activity. The relative abundance of Zenaida Doves appeared to be significantly higher than the relative abundance of Scaly-naped Pigeons during winter ($F = 6.188$; $df = 1, 49$; $P = 0.016$), spring ($F =$

12.275 ; $df = 1, 49$; $P = 0.001$), and summer ($F = 4.073$; $df = 1, 49$; $P = 0.049$).

COMMON GROUND-DOVES

Two years of data collection revealed a significant calling peak during spring ($F = 9.564$; $df = 3, 72$; $P < 0.0001$). Calling activity peaked between April and June; but, as in the case of Zenaida Doves, a second noticeable peak occurred between September and November in the dry zone ($F = 2.550$; $df = 3, 18$; $P = 0.088$). The number of calling birds detected in the dry zone was significantly different from the moist and wet zones ($F = 55.875$; $df = 2, 24$; $P < 0.0001$). Similarly, the number of visual detections in the dry zone was significantly different from the moist and wet zones ($F = 79.908$; $df = 2, 3$; $P = 0.002$). Visual detections in the dry and moist zones appeared to peak between June and November ($F = 9.178$; $df = 3, 9$; $P = 0.004$). Aural and visual detections of Common Ground-Doves in the PSUs of the wet zone were negligible during the sampling period covered. Five Common Ground-Doves were detected after conducting 720 point counts in the wet zone. The seasonal patterns of aural and visual detections in the dry and moist zones remained unchanged after two years of counts (aural: $F = 2.012$; $df = 1, 3$; $P = 0.251$; visual: $F = 0.016$; $df = 1, 3$; $P = 0.907$; total: $F = 0.824$; $df = 1, 3$; $P = 0.561$).

When the call counts of Common Ground-Doves and Zenaida Doves in the dry zone were pooled, May stood as the month of peak activity. The relative abundance of Common Ground-Doves appeared to be higher than the relative abundance of Zenaida Doves, but significance was reached only during fall ($F = 4.248$; $df = 1, 45$; $P = 0.045$).

RUDDY AND KEY WEST QUAIL-DOVES

Two years of data collection indicated that total detections (aural + visual) of quail-doves (pooled) peaked during the spring-summer period ($F = 3.717$; $df = 3, 72$; $P = 0.015$). The number of total detections in the moist and wet zones were significantly different from the dry zone ($F = 4.860$; $df = 2, 64$; $P = 0.017$). However, the counts of the moist zone were significantly different from the wet zone during spring ($F = 3.353$; $df = 2, 96$; $P = 0.039$), whereas they approached significance during summer ($F = 2.577$; $df = 2, 96$; $P = 0.081$). Detections of quail-doves in the dry zone were mainly restricted to the xerophytic

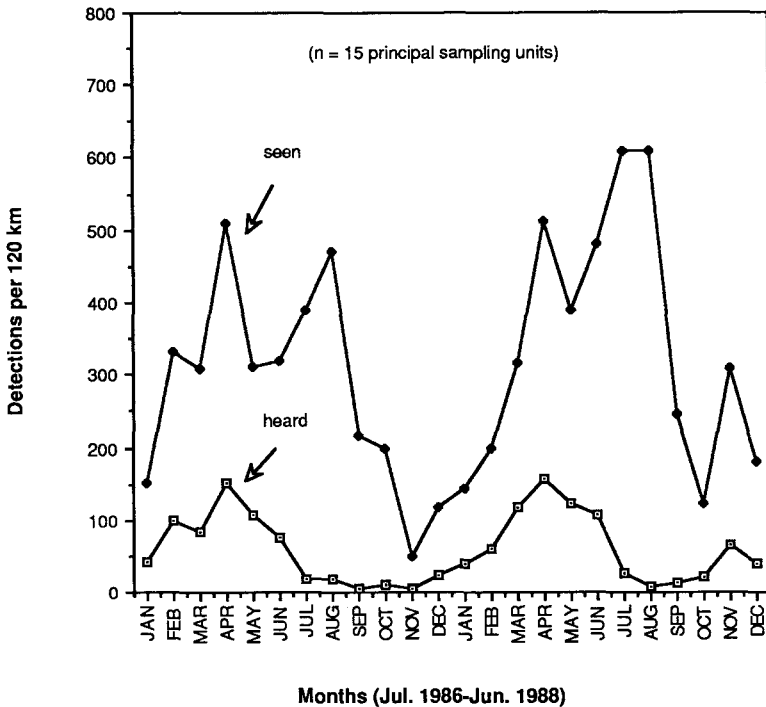


FIGURE 2. Columbids heard calling and seen in the 15 PSUs of the three major life zones of Puerto Rico.

forest of Guánica (PSU 14). Quail-doves were never detected in the dry coastal habitats of PSUs 15, 28, 29, and 36. The seasonal patterns of aural and visual detections (pooled) remained unchanged during the surveys (total: $F = 2.659$; $df = 1, 3$; $P = 0.361$).

WHITE-WINGED DOVES

Total detections of White-winged Doves peaked during summer ($F = 3.095$; $df = 3, 72$; $P = 0.032$). Relative abundance estimates in the dry zone were significantly different from the moist and wet zones ($F = 6.311$; $df = 2, 24$; $P = 0.006$). The counts of the dry zone were significantly different from the moist zone during spring ($F = 3.127$; $df = 2, 77$; $P = 0.049$), summer ($F = 6.186$; $df = 2, 77$; $P = 0.002$), and fall ($F = 5.415$; $df = 2, 77$; $P = 0.006$). Detections in the PSUs of the moist zone were mainly restricted to agricultural areas (e.g., PSU 32), whereas detections in the PSUs of the wet zone were negligible. The seasonal patterns of aural and visual detections (pooled) remained unchanged during the sampling period covered (total: $F = 0.001$; $df = 1, 3$; $P = 0.976$).

MOURNING DOVES

Total detections of Mourning Doves peaked during summer ($F = 3.095$; $df = 3, 72$; $P = 0.032$). Detections in the dry zone were significantly different from the moist and wet zones ($F = 6.311$; $df = 2, 24$; $P = 0.006$). The counts of the dry zone were significantly different from the moist zone during spring ($F = 3.127$; $df = 2, 77$; $P = 0.049$), summer ($F = 6.186$; $df = 2, 77$; $P = 0.002$), and fall ($F = 5.415$; $df = 2, 77$; $P = 0.006$). As in the case of White-winged Doves, detections in the PSUs of the moist zone were mainly restricted to agricultural areas (e.g., PSU 32), whereas detections in the PSUs of the wet zone were negligible. The seasonal patterns of aural and visual detections (pooled) remained unchanged during the surveys (total: $F = 3.176$; $df = 1, 3$; $P = 0.1728$).

COLUMBIDS

The relative abundance of all columbids in the three major life zones of the island peaked during the spring-summer period (March-August: $F = 21.575$; $df = 3, 108$; $P < 0.0001$; Fig. 2). Aural

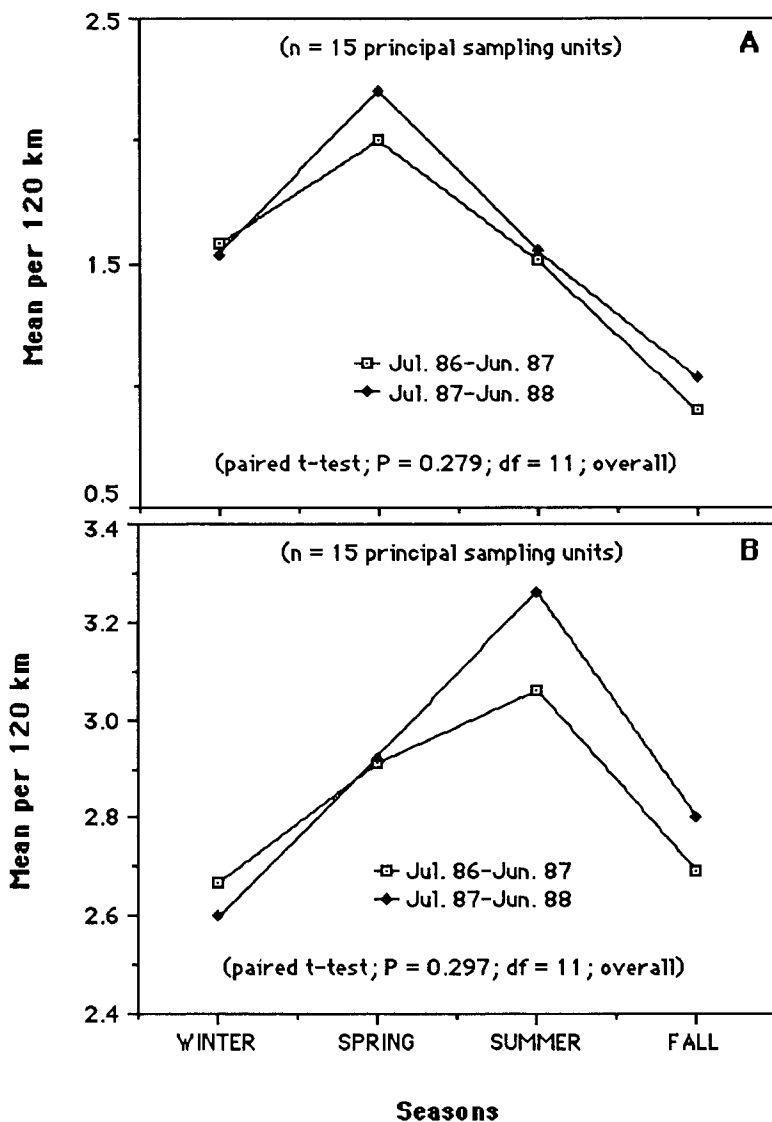


FIGURE 3. Seasonal patterns of aural (A) and total (B) detections of all columbids in the wet, moist, and dry zones (log-transformed).

detections peaked in April, before the peak of nesting activity in the life zones (May–June), whereas visual detections remained high between April and August. The second (July 1986–June 1987) and third (July 1987–June 1988) year of study showed similar patterns of relative abundance (aural: $F = 1.660$; $df = 1, 3$; $P = 0.288$; total: $F = 1.593$; $df = 1, 3$; $P = 0.296$; Fig. 3). The third year, however, resulted in higher summer counts than the second year of study (paired

t -test; $P < 0.05$). This significant difference appeared to be the result of an increase in the number and size of flocks of White-winged Doves and Mourning Doves detected in agricultural areas of the dry and moist zones (Rivera-Milán 1990).

The seasonal calling patterns of Zenaida Doves and Common Ground-Doves in the dry zone were obscured when the counts of the life zones were pooled (compare Figs. 2, 3 and 4). The

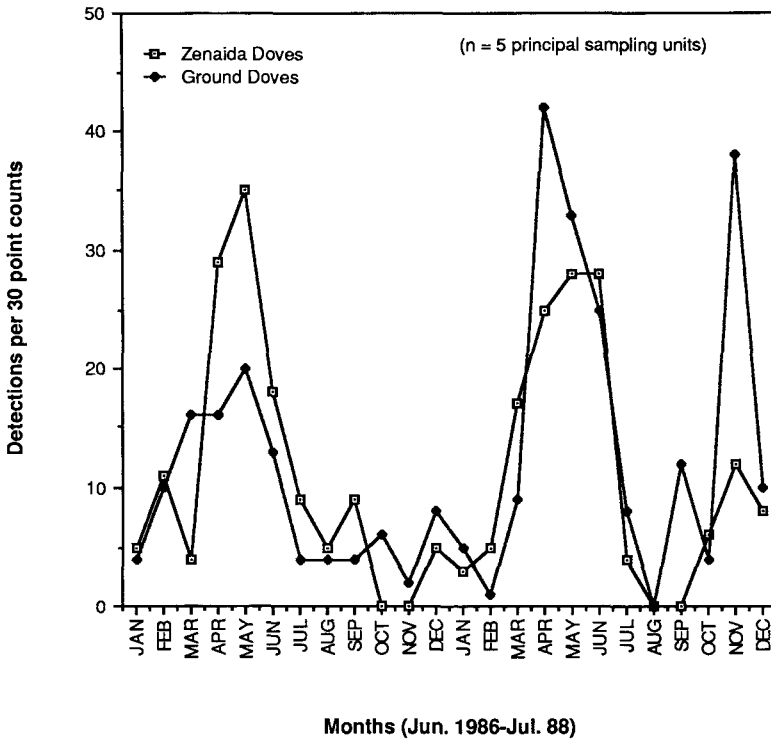


FIGURE 4. Calling patterns of Zenaida Doves and Common Ground-Doves in the PSUs of the dry zone.

calling patterns of Zenaida Doves and Common Ground-Doves in the PSUs of the dry zone were correlated and appeared to be triggered by the rainfall bimodality ($r = 0.7$; $P < 0.0001$; $r_s = 0.6$; $P < 0.001$; $n = 24$; Fig. 5). When the calling activity of Zenaida Doves in PSUs 14 and 15 was pooled, a significant correlation with rainfall was detected ($r_s = 0.4$; $P < 0.025$; and $r_s = 0.7$; $P < 0.001$; $n = 24$, respectively). Similarly, when the calling activity of Common Ground-Doves in PSUs 14 and 15 was pooled, the correlation with rainfall was significant ($r_s = 0.5$; $P < 0.01$ and $r_s = 0.5$; $P < 0.01$; $n = 24$, respectively). Common Ground-Doves, however, are probably less constrained than Zenaida Doves by rainfall seasonality. Common Ground-Doves forage mainly on annual and perennial grass seeds (e.g., Guinea grass [*Panicum maximum*]), whereas Zenaida Doves occupy both granivore and frugivore guilds. Frugivores can be expected to be highly sensitive to rainfall seasonality in xeric environments, since fruits tend to be patchily-distributed in space and time, and can be in short-supply during prolonged periods of dryness (Faaborg 1982). Moreover, the body mass of

Common Ground-Doves is ≈ 35 g, whereas the body mass of Zenaida Doves is ≈ 150 g. Hence, according to the model devised by MacMillen (1990), Common Ground-Doves should be more efficient than Zenaida Doves in deriving their energy and water requirements from a single for-

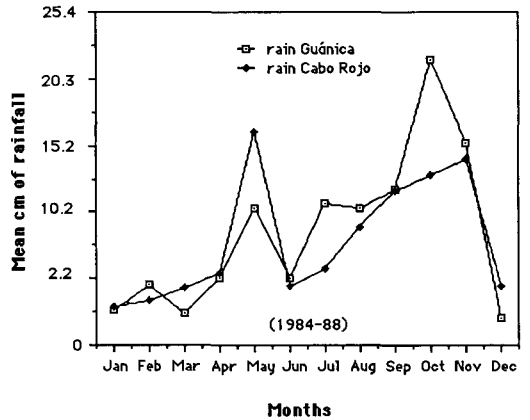


FIGURE 5. Monthly rainfall in the xerophytic forest of Guánica (PSU 14) and the dry coastal forest of Cabo Rojo (PSU 15).

aging resource (grass seeds) in xeric environments.

Rainfall can cause increases in soil moisture and primary productivity, and hence in the size and success of nesting populations of columbids in the dry zone. Rainfall, however, probably is less important than fruiting phenology of key tree species as a component of the environment of columbids in the moist and wet zones. The calling patterns of Zenaida Doves and Scaly-naped Pigeons in the PSUs of the moist and wet zones were correlated ($r = 0.7$; $P < 0.0001$; $r_s = 0.7$; $P < 0.001$; and $r = 0.7$; $P < 0.0001$; $r_s = 0.7$; $P < 0.0001$; $n = 24$, respectively). The calling activity of columbids can be expected to correlate with the fruiting phenology of tree species identified as major food sources in the moist and wet zones.

RAINFALL AND CALLING PATTERNS OF ZENAIDA DOVES IN THE DRY ZONE

There was a significant correlation between the calling activity of Zenaida Doves and rainfall in the dry zone during the sampling period covered ($r_s = 0.3$; $P = 0.028$; $n = 43$). Significant correlations were found between rainfall and calling activity of Zenaida Doves during winter ($r_s = 1.0$; $P < 0.0001$; $n = 3$), spring ($r_s = 1.0$; $P < 0.0001$; $n = 3$), summer ($r_s = 1.0$; $P < 0.0001$; $n = 3$), and fall ($r_s = 1.0$; $P < 0.0001$; $n = 3$) in PSUs 14 and 15 (pooled).

The relationship between the calling activity of Zenaida Doves and rainfall of the first six months of the year in PSU 14 was not significant ($y = 0.924 + 0.058x$; $r^2 = 0.072$; $P = 0.281$; $df = 17$). However, the calling activity of Zenaida Doves during the first six months of the year was significantly related with rainfall of the first six months of the previous year (i.e., a time lag of 1 year; $y = 4.011 + 1.503x$; $r^2 = 0.313$; $P = 0.027$; $df = 17$). The calling activity of the first six months of the year was marginally associated with rainfall of the first six months of two years before (i.e., a time lag of 2 years; $y = 0.897 + 0.098x$; $r^2 = 0.207$; $P = 0.060$; $df = 17$). The calling activity of Zenaida Doves during the first six months of the year was marginally associated with DFN values of the first six months of the year ($y = 0.831 + 0.150x$; $r^2 = 0.192$; $P = 0.069$; $df = 17$). However, the relationship between the calling activity of the first six months of the year and DFN values of the previous year was significant ($y = 0.671 + 0.237x$; $r^2 = 0.427$; $P =$

0.003 ; $df = 17$). The relationship between the calling activity of the first six months of the year and DFN values of two years before approached significance ($y = 0.822 + 0.188x$; $r^2 = 0.199$; $P = 0.064$; $df = 17$). The six rainfall variables examined above explained 74% of the variance associated with the calling activity of Zenaida Doves during the first six months of the year in PSU 14 ($y = 0.418 + 0.008x_1 - 0.118x_2 + 0.033x_3 - 0.08x_4 + 0.402x_5 - 0.036x_6$; $r^2 = 0.742$; $P = 0.0087$; $df = 17$).

The relationship between the calling activity of Zenaida Doves and rainfall of the first six months of the year in PSU 15 was not significant ($y = 0.645 + 0.015x$; $r^2 = 0.051$; $P = 0.369$; $df = 17$). However, time lags of 1 ($y = 0.452 + 0.053x$; $r^2 = 0.452$; $P = 0.001$; $df = 17$) and 2 ($y = 0.604 + 0.036x$; $r^2 = 0.242$; $P = 0.038$; $df = 17$) years were detected. The calling activity of Zenaida Doves was not significantly associated with DFN values of the same year ($y = 0.609 + 0.034x$; $r^2 = 0.117$; $P = 0.156$; $df = 17$). But, again, time lags of 1 ($y = 0.481 + 0.093x$; $r^2 = 0.462$; $P = 0.001$; $df = 17$) and 2 ($y = 0.549 + 0.069x$; $r^2 = 0.258$; $P = 0.031$; $df = 17$) years were detected. The six variables explained 79% of the variance associated with the call counts of Zenaida Doves during the first part of the year in PSU 15 ($y = 0.511 + 0.041x_1 + 0.027x_2 + 0.062x_3 - 0.047x_4 + 0.033x_5 - 0.052x_6$; $r^2 = 0.788$, $P = 0.0032$, $df = 17$). DFN values of the first six months of the previous year explained 54% of the variance associated with the calling activity of Zenaida Doves in PSUs 14 and 15 (pooled) ($y = 0.372 + 3.718x$, $r^2 = 0.544$, $P = 0.0005$, $df = 17$; Fig. 6).

FRUITING PHENOLOGY AND CALLING PATTERNS OF SCALY-NAPED PIGEONS AND ZENAIDA DOVES IN THE WET AND MOIST ZONES

A significant relationship was detected between the calling activity of Scaly-naped Pigeons and the availability of fruits of key tree species in the subtropical wet forest of Río Abajo ($y = -0.245 + 0.265x$; $r^2 = 0.618$; $P = 0.002$; $df = 11$; Fig 7). The calling activity of Zenaida Doves was also significantly related with the availability of fruits at Río Abajo forest ($y = -0.988 + 0.329x$; $r^2 = 0.469$; $P = 0.014$; $df = 11$). The availability of fruits of *S. jambos*, *R. borinquena*, *C. schreberiana*, and *Z. martinicensis* explained 76% and 80% of the variability associated with the calling

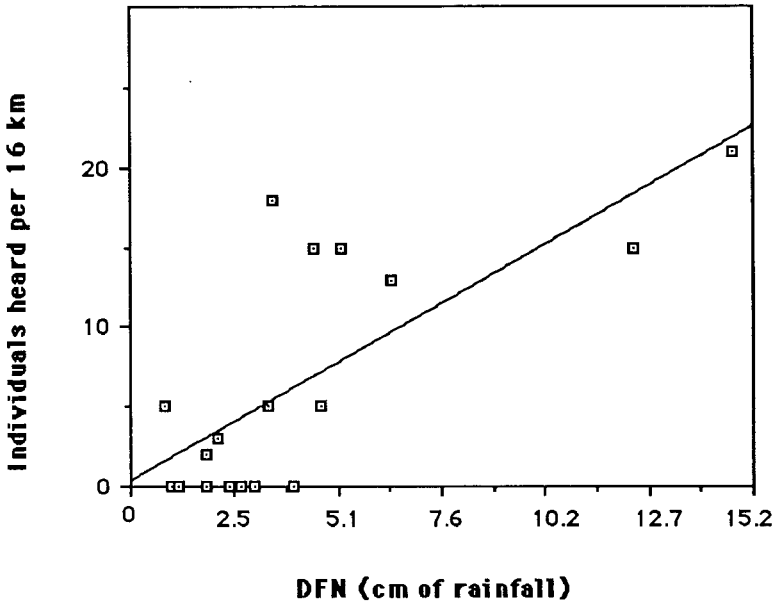


FIGURE 6. Number of Zenaida Doves calling vs. departures from normal (DFN) rainfall during the first six months of the year (1985–1988) in PSUs 14 and 15 ($n = 18$).

activity of Scaly-naped Pigeons ($y = -0.502 + 0.027x_1 + 0.02x_2 - 0.01x_3 + 0.018x_4$; $r^2 = 0.76$; $P = 0.0249$; $df = 11$) and Zenaida Doves ($y = -5.181 + 0.016x_1 + 0.07x_2 - 0.002x_3 + 0.011x_4$; $r^2 = 0.805$; $P = 0.0126$; $df = 11$), respectively, in Río Abajo forest.

A significant relationship was found between the calling activity of Scaly-naped Pigeons and Zenaida Doves (pooled) and the availability of fruits of key tree species in the riparian forest bordering Carite Lake and the secondary growth forests of Cidra and Comerío (pooled) ($y = 0.600 + 0.649x$; $r^2 = 0.318$; $P = 0.054$; $df = 11$). The calling activity of Scaly-naped Pigeons in PSU 12 was associated with the availability of fruits of *S. jambos* in the strip-transects bordering Carite Lake ($y = 1.579 + 4.822x$; $r^2 = 0.774$; $P < 0.001$; $df = 11$). A significant relationship was found between the calling activity of Scaly-naped Pigeons and Zenaida Doves (pooled) and the availability of fruits of *S. jambos* in the PSUs of the wet and moist zones (wet: $y = 0.93 + 0.031x$; $r^2 = 0.803$; $P = 0.001$; moist: $y = 1.379 + 0.018x$; $r^2 = 0.492$; $P = 0.011$; $df = 11$, respectively).

DISCUSSION

DISTRIBUTION AND RELATIVE ABUNDANCE PATTERNS

The counts of columbids resulted in repeatable patterns. The calling activity of columbids in the

wet and moist zones peaked during spring and then declined after early-summer (June). However, the seasonal calling patterns of Zenaida Doves and Common Ground-Doves in the dry zone were bimodal, with peaks occurring during spring and fall. Fall aural detections of White-winged Doves and Mourning Doves in the dry zone were negligible during the sampling period covered. The second and third week of July marked the beginning of the flocking period, and aural detections declined while visual detections became predominant. Zenaida Doves, Common Ground-Doves, White-winged Doves, and Mourning Doves formed foraging aggregations in agricultural areas of the dry and moist zones, whereas flocks of Scaly-naped Pigeons were detectable in wooded habitats of the interior and coast. A flocking period was not discernible for the quail-doves. Quail-doves were usually detected while calling (62%) or when foraging on the ground in small groups (≤ 11 birds) with variable degrees of cohesiveness (Rivera-Milán, unpubl. data). Overall, the flocking period of columbids coincided with the termination of a significant portion of their reproductive pulse in the island (Rivera-Milán 1990).

The seasonal patterns of relative abundance were detectable at local (PSUs) as well as at regional (life zones) scales of sampling, regardless of the observer involved and the counting tech-

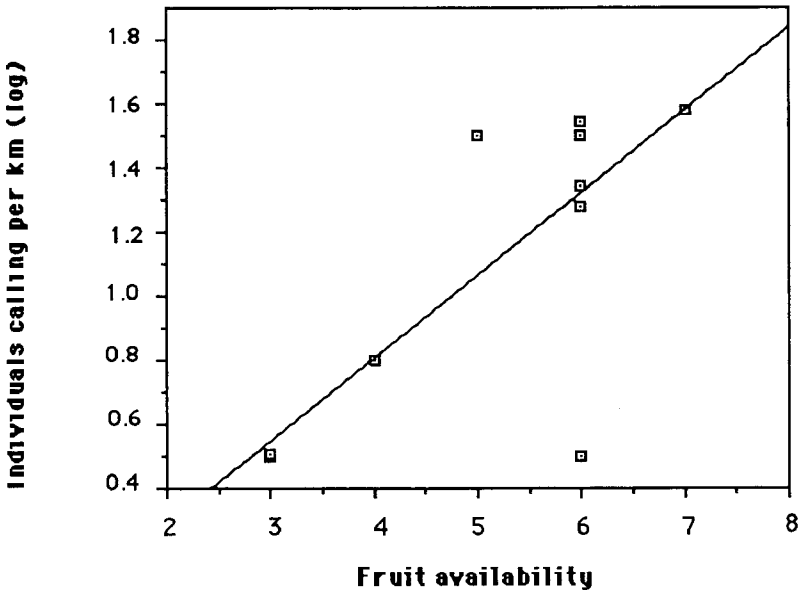


FIGURE 7. Number of Scaly-naped Pigeons calling vs. fruit availability of immature and mature fruits of key tree species (*S. jambos*, *R. borinquena*, *F. citrifolia*, *C. schreberiana*, *S. torvum*, *Z. martinicense*, *E. poeppigiana*, *G. spicata*, and *M. foetidissimum*; $k - 1 = 8$) in the subtropical wet forest of Río Abajo from 1984 to 1985 ($n = 12$). Data sources: Hammerson et al., 1984; Cardona et al., 1986.

nique applied (see, for example, Sedgwick 1976, 1977; Hammerson et al. 1983, 1984; Moreno-Brillón et al. 1986; Rivera-Milán, in prep.). The detected patterns are not considered to be either the result of sampling error (e.g., due to insufficient replication per life zone) or of statistical artifacts (e.g., created when pooling counts of populations with independent dynamics). However, relative abundance estimates based on aural and visual detections are commonly assumed to be valid indicators of population density changes at different spatial and temporal scales of sampling (but see Rotella and Ratti 1986). Seasonal estimates of relative abundance need to be adjusted for effective area of detection, especially when comparisons of different species in heterogeneous habitats are of interest (see Verner 1985). The PSUs under study, for example, are located in habitats with marked differences in vegetation structure and composition, weather, terrain, and urbanization levels among other things. If detection distances remain unfixed, even call counts of conspicuous species can be affected because of problems of acoustics and unknown rates of sound attenuation in different habitats (Emlen and DeJong 1981, Richards 1981, DeJong and Emlen 1985, Waide and Narins 1988). The problem is complicated when observers with

variable detection capacities are conducting the counts (see Bart 1985). A plausible alternative seems to be the calibration of unfixed and fixed counts via double-sampling (Cochran 1977, Eberhardt and Simmons 1987, Pollock and Kendall 1987, Rivera-Milán 1990). Counting standards should be as rigorous as possible to justify broad comparisons of species abundances. The seasonal patterns of relative abundance detected in the life zones probably represent the most general and repeatable aspect of the population dynamics of columbids in the island. Management and research decisions concerning columbid populations should be judged initially at a life zone and seasonal scale of resolution (see Wiens et al. 1986).

COMPONENTS OF THE ENVIRONMENT OF COLUMBIDS

On average, rainfall in PSUs 14 and 15 peaked in May and from October to November. The dry season normally extended from December until at least April. Therefore, the rains of May were expected to provide the most important environmental stimuli for the calling activity and reproduction of columbids in the dry zone. The first peak of rain (May) marks the end of the dry season, and normally is followed by a period of

increasing soil moisture and primary productivity (Lugo et al. 1978). On the other hand, the fall rainy season is followed by a period of extended dryness characterized by a deficit of soil moisture and a decline in vegetation cover and primary productivity (Lugo et al. 1978; Rivera-Milán, pers. observ.). Lugo et al. (1978) reported a positive correlation between rainfall and soil moisture availability, and a concomitant positive correlation between soil moisture and gross primary productivity in the xerophytic forest of Guánica (PSU 14). The increase in primary productivity should be linked with an increase in secondary productivity (e.g., biomass of herbivores). The combination of these forms of productivity should enhance the reproductive performance of birds in xeric environments (but see Rivera-Milán 1990, for complexities arising from the concomitant increase in the density of predators such as Pearly-eyed Thrashers [*Margarops fuscatus*] and Red-legged Thrushes [*Turdus plumbeus*] among others).

Faaborg and Arendt (in press) hypothesized that the reproductive success of birds in the xerophytic forest of Guánica was negatively correlated either with positive or negative rainfall extremes (DFN values) occurring during the first part of the year. However, they noted that after 15 years of study, DFN values were dominated by periods of severe drought, and suggested that the negative correlations found represented the impact of negative extremes on reproductive success. Above normal rainfall values (i.e., positive extremes) were positively correlated with the calling activity of Zenaida Doves during the first part of the year in PSUs 14 and 15. Time lags of one and two years were detectable in the responsiveness of calling Zenaida Doves to normal and above normal rainfall values. Hence, my data support the hypothesis of Faaborg and Arendt (in press) that the rainfall of the first six months of the year represents the most important environmental component influencing the reproduction of birds in the Guánica xerophytic forest. The calling and nesting activity of Zenaida Doves should be negatively correlated with below normal rainfall values occurring during the first part of the year in the xerophytic and dry coastal forests of the dry zone. Prolonged periods of dryness during the first part of the year might affect the abundance of columbids in the dry zone. The reproductive performance of Zenaida Doves is enhanced during years with above normal rain-

fall (Rivera-Milán, in prep.). The effects of rainfall on the reproduction of Zenaida Doves are detectable via the call count survey from April to June of the next two years, unless dramatic changes in the environment occur (e.g., hurricanes; Rivera-Milán, in prep.).

Frugivores, and to a lesser extent granivores, should be sensitive to rainfall seasonality in xeric environments (see, for example, Faaborg 1982). However, rainfall as a proximate factor probably is less important than fruiting phenology of key tree species in mesic environments. The relationship of rainfall and fruiting phenology in mesic environments is complex and species-specific; but, in general, the period of highest availability of fruits appears to occur from December to June, whereas the period of lowest availability appears to occur from July to November (see, for example, Cardona et al. 1986). The calling activity of Scaly-naped Pigeons and Zenaida Doves in the moist and wet zones appeared to be triggered by the availability of fruits of key tree species such as *S. jambos*. However, detailed studies about the foraging ecology of columbids in Puerto Rico are presently lacking (see, for example, Bancroft et al. 1990). Although food availability is often cited as a factor of ultimate importance in the reproduction of birds (Andrewartha and Birch 1954, 1984; Immelmann 1971; Lack 1976), it seems reasonable to hypothesize that the relative abundance patterns of columbids have not been molded solely by the availability of primary productivity in any of the life zones. In the moist and wet zones, columbids find fruits available on a year-round basis, especially in natural and human-induced forest gaps (e.g., *R. borinquena*, *C. schreberiana*, and *Zanthoxylum martinicense*, among others). Moreover, during prolonged periods of dryness and food scarcity columbids might easily disperse to neighboring forests in the ecotone of the dry and moist zones (Rivera-Milán, ongoing research).

The distribution and relative abundance patterns of columbids probably are under the influence of several components of the environment acting in a density-dependent or -independent mode. The relationship between biotic and climatological variables might be complex, and the observed patterns can be erroneously attributed to the effects of the most evident or measurable. Population fluctuations at local scales might be influenced by predators, parasites, diseases, and marginal deficiencies and imbalances of nutri-

ents among other things (Rivera-Milán 1990). Nevertheless, it seems reasonable to conclude that rainfall in the dry zone and fruiting phenology of key tree species in the moist and wet zones represent the most important environmental components influencing the seasonal patterns of relative abundance of columbids in the island.

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LITERATURE CITED

- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1984. The ecological web. Univ. of Chicago Press, Chicago.
- BANCROFT, G. T., R. BOWMAN, R. J. SAWICKI, AND A. M. STRONG. 1990. Relationship between the reproductive ecology of the White-crowned Pigeon and the fruiting phenology of tropical hardwood hammock trees. Florida Game Fresh Water Fish Comm., Nongame Wildl. Program Tech. Rep.
- BART, J. 1985. Causes of recording errors in singing bird surveys. *Wilson Bull.* 97:161-172.
- BEAL, K. G., AND H. J. KHAMIS. 1990. Statistical analysis of a problem data set: correlated observations. *Condor* 92:248-251.
- BEAL, K. G., AND H. J. KHAMIS. 1991. Reply to Quinn and Keough. *Condor* 93:202-203.
- BIRDSEY, R. A., AND P. L. WEAVER. 1982. The forest resources of Puerto Rico. U.S. Dep. Agric. For. Serv. Resour. Bull., SO-85, South For. Exp. Stn., New Orleans, LA.
- CARDONA, J., M. RIVERA, M. VÁZQUEZ, AND C. R. LABOY. 1986. Availability of food resources for the Puerto Rican Parrot and the Puerto Rican Plain Pigeon in Río Abajo Forest. Project W-10 (ES-1). Scientific Research Area. Puerto Rico Dept. Nat. Res.
- COCHRAN, W. G. 1977. Sampling techniques. 3rd ed. John Wiley and Sons, New York.
- COLLAZO-ALGARÍN, J., G. BONILLA, D. RAMOS, E. RAMOS, AND A. ORTIZ. 1985. Project W-11-4. Annual Performance Report. Scientific Research Area. Puerto Rico Dept. Nat. Res.
- DAY, R. W., AND G. P. QUINN. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59:433-463.
- DEJONG, M. J., AND J. T. EMLÉN. 1985. The shape of auditory detection function and its implications for songbird censusing. *J. Field Ornithol.* 56:213-320.
- DESANTE, D. F., AND G. R. GEUPEL. 1987. Landbird productivity in central coastal California: the relationship of annual rainfall, and a reproductive failure in 1986. *Condor* 89:636-653.
- DOLTON, D. D. 1985. Mourning Dove breeding population status. Adm. Rep. Dept. Int. U.S. Fish and Wildl. Serv.
- EBERHARDT, L. L., AND M. A. SIMMONS. 1987. Calibration of population indices by double sampling. *J. Wildl. Manage.* 51:665-675.
- EMLÉN, J. T., AND J. DEJONG. 1981. The application of song detection threshold distance to census operations, p. 346-352. In C. J. Ralph and J. M. Scott [eds.], Estimating numbers of terrestrial birds. *Stud. Avian Biol.* No. 6. Cooper Ornithol. Soc. Allen Press, Inc., Lawrence, KS.
- EWEL, J. J., AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and U.S. Virgin Islands. For. Serv. Res. Paper ITF-18.
- FAABORG, J. 1982. Avian population fluctuations during drought conditions in Puerto Rico. *Wilson Bull.* 94:20-30.
- FAABORG, J., AND W. J. ARENDT. In press. Rainfall correlates and bird population fluctuations in a Puerto Rican dry forest: a 15 year study. *Ornitol. Carib.*
- FAABORG, J., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. *Wilson Bull.* 96:575-593.
- GOODWIN, D. 1983. Pigeons and doves of the world. 3rd ed. Cornell Univ. Press, Ithaca, NY.
- GUREVITCH, J., AND S. T. CHESTER, JR. 1986. Analysis of repeated measures experiments. *Ecology* 67:251-255.
- HAMMERSON, J., G. BONILLA, D. RAMOS, E. RAMOS, AND F. RIVERA. 1983. Project W-11-2. Annual Performance Report. Scientific Research Area. Puerto Rico Dept. Nat. Res.
- HAMMERSON, J., G. BONILLA, D. RAMOS, E. RAMOS, AND F. RIVERA. 1984. Project W-11-3. Annual

- Performance Report. Scientific Research Area. Puerto Rico Dept. Nat. Res.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction, p. 341–389. *In* D. S. Farner and J. R. King [eds.], *Avian Biol.* Vol. 1. Academic Press, New York.
- KLEINBAUM, D. G., AND L. L. KUPPER. 1978. Applied regression analysis and other multivariate methods. Duxbury Press, Boston, MA.
- LACK, D. 1976. Island biology. Univ. of California Press, Berkeley and Los Angeles.
- LUGO, A. E., J. A. GONZÁLEZ-LIBOY, B. CINTRÓN, AND K. DUGGER. 1978. Structure, productivity, and transpiration of a subtropical dry forest. *Biotropica* 10:278–291.
- MACMILLEN, R. E. 1990. Water economy of granivorous birds: a predictive model. *Condor* 92:379–392.
- MORENO-BRILLÓN, J., G. BONILLA, D. RAMOS, E. RAMOS, AND A. ORTIZ. 1986. Apuntes sobre la distribución, abundancia relativa, y fenología reproductiva de la Tórtola Cardosanterra (*Zenaida aurita*) y la Paloma Turca (*Columba squamosa*) en Puerto Rico. *Ornitol. Carib.* 2:35–42.
- PÉREZ-RIVERA, R. A., AND J. COLLAZO-ALGARÍN. 1976. Distribución geográfica, hábitos alimentarios, y competencia por alimentos de la Paloma Sabanera (*Columba inornata wetmorei*) de Puerto Rico. *Science-Ciencia* 3:52–55.
- POLLOCK, K. H., AND W. L. KENDALL. 1987. Visibility bias in aerial surveys: a review of estimation procedures. *J. Wildl. Manage.* 51:502–509.
- QUINN, G. P., AND M. J. KEOUGH. 1991. Repeated measures analysis of variance: a comment on Beal and Khamis (1990). *Condor* 93:200–201.
- RAFFAELE, H. 1989. A guide to the birds of Puerto Rico and the Virgin Islands. 2nd ed. Princeton Univ. Press, Princeton, NJ.
- RICHARDS, D. G. 1981. Environmental acoustics and censuses of singing birds, p. 297–300. *In* C. J. Ralph and J. M. Scott [eds.], Estimating the numbers of terrestrial birds. *Stud. Avian Biol.* No. 6. Cooper Ornithol. Soc. Allen Press, Inc., Lawrence, KS.
- RIVERA-MILÁN, F. F. 1990. Distribution and abundance of columbids in Puerto Rico. Ph.D. diss. Univ. of Maryland, College Park, MD.
- RIVERA-MILÁN, F. F., G. BONILLA, D. RAMOS, E. RAMOS, AND A. ORTIZ. 1990. Project W-11. Final Performance Report. Puerto Rico Dept. Nat. Res.
- ROTELLA, J. J., AND J. T. RATTI. 1986. Test of a critical density index assumption: a case study with gray partridge. *J. Wildl. Manage.* 50:532–539.
- SEDGWICK, J. A. 1976. Project W-8-17. Annual Performance Report. Scientific Research Area. Puerto Rico Dept. Nat. Res.
- SEDGWICK, J. A. 1977. Project W-8-18. Annual Performance Report. Scientific Research Area. Puerto Rico Dept. Nat. Res.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co., New York.
- VERNER, J. 1985. Assessment of counting techniques, p. 247–302. *In* R. F. Johnston [ed.], *Current ornithology*. Vol. 2. Plenum Press, New York.
- WAIDE, R. B., AND P. M. NARINS. 1988. Tropical forest bird counts and the effect of sound attenuation. *Auk* 105:296–302.
- WIENS, J. A., J. F. ADICOTT, T. J. CASE, AND J. DIAMOND. 1986. Overview: the importance of spatial and temporal scale in ecological investigations, p. 145–153. *In* J. Diamond and T. J. Case [eds.], *Community ecology*. Harper and Row, New York.
- WILEY, J. W., AND B. N. WILEY. 1979. *The biology of the White-crowned Pigeon*. *Wildl. Monogr.* No. 64.
- WINER, B. J. 1971. *Statistical principles in experimental design*. 2nd ed. McGraw-Hill, New York.