

# NEST DENSITY AND SUCCESS OF COLUMBIDS IN PUERTO RICO<sup>1</sup>

FRANK F. RIVERA-MILÁN<sup>2</sup>

Department of Natural Resources, Scientific Research Area, Terrestrial Ecology Section, Stop 3 Puerta de Tierra, 00906, Puerto Rico

**Abstract.** A total of 868 active nests of eight species of pigeons and doves (columbids) were found in 210 0.1 ha strip-transects sampled in the three major life zones of Puerto Rico from February 1987 to June 1992. The columbids had a peak in nest density in May and June, with a decline during the July to October flocking period, and an increase from November to April. Predation accounted for 81% of the nest losses observed from 1989 to 1992. Nest cover was the most important microhabitat variable accounting for nest failure or success according to univariate and multivariate comparisons. The daily survival rate estimates of nests constructed on epiphytes were significantly higher than those of nests constructed on the bare branches of trees. Rainfall of the first six months of the year during the study accounted for 67% and 71% of the variability associated with the nest density estimates of the columbids during the reproductive peak in the xerophytic forest of Guánica and dry coastal forest of Cabo Rojo, but only 9% of the variability of the nest density estimates of the columbids in the moist montane second-growth forest patches of Cidra. In 1988, the abundance of fruits of key tree species (nine species combined) was positively correlated with the seasonal changes in nest density of the columbids in the strip-transects of Cayey and Cidra. Pairwise density correlations among the columbids suggested parallel responses of nesting populations to similar or covarying resources in the life zones of Puerto Rico.

**Key words:** Columbidae; strip-transects; nest density; nesting success; microhabitat; rainfall; fruit abundance; species covariations; seasons; life zones; Puerto Rico.

## INTRODUCTION

Ten native species of Columbidae (columbids hereafter) occur in Puerto Rico: Zenaida Dove (*Zenaida aurita*), White-winged Dove (*Z. asiatica*), Mourning Dove (*Z. macroura*), Common Ground-Dove (*Columbina passerina*), Scaly-naped Pigeon (*Columba squamosa*), White-crowned Pigeon (*C. leucocephala*), Plain Pigeon (*C. inornata*), Ruddy Quail Dove (*Geotrygon montana*), Key West Quail Dove (*G. chrysis*), and Bridled Quail Dove (*G. mystacea*). General information about the columbids in Puerto Rico can be found in Biaggi (1970) and Raffaele (1989). Additional information about their distribution and abundance can be found in Rivera-Milán (1990, 1992, 1993, 1995).

In Puerto Rico and on other Caribbean islands, there is a need to monitor bird populations, and to manage and protect nesting habitats that remain relatively undisturbed (Pérez-Rivera and

Collazo-Algarín 1976; Arendt et al. 1979; Wiley 1979, 1985, 1991; Wiley and Wiley 1979; Blockstein 1988; Bancroft et al. 1990; Godínez 1993). Habitat loss and illegal hunting have been ranked as the principal threats to species such as the Plain Pigeon and White-crowned Pigeon in Puerto Rico (Wiley 1985). Therefore, our management decisions should be guided by reliable estimates of the size and success of nesting populations at local scales (e.g., the 15 forest reserves of the Puerto Rican mainland, which range in size from ca. 140 to 11,300 ha; Birdsey and Weaver 1982, Silander et al. 1986).

In this study I examine: (1) the seasonal changes in nest density and covariation patterns for eight of ten native species of pigeons and doves in the three major life zones of Puerto Rico (1987-1988); (2) the annual changes in nest density in the moist montane second-growth forest patches of Cidra, the State Forest of Guánica (xerophytic forest hereafter), and the dry coastal forest of Cabo Rojo (1987-1992); (3) the relationship between changes in nest density during the reproductive peak and rainfall of the first six months of the year in Cabo Rojo, Cidra, and Guánica (1987-1992); (4) the associations between the seasonal changes in nest density and the abun-

<sup>1</sup> Received 16 May 1995. Accepted 5 September 1995.

<sup>2</sup> Current address: U.S. Fish and Wildlife Service, Office of International Affairs, 4401 North Fairfax Drive, Suite 860-ARLSQ, Arlington, VA 22203.

dance of fruits of key tree species in Cayey and Cidra (1988); and (5) the nesting success estimates of the columbids and the effects of six microhabitat variables on nest failure or success in Cabo Rojo, Cidra, and Guánica (1989–1992). The aim of this study is to promote a better understanding of the dynamics of columbid nesting populations at multiple spatial (habitats, life zones) and temporal (seasons, years) scales on the Puerto Rican mainland. The White-crowned Pigeon and Bridled Quail Dove were not included in this study because they were not observed nesting in any of the study areas sampled on the Puerto Rican mainland from 1987 to 1992.

## STUDY AREAS AND METHODS

### LIFE ZONES

Puerto Rico is the smallest (8,903 km<sup>2</sup>) and easternmost (55°17'–35°18'N, 37°65'–17°67'W) island of the Greater Antilles. Ewel and Whitmore (1973) classified the three major life zones of Puerto Rico as a subtropical moist zone (5,326 km<sup>2</sup>), a subtropical wet zone (2,124 km<sup>2</sup>), and a subtropical dry zone (1,216 km<sup>2</sup>; Fig. 1).

### NESTING HABITATS

The habitats sampled in the dry zone were the xerophytic forest of Guánica (ca. 4,006 ha; 4.6 ha sampled from 1987 to 1992), the dry coastal forest of Cabo Rojo (ca. 803 ha; 4.8 ha sampled from 1987 to 1992), and the mango (*Mangifera indica*) farms and surrounding dry coastal forest patches of Juana Diaz and Santa Isabel (ca. 292 ha; 6.4 ha sampled in 1988). The habitats sampled in the moist zone were the montane second-growth forest patches of Cidra (ca. 510 ha; 1.6 ha sampled from 1987 to 1992, and 3.6 ha sampled in 1988); and in the wet zone, the montane second-growth forest patches bordering Carite Lake that are adjacent to the Carite State Forest, Cayey (ca. 2,695 ha; 1.6 ha sampled from 1987 to 1991; Fig. 1). Refer to the Appendix for information about the vegetation of the mesic and xeric habitats sampled from 1987 to 1992.

### NEST DENSITY AND SUCCESS ESTIMATES

Nest counts were conducted on a year-round basis from February 1987 to December 1988. From 1989 to 1992, nest counts were conducted from the second week of May to the second week of June to cover the reproductive peak of the columbids on the Puerto Rican mainland (Rivera-Milán 1990).

A total of 210 0.1 ha (100 × 10 m) strip-transects (158 in the dry zone, 36 in the moist zone, and 16 in the wet zone) were sampled in 1988; 110 0.1 ha strip-transects (48 in Cabo Rojo, 46 in Guánica, and 16 in Cidra) were sampled from 1987 to 1992. A nest was considered active when eggs, nestlings, or incubating adults were present. When possible, incubating adults were not flushed from their nests to avoid unnecessary disturbance. Flagging was attached to branches or trunks at least 5 m from active nests. From 1987 to 1992, I sampled all the strip-transects with the assistance of two trained persons to minimize observer and habitat differences in nest detection probability (Nichols et al. 1986; Rivera-Milán 1990; Rivera-Milán et al. 1990, 1993; Rivera-Milán, unpubl. data). While searching for active nests, I kept a record of all the avian and mammalian predators seen inside the area of the strip-transects. The density estimates of predators are presented for all species combined at a locality; the density estimates of predator species per locality will be published elsewhere (Rivera-Milán, unpubl. data).

Nesting success was estimated according to the Mayfield method (Mayfield 1961, 1975; Johnson 1979). The lengths of the incubation and nestling periods were assumed to be 14 and 12 days for all the species (Hanson and Kossack 1963, Wiley 1991). A nest was classified as successful if at least one nestling reached day 12. Nests that were not found after the first visit, or that were found completely or partially destroyed and contained little or no feces, were classified as unsuccessful. Nest losses were recorded as caused by predators (avian or mammalian), human-induced (e.g., damage to nest trees), or natural (e.g., inclement weather). Active nests were visited a maximum of three times (at intervals of approximately 10 days) to minimize observer-induced disturbance (Nichols et al. 1984, Westmoreland and Best 1985, Götmark 1992, and references therein).

### MICROHABITAT VARIABLES

Six microhabitat variables were measured immediately after determining the fate of a nest: height of nest tree (m), height of nest above the ground (m), diameter at breast height (DBH) of nest tree (cm), perpendicular distance from below the nest to the center of the strip-transect (m), mean relative cover at 5 m from the nest (see below), and distance from the center of the nest-bowl to the trunk of the nest tree (cm).

Relative cover was calculated as the mean of four visibility measurements made at 5 m from a previously active nest in the four cardinal directions using a compass, a tape measure, and an ocular tube (James and Shugart 1970). Each relative cover measurement was recorded as 0 = poor, 1 = fair, 2 = good, or 3 = excellent. Nests were also classified as constructed on the bare branches of trees (0) or on epiphytes (1; bromeliads, lianas, and vines). From 1989 to 1992, I conducted all the microhabitat measurements with the assistance of two trained persons to avoid inter-observer effects (Block et al. 1987, Rivera-Milán et al. 1993).

#### RAINFALL

The rainfall data were obtained from pluviometers in the Guánica State Forest (Puerto Rico Department of Natural Resources, unpubl. data) and the Cabo Rojo National Wildlife Refuge (U.S. Fish and Wildlife Service, unpubl. data) from 1984 to 1992. The climatological summaries published by the National Oceanic and Atmospheric Administration (NOAA) were used to obtain the rainfall data of Cidra from 1984 to 1992.

#### FRUIT ABUNDANCE

In 1988, I conducted binocular observations from the ground in 15 of the 52 strip-transects established at Cayey ( $n = 8$ ) and Cidra ( $n = 7$ ) to determine the abundance of mature and immature fruits (combined) of Puerto Rican royal-palm (*Roystonea borinquena*), Martinique prickly-ash (*Zanthoxylum martinicense*), trumpet tree (*Cecropia shreberiana*), matchwood (*Dydimopanax morototoni*), punch berry (*Myrcia splendens*), camasey (*Miconia prasina*), India laurel-fig (*Ficus citrifolia*), apple rose (*Syzygium jambos*), and night shade (*Solanum torvum*). These tree species are considered important food sources of pigeons and doves in the montane second-growth forests of the moist and wet zones (Pérez-Rivera and Collazo-Algarín 1976, Maldonado-Colón and Pérez-Rivera 1977, Pérez-Rivera 1979, Cardona et al. 1986, Wiley 1991, Rivera-Milán, unpubl. data). While searching for active nests, I ranked fruit abundance per tree as 1 = low, 2 = moderate, or 3 = high, and calculated a mean per species per month (Rivera-Milán 1990, 1992).

Because of the number of strip-transects sampled in the dry zone in 1988 ( $n = 158$ ), I did not conduct detailed observations of the abundance of fruits of tree species in that zone. However, casual observations made inside and outside the areas sampled suggest that the fruits of trees such as pigeon berry (*Boureria succulenta*), turpentine tree (*Bursera simaruba*), and *Croton rigidus*, and the seeds of grasses such as *Argemone mexicana*, *Panicum maximum*, and *Amaranthus dubius* are important food sources for the columbids in the dry zone during the nesting season (also see Maldonado-Colón and Pérez-Rivera 1977, Pérez-Rivera 1987, Wiley 1991, and references therein).

#### STATISTICAL ANALYSES

The nest data were analyzed for each species separately and for all species combined at a locality. When necessary, the nest data were log-transformed to meet the assumptions of parametric tests (Sokal and Rohlf 1981).

Analysis of variance (ANOVA) with repeated measures at one factor (time) was used to examine the seasonal and annual changes in nest density of the columbids in the strip-transects of the life zones (Winer 1971; Gurevitch and Chester 1986; Beal and Khamis 1990, 1991; Quinn and Keough 1991). Polynomial contrasts (linear, quadratic, and cubic) were used to examine the relationships of time (seasons and years) and nest-counts (Winer 1971). Greenhouse-Geisser adjustment was used to correct the  $P$ -values of univariate ANOVAs with repeated measures (Gurevitch and Chester 1986; Beal and Khamis 1990, 1991; Quinn and Keough 1991).

Simple linear regression was used to examine the relationships between changes in nest density and rainfall of the first six months of the year in Cabo Rojo, Cidra, and Guánica. Pearson's Product-Moment Coefficient of Correlation ( $r$ ) was used to examine the relationships between changes in nest density and the abundance of fruits of key tree species in the strip-transects of Cayey and Cidra. Pearson's  $r$  was also used to measure the relative intensity of seasonal nest density covariations of the columbids in the life zones (Sokal and Rohlf 1981, Ludwig and Reynolds 1988).

ANOVA and multivariate analysis of variance (MANOVA) were used to carry out univariate and multivariate comparisons of the six micro-

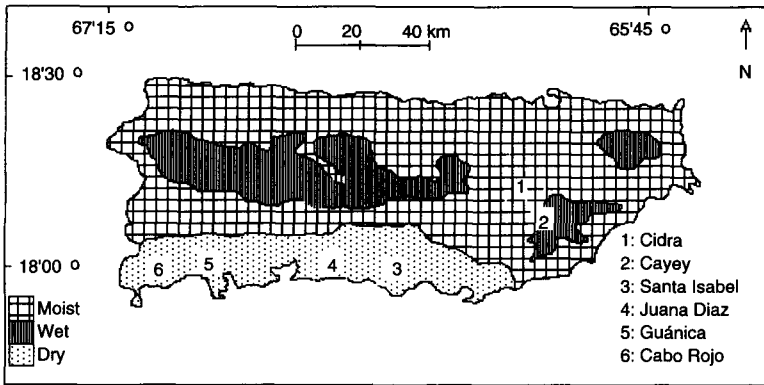


FIGURE 1. Map of Puerto Rico showing the study areas sampled in the three major life zones of the Puerto Rican mainland.

habitat variables measured at nest trees (Dillon and Goldstein 1984, Block et al. 1987). Estimates of daily survival rate (DSR) were used to carry out a one-tailed Z-test of the equality of nesting success of the columbids in Cabo Rojo, Cidra, and Guánica (i.e., intra- and interspecific comparisons within and between the localities; Steel and Torrie 1980). A one-tailed Z-test was also used to compare the DSRs of nests constructed on epiphytes and on the bare branches of trees (Steel and Torrie 1980).

Statistical analyses were performed with the programs SuperANOVA and StatView II (Abacus Concepts, Inc., Berkeley, CA). Significance was accepted at  $P \leq 0.05$ .

RESULTS

SEASONAL CHANGES IN NEST DENSITY IN THE LIFE ZONES

In 1988, a total of 341 active nests were found in the 158 0.1 ha strip-transects of the dry zone, whereas 193 active nests were found in the 52 0.1 ha strip-transects of the wet and moist zones. The columbids (eight species combined) had a peak in nest density in May and June, with a decline from July to October (the flocking period), and an increase from November to April (Table 1, Figs. 2 and 3A, B). The significant second degree polynomial contrast suggested a curvilinear relationship between time and nest-

TABLE 1. Analysis of variance (ANOVA) with repeated measures at one factor (seasons) for nest counts of the columbids (combined) in the three major life zones of Puerto Rico. Sampling period: January–December 1988\*.

Source Variation	df	SS	MS	F	P
Life zone	1	0.011	0.011	0.007	0.9347
Species (Life zone)	7	10.413	1.488		
Season	3	15.904	5.301	22.928	0.0001
Season × life zone	3	0.602	0.201	0.868	0.4437
Season × species (Life zone)	21	4.856	0.231		
Repeated Measures:					
		Winter	Spring	Summer	Autumn
Life zone:					
Moist-wet	0.976	2.164	2.388	0.500	
Dry	1.208	1.871	2.247	0.841	
Means table:					
Effect: season	1.105	2.002	2.310	0.689	
Linear contrast			$F = 1.789, P = 0.1931$		
Quadratic contrast			$F = 63.639, P = 0.0001$		
Cubic contrast			$F = 3.356, P = 0.0961$		

\* The ANOVA model used was:  $\bar{Y}_{ijk} = \mu + \alpha_i + \pi_{k(i)} + \beta_j + \alpha\beta_{ij} + \beta\pi_{j(k)} + \epsilon_{m(ijk)}$  (Winer 1971:518–539). Nest counts were log-transformed.

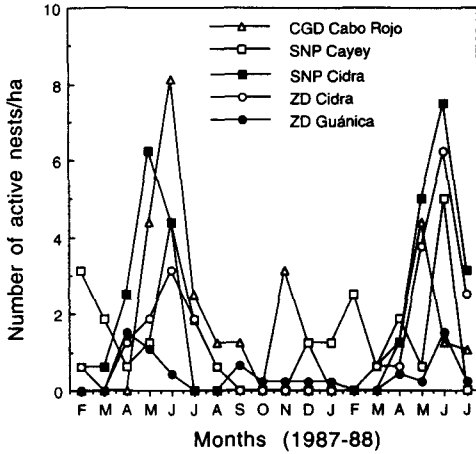


FIGURE 2. Nest density estimates of Common Ground-Doves (CGD), Scaly-naped Pigeons (SNP), and Zenaida Doves (ZD) in 126 0.1-ha strip-transects sampled in Cabo Rojo, Cayey, Cidra, and Guánica, Puerto Rico, from February 1987 to July 1988. Ground Doves, White-winged Doves, and Mourning Doves were not observed nesting in any of the strip-transects sampled in the moist and wet zones from 1987 to 1988. Scaly-naped Pigeons, Plain Pigeons, and Ruddy Quail Doves were not observed nesting in any of the strip-transects sampled in the dry zone from 1987 to 1988.

counts (i.e., a seasonal increase followed by a decrease in nest density in the life zones; Table 1). The seasonal nesting pattern remained unchanged from 1987 to 1988, with June having the highest nest density in both years (Figs. 2 and 3A, B). Although active nests of species such as Common Ground-Doves, Zenaida Doves, and Scaly-naped Pigeons were found on a year-round basis in the strip-transects of the life zones, the nesting activity occurring from September to November was minimal (Table 1, Figs. 2 and 3A, B).

ANNUAL CHANGES IN NEST DENSITY IN CIDRA, GUÁNICA, AND CABO ROJO

A total of 105 active nests were found in the strip-transects of the moist montane second-growth forest patches of Cidra from 1987 to 1992. There was a decrease in the mean nest density estimates of the columbids in 1989 and 1990, followed by an increase in 1991 and 1992 (Table 2, Fig. 4A).

A total of 46 active nests were found in the strip-transects of the xerophytic forests of Guánica from 1987 to 1992. There was a decrease in the mean nest density estimates of the columbids

in 1989 and 1991, followed by an increase in 1992 (Table 2, Fig. 4B).

A total of 82 active nests were found in the strip-transects of the dry coastal forest of Cabo Rojo from 1987 to 1992. There was a decrease in the mean nest density estimates of the columbids in 1990 and 1991, followed by an increase in 1992 (Table 2, Fig. 4C).

ANNUAL CHANGES IN NEST DENSITY AND RAINFALL

The rainfall of the first six months of the year explained 67% and 71% of the variability asso-

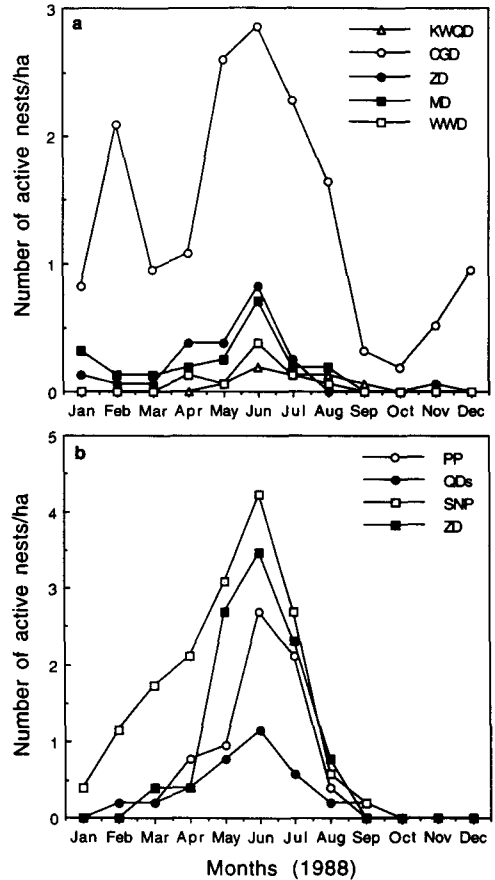


FIGURE 3. (A) Nest density estimates of Key West Quail Doves (KWQD), Ground Doves (CGD), Zenaida Doves (ZD), Mourning Doves (MD), and White-winged Doves (WWD) in 158 0.1 ha strip-transects sampled in the dry zone of Puerto Rico from January–December 1988. (B) Nest density estimates of Plain Pigeons (PP), Ruddy and Key West Quail Doves (QDs), Scaly-naped Pigeons (SNP), and Zenaida Doves (ZD) in 52 0.1 ha strip-transects sampled in the moist and wet zones from January to December 1988.

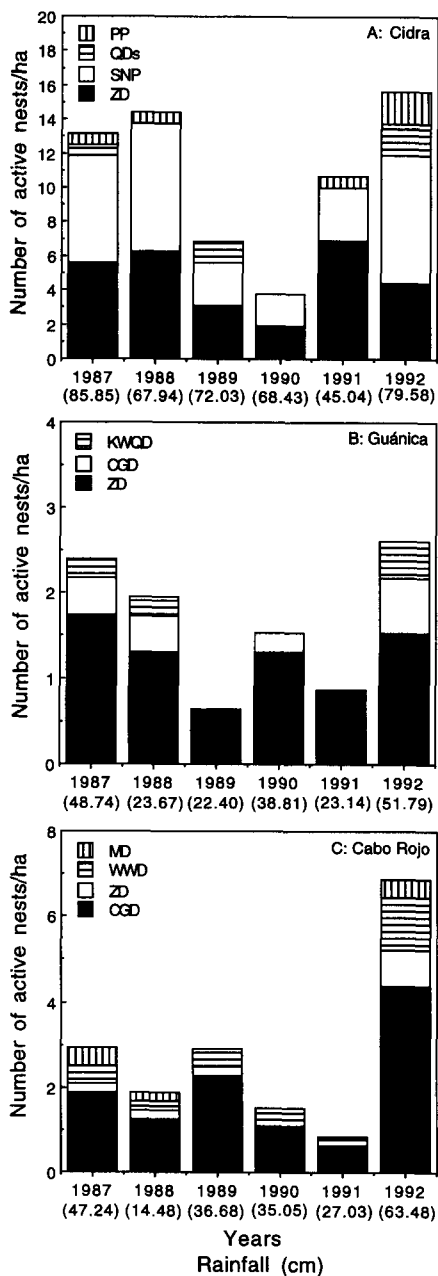


FIGURE 4. Annual changes in the mean nest density estimates of the columbids in the moist montane second-growth forest patches of Cidra (A;  $n = 16$  strip-transects), the xerophytic forest of Guánica (B;  $n = 46$ ), and the dry coastal forest of Cabo Rojo (C;  $n = 48$ ) from May–June 1987 to 1992. The rainfall of the first six months of the year is given within parentheses in the x-axis. Abbreviations are as in Figs. 2 and 3A, B.

ciated with the nest density estimates of all columbids combined during the reproductive peak of May and June in the strip-transects of the xerophytic forest of Guánica (1987–1992;  $\beta_1 = 0.048$ , 95% confidence intervals (CI) = 0.002–0.095,  $P = 0.05$ ; Fig. 4B) and the dry coastal forest of Cabo Rojo (1987–1992;  $\beta_1 = 0.107$ , 95% CI = 0.012–0.203,  $P = 0.04$ ; Fig. 4C). It only explained 9% of the variability of the nest density estimates in the strip-transects of the moist montane second-growth forest patches of Cidra (1987–1992;  $\beta_1 = 0.101$ , 95% CI =  $-0.339$ – $0.541$ ,  $P = 0.69$ ; Fig. 4A).

SEASONAL CHANGES IN NEST DENSITY AND FRUIT ABUNDANCE

In 1988, the seasonal changes in nest density of the columbids (Scaly-naped Pigeons, Zenaida Doves, Plain Pigeons, Ruddy Quail Doves, and Key West Quail Doves combined) were positively correlated with the abundance of mature and immature fruits of key tree species (nine species combined) in the strip-transects of Cayey and Cidra ( $r = 0.54$ ,  $P = 0.071$ ,  $n = 12$ ). The apple rose ( $r = 0.71$ ,  $P = 0.009$ ), night shade ( $r = 0.59$ ,  $P = 0.045$ ), and trumpet tree ( $r = 0.55$ ,  $P = 0.064$ ) had the highest correlations with the nest density estimates of the columbids (also see Rivera-Milán 1990, 1992).

NESTING SUCCESS ESTIMATES AND MICROHABITAT VARIABLES

Of 224 active nests, 144 (64%) were unsuccessful. Predation accounted for 81% (116 of 144) of the nest losses observed from 1989 to 1992 (Table 3). The density of avian and mammalian predators combined was higher in the strip-transects of Cabo Rojo than in those of Cidra and Guánica; but it was higher in the strip-transects of Cidra than in those of Guánica (Table 3). Human-induced disturbance such as damage to nest trees accounted for 12%, and inclement weather for 7% of the nest losses observed from 1989 to 1992.

The Zenaida Doves had a nesting success of 49% in Guánica, 47% in Cidra, and 22% in Cabo Rojo. The Scaly-naped Pigeons had a nesting success of 44% in Cidra. In Cabo Rojo, the White-winged Doves had a nesting success of 29%, and the Mourning Doves of 21%, and the Ground Doves of 17% (Table 3). The nests of Zenaida Doves in Guánica and Cidra had higher estimates of daily survival rate (DSR) than those of the other columbids in Cidra and Cabo Rojo. In

TABLE 2. One-way analysis of variance (ANOVA) with repeated measures at one factor (years) for nest counts of the columbids (combined) in the moist montane second-growth forest of Cidra, the xerophytic forest of Guánica, and the dry coastal forest of Cabo Rojo. Sampling period: May–June 1987–1992<sup>a</sup>.

Source Variation	df	SS	MS	F	P	
Locality	2	63.955	31.977	2.174	0.1762	
Species (locality)	8	117.676	14.709			
Year	5	17.519	3.504	3.928	0.0339	
Year × locality	10	13.532	1.353	1.517	0.2359	
Year × species (locality)	40	36.676	0.892			
Repeated Measures:	1987	1988	1989	1990	1991	1992
Locality:						
Cidra	3.283	3.595	1.717	0.940	2.660	3.910
Guánica	0.797	0.650	0.217	0.507	0.290	0.867
Cabo Rojo	0.733	0.470	0.730	0.380	0.210	1.720
Means Table:						
Effect: Year	1.677	1.655	0.949	0.618	1.123	2.284
Linear contrast			$F = 0.164, P = 0.4889$			
Quadratic contrast			$F = 15.099, P = 0.0057$			
Cubic contrast			$F = 3.833, P = 0.0834$			

<sup>a</sup> The ANOVA model used was:  $\bar{Y}_{ijk} = \mu + \alpha_i + \pi_{k(i)} + \beta_j + \alpha\beta_{ij} + \beta\pi_{k(i)} + \epsilon_{m(ijk)}$  (Winer 1971:518–539). Nest counts were log-transformed.

contrast, the nests of the columbids in Cabo Rojo had lower DSRs than those in Guánica and Cidra (Table 3). The estimated DSR of nests constructed on epiphytes (DSR = 0.971, 95% CI = 0.9591–0.9829,  $n = 78$ ) was significantly higher than that of nests constructed on the bare branches of trees (DSR = 0.944, 95% CI = 0.9217–0.9556,  $n =$

146) in Cabo Rojo, Cidra, and Guánica (combined;  $Z$ -value = 5.487,  $P < 0.001$ ).

According to univariate and multivariate comparisons, the mean relative cover at 5 m from active nests was the most important microhabitat variable accounting for the reproductive failure or success of the columbids in Cidra,

TABLE 3. Nesting success estimates of the columbids in the moist montane second-growth forest of Cidra, the xerophytic forest of Guánica, and the dry coastal forest of Cabo Rojo. Sampling period: May–June 1989–1992<sup>a</sup>.

Species <sup>b</sup>	Number of nests	DSR (SE <sub>DSR</sub> ) <sup>c</sup>	Success estimate (%) <sup>d</sup>	Predation/ nest losses <sup>e</sup>	Predator mean density (SE) <sup>f</sup>
Cidra: moist montane second-growth forest <sup>g</sup>					
SNP	40	0.968 (0.0072) <sup>A</sup>	44	16/18 (89%)	5.94 (1.133)
ZD	31	0.971 (0.0062) <sup>B</sup>	47	17/21 (81%)	
Guánica: xerophytic forest <sup>h</sup>					
ZD	42	0.973 (0.0076) <sup>B</sup>	49	24/30 (80%)	2.65 (0.592)
Cabo Rojo: dry coastal forest					
CGD	51	0.935 (0.0105) <sup>E</sup>	17	33/36 (92%)	9.39 (1.668)
MD	27	0.941 (0.0132) <sup>D</sup>	21	13/19 (68%)	
WWD	20	0.953 (0.0133) <sup>C</sup>	29	8/12 (67%)	
ZD	13	0.943 (0.0195) <sup>D</sup>	22	5/8 (63%)	

<sup>a</sup> A nesting period of 26 days was assumed for all the species.

<sup>b</sup> Abbreviations: Scaly-naped Pigeon (SNP); Zenaida Dove (ZD); Common Ground-Dove (CGD); Mourning Dove (MD); and White-winged Dove (WWD).

<sup>c</sup> Daily survival rates ( $\pm$  standard error) followed by different superscripts differed significantly at  $P \leq 0.05$  (one-tailed  $Z$ -tests). Daily survival rates followed by similar superscripts did not differ significantly at  $P \leq 0.05$ .

<sup>d</sup> Mayfield's method.

<sup>e</sup> Number of nests predated divided by the total number of nest losses recorded due to predation (avian or mammalian) or any other natural (e.g., inclement weather) or human-induced (e.g., damage to nest trees) cause.

<sup>f</sup> Mean number of avian and mammalian predators (combined) per ha ( $\pm$  standard error).

<sup>g</sup> It was not possible to estimate nesting success for all the nests found active in the moist montane second-growth forest patches because of nest height and inaccessibility (see Table 4).

<sup>h</sup> Some active nests found outside of the strip-transects of the xerophytic and dry coastal forests were included in the estimates of nesting success of White-winged Doves, Mourning Doves, and Zenaida Doves to increase the sample-sizes per habitat type.

TABLE 4. Univariate comparisons of nest tree microhabitat variables of successful and unsuccessful nests of the columbids (combined) in the moist montane second-growth forest of Cidra, the xerophytic forest of Guánica, and the dry coastal forest of Cabo Rojo. Sampling period: May–June 1989–1992.\*

Variables <sup>b</sup>	$\bar{x}$	SE <sub><math>\bar{x}</math></sub>	<i>n</i>	<i>F</i>	<i>P</i>
Cidra: moist montane second-growth forest					
1. Nest tree height (m)					
Unsuccessful	12.81	2.024	14	0.095	0.761
Successful	13.87	2.897	10		
2. Nest height (m)					
Unsuccessful	7.61	0.888	14	3.306	0.083
Successful	5.54	0.506	10		
3. Nest tree DBH (cm)					
Unsuccessful	21.98	3.393	14	1.107	0.304
Successful	29.31	6.600	11		
4. Perpendicular distance from nest to transect center (m)					
Unsuccessful	10.84	1.967	14	0.655	0.427
Successful	12.83	1.155	11		
5. Mean relative cover of nest at 5 m					
Unsuccessful	1.68	0.217	14	23.982	0.0001
Successful	2.90	0.049	11		
6. Distance from nest-bowl center to tree trunk (cm)					
Unsuccessful	240.07	47.252	14	2.562	0.124
Successful	128.10	49.618	10		
Cabo Rojo and Guánica: xerophytic and dry coastal forest					
1. Nest tree height (m)					
Unsuccessful	3.87	0.286	28	2.367	0.131
Successful	4.69	0.503	17		
2. Nest height (m)					
Unsuccessful	2.19	0.176	28	0.567	0.455
Successful	2.43	0.282	17		
3. Nest tree DBH (cm)					
Unsuccessful	12.77	1.521	28	0.350	0.557
Successful	14.16	1.684	17		
4. Perpendicular distance from nest to transect center (m)					
Unsuccessful	6.64	1.253	28	4.329	0.043
Successful	11.83	1.957	17		
5. Mean relative cover of nest at 5 m					
Unsuccessful	2.09	0.104	28	11.182	0.002
Successful	2.60	0.093	17		
6. Distance from nest-bowl center to tree trunk (cm)					
Unsuccessful	24.44	47.252	28	0.267	0.871
Successful	26.18	10.276	17		

\* One-way ANOVAs. The nests of Zenaida Doves, Scaly-naped Pigeons, and Plain Pigeons were combined in Cidra. The nests of Common Ground-Doves, White-winged Doves, Mourning Doves, and Zenaida Doves were combined in Cabo Rojo and Guánica.  
<sup>b</sup> See Methods.

Cabo Rojo and Guánica (MANOVAs: Cidra:  $F_{1,16} = 5.981, P = 0.0264$ ; Cabo Rojo and Guánica:  $F_{1,37} = 7.983, P = 0.0076$ ; overall:  $F_{1,61} = 20.877, P = 0.0001$ ; Table 4). The second most important microhabitat variable measured in the xerophytic and dry coastal forests was the perpendicular distance from the nests to the center of the strip-transects (MANOVA:  $F_{1,37} = 1.626, P = 0.2102$ ). Nest height was the second most important microhabitat variable measured in the moist montane second-growth forest patches

(MANOVA:  $F_{1,16} = 1.172, P = 0.2951$ ; see Table 4 for ANOVAs and descriptive statistics of microhabitat variables). A list of the number of active nests found per tree species per locality is given in the Appendix.

SEASONAL SPECIES COVARIATIONS IN NEST DENSITY IN THE LIFE ZONES

Pearson's (*r*) correlation coefficients showed similar patterns of species covariations in the strip-transects of the life zones (Table 5). The nest



density estimates of Scaly-naped Pigeons, Plain Pigeons, Zenaida Doves, and Ruddy and Key West Quail Doves (combined) were positively correlated in the strip-transects of the moist and wet zones, whereas the nest density estimates of Ground Doves, Zenaida Doves, Mourning Doves, White-winged Doves, and Key West Quail Doves were positively correlated in the strip-transects of the dry zone (Table 5). The predominantly positive and significant correlations (13 of 16) suggested parallel responses of columbid nesting populations to similar or covarying resources in the life zones of Puerto Rico (Rivera-Milán 1990, 1992, 1995).

## DISCUSSION

### SEASONAL AND ANNUAL CHANGES IN NEST DENSITY

A peak in the nest density of the columbids occurred in May and June, followed by a decrease during the July to October flocking period (see Rivera-Milán 1990, 1992, 1993, 1995), and an increase from November to April (Figs. 2 and 3A, B, Table 1). A second degree (quadratic) polynomial model showed an adequate fit to the observed seasonal changes in nest density of the columbids in the life zones from 1987 to 1988 (Table 2). Although a peak in nest density occurred in May and June, active nests of species such as Ground Doves, Zenaida Doves, and Scaly-naped Pigeons were observed throughout the year in the study areas sampled from 1987 to 1988 (see below).

A quadratic polynomial model showed an adequate fit to the changes observed in Cabo Rojo, Cidra, and Guánica from 1987 to 1992 (Fig. 4A-C, Table 2). The mean nest density estimates of the columbids (Scaly-naped Pigeons, Zenaida Doves, Plain Pigeons, Ruddy Quail Doves, and Key West Quail Doves combined) decreased in Cidra in 1990, probably due to the effect of the passage of Hurricane Hugo through the north-eastern corner of Puerto Rico on 18 September 1989 (see Brennan 1991, Boose et al. 1994, and references therein). Some frugivore and seed-eating bird populations were severely affected both short-term direct effects and long-term indirect effects by this large-scale environmental perturbation (e.g., Ruddy Quail Doves; see Waide 1991, Wauer and Wunderle 1992, Wiley and Wunderle 1993, Rivera-Milán, unpubl. data), but in Cidra

TABLE 5. Pearson's Product-Moment Coefficients of Correlation ( $r$ ; upper-right triangle) and covariances (lower-left triangle) of nest-counts of the columbids in the three major life zones of Puerto Rico. Sampling period: January–December 1988.<sup>a</sup>

Life zone	Species				
Dry Zone (area sampled: 15.8 ha)					
	ZD <sup>b</sup>	CGD	MD	WWD	KWQD
ZD	—	0.65*	0.83*	0.80*	0.38 <sup>ns</sup>
CGD	0.10	—	0.71*	0.64*	0.53 <sup>ns</sup>
MD	0.12	0.10	—	0.76*	0.50 <sup>ns</sup>
WWD	0.10	0.06	0.08	—	0.74*
KWQD	0.04	0.04	0.04	0.05	—
Moist and Wet Zones (area sampled: 5.2 ha)					
	SNP	ZD	PP	QDs	
SNP	—	0.83*	0.88*	0.91*	
ZD	0.22	—	0.94*	0.90*	
PP	0.20	0.21	—	0.93*	
QDs	0.13	0.13	0.12	—	

<sup>a</sup> A total of 210 0.1 ha strip-transects were sampled in 1988 (158 in the dry zone, 36 in the moist zone, and 16 in the wet zone). Nest counts were log-transformed.

<sup>b</sup> Abbreviations as in Table 1.

\* Significant at  $P \leq 0.05$ .

<sup>ns</sup> Not significant at  $P \leq 0.05$ .

the columbid nesting populations rebounded to pre-Hurricane levels from 1991 to 1992 (Fig. 4A).

Cabo Rojo and Guánica were not affected by Hurricane Hugo. The mean nest density estimates of the columbids (Zenaida Doves, Common Ground-Doves, and Key West Quail Doves combined) decreased in Guánica in 1989 and 1991 (Fig. 4B), whereas the mean nest density estimates of the columbids (Ground Doves, Zenaida Doves, White-winged Doves, and Mourning Doves combined) decreased in Cabo Rojo in 1990 and 1991 (Fig. 4C). The mean nest density estimates in Cabo Rojo and Guánica increased in 1992. The rainfall of the first six months of the year influenced the changes observed from 1987 to 1992 (see below).

### NESTING SUCCESS, MICROHABITAT VARIABLES, AND PREDATION

The estimates of nesting success of the columbids in Guánica and Cidra were significantly higher than those in Cabo Rojo (Table 3). Nest cover was the most important microhabitat variable accounting for failure or success (Table 4). Predation on eggs or nestlings was the major cause of failure. Nests constructed on epiphytes (bromeliads, lianas, and vines) had higher DSRs than those constructed on the bare branches of trees,

probably because epiphytes provided additional support and concealment against predators (Nice 1922, 1923; Coon et al. 1981; Best and Stauffer 1980; Yahner 1982; Martin and Roper 1988). Epiphytes were uncommon in the dry coastal forest of Cabo Rojo, but were used as nest substrates in areas dominated by oxborn bucida (*Bucida buseras*). The use of epiphytes was also reported by Barbour (1923) and Maldonado-Colón and Pérez-Rivera (1977; see below).

Predator density was higher in Cabo Rojo than in Cidra and Guánica (Table 3). Common Ground-Doves had lower nesting success and higher predation rates than the other columbids in Cabo Rojo, probably because they had a higher density of active nests and used a wide variety of microhabitats frequently with poor-fair cover (e.g., dry tree stumps near the ground). From 1987 to 1992, Common Ground-Doves ( $n = 2$ ), Zenaida Doves ( $n = 1$ ), and Mourning Doves ( $n = 2$ ) were observed nesting on top of old Bananaquit (*Coereba flaveola*) and Puerto Rican Bullfinch (*Loxigilla portoricensis*) nests in Cabo Rojo. Scaly-naped Pigeons were observed nesting on top of old rat (*Rattus* spp.;  $n = 2$ ) and Green Heron (*Butorides virescens*;  $n = 1$ ) nests in Cidra and Cayey (Rivera-Milán, unpubl. data). The other pigeons and doves were not observed using the old nests of other species as substrates, but this appears to be a widespread nesting strategy among the columbids (Nice 1922, 1923; McClure 1943; Hanson and Kossack 1963; Coon et al. 1981; Goodwin 1983; Westmoreland et al. 1986; Sayre and Silvy 1993).

While sitting quietly and motionless on eggs or nestlings, the columbids appeared to rely on the concealment provided by their plumage coloration and on vegetation cover to reduce the risk of detection by predators (Swank 1955, Murton 1965, Best and Stauffer 1980, Tomialojc 1980, Yahner 1982, Westmoreland and Best 1987, Burger et al. 1989, Martin 1992). Nesting Common Ground-Doves, Zenaida Doves, and Mourning Doves often performed distraction displays when approached by an observer, but sometimes they could be approached very closely before flushing from the nest, especially when brooding recently hatched nestlings (Swank 1955, Burger et al. 1989, Sayre and Silvy 1993, Wiley 1991, Rivera-Milán unpubl. data).

Wiley (1991) concluded that the Zenaida Doves used nest trees in relation to their abundance in

the areas sampled, and estimated that an average of 40.9% ( $n = 22$ ) of the nests with eggs were successful (i.e., at least one nestling fledged) in southwestern Puerto Rico (Guánica and Susúa forests combined) from 1974 to 1975, and 62.6% ( $n = 91$ ) were successful in Cidra from 1974 to 1982. Maldonado-Colón and Pérez-Rivera (1977) estimated a mean nesting success of 63% ( $n = 78$ ) for the Zenaida Doves in Cayey, Cidra, and Guánica (combined) and reported that 54% ( $n = 37$ ) of the nests found in Cayey were constructed on bromeliads (*Tillandsia* sp. and *Guzmania* sp.). However, Maldonado-Colón and Pérez-Rivera (1977) and Wiley (1991) apparently used the traditional method to estimate nesting success; hence their estimates are probably biased high (see Mayfield 1961, 1975; Johnson 1979). The Zenaida Dove is a multibrooded habitat generalist that may change its nesting and foraging preferences throughout the year in an opportunistic manner; but, as with the other columbids, it needs to find sites with adequate horizontal support and concealment against predators to increase the probability of nesting successfully (see Martin 1992 for a review).

#### SEASONAL PATTERNS OF SPECIES COVARIATIONS

The density of active nests found between the second week of May and the second week of June in the xerophytic forest of Guánica and dry coastal forest of Cabo Rojo was significantly influenced by the rainfall of the first six months of the year (also see Faaborg 1982, Faaborg et al. 1984). On average, the rainfall in the xerophytic and dry coastal forests peaked in May and from October to November (Rivera-Milán 1990, 1992). The first and smaller peak of rain in May marked the end of the December to March dry season and normally was followed by a period of increasing soil moisture and primary productivity. The second and greater peak of rain during October and November was normally 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). The dry season probably prevents the occurrence of a second peak in nest density from September to November by exerting a strong selective force against reproductive success in the xerophytic forest of Guánica and dry coastal forest of Cabo Rojo. The decline in vegetation cover

during the dry season can increase the exposure of active nests to predators such as Pearly-eyed Thrashers (*Margarops fuscatus*), Red-legged Thrushes (*Turdus plumbeus*), Mangrove Cuckoos (*Coccyzus minor*), Puerto Rican Lizard-Cuckoos (*Saurothera vieilloti*), and rats among others (Rivera-Milán 1990, 1992; Rivera-Milán et al. 1993; Rivera-Milán and Schaffner, unpubl. data).

Since columbids are capable of multiple brooding and crop-milk production, and they have a diverse frugivorous and granivorous diet, complete synchronization of nesting events with foraging resources is not necessary to enhance their reproductive success (Westmoreland and Best 1987, Blockstein 1989, Wiley 1991; but see Bancroft et al. 1990). For example, active nests of Zenaida Doves and Ground Doves were found at any time during the year in the strip-transects of the dry zone. Both species molted throughout the year (Rivera-Milán, unpubl. data). Male calling activity was stimulated by rainfall in a bimodal fashion (Rivera-Milán 1990, 1992); and probably they were ready to mate and breed whenever the environmental conditions became favorable enough (e.g., adequate food supply and vegetation cover; Miller 1962, Immelmann 1971, Fogden 1972, Murton and Westwood 1977, Avery 1980, Wiley 1991).

In the dry zone, the nesting activity of Common Ground-Doves was less constrained than that of the other columbids by rainfall (Figs. 2 and 3A). Common Ground-Doves feed mainly on grass seeds (Pérez-Rivera 1987), whereas the other columbids feed on both seeds and fruits (Pérez-Rivera and Collazo-Algarín 1976, Maldonado-Colón and Pérez-Rivera 1977, Pérez-Rivera 1979, Wiley and Wiley 1979, Wiley 1991, and references therein). The fruits of key tree species in xeric habitats can be in short supply during dry years (Faaborg 1982, Faaborg et al. 1984). Moreover, the mean body mass of the Common Ground-Dove is about 35 g, whereas the mean body mass of the other columbids in the dry zone is over 100 g (Rivera-Milán, unpubl. data). Hence, Common Ground-Doves can probably derive their energy and water requirements more easily than the other columbids from a single foraging resource (grass seeds) that is available throughout the year, especially during the peaks of rain in the dry zone (see MacMillen 1990). With a mean density of 210.9 birds/km<sup>2</sup> (95% CI = 102.9–318.8), the Common Ground-Dove ranked as the most abundant among the

columbids in the dry zone from 1987 to 1988 (Rivera-Milán 1990, 1995).

The total amount of rainfall occurring during the first six months of the year was probably less important than the abundance of fruits of key tree species (e.g., *Syzygium jambos*, *Solanum torvum*, and *Cecropia shreberiana*) as a predictor of the seasonal and annual changes in nest density of the columbids in the moist and wet zones (Cardona et al. 1986; Rivera-Milán 1990, 1992, unpubl. data). Quantitative studies about the relationships between seasonal and annual changes in nest density and fruiting phenology of key tree species are needed to improve our understanding of the dynamics of columbid nesting populations in mesic and xeric habitats (see, for example, Cardona et al. 1986, Bancroft et al. 1990). Nevertheless, the predominantly positive species covariations suggested parallel responses of the columbid nesting populations to similar or co-varying resources in the life zones of the Puerto Rican mainland (Table 5). Quantification of nesting and foraging resource use and availability is particularly important for the conservation and management of columbid populations inside the forest reserves of Puerto Rico.

#### ACKNOWLEDGMENTS

Part of this study was performed in partial fulfillment of the requirements for the degree of Ph.D. from the University of Maryland at College Park (UMCP). I thank J. Faaborg, F. Schaffner, and J. Wiley for reviewing the manuscript. I also thank G. Bonilla, E. González, A. Matos, S. Medina, A. Ortiz, J. Pagán, D. Ramos, E. Ramos, and C. Vázquez for sharing many hours afield. J. Vivaldi (deceased) and J. Moreno provided support as coordinators of Pittman-Robertson Funds grant-in-aid to Project W-11, Section of Terrestrial Ecology, Scientific Research Area, Puerto Rico Department of Natural Resources (PRDNR). M. Canals (PRDNR) provided the rainfall data of the Guánica State Forest. J. Collazo, S. Rice, and F. Schaffner (U.S. Fish and Wildlife Service, Caribbean Islands National Wildlife Refuge) provided the rainfall data of the Cabo Rojo National Wildlife Refuge. G. Proctor (PRDNR) helped with the identification of plants, seeds, and fruits whenever it was requested. From 1987 to 1988, I also received support through a research assistantship from the Graduate Program in Marine and Estuarine Environmental Sciences and the Agricultural and Life Sciences Division at UMCP.

#### LITERATURE CITED

- ARENDET, W. J., T.A.V. MORA, AND J. W. WILEY. 1979. White-crowned Pigeon: status rangewide in the Dominican Republic. Proc. Ann. Conf. S.E. Assoc. Fish Wildl. Agencies 33:111–122.
- AVERY, M. L. 1980. Diet and breeding seasonality

- among a population of Sharp-tailed Munias, *Lonchura striata*, in Malaysia. *Auk* 97:160-166.
- 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. Tallahassee, FL.
- BARBOUR, T. 1923. The birds of Cuba. Nuttall Ornithol. Club, No. 6.
- 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.
- BEST, L. B., AND D. F. STAUFFER. 1980. Factors affecting the nesting success in riparian bird communities. *Condor* 82:149-158.
- BIAGGI, V. 1970. Las aves de Puerto Rico. Segunda edición. Plus Ultra Educational Publishers, NY.
- BIRDSEY, R. A., AND P. L. WEAVER. 1982. The forest resources of Puerto Rico. U.S. Forest Serv. Resour. Bull. SO-85, Southern Forest Experiment Station, New Orleans, LA.
- BLOCK, W. M., K. A. WITH, AND M. L. MORRISON. 1987. On measuring bird habitat: influence of observer variability and sample size. *Condor* 89:241-251.
- BLOCKSTEIN, D. E. 1988. Two endangered birds of Grenada, West Indies: Grenada Dove and Grenada Hook-billed Kite. *Carib. J. Sci.* 24:127-136.
- BLOCKSTEIN, D. E. 1989. Crop milk and clutch size in Mourning Doves. *Wilson Bull.* 101:11-25.
- BOOSE, E. R., D. R. FOSTER, AND M. FLUET. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64:369-400.
- BRENNAN, J. W. 1991. Meteorological summary of Hurricane Hugo. *J. Coastal Res.* 8:1-12.
- BURGER, J., M. GOCHFELD, D. J. GOCHFELD, AND J. E. SALIVA. 1989. Nest site selection in Zenaida Dove (*Zenaida aurita*) in Puerto Rico. *Biotropica* 21:244-249.
- CARDONA, J., M. RIVERA, M. VÁZQUEZ, AND C. R. LABOY. 1986. Availability of food resources for the Puerto Rican Parrot and Puerto Rican Plain Pigeon in Río Abajo Forest. Project W-10 (ES-1). Scientific Research Area. Puerto Rico Dept. Nat. Res.
- COON, R. A., J. D. NICHOLS, AND H. F. PERCIVAL. 1981. Importance of structural stability to success of Mourning Dove nests. *Auk* 98:389-391.
- DILLON, W. R., AND M. GOLDSTEIN. 1984. Multivariate analysis. John Wiley and Sons, NY.
- 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., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates and bird population fluctuations in a Puerto Rican dry forest: a nine year study. *Wilson Bull.* 96:575-593.
- FOGDEN, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307-343.
- GODÍNEZ, E. 1993. Situación de las poblaciones de *Columba leucocephala* (Aves: Columbidae) en Cuba entre 1979 y 1987. Editorial Academia, La Habana, Cuba.
- GOODWIN, D. 1983. Pigeons and doves of the world. 3rd edition. Cornell Univ. Press, NY.
- GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds, p. 63-94. *In* D. M. Power [ed.], Current ornithology. Vol. 9. Plenum Press, NY.
- GUREVITCH, J., AND S. T. CHESTER, JR. 1986. Analysis of repeated measures experiments. *Ecology* 67:251-255.
- HANSON, H. C., AND C. W. KOSSACK. 1963. The Mourning Dove in Illinois. Illinois Dept. of Cons. Tech. Bull. No. 2.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction, p. 341-389. *In* D. S. Farner and J. R. King [eds.], Avian biology. Academy Press, NY.
- JAMES, F. C., AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727-736.
- JOHNSON, D. H. 1979. Estimating nesting success: the Mayfield method and an alternative. *Auk* 96:651-661.
- LITTLE, E. L. JR., F. H. WADSWORTH, AND J. MARRERO. 1977. Árboles comunes de Puerto Rico y las Islas Virgenes. Editorial Universitaria, Río Piedras, Puerto Rico.
- LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical ecology. John Wiley & Sons, NY.
- LUGO, A. E., J. A. GONZÁLEZ, 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.
- MALDONADO-COLÓN L. A., AND R. A. PÉREZ-RIVERA. 1977. Factores de supervivencia de la tórtola cardosantera (*Zenaida aurita aurita*) en Puerto Rico. *Science-Ciencia* 4:66-70.
- MARTIN, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies, p. 163-197. *In* D. M. Power [ed.], Current Ornithology. Vol. 9. Plenum Press, NY.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90:51-57.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.
- MAYFIELD H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- MCCLURE, H. E. 1943. Ecology and management of the Mourning Dove, *Zenaida Macroura* (Linn.) in Cass County, Iowa. Iowa Agric. Exper. Sta. Res. Bull. 310:335-415.
- MILLER, A. H. 1962. Biomodal occurrence of breeding in an equatorial sparrow. *Proc. Natl. Acad. Sci.* 48:396-400.
- MURTON, R. K. 1965. The Wood Pigeon. New Nat. Monogr. Ser. Collins, London.

- MURTON, R. K., AND N. J. WESTWOOD. 1977. Avian breeding cycles. Clarendon Press, Oxford.
- NICE, M. M. 1922. A study of the nesting of Mourning Doves. Part 1. *Auk* 39:457-474.
- NICE, M. M. 1923. A study of the nesting of Mourning Doves. Part 2. *Auk* 40:37-58.
- NICHOLS, J. D., H. F. PERCIVAL, R. A. COON, M. J. CONROY, G. L. HENSLER, AND J. E. HINES. 1984. Observer visitation frequency and success of Mourning Dove nests: a field experiment. *Auk* 101:398-402.
- NICHOLS, J. D., R. E. TOMLINSON, AND G. WAGGERMAN. 1986. Estimating nest detection probabilities for White-winged Dove nest transects in Tamaulipas, Mexico. *Auk* 103:825-828.
- PÉREZ-RIVERA, R. A. 1979. Trabajo preliminar sobre la biología y el ciclo de vida de la perdiz pequeña (*Getrygon montana montana*). *Science-Ciencia* 6:85-90.
- PÉREZ-RIVERA, R. A. 1987. Aspectos de la alimentación de la rolita de Puerto Rico (*Columbina passerina portoricensis*). *Science-Ciencia* 14:27-30.
- PÉREZ-RIVERA, R. A. 1990. Situación actual de la paloma ceniza o sabanera (*Columba inornata*) en las Antillas Mayores. *Science-Ciencia* 17:21-25.
- 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.
- 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.
- 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. 1992. Distribution and abundance patterns of columbids in Puerto Rico. *Condor* 94:224-238.
- RIVERA-MILÁN, F. F. 1993. Standardization of roadside counts of columbids in Puerto Rico and on Vieques Island. U.S. Natl. Biol. Surv. Publ. No. 197.
- RIVERA-MILÁN, F. F. 1995. Spatial and temporal variation in the detectability and density of columbids in Puerto Rico and on Vieques Island. *Ornitología Neotropical* 6:1-17.
- RIVERA-MILÁN, F. F., G. BONILLA, A. ORTIZ, D. RAMOS, AND E. RAMOS. 1990. Final Report. Project W-11, Puerto Rico Dept. Nat. Res.
- RIVERA-MILÁN, F. F., E. GONZÁLEZ, A. MATOS, S. MEDINA, AND C. VÁZQUEZ. 1993. Final Report. Project W-11, Puerto Rico Dept. Nat. Res.
- SILANDER, S., H. G. DE RUBIO, M. MIRANDA, AND M. VÁZQUEZ. 1986. Compendio enciclopédico de los recursos naturales de Puerto Rico. Estudio IV. Vol. 10. Los bosques de Puerto Rico. Puerto Rico Dept. Nat. Res.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co., San Francisco.
- SAYRE, M. W., AND N. J. SILVY. 1993. Nesting and production, p. 81-104. *In* T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi [eds.], *Ecology and management of the Mourning Dove*. Stackpole Books, Harrisburg, PA.
- STEEL, R. G. D., AND J. H. TORRIE. 1980. *Principles and procedures of statistics*. 2nd ed. McGraw-Hill Book Co., NY.
- SWANK, W. G. 1955. Nesting and production of the Mourning Dove in Texas. *Ecology* 36:495-505.
- TOMIALOJC, L. 1980. The impact of predation on urban and rural Wood Pigeon (*Columba palumbus* [L.]) populations. *Polish Ecol. Stud.* 5:141-220.
- WAIDE, R. B. 1991. The effect of Hurricane Hugo on birds populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:475-480.
- WAUER, R. H., AND J. M. WUNDERLE, JR. 1992. The effect of Hurricane Hugh on bird populations on St. Croix, U.S. Virgin Islands. *Wilson Bull.* 104:656-673.
- WESTMORELAND, D. L., AND B. BEST. 1985. Effects of researcher disturbance on Mourning Dove nesting success. *Auk* 102:774-780.
- WESTMORELAND, D. L., AND B. BEST. 1987. What limits Mourning Doves to a clutch of two eggs? *Condor* 89:486-493.
- WESTMORELAND, D. L., B. BEST, AND D. E. BLOCKSTEIN. 1986. Multiple brooding as a reproductive strategy: time-conserving strategies in Mourning Doves. *Auk* 103:196-203.
- WILEY, J. W. 1979. The White-crowned Pigeon in Puerto Rico: status, distribution, and movements. *J. Wildl. Manage.* 43:402-413.
- WILEY, J. W. 1985. Bird conservation in the United States Caribbean, p. 107-160. *In* S. A. Temple [ed.], *Bird conservation*. No. 2. The Univ. of Wisconsin Press, Madison, WI.
- WILEY, J. W. 1991. Ecology and behavior of the Zenaida Dove. *Ornitología Neotropical* 2:49-75.
- WILEY, J. W. AND B. N. WILEY. 1979. The biology of the White-crowned Pigeon. *Wildl. Monogr.* No. 64.
- WILEY, J. W., AND J. M. WUNDERLE, JR. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Cons. Intl.* 3:319-349.
- WINER, B. J. 1971. *Statistical principles in experimental design*. 2nd ed. McGraw-Hill Book Co., NY.
- YAHNER, R. H. 1982. Avian nest densities and nest-site selection in farmstead shelterbelts. *Wilson Bull.* 94:156-175.

APPENDIX. Nest trees used by the columbids (eight species combined) in the strip-transects of the moist montane second-growth forest of Cidra, the xerophytic forest of Guánica, and the dry coastal forest of Cabo Rojo. Sampling period: February 1987-June 1992.

Locality Nest tree <sup>a</sup>	Number of nests
Cidra: moist montane second-growth foerst ( $n = 272$ ) <sup>b</sup>	
Apple rose ( <i>Syzygium jambos</i> )	76
Bamboo ( <i>Bambusa vulgaris</i> )	49

## APPENDIX. Continued.

Locality Nest tree <sup>a</sup>	Number of nests
African tuliptree ( <i>Spathodea campanulata</i> )	43
American muskwood ( <i>Guarea trichilioides</i> )	41
White cedar ( <i>Tabebuia heterophylla</i> )	22
Martinique prickly-ash ( <i>Zanthoxylum martinicense</i> )	14
Mountain immortelle ( <i>Erythrina poeppigiana</i> )	14
Trumpet tree ( <i>Cecropia shreberiana</i> )	8
White manjack ( <i>Cordia sulcata</i> )	3
Puerto Rican royal-palm ( <i>Roystonea borinquena</i> )	2
Guánica: xerophytic forest ( $n = 71$ ) <sup>c</sup>	
Dildo ( <i>Cephalocereus royenii</i> )	21
Prickly pear ( <i>Opuntia rubescens</i> )	17
Oxhorn bucida ( <i>Bucida buceras</i> )	16
Mahogany ( <i>Swietenia mahagoni</i> )	11
Box briar ( <i>Randia aculeata</i> )	3
Turpentine tree ( <i>Bursera simaruba</i> )	2
Caribbean princewood ( <i>Exostema caribaeum</i> )	1
Cabo Rojo: dry coastal forest ( $n = 254$ ) <sup>d</sup>	
Dildo	64
Prickly pear	51
Mesquite ( <i>Prosopis</i> spp.)	43
Guamuchil ( <i>Pithecellobium dulce</i> )	32
Oxhorn budica	28
Turpentine tree	15
Red mangrove ( <i>Rhizophora mangle</i> )	10
Black mangrove ( <i>Avicennia germinans</i> )	7
Button mangrove ( <i>Conocarpus erectus</i> )	4

<sup>a</sup> Scientific names followed Little et al. (1977). I kept a complete record of the nest trees used by each species per locality from 1989 to 1992. Refer to Pérez-Rivera and Collazo-Algarín (1976), Maldonado-Colón and Pérez-Rivera (1977), Wiley and Wiley (1979), and Wiley (1991) for more information about the nest trees used by the columbids in Puerto Rico.

<sup>b</sup> Ruddy and Key West Quail Dove nests were commonly found on leaf clumps in unidentified shrubs, ferns, and tree stumps near the ground (also see Pérez-Rivera 1979). The nests of Zenaida Doves, Scaly-naped Pigeons, and Plain Pigeons were combined. Epiphytes (bromeliads, lianas, and vines) were commonly used as nest substrates. The vegetation in Cidra was characterized by Puerto Rican royal-palm, West Indies tremma (*Trema lamarckiana*), trumpet tree, India laurel-fig (*Ficus citrifolia*), machette (*Erythrina berteroaana*), mountain immortelle, guaba (*Inga vera*), Martinique prickly-ash, American muskwood, wild mamee (*Clusia rosea*), punch berry (*Myrcia splendens*), camasey (*Miconia prasina*), apple rose, matchwood (*Dydimopanax morototoni*), white manjack, night shade, African tuliptree, bamboo, and white cedar among others.

<sup>c</sup> The nests of Zenaida Doves, Ground Doves, and Key West Quail Doves were combined. Bromeliads (*Tillandsia* sp. and *Guzmania* sp.) were commonly used as nest substrates. The vegetation in Guánica was characterized by oxhorn bucida, turpentine tree, dildo, prickly pear, pigeon berry (*Boureria succulenta*), caribbean princewood (*Exostema caribaeum*), sea amyril (*Amyris elemifera*), lignumvitae (*Guaiacum officinale*), mahogany, box briar, and fustic (*Pictetia aculeata*) among others.

<sup>d</sup> The nests of Common Ground-Doves, White-winged Doves, Mourning Doves, and Zenaida Doves were combined. Bromeliads were uncommon, but were used as nest substrates in forest patches dominated by oxhorn bucida. The vegetation in Cabo Rojo, Juana Diaz, and Santa Isabel was characterized by mesquite, tamarind (*Tamarindus indica*), guamuchil (*Pithecellobium* sp.), leadtree (*Leucaena glauca*), corcho bobo (*Pisonia albidia*), lebbek albizia (*Albizia lebbek*), red mangrove, white-mangrove (*Laguncularia rademosa*), black-mangrove, button-mangrove, oxhorn bucida, turpentine tree, dildo, prickly pear, pigeon berry, lignumvitae, box briar, and fustic among others.