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SPATIAL AND TEMPORAL VARIATION IN THE DETECTABILITY AND DENSITY OF COLUMBIDS IN PUERTO RICO AND ON VIEQUES ISLAND

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Resumen. Es común que se presuma la existencia de una correlación entre los estimados de abundancia relativa y densidad en escalas múltiples de espacio y tiempo. Sin embargo, los estimados anuales y estacionales de abundancia relativa deben ser ajustados para el área de detección, especialmente cuando existe un interés en hacer comparaciones de la abundancia de varias especies en hábitats heterogéneos. Entre 1986—92 combiné puntos de conteo con un radio fijo (radio = 60 m) y sin un radio fijo para muestrear las poblaciones de las diez especies nativas de palomas y tórtolas (colúmbidos en lo subsiguiente) en las tres zonas de vida de mayor tamaño en Puerto Rico (zona húmeda, mojada y seca). Vieques (la isla municipio de mayor tamaño de Puerto Rico) fué muestreada en mayo de 1991 y 1992. En este estudio examino (1) los cambios en detección ($\hat{C}$) y densidad ($\hat{D}$) de los colúmbidos en escalas múltiples de espacio (rutas, zonas de vida, islas) y tiempo (meses, estaciones, años), y (2) la viabilidad de combinar técnicas de conteos intensivas (puntos de conteo con un radio fijo) y extensivas (puntos de conteo sin un radio fijo) para monitorear a largo plazo (> 10 años) los cambios poblacionales de los colúmbidos en las zonas de vida. La $\hat{C}$ y $\hat{D}$ de los colúmbidos varió de acuerdo a las escalas de tiempo y espacio establecidas. Con la excepción de la paloma turca (*Columba squamosa*) en la zona húmeda, los conteos de los colúmbidos efectuados en los puntos con un radio fijo y sin un radio fijo correlacionaron significativamente en las zonas de vida. El aumento en el número de individuos detectados fuera de los puntos con un radio fijo no implicó necesariamente un aumento en el número de individuos detectados dentro de los mismos, ni un aumento en los estimados de $\hat{D}$ de la paloma turca en la zona húmeda. Los coeficientes de variación (CVs) de los conteos de 3-minutos demostraron que la variación en el número de detecciones dentro de los puntos con un radio de 60 m fué un componente importante de la variación total de los estimados de $\hat{D}$ a nivel estacional y anual en las zonas de vida. Los estimados de $\hat{D}$ de la tórtola cardosantera (*Zenaida aurita*) y la paloma turca aumentaron levemente entre mayo y junio de 1987 a 1992. Los índices de correlación de los colúmbidos fueron indicativos de fluctuaciones paralelas de las poblaciones a recursos similares o covariables en las zonas de vida.

Abstract. Relative abundance (birds/km) and density (birds/km^2) estimates are commonly assumed to be correlated at multiple spatio-temporal scales. However, annual and seasonal estimates of relative abundance should be adjusted for detection area, especially when comparisons of species abundances in heterogeneous habitats are of interest. From 1986—92, I combined unfixed- and fixed-radius point counts (radius = 60 m) of all the ten native species of pigeons and doves (columbids hereafter) in the three major life zones of the Puerto Rican mainland (moist, wet, and dry zone). Vieques Island (Puerto Rico's largest offshore territory) was sampled in May 1991 and 1992. In this study I examine (1) the detectability ($\hat{C}$) and density ($\hat{D}$) estimates of the columbids at multiple spatial (routes, life zones, islandwide) and temporal (months, seasons, years) scales, and (2) the feasibility of combining intensive (fixed-radius point counts) and extensive (unfixed-radius point counts) counting techniques to monitor long-term (>10 years) population changes of the columbids in the life zones. The $\hat{C}$ and $\hat{D}$ estimates of the colum-

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bids varied according to the established spatio-temporal scales. With the exception of the Scaly-naped Pigeon (*Columba squamosa*) in the moist zone, the unfixed- and fixed-radius point counts of the columbids were significantly correlated in the life zones. An increase in the number of aural (call-count) and visual (sight-count) detections outside the fixed-radius did not necessarily imply an increase in the number of detections inside the fixed-radius of the 3-min stations or an increase in the $\hat{D}$ of Scaly-naped Pigeons in the moist zone. The coefficients of variation (CVs) of the fixed and unfixed call- and sight-counts of the columbids showed that the variability in the number of detections inside the 60 m radius of the 3-min stations was an important component of the total variation of the seasonal and annual $\hat{D}$ estimates in the life zones. The $\hat{D}$ estimates of the Zenaida Doves (*Zenaida aurita*) and Scaly-naped Pigeons increased slightly from May-June 1987—92. Pair-wise $\hat{D}$ correlations of the columbids were indicative of parallel fluctuations to similar or covarying resources in the life zones. *Accepted 27 November 1994.*

Key words: Columbidae, detectability, density, relative abundance, point counts, spatio-temporal scales, Puerto Rico, Vieques Island.

INTRODUCTION

There are ten native species of pigeons and doves (columbids hereafter) in Puerto Rico and its offshore territories: 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. chrysia*), and Bridled Quail-Dove (*G. mystacea*) (see Goodwin 1983 and Raffaele 1989 for general information about the species). From July 1986—June 1992, I conducted standardized call- and sight-counts of all the columbids to determine their status, distribution, and abundance (Rivera-Milán 1990a, 1992, 1993).

Relative abundance estimates based on aural and visual detections are commonly assumed to be valid indicators of population density changes at multiple spatial and temporal scales. Rotella & Ratti (1986) questioned the validity of the index-density relationship and demonstrated via double sampling the risk of not screening an index of abundance for spatial and temporal variation in the detectability of the Gray Partridge (*Perdix perdix*). The index-density relationship is not necessarily linear, or even positive in some instances (Caughley 1977, Eberhardt & Simmons 1987).

Annual and seasonal estimates of relative abundance should be adjusted for detection area, especially when comparisons of species abundances in heterogeneous habitats are of interest (Verner 1985, Bock 1987, Raphael 1987). However, attempts to estimate density can be plagued by bias and error. Detections accumulated in a given area during a fixed interval of time are an intricate function of species behavior, abundance, season, time of day, habitat type, weather, observer, and sampling scheme (Verner 1985). Density estimation from variable-distance line transects (Burnham *et al.* 1980, 1981) and variable-radius point counts (Reynolds *et al.* 1980, Scott *et al.* 1986) is often impractical because prolonged periods of personnel training are required to minimize the bias and error associated with distance measurements, especially when counts are conducted by several observers in dense habitats and birds are frequently heard but not seen. Exact distance measurements are not necessary when working with categories (e.g., 0—30, 30—60, 60—120, >120 m; Rivera-Milán 1990a, unpubl. data), but observers must be able to discriminate and assign aural and visual detections to the correct categories (Burnham & Anderson 1984).

The problem of density estimation can be circumvented by exploring less sophisticated, but more practical, counting techniques that deal with a fixed radial or lateral distance for the species of interest; e.g., circular plots or fixed-radius point counts (Petraborg *et al.* 1953; Järvinen & Väisänen 1975; Järvinen 1976, 1978; Emlen 1977; Emlen & DeJong 1981; Ramsey & Scott 1981; Christman 1984; DeJong & Emlen 1985; Hutto *et al.* 1986; Rivera-Milán 1990a, and unpubl. data).

In this study I examine (1) the detectability and density estimates of the columbids at multiple spatial (routes, life zones, islandwide) and temporal (months, seasons, years) scales, and (2) the feasibility of combining intensive (fixed-radius point counts) and extensive (unfixed-radius point counts) counting techniques to monitor the long-term (>10 years) population changes of the columbids in the life zones in Puerto Rico and on Vieques Island. Special attention is given to the most general and repeatable distribution and abundance patterns of the columbids. Puerto Rico and its offshore territories comprise a small fraction of the Caribbean region. Similar studies are needed on other islands (e.g., Cuba, Jamaica, Dominican Republic, and Grenada) where little is known about the status, distribution, and abundance of the columbids.

STUDY AREAS

The main part of the study was conducted in the three major life zones of the Puerto Rican mainland (17° 55'–18° 35' N, 65° 37'–67° 17' W; 8,903 km^2) from July 1986—June 1992. Vieques Island (18° 01'–18° 09' N, 65° 16'–67° 27' W; 162 km^2) was sampled in May 1991 and 1992 to assess the impact of Hurricane Hugo on the columbid populations (Rivera-Milán 1990b, unpubl. data).

The three major life zones cover approximately 98 % of the total land area of Puerto Rico (Ewel & Whitmore 1973). The subtropical moist zone covers 5,326 km^2 (ca. 60 %); the subtropical wet zone covers 2,124 km^2 (ca. 24 %); and the subtropical dry zone covers 1,216 km^2 (ca. 14 %; Ewel & Whitmore 1973). The forest area of Puerto Rico covered approximately 2,790 km^2 (ca. 32 %) in the late 1970s (Birdsey & Weaver 1982); and it increased to about 3,399 km^2 (ca. 38 %) in the late 1980s (Ortiz 1989). Details of the life zones and the sampling units can be found in Rivera-Milán (1990a, 1992, 1993).

METHODS

From July 1985—June 1986, 5 routes (each 8-km long) were sampled/life zone using a stratified random sampling design (Collazo-Algarín *et al.* 1985, Scheaffer *et al.* 1979). The routes were on secondary and tertiary roads that were lightly travelled during the early morning hours. Six stations/route were spaced at regular intervals of 1.6 km. Call- and sight-counts were conducted for 3-min at each station. Counts started at 06:00 and finished at 10:30 hours.

From July 1986—June 1992, a 60 m radius was marked with orange fluorescent paint at each of the 90 3-min stations (i.e., 30 stations/life zone). A fixed-radius of 60 m was sufficiently large to obtain an adequate number of detections of the pigeons and doves (Rivera-Milán 1990a, and unpubl. data). The vocalizations (e.g., advertisement and nest calls) and movements (e.g., short flights between calling perches) of the columbids were easily detected at 60 m, even when the vegetation was dense and the canopy was high. Detections were assigned as "inside" or "outside" the fixed area of the 3-min stations following a premeditated standard similar to that developed by Hutto *et al.* (1986). Birds that flushed from within the fixed area upon arrival of the observers to the stations were recorded as inside. Similarly, birds that initially were detected outside but moved within the fixed area during the 3-min were also considered as inside the stations. Inside and outside detections were always recorded by consensus of two trained observers. One observer was always responsible for corroborating detection distances (e.g., using tapelines, rangefinders, or pacing). Detections that required special efforts (e.g., tapeline measurements) were corroborated immediately after the 3-min counts. Birds detected after the 3-min were recorded, but not used to estimate density or relative abundance (F. F. Rivera-Milán, unpubl. data).

From May—June 1988—92, the counts were conducted between the second week of May and the second week of June to obtain samples representative of the calling and nesting peaks of the columbids (Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

The relative abundance estimates (birds/km) were obtained from the total number of aural (call-count) and visual (sight-count) detections of pigeons and doves/40 km. During the 3-min counts, the number of aural and visual detections were recorded regardless of the radial distance involved (i.e., unfixed-radius point counts).

The density estimates (birds/km^2) were obtained from the fixed-radius point counts. Detections that were outside the 60 m radius were used as supplementary data to create a species-specific constant to approximate the distance at which detectability dropped to 0 (Järvinen & Väisänen 1975, Järvinen 1978). Detectability was defined as a monotonically decreasing function of distance. Several models of best-fit have been proposed to explain the shape of the detection function (Järvinen & Väisänen 1975; Burnham *et al.* 1980, 1981; Verner & Ritter 1985, 1988, but see DeJong & Emlen 1985). Here I have assumed (1) that the detectability of the columbids dropped linearly with the radial distance from the center of each station (Järvinen & Väisänen 1975, Järvinen 1976, 1978), (2) that there was a 100 % probability of detection of the individuals of each species at the center of each station (i.e., $g[0] = 1$), (3) that the movements of the individuals of each species inside the fixed area of the stations were always detectable, (4) that the individuals of each species were counted only once during the 3-min counts, (5) that there were no errors in the discrimitation of inside and outside (60 m) detections, and (6) that the counts between the 3-min stations represented independent events.

Density from fixed-radius point counts was estimated as $\hat{D} = 3\ (10^6)\ N\ \hat{C}^2/\pi$ (Järvinen 1978).

TABLE 1. Mean detectability estimates ($\hat{C}$) of the columbids in the three major life zones of the Puerto Rican mainland, July 1986—June 1988.

Species	Sampling Periods		Mean $\hat{D}$[a]	SE
Dry Zone				
Zenaida aurita	July 1986—June 1987	12	0.00631	0.00150
Zenaida aurita	July 1987—June 1988	12	0.00410	0.00071
Zenaida aurita	July 1986—June 1988	24	0.00521A	0.00084
Zenaida asiatica	July 1986—June 1987	12	0.00090	0.00039
Zenaida asiatica	July 1987—June 1988	12	0.00244	0.00017
Zenaida asiatica	July 1986—June 1988	24	0.00167B	0.00062
Zenaida macroura	July 1986—June 1987	12	0.00279	0.00014
Zenaida macroura	July 1987—June 1988	12	0.00735	0.00213
Zenaida macroura	July 1986—June 1988	24	0.00507A	0.00133
Columbina passerina	July 1986—June 1987	12	0.00703	0.00080
Columbina passerina	July 1987—June 1988	12	0.00703	0.00013
Columbina passerina	July 1986—June 1988	24	0.00653A	0.00075
Moist Zone				
Zenaida aurita	July 1986—June 1987	12	0.00360	0.00133
Zenaida aurita	July 1987—June 1988	12	0.00273	0.00132
Zenaida aurita	July 1986—June 1988	24	0.00317ABC	0.00092
Columba squamosa	July 1986—June 1987	12	0.00197	0.00053
Columba squamosa	July 1987—June 1988	12	0.00134	0.00043
Columba squamosa	July 1986—June 1988	24	0.00166ABD	0.00034
Columba inornata	July 1986—June 1987	12	0.00131	0.00039
Columba inornata	July 1987—June 1988	12	0.00166	0.00083
Columba inornata	July 1986—June 1988	24	0.00148D	0.00017
Columbina passerina	July 1986—June 1987	12	0.00404	0.00187
Columbina passerina	July 1987—June 1988	12	0.00553	0.00208
Columbina passerina	July 1986—June 1988	24	0.00478BC	0.00138
Geotrygon spp[b]	July 1986—June 1987	12	0.00770	0.00207
Geotrygon spp.	July 1987—June 1988	12	0.00355	0.00151
Geotrygon spp.	July 1986—June 1988	24	0.00563C	0.00132
Wet Zone				
Zenaida aurita	July 1986—June 1987	12	0.00066	0.00035
Zenaida aurita	July 1987—June 1988	12	0.00198	0.00146
Zenaida aurita	July 1986—June 1988	24	0.00131A	0.00075
Columba squamosa	July 1986—June 1987	12	0.00145	0.00026
Columba squamosa	July 1987—June 1988	12	0.00120	0.00020
Columba squamosa	July 1986—June 1988	24	0.00132A	0.00034
Geotrygon spp.	July 1986—June 1987	12	0.00571	0.00143
Geotrygon spp.	July 1987—June 1988	12	0.00556	0.00208
Geotrygon spp.	July 1986—June 1988	24	0.00570B	0.00143

[a]) Species detectability ($\hat{C}$) was estimated empirically as $\hat{C} = 1 - (1 - p)^{0.5}/r$; where p = the number of aural and visual detections inside 60 m (fixed-count) divided by the number of aural and visual detections, regardless of detections distance (unfixed-count). Means followed by different letters differed significantly at $P \leq 0.05$ (one tailed t-tests; see methods). SE = standard error of the mean.

[b]) The counts of the three species of quail-doves (*Getrygon montana*, *G. chrysia*, and *G. mystacea*) were combined.

The constant 10^6 was used simply to express the density of the columbids in km^2. Species detectability ($\hat{C}$) was estimated empirically as $\hat{C} = 1 - (1 - p)^{1/2}/r$, where p = the number of aural and visual detections made inside 60 m (i.e., N) divided by the number of aural and visual detections made, regardless of radial distance (i.e., inside 60 m/inside + outside 60 m).

Statistical Analyses

Analyses of variance (ANOVA) with repeated measures at one factor (time) was used to examine the seasonal (July 1986—June 1988) and annual (May—June 1987—92) changes in $\hat{D}$ estimates of the columbids in the life zones (Winer 1971; Gurevitch & Chester 1986; Beal & Khamis 1990, 1991; Quinn & Keough 1991). Polynomial contrasts (linear, quadratic, and cubic) were used to examine the relationships of time (seasons, years) and point counts (Winer 1971: 177—185). Greenhouse-Geisser adjustment was used to correct the P-values of univariate ANOVAs with repeated measures (Gurevitch & Chester 1986; Beal & Khamis 1990, 1991; Quinn & Keough 1991).

Simple linear regression and Pearson's Product-Moment Coefficient of Correlation (r) were used to examine the relationships between unfixed- and fixed-radius point counts at multiple spatial and temporal scales (Sokal & Rohlf 1981, Ludwig & Reynolds 1988). The call- and sight-count data (combined) were analyzed before and after being log-transformed. The log-transformation helped to normalize and stabilize the variances of unfixed and fixed-radius (60 m) call- and sight-counts (Sokal & Rohlf 1981; Rivera-Milán 1990a, 1992, 1993). A one-tailed unpaired *t*-test was used to carry out intra-specific comparisons of $\hat{C}$ and $\hat{D}$ estimates between the life zones from July 1986—June 1988; a one-tailed unpaired *t*-test was also used to carry out inter-specific comparisons within and between the life zones from July 1986—June 1988; whereas a one-tailed paired *t*-test was used to carry out intra-specific comparisons within the life zones from July 1986—June 1988 (Sokal & Rohlf 1981). Details of other statistical analyses are given with the corresponding results. Statistics were performed with the programs SuperANOVA and STATVIEW II (Abacus Concepts, Inc., Berkeley, CA, 1987, 1989). Significance was accepted at $P \leq 0.05$.

RESULTS

Detectability ($\hat{C}$) and Density ($\hat{D}$) Estimates of the Columbids in the Life Zones of the Puerto Rican Mainland

The detectability ($\hat{C}$) and density ($\hat{D}$) estimates of the columbids varied according to the spatial (route, life zone, islandwide) and temporal (months, seasons, years) scales under consideration (Tables 1—7). Summaries of the mean $\hat{C}$ and $\hat{D}$ estimates of the columbids from July 1986—June 1988 are given in Tables 1 and 2.

Zenaida Doves

The mean $\hat{C}$ estimate of the Zenaida Doves in the dry zone was significantly higher from July 1986—June 1987 than from July 1987—June 1988 ($P = 0.034$); but it did not differ significantly from July 1986—June 1988 in the moist ($P = 0.318$) and wet zones ($P = 0.147$); their mean $\hat{C}$ estimate was significantly higher in the dry zone than in the moist ($P = 0.053$) and wet ($P = 0.001$) zones; but their mean $\hat{C}$ estimate in the moist zone was only marginally higher than in the wet zone ($P = 0.072$; Table 1).

The mean $\hat{D}$ estimate of the Zenaida Doves did not differ significantly from July 1986—June 1988 in the dry ($P = 0.302$), moist ($P = 0.415$), and wet ($P = 0.156$) zones; their mean $\hat{D}$ estimate was significantly higher in the dry zone than in the moist ($P = 0.003$) and wet ($P = 0.0001$) zones; whereas their mean $\hat{D}$ estimate was significantly higher in the moist zone than in the wet zone ($P = 0.004$; Table 2).

Scaly-naped Pigeons

The mean $\hat{C}$ estimate of the Scaly-naped Pigeons did not differ significantly from July 1986—June 1988 in the moist ($P = 0.151$) and wet ($P = 0.275$) zones; and their mean $\hat{C}$ estimate in the wet zone did not differ significantly from the moist zone ($P = 0.211$; Table 1).

The mean $\hat{D}$ estimate of Scaly-naped Pigeons in the wet zone did not differ significantly from July 1986—June 1988 ($P = 0.473$); neither was their mean $\hat{D}$ estimate in the moist zone significantly different from July 1986—June 1988 ($P = 0.224$); their mean $\hat{D}$ estimate in the wet zone did not differ significantly from the moist zone ($P = 0.117$; Table 2). Scaly-naped Pigeons were rarely observed in the sampling units of the dry zone (Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

Plain Pigeons

The mean $\hat{C}$ estimate of the Plain Pigeons did not differ significantly from July 1986—June 1988 in the moist zone (P = 0.571; Table 1); and their mean $\hat{D}$ estimate in the moist zone did not differ significantly from July 1986—June 1988 (P = 0.338; Table 2). Plain Pigeons were never observed in the sampling units of the dry zone; and they were rarely detected in the sampling units of the wet zone (Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

Common Ground-Doves

The mean $\hat{C}$ estimate of the Common Ground-Doves did not differ significantly from July

TABLE 2. Mean density estimates ($\hat{D}$) of the columbids in the three major life zones of the Puerto Rica mainland, July 1986—June 1988.

Species	Sampling Periods		Mean $\hat{D}^a$	SE
Dry zone				
Zenaida aurita	July 1986—June 1987	12	63.92	9.508
Zenaida aurita	July 1987—June 1988	12	77.75	29.247
Zenaida aurita	July 1986—June 1988	24	70.83A	15.108
Zenaida asiatica	July 1986—June 1987	12	6.64	3.841
Zenaida asiatica	July 1987—June 1988	12	331.99	315.992
Zenaida asiatica	July 1986—June 1988	24	169.32AB	158.214
Zenaida macroura	July 1986—June 1987	12	7.05	3.860
Zenaida macroura	July 1987—June 1988	12	116.01	69.922
Zenaida macroura	July 1986—June 1988	24	61.53A	36.080
Columbina passerina	July 1986—June 1987	12	268.85	95.359
Columbina passerina	July 1987—June 1988	12	152.94	40.901
Columbina passerina	July 1986—June 1988	24	210.89B	52.160
Moist Zone				
Zenaida aurita	July 1986—June 1987	12	23.02	7.193
Zenaida aurita	July 1987—June 1988	12	20.39	8.834
Zenaida aurita	July 1986—June 1988	24	21.71A	5.578
Columba squamosa	July 1986—June 1987	12	12.60	5.414
Columba squamosa	July 1987—June 1988	12	7.80	3.140
Columba squamosa	July 1986—June 1988	24	10.20B	3.100
Columba inornata	July 1986—June 1987	12	0.67	0.233
Columba inornata	July 1987—June 1988	12	1.54	0.906
Columba inornata	July 1986—June 1988	24	1.10C	0.435
Columbina passerina	July 1986—June 1987	12	30.29	18.175
Columbina passerina	July 1987—June 1988	12	18.32	6.770
Columbina passerina	July 1986—June 1988	24	24.30AD	9.570
Geotrygon spp[b]	July 1986—June 1987	12	62.18	23.263
Geotrygon spp.	July 1987—June 1988	12	27.43	11.704
Geotrygon spp.	July 1986—June 1988	24	44.80D	13.240
Wet Zone				
Zenaida aurita	July 1986—June 1987	12	2.15	1.259
Zenaida aurita	July 1987—June 1988	12	6.79	4.823
Zenaida aurita	July 1986—June 1988	24	4.47A	2.485
Columba squamosa	July 1986—June 1987	12	16.91	4.170
Columba squamosa	July 1987—June 1988	12	16.35	6.845
Columba squamosa	July 1986—June 1988	24	16.64B	3.920
Geotrygon spp.	July 1986—June 1987	12	31.80	17.455
Geotrygon spp.	July 1987—June 1988	12	20.81	7.257
Geotrygon spp.	July 1986—June 1988	24	26.30B	9.310

[a]) The density ($\hat{D}$) from the fixed-radius point counts was estimated as $\hat{D} = 3(10^6)N\hat{C}^2/\pi$. The constant 10^6 was used to express the density estimates of the columbids in km^2; N = the number of aural and visual detections inside the 60 m of the 3-min stations/month/life zone. Means followed by different letters differed significantly at $P \leqq 0.05$ (one tailed t-tests; see methods). SE = standard error of the mean.

[b]) The counts of the three species of quail-doves (*Getrygon montana*, *G. chrysia*, and *G. mystacea*) were combined.

TABLE 3. Mean detectability ($\hat{C}$) and density ($\hat{D}$) estimates of the columbids on Vieques Island[a].

Species	n	Mean $\hat{C}$[b]	$\hat{C}$ (SE)	Mean $\hat{D}$[c]	$\hat{D}$ (SE)
Columbina passerina	6				
Columba squamosa	6				
Zenaida asiatica	6				
Zenaida aurita	6				
Columba leucocephala	6				

[a] Three routes of unequal length (road #995: 3.2 km; Camp García and road #997: 4.0 km; and the Naval Base Storage Facility: 8.0 km) were sampled in May 1991 and 1992. The 3-min stations were at 0.8 km from each other (i. e., 4 stations along road #995; 6 stations in Camp García and road #997; and 10 stations inside the Naval Base Storage Facility).
[b] Mean detectability ± standard error (see Table 1).
[c] Mean density (birds/km^2) ± standard error (see Table 2).

1986—June 1988 in the dry (P = 0.265) and moist (P = 0.222) zones; and their mean $\hat{C}$ in the dry zone did not differ significantly from the moist zone (P = 0.116; Table 1).

The mean $\hat{D}$ estimate of the Common Ground-Doves in the dry zone was marginally higher from July 1986—June 1987 than from July 1987—June 1988 (P = 0.063); but their mean $\hat{D}$ estimate in the moist zone did not differ significantly from July 1986—June 1988 (P = 0.238); their mean $\hat{D}$ estimate was significantly higher in the dry zone than in the moist zone (P = 0.0002; Table 2). Common Ground-Doves were rarely observed in the sampling units of the wet zone (Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

Ruddy, Key West, and Bridled Quail-Doves

The mean $\hat{C}$ estimate of the three quail-dove species (combined) in the moist zone was marginally higher from July 1986—June 1987 than from July 1987—June 1988 (P = 0.086); but it was not significantly different in the wet zone from July 1986—June 1988 (P = 0.462); their mean $\hat{C}$ estimate in the moist zone did not differ significantly from the wet zone (P = 0.486; Table 1).

The mean $\hat{D}$ estimate of the quail-doves (combined) did not differ significantly from July 1986—June 1988 in the moist (P = 0.109) and wet (P = 0.299) zones; but their mean $\hat{D}$ was marginally higher in the moist zone than in the wet zone (P = 0.083; Table 2). The three species of quail-doves were rarely observed in the sampling units of the dry zone (Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

White-winged Doves

The mean $\hat{C}$ estimate of the White-winged Doves in the dry zone was marginally higher from July 1987—June 1988 than from July 1986—June 1987 (P = 0.073; Table 1); but their mean $\hat{D}$ estimate in the dry zone did not differ significantly from July 1986—June 1988 (P = 0.160; Table 2). White-winged Doves were rarely observed in the sampling units of the moist and wet zones; but single-species flocks of variable sizes were commonly seen in the agricultural areas of the dry, moist, and wet zones, especially during the flocking period (July—November; Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

Mourning Doves

The mean $\hat{C}$ estimate of the Mourning Doves in the dry zone was marginally higher from July 1987—June 1988 than from July 1986—June 1987 (P = 0.064; Table 1); and their mean $\hat{D}$ estimate was marginally higher from July 1987—June 1988 than from July 1986—June 1987 (P = 0.072; Table 2). Mourning Doves were rarely observed in the sampling units of the moist and wet zones; but single- and mixed-species flocks (usually with Zenaida Doves) were commonly seen in the agricultural areas of the dry, moist, and wet zones, especially during the flocking period (July—November; Rivera-Milán 1990a, 1992, 1993, and unpubl. data).

Interspecific Comparisons in the Dry Zone

The mean $\hat{C}$ estimate of the Zenaida Doves was significantly higher than that of White-winged Doves (P = 0.0026); but it did not differ significantly from that of Mourning Doves (P =

TABLE 4. Correlations of unfixed- and fixed-radius point counts of (call- and sight-counts combined) of the columbids in the life zones of the Puerto Rican mainland, July 1986—June 1988 (n = 24)[a].

Species	Life Zone		*P*
Zenaida aurita	Dry Zone	0.83	0.0001
Zenaida asiatica	Dry Zone	0.98	0.0001
Zenaida macroura	Dry Zone	0.87	0.0001
Columbina passerina	Dry Zone	0.86	0.0001
Zenaida aurita	Moist Zone	0.87	0.0001
Columba squamósa	Moist Zone	0.06	0.7893
Columba inornata	Moist Zone	0.76	0.0001
Columbina passerina	Moist Zone	0.70	0.0001
Geotrygon spp.[b]	Moist Zone	0.91	0.0001
Zenaida aurita	Wet Zone	0.82	0.0001
Columba squamosa	Wet Zone	0.80	0.0001
Geotrygon spp.	Wet Zone	0.85	0.0001
Columbids (combined)	Dry, Moist, & Wet Zone	0.84	0.0001

Pearson's Product-Moment Coefficient of Correlation.

The counts of the three species of quail-doves (*Getrygon montana*, *chrysia*, and *mystacea*) were combined.

0.469) and Common Ground-Doves ($P = 0.127$); the mean $\hat{C}$ estimate of the Common Ground-Doves did not differ significantly from that of Mourning Doves ($P = 0.169$); but it was significantly higher than that of White-winged Doves ($P = 0.0001$); the mean $\hat{C}$ estimate of the Mourning Doves was also significantly higher than that of White-winged Doves ($P = 0.007$; Table 1).

The mean $\hat{D}$ estimate of the Zenaida Doves did not differ significantly from that of White-winged Doves ($P = 0.437$) and Mourning Doves ($P = 0.272$); neither was the mean $\hat{D}$ estimate of the White-winged Doves significantly different from that of Mourning Doves ($P = 0.257$); the mean $\hat{D}$ estimate of the Common Ground-Doves was significantly higher than that of Zenaida Doves ($P = 0.008$) and Mourning Doves ($P = 0.017$); and the mean $\hat{D}$ estimate of the Common Ground-Doves did not differ significantly from that of White-winged Doves ($P = 0.407$; Table 2).

TABLE 5. Analysis of variance (ANOVA) with repeated measures at one factor (seasons) of fixed-radius point of the columbids in the three major life zones of the Puerto Rican mainland[a].

Source of Variation	df	Sum Squares	Mean Squares	F	*P*
					0.1132
				8.319	0.0004
				1.631	0.1718
				Summer	Autumn
				1.728	1.254
				1.250	0.608
				2.117	1.618
				1.740	1.206

F = 23.220, *P* 0.0001

[a]) Fifteen 8-km routes (5/life zone) were sampled monthly from July 1986—June 1988. Seasonal arithmetic means were calculated by pooling call- and sight-counts of all the columbids (10 species combined) in the life zones as follows: winter — December, January, and February; spring — March, April, and May; summer — June, July, and August; autumn — September, October, and November. The call- and sight-count data were log-transformed. A second degree (quadratic) polynomial was used to depict the relationship between time (seasons) and fixed-counts (see methods).

Interspecific Comparisons in the Moist Zone

The mean $\hat{C}$ estimate of the Scaly-naped Pigeons was significantly lower than that of the three species of quail-doves (combined; $P = 0.003$) and Common Ground-Doves ($P = 0.027$); but it was only marginally lower than that of Zenaida Doves ($P = 0.076$); and it did not differ significantly from that of Plain Pigeons ($P = 0.477$); the mean $\hat{C}$ estimate of the Plain Pigeons was significantly lower than that of the quail-doves (combined; $P = 0.002$), Zenaida Doves ($P = 0.024$), and Common Ground Doves ($P = 0.001$); the mean $\hat{C}$ estimate of the Zenaida Doves was marginally lower than that of the quail-doves (combined; $P = 0.078$); and the mean $\hat{C}$ estimate of the Common Ground-Doves did not differ significantly from that of the quail-doves (combined; $P = 0.335$) and Zenaida Doves ($P = 0.139$; Table 1).

The mean $\hat{D}$ estimate of the Scaly-naped Pigeons was significantly lower than that of the quail-doves (combined; $P = 0.010$), Zenaida Doves ($P = 0.045$), and Common Ground-Doves ($P = 0.101$); the mean $\hat{D}$ estimate of the Plain Pigeons was significantly lower than that of Scaly-naped Pigeons ($P = 0.012$), Zenaida Doves ($P = 0.002$), the quail-doves (combined; $P = 0.001$), and Common Ground-Doves ($P = 0.002$); the mean $\hat{D}$ estimate of the quail-doves (combined) was significantly higher than that of Zenaida Doves ($P = 0.045$); but it was only marginally higher than that of Common Ground-Doves ($P = 0.080$); whereas the mean $\hat{D}$ estimate of the Zenaida Doves did not differ significantly from that of Common Ground-Doves ($P = 0.401$; Table 2).

Interspecific Comparisons in the Wet Zone

The mean $\hat{C}$ estimate of the quail-doves (combined) was significantly higher than that of Scaly-naped Pigeons ($P = 0.003$) and Zenaida Doves ($P = 0.006$); but the mean $\hat{C}$ estimate of the Scaly-naped Pigeons did not differ significantly from that of Zenaida Doves ($P = 0.496$; Table 1).

The mean $\hat{D}$ estimate of the quail-doves (combined) did not differ significantly from that of Scaly-naped Pigeons ($P = 0.171$); but it was significantly higher than that of Zenaida Doves ($P = 0.003$); the mean $\hat{D}$ estimate of the Scaly-naped Pigeons was also significantly higher than that of Zenaida Doves ($P = 0.018$; Table 2).

Detectability ($\hat{C}$) and Density ($\hat{D}$) Estimates of the Columbids on Vieques Island

A summary of the mean $\hat{C}$ and $\hat{D}$ estimates of the columbids on Vieques Island is given in Table 3. Due to the small number of routes sampled on Vieques Island in May 1991 (n = 3)

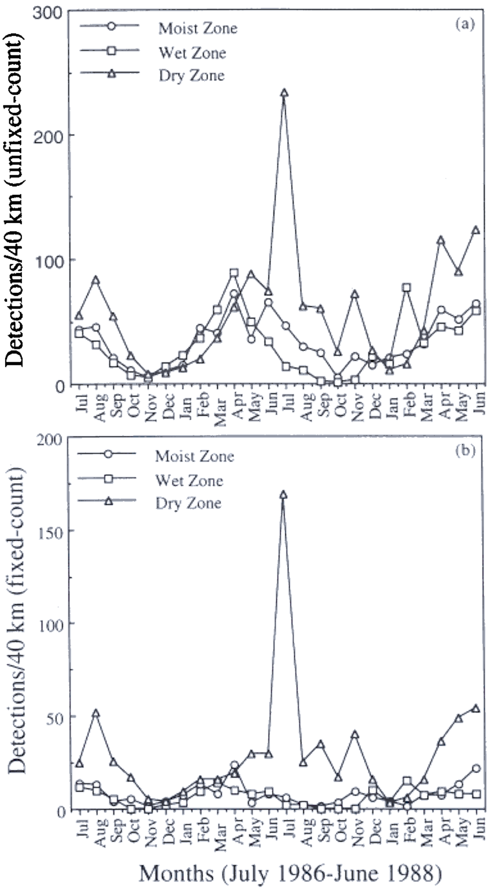

FIG. 1. (A) Unfixed- and (B) fixed-radius point counts (radius = 60 m) of the columbids (10 species combined) in the three major life zones of the Puerto Rican mainland from July 1986—June 1988. Species included in the analysis: Zenaida Dove (*Zenaida aurita*), White-winged Dove (*Z. asiatica*), Mourning Dove (*Z. macroura*), Common Ground-Dove (*Columbina passerina*), Scaly-naped Pigeon (*Columba squamosa*), Plain Pigeon (*C. inornata*), White-crowned Pigeon (*C. leucocephala*), Ruddy Quail-Dove (*Geotrygon montana*), Key West Quail-Dove (*G. chrysia*), and Bridled Quail-Dove (*G. mystacea*). See Tables 1—2 for more information about detectability ($\hat{C}$) and density ($\hat{D}$) estimates in the life zones.

and 1992 (n = 3) statistical comparisons of the mean $\hat{C}$ and $\hat{D}$ estimates were not attempted. Mourning Doves, Key West Quail-Doves, and Bridled Quail-Doves were rarely observed in the sampling units of Vieques Island; whereas the Ruddy Quail-Doves and Plain Pigeons were never observed in the sampling units of Vieques Island.

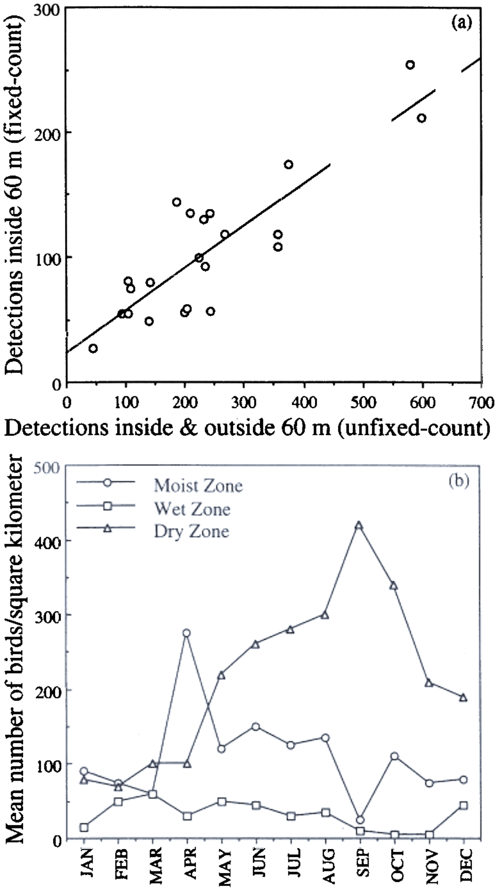

FIG. 2. (a) Relationship of unfixed- and fixed-radius point counts (radius = 60 m) of the columbids (10 species combined) in the three major life zones (combined) of the Puerto Rican mainland from July 1986—June 1988. (b) Seasonal density ($\hat{D}$) changes of the columbids (10 species combined) in the three major life zones of the Puerto Rican mainland from July 1986—June 1988. See the legend of Fig. 1 a, b for more information about the species included in the analysis, and Tables 1 and 2 for more information about the detectability ($\hat{C}$) and density ($\hat{D}$) estimates of the columbids in the life zones.

Columbid populations on Vieques Island and the northeastern corner of Puerto Rico were affected by the passage of Hurricane Hugo in September 1989. The combination of unfixed-radius and fixed-radius point counts along secondary and tertiary roads helped in compensating for changes in $\hat{C}$ associated with an increase in the visibility of the columbids (e.g., Scaly-naped Pigeons) that were moving from high to low effect areas in search of food and cover (Rivera-Milán 1990 b, unpubl. data).

Unfixed- and Fixed-radius Point Counts and Seasonal Density ($\hat{D}$) Patterns of the Columbids in the Life Zones of the Puerto Rican Mainland

With the exception of the Scaly-naped Pigeons in the moist zone, the unfixed- and fixed- radius point counts of the columbids were significantly correlated in the life zones (Table 4, Figs. 1 a,b and Fig. 2 a). The $\hat{D}$ estimates of the columbids in the dry zone increased from about 80 birds/km^2 in January to about 400 birds/km^2 in September; in the moist zone, the $\hat{D}$ estimates increased from about 90 birds/km^2 in January to about 275 birds/km^2 in April; and, in the wet zone, the $\hat{D}$ estimates increased from about 25 birds/km^2 in January to about 60 birds/km^2 in March (Fig. 2 b). A peak in the $\hat{D}$ estimates of the columbids occurred between March and August because the number of aural and visual detections in the sampling units of the life zones increased before and during the peak of the nesting (May—June) and flocking periods (July—November; Table 5, Fig. 1 a,b and Fig. 2 b). During the flocking period, single and mixed-species flocks became conspicuous in areas with abundant food (e.g., agricultural and mixed-habitats in the dry, moist, and wet zones; Rivera-Milán 1990 a, 1992, 1993, and unpubl. data).

Annual Changes in Detectability ($\hat{C}$) and Density ($\hat{D}$) Estimates of the Zenaida Doves and Scaly-naped Pigeons in the Life Zones of the Puerto Rican Mainland

The mean annual $\hat{C}$ estimate of Zenaida Doves in the life zones (combined) was 0.00232; and the estimated mean annual $\hat{D}$ was 143.31 birds/km^2

TABLE 6. Changes in annual detectability ($\hat{C}$) and density ($\hat{D}$) estimates of the Zenaida Doves (*Zenaida aurita*) in the three major life zones (combined) of the Puerto Rican mainland[a].

Year	Unfixed-counts	Fixed-counts	$\hat{C}$	$\hat{D}$
			0.00306	196.71
			0.00258	114.49
			0.00202	97.01
			0.00203	106.30
			0.00202	116.41
			0.00219	228.93
$\bar{x}$			0.00232	143.308
SE			0.00017	22.546
CV (%)			18.274	38.537
95 % CI			0.00187—	85.351—
			0.00276	201.265

[a] Fifteen 8-km routes (5/life zone) were sampled from the second week of May to the second week of June (1987—92) to cover the reproductive peak of the columbids (Rivera-Milán 1990 a, unpubl. data).

(Table 6). The $\hat{D}$ estimates of the Zenaida Doves increased slightly from May—June 1987—92 ($y = 125.69 + 5.03\ [14.544\ \mathrm{SE}]x$, $r^2 = 0.029$, df = 5, $P = 0.747$) because there was a non-significant decrease in the number of detections inside 60 m in 1988 followed by a non-significant increase from 1989—92 (Tables 6 and 7). The significant first degree polynomial contrast was indicative of a linear relationship between the fixed-counts of Zenaida Doves in the life zones and year (1987—92; Table 7).

From May—June 1987—92, there was a significant correlation between the unfixed and fixed call- and sight-counts of the Zenaida Doves in the life zones of the Puerto Rican mainland ($r = 0.83$, df = 5, $P = 0.040$); and the variability of the fixed-counts was smaller than the variability of the unfixed-counts in the life zones (coefficients of variation [CVs] = 21 % and 29 %; Table 6). According to the observed CVs, the number of aural and visual detections inside the 60 m radius of the 3-min stations was an important component of the total variation of the Zenaida Doves $\hat{D}$ estimates in the life zones. The fixed-counts were less affected than the unfixed-counts by the flocking behavior of Zenaida Doves in the life zones. Zenaida Doves were widely distributed in the life zones and were

TABLE 7. Analysis of variance (ANOVA) with repeated measures at one factor (years) of fixed-radius point counts of the Zenaida Doves (*Zenaida aurita*) in the three major life zones of the Puerto Rican mainland[a].

Source of Variation	df	Sum Squares	Mean Squares	F	P
				1.738	
				2.276	0.0977
				1.846	0.1186

	1987			1990	1991	1992
	1.241	1.371	1.589	1.832	1.670	1.642
	1.060	1.060	1.241	1.120	1.095	1.276
	1.661	1.330	1.477	1.532	1.212	1.616
	1.342	1.259	1.427	1.497	1.319	1.518
	$F = 4.577$, $P = 0.0561$					

[a] Fifteen 8-km routes (5/life zone) were sampled monthly from July 1986—June 1988. The call- and sight-count data were log-transformed. A first degree (linear) polynomial was used to depict the relationship between time (years) and fixed-counts (see methods).

commonly detected foraging on the ground near trails or roads (F. F. Rivera-Milán, unpubl. data).

The mean annual Ĉ estimate of Scaly-naped Pigeons in the moist and wet zones (combined) was 0.00168; and the estimated mean annual D̂ was 51.37 birds/km^2 (Table 8). The D̂ estimates of the Scaly-naped Pigeons increased slightly from May—June 1987—92 ($y = 27.781 + 6.740$ [9.617 SE]x, $r^2 = 0.109$, $df = 5$, $P = 0.522$) because there was a non-significant increase in the number of detections inside 60 m from 1989—92 (Tables 8 and 9). As in the case of the Zenaida Doves, the significant first degree polynomial contrast was indicative of a linear relationship between the fixed-counts of Scaly-naped Pigeons in the moist and wet zones and year (1987—92; Table 9).

From May—June 1987—92, there was a significant correlation between the unfixed and fixed call- and sight-counts of the Scaly-naped Pigeons in the moist and wet zones of the Puerto Rican mainland ($r = 0.98$, $df = 5$, $P = 0.0006$). The variability of the fixed-counts was larger than the variability of the unfixed-counts of Scaly-naped Pigeons in the moist and wet zones (CVs = 27 % and 43 %; Table 8). According to the observed CVs, the number of aural and visual detections inside the 60 m radius of the 3-min stations was an important component of the total variation of the Scaly-naped Pigeons D̂ estimates in the moist and wet zones. The fixed-counts of Scaly-naped Pigeons were affected by the relative small number of aural and visual detections inside the 60 m radius of the 3-min stations. Most of the aural and visual detections of the Scaly-naped Pigeons came from individuals that were flying singly, in couples, or in flocks of variable sizes at distances beyond the 60 m radius of the 3-min stations (F. F. Rivera-Milán, unpubl. data).

Parallel Density (D̂) Fluctuations of the Columbids in the Life Zones of the Puerto Rican Mainland

There was a preponderance of positive D̂ correlations among the columbids in the sampling units of the life zones of the Puerto Rican mainland (Tables 10). Seven of 15 (47 %) positive correlations were significant at $P \leqq 0.05$. Moreover, the ratio of the sum of the individual species variances to the variance of their sum was less than 1.0, which is indicative of parallel D̂ fluctuations to similar or covarying resources in the life zones (Järvinen 1979; James & Boecklen 1984; Rivera-Milán 1990a, 1992, 1993, and unpubl. data; Table 11).

DISCUSSION

Detectability (Ĉ) and Density (D̂) Estimates

The Ĉ and D̂ estimates of the columbids varied according to the established spatio-temporal scales. Population changes were discernible at a relative scale of abundance (e.g., birds/km); but it was necessary to adjust counts for differences in Ĉ to justify the comparisons of species abundances at multiple sampling scales. The variation in the number of aural and visual detections in-

TABLE 8. Changes in annual detectability (Ĉ) and density (D̂) estimates of the Scaly-naped Pigeons (*Columba squamosa*) in the moist and wet zones (combined) of the Puerto Rican mainland[a].

Year	Unfixed-counts	Fixed-counts	Ĉ	D̂
			0.00113	9.75
			0.00158	35.80
			0.00192	60.13
			0.00210	121.74
			0.00166	36.80
			0.00181	44.01
$\overline{x}$			0.00168	51.372
SE			0.00013	15.567
CV (%)			19.263	74.225
95 % CI			0.00134— 0.00202	11.356— 91.387

[a]) Ten 8-km routes (5/life zone) were sampled from the second week of May to the second week of June (1987—92) to cover the reproductive peak of the columbids (Rivera-Milán 1990a, unpubl. data).

TABLE 9. Analysis of variance (ANOVA) with repeated measures at one factor (years) of fixed-radius point counts of the Scaly-naped Pigeons (*Columba squamosa*) in the moist and wet zones of the Puerto Rican mainland[a].

Source of Variation	df	Sum Squares	Mean Squares	F	
	1				0.0070
	8				
	5			2.165	0.1234
	5			0.503	0.6727
	40				

	1987			1990	1991	1992
	1.169	1.156	1.156	1.276	1.311	1.251
	1.177	1.619	1.700	2.022	1.927	1.987
	1.473	1.387	1.428	1.649	1.619	1.619

F = 6.536, P = 0.0318

[a] Ten 8-km routes (5/life zone) were sampled monthly from July 1986—June 1988. The call- and sight-count data were log-transformed. A first degree (linear) polynomial was used to depict the relationship between time (years) and fixed-counts (see methods).

side the 60 m radius of the 3-min stations was an important component of the total variation of $\hat{D}$ of columbids in the life zones (see, for example, the CVs of the annual counts of the Zenaida Doves and Scaly-naped Pigeons in the life zones of the Puerto Rican mainland; Tables 6 and 8).

Hutto *et al.* (1986) found serious inconsistencies in the ranking by relative abundance of species with high detection ratios when they compared fixed-radius point counts (radius = 25 m) and unfixed-radius point counts in woodland interior and edge habitats of western Mexico. They recorded individuals of some species more often outside than inside the 25 m radius of the stations, and suggested that the high detection ratios resulted either because the birds were rare but highly vocal, or because the species were common but inconspicuous when close to the observers. Hutto *et al.* (1986) calculated a detection ratio of 0.77 for Mourning Doves and of 0.90 for Band-tailed Pigeons (*Columba fasciata*).

The variability of the fixed-radius point counts of the columbids increased in relation to the number of detections outside the fixed area of the stations. However, the selection of a fixed radius of detection was not a simple optimization process (Hutto *et al.* 1986, Rivera-Milán 1990 a, unpubl. data). Detectability varied in relation to many variables that were not effectively controlled by the observers (e. g., species abundance and distribution, flocking behavior, traffic of vehicles along secondary and tertiary roads, noise levels in suburban and rural areas, etc.). Depending on the habitat sampled, certain behavioral differences probably contributed to detecting some species more often at shorter or at longer distances than others. For example, the Scaly-naped Pigeons were mainly arboreal, and were highly detectable when flying between vegetation patches, or when feeding on fruits or drinking water on tops of trees at some distance from secondary and tertiary roads. On the other hand, the Zenaida Doves were both arboreal and ground-dwellers, and were commonly attracted to secondary and tertiary roads in search of water, food, and grit. As expected, the Scaly-naped Pigeons had higher detection ratios than Zenaida Doves in the moist (0.86 *versus* 0.79) and wet (0.83 *versus* 0.61) zones of the Puerto Rican mainland (Rivera-Milán 1990 a).

Zenaida Doves and Scaly-naped Pigeons were neither rare or inconspicuous when close to observers. On the contrary, both species were highly vocal during the nesting season (January—August), and their movements were highly detectable at least within the fixed area of the 3-min stations. Consequently, the variability of the fixed-radius point counts depended, in part, upon the number of units (stations/routes) that were effectively sampled at any fixed spatial (life zone) and temporal (season) scale. When the number of sampling units was too small and the selected radius too restricted (e.g., 30 versus 60 and 120 m; Rivera-Milán 1990 a), the number of inside detections decreased and the index-density relationship became inconsistent. The index-density relationship was strong during the calling and nesting peaks (May—June), when presumably the home ranges of the columbids were compressed (e.g., due to site tenacity of territorial ♂). On the other hand, the index-density relationship was weak after the peak of the nesting season, when flocks became more conspicuous in areas with abundant food and the home ranges of the columbids were expanded (Rivera-Milán 1990a).

The $\hat{C}$ estimates of columbids were in the range of "intermediate" (e.g., Common Ground-Doves and Zenaida Doves) to "long" (e.g., Scaly-naped Pigeons and Plain Pigeons) distance (Järvinen & Väisänen 1975). The data of the Scaly-naped Pigeons in the moist zone represents evidence against the use of untested relative abundance indices. As stated by Rotella & Ratti (1986: 532), "a valid population index is one that is directly related to density; i.e., one that accurately indicates spatial and temporal differences in density". The unfixed- and fixed-radius point counts of the columbids were correlated significantly, except in the case of the Scaly-naped Pigeons in the moist zone. An increase in the number of detections outside the fixed-radius did not necessarily imply an increase in the number of detections inside the fixed-radius of the 3-min stations or an increase in the $\hat{D}$ estimates of the Scaly-naped Pigeons in the moist zone. The lack of correlation appeared to be, in part, the result of the number of visual detections made beyond the fixed-area of the 3-min stations. The Scaly-naped Pigeons were highly conspicuous when flying (as singles, in couples, or in flocks of variable sizes) across vegetation gaps. In open and fragmented habitats (e.g., second-growth forests in the moist zone) most of the visual detections were of pigeons moving at distances greater than 60 m. The efficiency (see the definition of "p" in the methods) of the fixed-radius point counts was affected by the abundance and behavior of Scaly-naped Pigeons in the moist zone during the breeding and non-breeding periods of the year. The unfixed- and fixed-radius point counts coincided in the recognition of the most general and repeatable patterns of distribution and abundance of the columbids in the life zones during the different seasons of the year (Rivera-Milán 1990a, 1992, 1993). But comparisons of the abundance of Scaly-naped Pigeons among the life

TABLE 10. Pearson Product-Moment Coefficients of Correlation (r; upper-right triangle) and covariances (lower-left triangle) of fixed-radius point counts of the columbids in the life zones of the Puerto Rican mainland[a].

	Species/Life Zone			
Dry Zone	ZD[b]		WWD	CGD
ZD			0.34	0.40*
MD	28.58		0.14	0.20
WWD	205.52	24.18		−0.08
CGD	110.36	16.07	—49.25	
Moist Zone	ZD	SNP	QDS	CGD
ZD		0.19	0.62**	0.38*
SNP	20.46		0.16	0.21
QDS	25.63	3.53		0.51**
CGD	8.79	2.68	2.58	
Wet Zone	SNP	QDS	ZD	
SNP		0.56**	0.49**	
QDS	21.69		0.58**	
ZD	29.05	2.96		

[a]) Fife 8-km routes/life zone were sampled monthly from July 1986—June 1988.

[b]) Abbreviations: ZD — Zenaida Doves; MD — Mourning Doves; WWD — White-winged Doves; CGD — Common Ground-Doves; SNP — Scaly-naped Pigeons; and QDS — quail-doves (combined).

*) Significant at $P \leqq 0.05$.

**) Significant at $P \leqq 0.01$.

zones and seasons were not justified until the counts were adjusted for differences in $\hat{C}$.

The fixed-radius point counts were used in the corroboration and calibration of changes in annual relative abundance estimates (birds/km) obtained from unfixed-radius point counts. The fixed- and unfixed-radius point counts were significantly correlated in the life zones from May—June 1987—1992. According to the observed CVs of the call- and sight-counts of the columbids, the combination of intensive (fixed-radius point counts) and extensive (unfixed-radius point counts) counting techniques in the life zones was cost-effective at least for common and widely-distributed species such as Zenaida Doves and Scaly-naped Pigeons. Although relative abundance and density estimates obtained from roadside counts can be misleading indicators of habitat quality (Van Horne 1983) and the size and success of nesting populations at local scales (Armbruster *et al.* 1978; Baskett *et al.* 1978; Wilson & Bart 1985; Rivera-Milán 1990 a, unpubl. data), their standardization represents the most cost-effective alternative to study long-term ($>$ 10 years) population changes (trends) in the life zones of the Puerto Rican mainland and Vieques Island (Rivera-Milán 1993).

TABLE 11. Variances of fixed-radius point count of the columbids in the life zones of the Puerto Rican mainland[a].

Species/Life Zone	Individual Species Variances
Dry Zone	
Zenaida asiatica	1 271.520
Zenaida aurita	283.085
Zenaida macroura	23.587
Columbina passerina	273.129
Sum of Individual Species Variances	1 851.321
Variance of Species Sums	2 520.071
Ratio[b]	0.735
Moist Zone	
Zenaida aurita	194.775
Columba squamosa	57.216
Geotrygon spp.[c]	8.891
Columbina passerina	2.810
Sum of Individual Species Variances	263.692
Variance of Species Sums	385.739
Ratio	0.684
Wet Zone	
Columba squamosa	455.036
Zenaida aurita	7.694
Geotrygon	3.346
Sum of Individual Species Variances	466.076
Variance of Species Sums	573.471
Ratio	0.813

[a]) Five 8-km routes/life zone were sampled monthly from July 1986—June 1988.

[b]) Ratio of the sum of the individual species variances to the variance of their sum (Järvinen 1979; James & Boecklen 1984; Rivera-Milán 1990 a, 1992, 1993, and unpubl. data).

[c]) The counts of the three species of quail-doves (*Geotrygon montana*, *G. chrysia*, and *G. mystacea*) were combined.

Parallel Density ($\hat{D}$) Fluctuations

Järvinen (1979) indicated that the ratio of the sum of the individual species variances to the variance of their sum would be equal to 1.0 in the case that the $\hat{D}$ estimates of each species represented independent random variables; a ratio greater than 1.0 would imply compensatory fluctuations (say, via competition for limiting nesting and foraging resources); while a ratio less than 1.0 would imply parallel fluctuations among species pairs. The pair-wise $\hat{D}$ correlations of the columbids were indicative of parallel responses to similar or covarying resources in their environments (Rivera-Milán 1990 a, 1992, 1993, unpubl. data). This, however, does not represent a rejection of biotic interactions (via competition, predation, and/or parasitism) with other species that might influence their status, distribution, and abundance in the life zones. Interactions with both avian and non-avian species might be enhanced, for example, during prolonged periods of food scarcity due to hurricanes and drought conditions ("ecological crunches"; Wiens 1977; Faaborg 1982; Wiley & Wunderle 1993; Rivera-Milán 1990 b, unpubl. data). But, in general, the columbids appeared to be well-adapted to the environmental conditions found in xeric and mesic habitats. They have a great power of dispersion; and are generalists with respect to their nesting and foraging resources in the life zones. The revealed distribution and density patterns are thought to represent the influence of factors in the environment of the columbids working at variable intensities in a scale-dependent fashion (Rivera-Milán 1990 a, 1992, 1993, unpubl. data).

The methodology of this study can be easily adapted to the local conditions of other Caribbean islands. For example, Nellis *et al.* (1984) and

Wauer & Wunderle (1992) conducted roadside counts in the U. S. Virgin Islands; while F. F. Rivera-Milán & J.W. Wiley (unpubl. data) used bicycles to conduct roadside counts in Ciénaga Zapata, Cuba, in 1993. Standardized roadside counts are needed to monitor population changes at multiple spatio-temporal scales and guide management actions in nesting, roosting, and foraging habitats of the columbids in the Caribbean region (see Rivera-Milán 1993 for guidelines).

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