The Condor 98:745-768
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WINTER SURVEYS OF FOREST-DWELLING NEOTROPICAL MIGRANT AND RESIDENT BIRDS IN THREE REGIONS OF CUBA[1]

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Abstract. We used mist nets and fixed-radius point counts to survey the distribution and relative abundance of Neotropical migrant and resident birds at 18 sites, six in each of three regions, in Cuba, representing six forest types. Eighty-two species and one hybrid were recorded, of which 32 species (39.0%) were Neotropical migrants. Strong differences were observed in the numbers of migrant and resident individuals and species detected, and the proportions of migrant individuals and species among regions, but results obtained by mist nets and point counts often differed. Combined results suggest that the western montane region contains the most resident species, and Cayo Coco in eastern Cuba holds the most migrant species. Relative abundances of migrants and residents were compared among forest types within regions. Based on mist net captures, the number of migrant and resident individuals and species at each site were significantly positively correlated. A Principal Components Analysis correlating vegetation structure characteristics with mist net captures suggested that residents occupy a broader spectrum of vegetation structure types than migrants which favor sites with structure typical of secondary forests. We observed habitat segregation among dichromatic migrant warblers both among forest types within regions and among regions within forest types. Generally, Cuba supports greater numbers of migrant individuals and species than other sites in the Caribbean. Compared to the Yucatán Peninsula and Belize, Cuba supports fewer migrant species, but they account for a greater proportion of all species and a lower proportion of all individuals. The efficacy and biases of mist nets and point counts are discussed.

Key words: Cuba; Neotropical migrant birds; resident birds; habitat use; mist nets; point counts.

INTRODUCTION

In recent years, concern has mounted over the status of landbirds that breed in the Nearctic and migrate to winter in the Neotropics (hereafter referred to as Neotropical migrants) (Terborgh 1980, 1989), and there is increasing evidence that populations of some Neotropical migrants are declining (reviewed by Askins et al. 1990). While debate continues over when and where during the annual cycle migrants are most limited (Morse 1980, Hutto 1988, Sherry and Holmes 1993, Rappole and McDonald 1994), knowledge of declines has promoted an increase in research efforts in the Neotropics to understand migrant ecology in relation to habitat use and resident species (e.g., western Mexico, Hutto 1992; Yu-

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[1] Received 22 September 1995. Accepted 18 June 1996.

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catán Peninsula, Lynch 1989; Belize, Petit et al. 1992; Costa Rica, Blake and Loiselle 1992; Central America and Caribbean, Robbins et al. 1992; Jamaica, Holmes et al. 1989; Bahamas and Greater Antilles, Wunderle and Waide 1993). However, relatively little is known about the status, relative abundance, and habitat use of Neotropical migrants and residents in Cuba.

Cuba, with an area of 114,524 km², comprises approximately half of the landmass of the West Indies (Rand McNally and Co. 1986) and has long been recognized for its rich avifauna (Gundlach 1876, Barbour 1923, Bond 1956–1987, Garrido and García Montaña 1975) and as a wintering area and migration stopover for many species of Neotropical migrants (Bond 1956–1987, Garrido 1988). Although Cuba has a growing network of reserves and national parks, ranching, logging, and agriculture have contributed greatly to deforestation and forest fragmentation in the past 100 years (Herrero et al. 1983, Silva Taboada 1983). However, as Santana (1991) noted, Cuba has one of the lowest rates of deforestation in the Caribbean. In fact, between 1974–1976 and 1984, forest area increased in Cuba from 16.0% to 16.9% (Food and Agriculture Organization 1986). Nonetheless, the country's economic situation has worsened dramatically in recent years, and forested areas face renewed threats from agricultural expansion, mining, tourism, and wood cutting for fuel in spite of the efforts and research of various conservation organizations.

Among previous studies, Eaton (1953) presented anecdotal information on the wintering behavior of Neotropical migrant warblers and mixed-species flocks of wintering migrants and residents near Cienfuegos. Dathe and Fisher (1979) summarized observations of a wide variety of migrant and resident species. During January–February 1988 and 1989, a joint Cuban/Canadian team initiated a study of the relative abundance and habitat use of migrant and resident species wintering at Los Sábalos in the Ciénaga de Zapata, Matanzas Province as an off-shoot of an effort to train Cuban ornithologists and technicians in bird banding (González Alonso et al. 1990, 1992). The study was the first international cooperative banding project in Cuba since 1959. In February–March 1989, Wunderle and Waide (1993) assessed the relative abundance of 17 species of Neotropical migrant landbirds at five sites (one site in each of five habitat types) in Pinar del Río Province.

We designed a multi-year project to: (1) test the hypotheses that the relative abundance and habitat use of Neotropical migrant and resident landbirds differ regionally across Cuba and vary among forest types and forest micro-habitats in Cuba and (2) collect information that will enhance conservation efforts in Cuba. Here, we present results from the first phase of the project and compare those results to other sites in the Caribbean basin.

METHODS

STUDY AREAS

During late January and early February 1991–1994, we surveyed forest-dwelling Neotropical migrant and resident landbirds at 18 sites, six in each of three regions (Fig. 1, Table 1): Mil Cumbres in La Cordillera de Guaniguanico, approximately 115 km WSW of La Habana in Pinar del Río Province; La Ciénaga de Zapata, approximately 160 km SE of La Habana in Matanzas Province; and Cayo Coco, Archipiélago de Sabana-Camagüey, approximately 400 km ESE of La Habana in Ciego de Ávila Province. Mil Cumbres is characterized by numerous, deeply eroded, bread-loaf shaped, limestone mountains up to 692 m. Dense forests growing in predominantly laterite soils occur at moderate to high elevation. The local land use consists mostly of cattle ranching, vegetable farming, tobacco, and coffee growing. Ciénaga de Zapata is Cuba's largest wetland area, consisting of over 3,400 km² of freshwater, brackish water, and marine wetlands (Scott and Carbonell 1986). Vast mangrove swamps prevail at sea level with freshwater marshes and swamps, and forested wetlands inland. The Bahía de Cochinos is bordered by seasonally flooded lowland forest growing on thin soils overlying limestone. The terrain is flat and elevations do not exceed 10 m. Land use consists mainly of wood cutting for charcoal in forested areas and rice cultivation in freshwater marshes. Cayo Coco, a 45 km long island lying approximately 15 km offshore, is connected to the mainland by a recently constructed causeway. The island is flat with elevations under 5 m. Forest on thin soils covering limestone bedrock dominates the island and is subject to flooding during the rainy season. There is some wood cutting for charcoal. With the construction of the causeway and a hotel, tourism is fast becoming the island's main industry, and most of the few residents are construction workers. The three

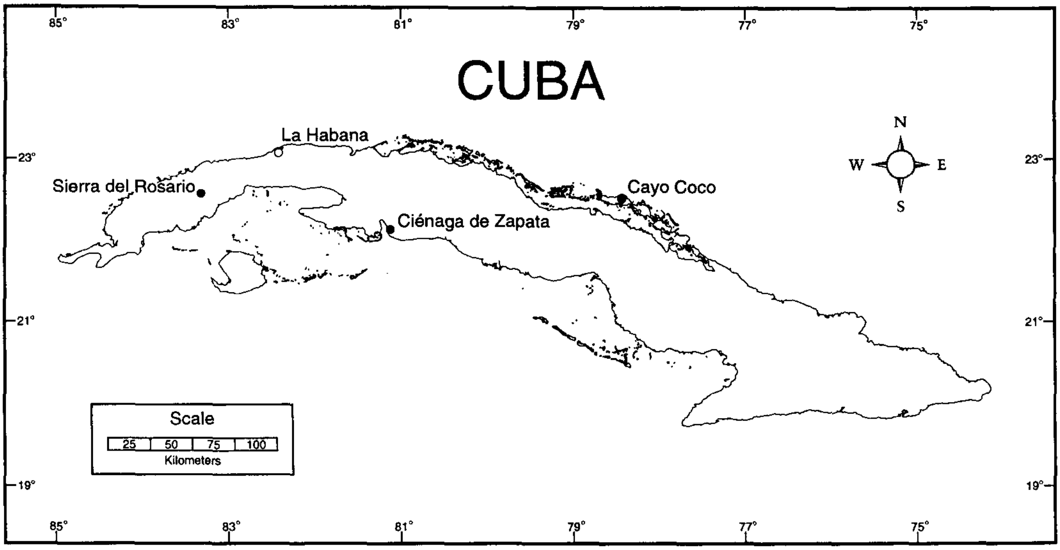

FIGURE 1. The island of Cuba showing the location of the three study regions relative to the capital city, La Habana.

regions are tropical with annual average temperatures of 22.7°C in Mil Cumbres, 24.2°C in Zapata, and 25.3°C on Cayo Coco. All three regions have a pronounced rainy season from April–October (Instituto de Geografía de la Academia de Ciencias y Instituto Cubano de Geodesia y Cartografía 1989).

Site choice was based on perceived conservation value, the desirability of acquiring detailed survey information that could be used for

TABLE 1. Geographic location, forest type, sampling effort, and dates for each study location. Forest types: A—mesic, sub-montane, pine; B—mesic, sub-montane, semideciduous; C—mesic, sub-coastal, semideciduous; D—xeric, sub-coastal, semideciduous; E—xeric, coastal scrub; F—sub-coastal mangrove.

Location	Forest type	Net hours	No. point count sites	No. vegetation sampling sites	Bird sampling dates
Mil Cumbres					
Cabañas	A	727.5	8	10	6–9 Feb 94
Cajalbana	A	657.0	8	9	4–7 Feb 93
El Cayo	A	642.0	8	9	8–11 Feb 93
Salvador	B	720.0	8	10	27–30 Jan 94
Venado	B	772.5	8	10	1–5 Feb 94
San Marcos	B	643.5	8	9	30 Jan–2 Feb 93
Zapata					
Camilo	C	692.4	8	15	6–9 Feb 91, 29 Jan–1 Feb 92
El Cenote	C	687.3	8	15	11–14 Feb 91, 29 Jan–1 Feb 92
C. Buena	C	677.4	8	8	8–12 Feb 92
Lindero	D	615.0	7	7	3–7 Feb 92
El Brinco	D	687.6	8	8	3–7 Feb 92
C. Toro	D	680.1	8	8	8–12 Feb 92
Cayo Coco					
Sitio Viejo	C	720.5	8	10	27–30 Jan 94
Vereda	C	742.5	8	10	30 Jan–2 Feb 93
Potrero	C	686.5	8	10	3–6 Feb 93
Dorada	E	735.0	7	11	7–10 Feb 93
Coloradas	E	720.0	8	10	31 Jan–3 Feb 94
Petrolera	F	714.1	8	10	4–7 Feb 94

site management, and the degree to which the forest type of a site was both extensive (minimum 100 ha) and representative of a region. Surveys were conducted in six of Cuba's 23 major forest types (Instituto de Geografía de la Academia de Ciencias y Instituto Cubano de Geodesia y Cartografía 1989) (Table 1). In Mil Cumbres, the San Marcos site was within the protected Reserva San Marcos. El Cayo was chosen because logging has largely been excluded and it closely resembles the ancestral forest. Cajalbana was on serpentine soils with an unusual plant assemblage, including several endemics. The remaining three sites lay within the Parque Nacional La Güira. In Zapata, all sites were within the Plan Victoria de Girón, an integrated management plan for the Parque Nacional Zapata and vicinity. On Cayo Coco, all sites lay within the Cayo Coco Faunal Reserve, an area potentially threatened by a major tourist development. The coastal scrub on Cayo Coco has a low canopy, limited economic value, and to our knowledge has never been cut. However, some trees, particularly the palms *Coccothrinax littoralis* and *Pseudophoenix sargentii,* are being extracted for replanting on hotel grounds. All other sites, except El Cayo and the coastal scrub sites, have been logged in the past. Feral pigs occur in the forests of all three regions, and feral cattle are present at Mil Cumbres and on Cayo Coco. Further details on each of the study areas are outlined in Wallace (1991, 1993, 1994) and McNicholl (1992).

BIRD SAMPLING

We restricted our surveys to forest-dwelling landbirds. We did not consider waterbirds, shorebirds, aerial species that occurred above the forest canopy, and non-forest raptors. We assessed the relative abundance of each bird species using mist nets and fixed-radius point counts. At each site, two mist nets (9 × 2.6 m, 30 mm mesh) were placed at each of 15 locations. The net pairs were positioned objectively and independent of bird activity at 100 m intervals determined by pacing or with a pedometer. Nets were typically run 6 hr per day, beginning approximately at sunrise, for four days, and were checked every 30 min. With the exception of very small birds (e.g., hummingbirds, gnatcatchers, and todies) for which the North American band size 0 was too large and Cuban Pygmy-Owls (*Glaucidium siju*) for which a suitable band was not available, each bird trapped was banded with a standard U.S. National Biological Service/Canadian Wildlife Service numbered aluminum band. Unbanded birds were marked by clipping the corner of one or more rectrices enabling them to be identified individually if recaptured during the four-day study period. The net in which each bird was captured was recorded and all birds were released from a central banding station. Neotropical migrants were aged and sexed to the extent possible based on the North American Bird Banding Manual (Anonymous 1977) or Pyle et al. (1987). Residents were aged and sexed using plumage, cranial pneumatization, published descriptions (Bond 1985), and personal experience. Relative abundance for each species was calculated in terms of individuals captured per 100 net-hours.

At each study site, fixed-radius point-count locations (Hutto et al. 1986) were established immediately adjacent to eight net locations, separated from each other by 200 m intervals. Each point-count location was censused twice during the four-day netting period before 10:30 E.S.T. and the mean number of each bird species detected during the two censuses was counted as the final census tally. At Lindero, count data were derived from one count per point at seven locations. At Dorada, count data were derived from two counts per point at seven locations. Counts lasted 10 minutes and observers recorded all birds within a 25 m radius and all birds beyond the 25 m radius. Point counts provided indices of relative abundance for each species based on the average number seen or heard within 25 m, frequency of occurrence within 25 m, and frequency of occurrence beyond 25 m.

Bird sampling data collected at Camilo and El Cenote in 1991 are not included here because the methodology was not consistent with subsequent years.

VEGETATION SAMPLING

Vegetation at each study site was characterized at all locations at which both netting and point counts were conducted (minimum seven locations) and at other net locations as time allowed (Table 1) using methods based on James and Shugart (1970) and Noon (1981). Circular plots (0.04 ha) were established immediately adjacent to net/point count locations. In each circle, we counted the number of saplings and standing trees in each of nine diameter at breast height (dbh, 1.3 m) classes (S: > 3–8 cm, A: > 8–15 cm, B: > 15–23 cm, C: > 23–38 cm, D: > 38–53 cm, E: > 53–69 cm, F: > 69–84 cm, G: > 84–102 cm, H: > 102 cm) using a reach stick. Shrub stem density was assessed by counting all stems ≤ 3 cm dbh touched by an observer's outstretched arms along two 22.6 m transects aligned on the cardinal axes of the plot. Percent canopy cover and ground cover were derived from 40 positive or negative readings through an ocular tube along the plot axes. Average canopy height was calculated from the heights of ten canopy trees measured with a clinometer. Understory foliage volume was measured in four height classes (0–0.3 m, > 0.3–1 m, > 1–2 m, > 2–3 m) with a density board drop cloth held upright 11.3 m from the center of the plot at each of the four cardinal directions. All saplings and trees were identified to species when possible, and the five principal ground cover and shrub species were recorded for each plot. To avoid disturbance during the bird-sampling period, we sampled vegetation either after all bird sampling was completed at a site or a minimum of three days before bird sampling was initiated.

DATA ANALYSIS

We analyzed differences in captures and counts of Neotropical migrants and residents combined among regions and forest types and for all migrant and resident species combined as well as individually among forest types. Data were analyzed for homogeneity of variances using the $F_{\max}$-test for multiple-group tests and F-test for two-group tests. In cases where variances were not homogeneous, data were transformed using square root, log, and arcsine functions. If the variances were homogeneous initially, or after transformation, among-group differences were tested using ANOVA or two-tailed t-tests. If variances were unresponsive to transformation, we used the Kruskal-Wallis test for multi-group comparisons and the Mann-Whitney U-test for two-group comparisons. The Tukey multiple comparison test was used as a follow-up to ANOVAs. Analysis of differences in capture and count data for migrant and resident species combined and individually among forest types on Cayo Coco presented special problems because of very small and unequal sample sizes (e.g., testing one mangrove site against two coastal scrub and three semideciduous). For these analyses, we used ANOVA because non-parametric tests cannot show differences among treatments in this case even if differences are very large. We believe that while these tests are extremely conservative, they have illustrative value. Linear regression was used to test the hypothesis that migrant and resident species differed with respect to their estimates of relative abundance from banding and point counts. Heterogeneity of male:female sex ratios among forest types was tested with a χ^2 test. Pearson product-moment correlations (r) were used with normally distributed data and Spearman rank correlations (r_s) were used with non-normal data and data in the form of percentages. Means are presented ± SE. We used a probability of Type I error of 0.05 or less as significant for all tests.

An ordination of migrant and resident bird species capture data with respect to vegetation structure variables was accomplished using Principal Components Analysis (PCA). We used vegetation data collected from the circular plots associated with 179 net locations (Mil Cumbres, $n = 57$; Ciénaga de Zapata, $n = 61$; Cayo Coco, $n = 61$). PCA was run with SAS (SAS Institute 1989) using a correlation matrix and varimax rotation. Capture data for the seven most abundant Neotropical migrants and 14 most abundant residents from the 179 net sites were correlated with the principal components using Pearson product-moment correlation.

RESULTS

REGIONAL DIFFERENCES

Banding. The relative abundance of Neotropical migrant and resident individuals reflected by mist net capture rates (Fig. 2a) differed significantly among regions. With respect to migrants, Cayo Coco capture rates were significantly greater than those at Zapata and Mil Cumbres, whereas Zapata and Mil Cumbres rates were not significantly different from each other. With respect to residents, Cayo Coco capture rates were significantly greater than rates at Zapata, but not significantly different from those at Mil Cumbres. Resident capture rates in Zapata were not significantly different from rates at Mil Cumbres. The proportion of migrant individuals captured (Fig. 2b) was significantly higher on Cayo Coco than in Mil Cumbres, whereas the proportion of migrants in Zapata was not significantly different from Cayo Coco or Mil Cumbres.

With respect to both migrants and residents, more species (Fig. 2c) were captured on Cayo

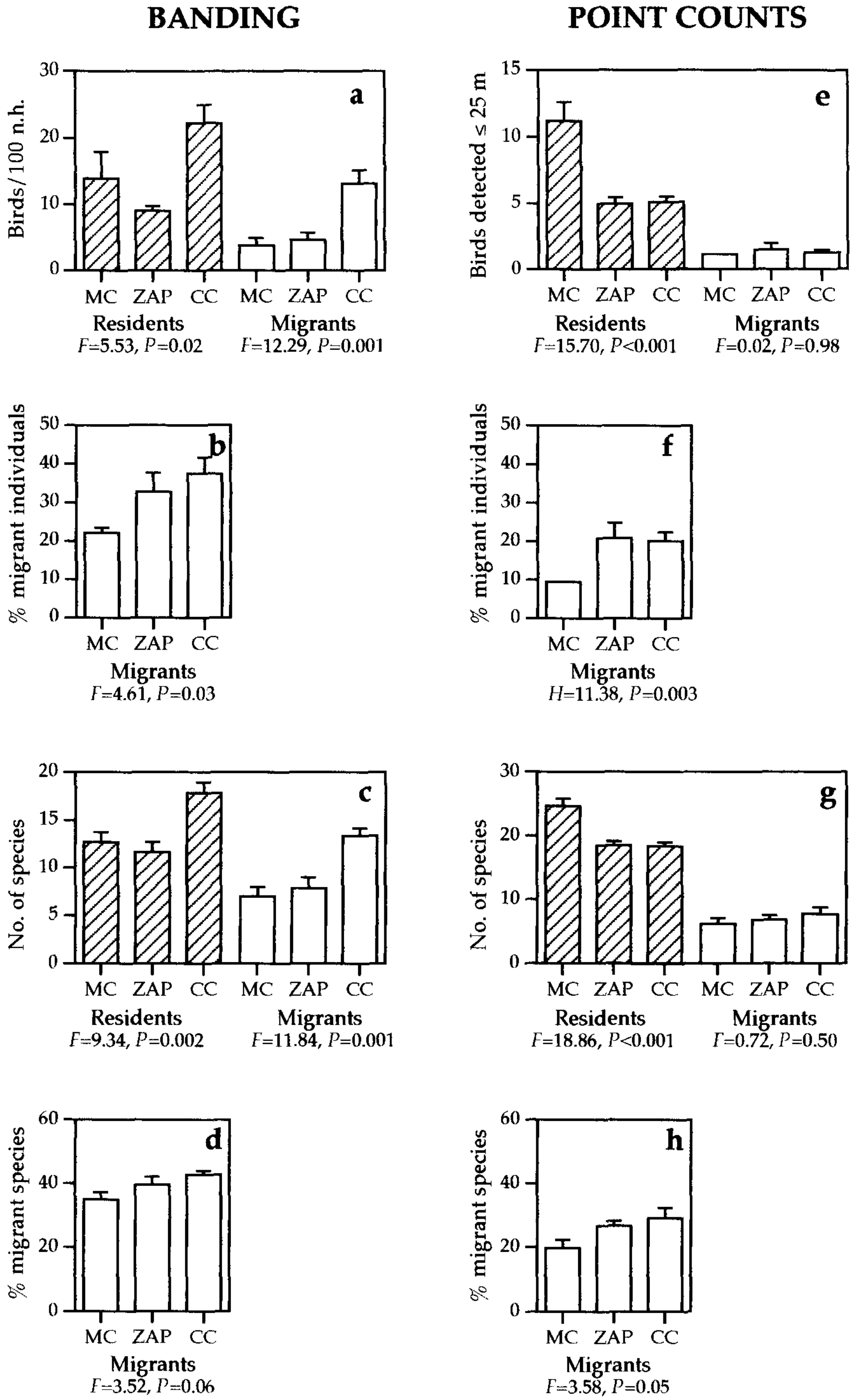

FIGURE 2. Comparison of relative abundance and species richness of Neotropical migrants and residents among three regions in Cuba using banding and point counts. Parts a–d: banding. Parts e–h: point counts. MC—Mil Cumbres, ZAP—Ciénaga de Zapata, CC—Cayo Coco. Error bars equal one standard error. Tests among regions were performed using ANOVA, except in Part f where a Kruskal-Wallis test was used. Tests were performed on log-transformed data in Parts a and e and on square-root transformed data in Part b.

TABLE 2. Selected vegetation structure statistics from 18 study sites. Forest types: A—mesic, sub-montane, pine; B—mesic, sub-montane, semideciduous; C—mesic, sub-coastal, semideciduous; D—xeric, sub-coastal, semideciduous; E—xeric, coastal scrub; F—sub-coastal mangrove. All data are means of the values from the vegetation plots sampled at each area.

Location	Forest type	Tree stems/ha	Basal area m²/ha	Shrub stems/ha	% canopy cover	% ground cover	Canopy height, m	% foliage 0–0.3 m	% foliage 0.3–1.0 m	% foliage 1.0–2.0 m	% foliage 2.0–3.0 m	No. tree species/ plot
Mil Cumbres												
Cabañas	A	1,290	28.6	10,725	90.3	45.5	19.2	71.5	62.5	67.1	60.1	13.9
Cajalbana	A	1,592	18.6	17,889	71.7	45.6	16.5	93.3	86.3	72.2	69.2	10.3
El Cayo	A	1,200	25.1	19,153	80.3	59.7	17.5	93.1	75.4	73.3	74.7	10.8
Salvador	B	1,728	29.6	15,425	94.8	27.5	17.2	71.0	62.9	57.8	58.9	17.1
Venado	B	1,963	23.9	15,550	94.3	29.3	11.9	77.5	66.6	66.3	65.7	18.9
San Marcos	B	1,817	24.4	16,972	96.9	53.1	14.6	74.4	57.1	42.4	48.5	16.8
Zapata												
Camilo	C	2,658	20.1	13,225	83.5	24.2	10.5	59.0	54.0	59.9	65.0	10.9
El Cenote	C	4,172	24.3	13,725	95.3	24.5	13.5	78.8	70.9	69.7	77.7	9.5
C. Buena	C	3,741	29.2	16,750	84.4	38.4	11.9	–	–	–	–	24.3
Lindero	D	2,504	30.1	9,518	81.1	27.1	12.1	–	–	–	–	14.6
El Brinco	D	2,291	21.7	14,813	81.9	36.6	10.3	–	–	–	–	11.5
C. Toro	D	3,050	21.7	6,000	76.3	21.6	10.4	–	–	–	–	17.1
Cayo Coco												
Sitio Viejo	C	2,580	19.2	13,838	96.8	51.8	10.4	93.2	91.5	91.0	93.0	11.3
Vereda	C	3,758	16.9	23,163	92.0	21.5	7.4	85.7	82.4	85.6	91.5	8.9
Potrero	C	3,073	17.7	17,750	94.5	28.5	9.2	90.0	76.1	79.8	84.2	8.7
Dorada	E	3,331	16.1	15,580	80.8	45.2	4.1	87.7	90.1	95.5	96.8	12.3
Coloradas	E	2,560	13.8	15,275	91.8	48.8	5.8	95.8	90.7	85.7	92.7	16.3
Petrolera	F	2,333	7.5	14,863	75.5	64.0	4.6	80.5	77.6	80.9	90.2	5.0

Coco than in Mil Cumbres or Zapata. Numbers of migrant and resident species were not significantly different between Mil Cumbres and Zapata. The proportion of migrant species captured did not vary significantly among the three regions (Fig. 2d), although the mean proportion of migrant species was greater on Cayo Coco than in Zapata and Mil Cumbres.

Point Counts. The relative abundance of Neotropical migrant and resident individuals reflected by birds detected at ≤ 25 m on point counts (Fig. 2e) varied significantly among regions with respect to residents, but not with respect to migrants. Significantly more residents were detected at Mil Cumbres than in Zapata or on Cayo Coco, whereas Zapata and Cayo Coco did not differ significantly from each other. The proportions of migrant individuals detected (Fig. 2f) on Cayo Coco and in Zapata were not significantly different but were significantly greater than in Mil Cumbres.

The numbers of species detected by counts (Fig. 2g) differed significantly among regions with respect to residents, but not with respect to migrants. Significantly more resident species were detected in Mil Cumbres than on Cayo Coco or in Zapata, but numbers of species did not differ significantly between the latter two areas. The proportions of migrant species detected (Fig. 2h) were significantly greater on Cayo Coco and in Zapata than in Mil Cumbres, but the proportions on Cayo Coco and in Zapata were not significantly different from each other.

FOREST HABITAT COMPARISONS

Characterization of forest types. We conducted surveys in six forest types (Table 1, 2). Note that whereas Cajalbana is considered by some authors to be an example of a pine/cuabal forest (Capote and Berazain 1984, Capote et al. 1988), we have placed it in the pine forest group for purposes of this study. In addition, we treat all forests on Cayo Coco, with the exception of the sub-coastal mangrove site, as semideciduous. Chiappy et al. (1989) classed these forests as evergreen, but we feel that the large proportion of deciduous trees suggests they are more correctly classed as semideciduous. Structural characteristics of sites are summarized in Table 2. In terms of relative dominance, sub-montane pine forests in Mil Cumbres were composed of at least 67% *Pinus caribaea* with lesser amounts of *Matayba oppositifolia, Calophyllum pinetorum,* and *Copernicia* sp. The total number of tree species ranged from 35–41. The understory was complex and included over 41 species with *Matayba oppositifolia* being the only species common at all three sites. Sub-montane semideciduous forests in Mil Cumbres were more diverse with 60–67 tree species including *Matayba oppositifolia, Spondias mombin,* and *Pseudolmedia spuria.* Like pine forest, the understory was complex, but more clearly dominated by *Oxandra lanceolata* and *Matayba oppositifolia.*

Lowland forests tended to be simpler communities. Mesic, sub-coastal semideciduous forests in Zapata were dominated by *Lysiloma latisiliquum* with lesser amounts of *Bursera simaruba, Swietenia mahogani, Oxandra lanceolata,* and *Mastichodendron foetidissimum.* Important understory plants included *Oxandra lanceolata, Gymnanthes lucida,* and *Atherammus lucidus.* Xeric, sub-coastal semideciduous forests in Zapata were composed principally of *Lysiloma latisiliquum, Bursera simaruba,* and *Eugenia maleolens* with an understory comprised largely of *Eugenia maleolens* and *E. glabrata, Erythroxylum havanense,* and *Atherammus lucidus.*

In mesic, sub-coastal semideciduous forests on Cayo Coco, the dominant tree was *Coccoloba diversifolia* and was typically accompanied by *Lysiloma latisiliquum, Bursera simaruba,* and *Metopium brownii.* Common understory species were *Coccoloba diversifolia, Dipholis celastrina, Nectandra coriacea,* and *Psychotria undata.* The dominant tree species in xeric, coastal scrub, known as "matorral" or "manigua," were *Coccoloba diversifolia, Coccothrinax littoralis, Pseudophoenix sargentii,* and *Bursera simaruba.* Main understory species included *Coccothrinax littoralis, Croton lucidus, Amyris elemifera,* and *Coccoloba diversifolia.* The single sub-coastal mangrove site, or "yanal," had a plant community composed almost entirely of *Conocarpus erecta, Avicennia germinans,* and *Coccoloba diversifolia.* The understory was composed mostly of *Dipholis celastrina* and *Conocarpus erecta.*

Even though mesic, sub-coastal semideciduous forests were surveyed in more than one area, we restricted comparison of birds among forest types to within regions because of strong among region differences. Inter-forest type comparisons of birds within regions are summarized in Table 3.

Mil Cumbres. Estimates of relative abundance from banding and point counts both suggest that residents were significantly more abundant in submontane pine than in sub-montane semideciduous. Banding suggested that migrants were more abundant in pine, but the difference was not statistically significant. Point counts indicated migrants were on average more abundant in pine, but the difference was not significant. Banding did not indicate a significant difference in the proportion of migrant individuals, but point counts suggested a significantly greater proportion in semideciduous than in pine. The numbers of migrant and resident species captured and detected were greater in pine than in semideciduous, but the differences were not significant. The proportions of migrant species did not differ significantly among pine and semideciduous forests using banding or point counts.

Ciénaga de Zapata. Estimates of relative abundance from banding and point counts suggest that there was no significant difference between the numbers of migrants or residents among mesic, sub-coastal semideciduous forest and xeric, sub-coastal semideciduous forest. Neither captures nor point counts showed significant differences in the proportions of migrant individuals. Significantly more resident species were captured in xeric, sub-coastal semideciduous forest than in mesic, sub-coastal semideciduous forest, although there was no significant difference in the number of resident species detected by point counts. The numbers of migrant species captured and detected on counts did not differ significantly among the forests. Neither captures nor point counts showed differences among forest types in the proportion of migrant species.

Cayo Coco. Estimates of relative abundance from banding and point counts suggest that there was no significant difference among mesic, subcoastal semideciduous forest, xeric coastal scrub, and sub-coastal mangrove with respect to residents. Banding results suggest that migrants were more abundant in mangrove than in semideciduous forest and scrub, but the difference was not significant. Point counts reveal no significant difference in the abundance of migrants among the three habitats. The proportion of migrant individuals captured was greater in mangrove than in semideciduous forest and scrub, and greater in semideciduous forest than in scrub, but the differences were not significant. There was no significant difference among the three habitats in the proportion of migrants detected by point counts. The numbers of resident species captured tended to be greater in mangrove than in semideciduous forest and scrub, but the difference was not significant. Point counts suggest that the numbers of resident species tended to be greater in scrub than in mangrove and semideciduous forest, but the difference was not significant. The numbers of migrant species did not differ significantly among the forest types using either method. Similarly, the proportions of migrant species captured and detected on point counts did not differ significantly among the forest types.

PATTERNS OF SPECIES DISTRIBUTION AND ABUNDANCE

Neotropical migrants. We collected relative abundance data for 23 species of Neotropical migrants. Here, unless stated otherwise, we discuss banding data as there were greater numbers of detections of migrant species using banding and there was higher variability across regions.

The five most frequently encountered migrant species were Gray Catbird (*Dumetella carolinensis*), Black-throated Blue Warbler (*Dendroica caerulescens*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), and Ovenbird (*Seiurus aurocapillus*), all being found in at least 75% of the areas surveyed. All but Ovenbird were most abundant on Cayo Coco and least abundant in Mil Cumbres. Ovenbirds were slightly more common in Mil Cumbres than in Zapata. On Cayo Coco, Gray Catbirds were more common in mesic, semideciduous forest than in scrub or mangrove, although the difference among habitats was not significant (banding: $F_{2,3}$ = 5.27, P = 0.10). In Mil Cumbres, Black-throated Blue Warblers were significantly more common in pine than in semideciduous (banding: t_4 = 3.74, P = 0.02). On Cayo Coco, Black-throated Blue Warblers were more common in xeric, coastal scrub, although the difference among habitats was not significant (banding: $F_{2,3}$ = 4.12, P = 0.14). Black-and-white Warblers were significantly more common in subcoastal mangrove on Cayo Coco (banding: $F_{2,3}$ = 21.09, P = 0.02). American Redstarts reached peak abundances in mesic, semideciduous forest on Cayo Coco, and at El Cayo, a pine forest site in Mil Cumbres. In Zapata, American Redstarts were only slightly more common in mesic, semideciduous forest than xeric, semideciduous forest based on banding, but point counts indicated a significant difference (point count: t_4 = 4.26, P = 0.01). Mesic, semideciduous forests on Cayo Coco also held the most Ovenbirds. Two species, Worm-eating Warbler (*Helmitheros vermivorus*) and Swainson's Warbler (*Limnothlypis swainsonii*), occurred in low-moderate numbers in a broad range of forest types, tending to be more common in semideciduous forest types.

Several migrant species showed distinct regional preferences and a few exhibited statistically significant habitat preferences within regions. Yellow-bellied Sapsuckers (*Sphyrapicus varius*) were found mainly in Mil Cumbres where they were detected in low numbers by point counts. Blue-gray Gnatcatchers (*Polioptila caerulea*) were present in low numbers almost exclusively in Zapata where they were significantly more common in xeric, semideciduous forest than mesic, semideciduous forest (point count: t_4 = 3.52, P = 0.02). A single bird was detected on a point count on Cayo Coco, and it was observed only incidentally at two montane sites in Mil Cumbres. Yellow-throated Vireos (*Vireo flavifrons*), considered rare in winter in Cuba (Garrido and García Montaña 1975), occurred at four sites, three on Cayo Coco where four were banded at the mangrove site. Northern Parulas (*Parula americana*) were recorded mainly in Zapata and on Cayo Coco where they occurred in most forest types, but were somewhat more common in xeric sites. Magnolia Warblers (*Dendroica magnolia*) were recorded at seven sites. The greatest numbers were at El Cayo, a pine site in Mil Cumbres, and at the mangrove site on Cayo Coco. Cape May Warblers (*Dendroica tigrina*) were found mainly on Cayo Coco, where they were significantly more abundant in xeric coastal scrub (banding: $F_{2,3}$ = 32.37, P = 0.01). Black-throated Green Warblers (*Dendroica virens*) occurred in low numbers at six sites, four on Cayo Coco and primarily in semideciduous forest. Prairie Warblers (*Dendroica discolor*) were found only in Zapata and on Cayo Coco. In Zapata, they were most common at El Brinco, a xeric sub-coastal semideciduous forest. On Cayo Coco, banding data showed that they were more abundant in mangrove than in other habitats, but the difference was not significant ($F_{2,3}$ = 5.3, P = 0.10). Northern Waterthrushes (*Seiurus noveboracensis*) were significantly more abundant in

TABLE 3. Within region comparisons among forest types of relative abundance estimates (banding—birds/100 n.h.; point counts—birds detected ≤ 25 m), species richness, and proportions of Neotropical migrant individuals and species. All statistical tests were performed on untransformed data except for Mil Cumbres relative abundance of residents and Zapata number of migrant species for which square root transformations were used. Degrees of freedom for test statistics: Mil Cumbres and Zapata, t, $df = 4$; Cayo Coco, F, $df = 2,3$. Significant differences are indicated. Forest types: A—mesic, sub-montane, pine; B—mesic, sub-montane, semideciduous; C—mesic, sub-coastal, semideciduous; D—xeric, sub-coastal, semideciduous; E—xeric, coastal scrub; F—sub-coastal mangrove.

		Banding					Point counts				
Region	Forest type	Mean	SE	Test	*P*	Diff.	Mean	SE	Test	*P*	Diff.
Mil Cumbres											
Relative abundance of residents	A	21.6	4.7	$t = 4.13$	0.02	A > B	13.7	1.7	$t = 2.70$	0.05	A > B
	B	6.2	0.7				8.6	0.8			
Relative abundance of migrants	A	5.7	1.4	$t = 2.62$	0.06	—	1.3	0.1	$t = 1.78$	0.15	—
	B	2.0	0.4				1.0	0.1			
Proportion migrant individuals (%)	A	20.6	1.8	$t = 1.19$	0.30	—	8.6	0.3	$t = 3.97$	0.02	B > A
	B	23.6	1.8				10.2	0.3			
Number of resident species	A	14.3	1.8	$U = 7.50$	0.12	—	26.3	1.9	$t = 1.71$	0.16	—
	B	11.0	0.0				23.0	0.6			
Number of migrant species	A	8.0	1.5	$t = 1.04$	0.36	—	6.0	1.7	$t = 0.17$	0.87	—
	B	6.0	1.2				6.3	1.5			
Proportion of migrant species (%)	A	35.3	2.0	$t = 0.10$	0.91	—	18.1	4.5	$t = 0.66$	0.55	—
	B	34.7	4.5				21.5	2.7			
Zapata											
Relative abundance of residents	C	9.5	0.7	$t = 1.55$	0.20	—	5.5	1.5	$t = 1.30$	0.27	—
	D	10.0	0.3				4.3	0.3			
Relative abundance of migrants	C	5.3	1.9	$t = 0.59$	0.59	—	1.7	1.0	$t = 0.41$	0.71	—
	D	4.0	2.1				1.3	0.3			
Proportion migrant individuals (%)	C	38.1	7.6	$t = 1.10$	0.33	—	20.0	7.9	$t = 0.20$	0.85	—
	D	27.4	5.9				21.8	3.7			
Number of resident species	C	9.7	0.7	$t = 3.62$	0.02	D > C	19.0	0.6	$t = 0.77$	0.48	—
	D	13.7	0.9				18.0	1.2			
Number of migrant species	C	6.7	0.3	$t = 0.91$	0.41	—	7.0	0.6	$t = 0.22$	0.88	—
	D	9.0	2.3				6.7	1.3			
Proportion migrant species (%)	C	40.1	1.5	$t = 0.45$	0.68	—	26.9	1.4	$t = 0.10$	0.92	—
	D	38.4	5.4				26.4	3.3			

TABLE 3. Continued.

Region	Forest type	Banding					Point counts				
		Mean	SE	Test	P	Diff.	Mean	SE	Test	P	Diff.
Cayo Coco											
Relative abundance of residents	C	19.0	5.1	$F = 0.75$	0.54	—	5.4	0.3	$F = 0.90$	0.49	—
	E	27.1	0.7				5.2	1.3			
	F	22.0					3.7				
Relative abundance of migrants	C	12.3	1.7	$F = 6.71$	0.08	—	1.3	1.0	$F = 1.33$	0.39	—
	E	9.8	1.6				0.9	0.0			
	F	22.0					1.3				
Proportion migrant individuals (%)	C	40.5	3.7	$F = 6.61$	0.08	—	21.7	2.8	$F = 2.46$	0.23	—
	E	26.4	2.7				14.7	2.7			
	F	50.0					26.1				
Number of resident species	C	16.0	1.0	$F = 4.05$	0.14	—	17.3	0.3	$F = 4.87$	0.11	—
	E	18.5	1.5				20.0	1.0			
	F	22.0					18.0				
Number of migrant species	C	12.0	1.7	$F = 1.55$	0.35	—	9.0	2.0	$F = 0.66$	0.58	—
	E	14.5	2.1				6.5	0.5			
	F	15.0					6.0				
Proportion migrant species (%)	C	42.8	0.6	$F = 0.27$	0.78	—	33.4	5.9	$F = 0.84$	0.51	—
	E	43.9	4.5				24.5	0.5			
	F	40.5					25.0				

mangrove than in other habitats on Cayo Coco (banding: $F_{2,3} = 111.04$, $P = 0.002$). All other sites where they were recorded bordered mangrove. Louisiana Waterthrushes (*Seiurus motacilla*) were found in stream beds in four of the Mil Cumbres sites. Most Common Yellowthroats (*Geothlypis trichas*) were found either in pine sites in Mil Cumbres or at the mangrove site on Cayo Coco, although it was the most commonly captured species at Linea de Quintela in Zapata in 1988 (Sirois et al. 1990). Summer Tanager (*Piranga rubra*) is considered very rare and local in Cuba during winter (Garrido and García Montaña 1975) and was recorded at three sites in Mil Cumbres, one pine and two semideciduous. Indigo Bunting (*Passerina cyanea*) was recorded in low numbers at five of the six Mil Cumbres sites. Elsewhere, single birds were recorded in each of five sites, principally xeric.

Several species were recorded in comparable numbers in all three regions with some similarity of habitat preference across regions. White-eyed Vireo (*Vireo griseus*) was detected only in low numbers mostly in xeric forest types. Palm Warbler (*Dendroica palmarum*) favored open areas along broad trails in mesic and xeric, sub-coastal semideciduous forest, and forests with more open structure such as pine forest. On Cayo Coco, Palm Warbler was significantly more common in mangrove than in coastal scrub or semideciduous forest (banding: $F_{2,3} = 18.08$, $P = 0.02$). Hooded Warbler (*Wilsonia citrina*), considered rare, but annual, in Cuba (Garrido and García Montaña 1975, Garrido 1988) was recorded in low numbers and only in mesic, semideciduous forest types.

An additional nine species and one hybrid were detected by banding and/or point counts, or were observed incidentally, at less than four areas. Among rare species, one Sharp-shinned Hawk (*Accipiter striatus*) of the North American subspecies (ssp. *velox*) was netted at Dorada on Cayo Coco in 1993. This subspecies is considered an accidental migrant in Cuba (Garrido and García Montaña 1975) and has not been recorded previously on Cayo Coco (Kirkconnell, in press). Observations of Blue-winged Warbler (*Vermivora pinus*) at two sites on Cayo Coco add to the increasing number of winter records. Whereas it was formerly considered only a hypothetical rare winter resident in Cuba (Garrido and García Montaña 1975), it can now be considered a regular, but rare, winter resident (Garrido, in litt. in González Alonso et al. 1992). A Blue-winged × Golden-winged Warbler hybrid (*Vermivora pinus* x *chrysoptera*) banded at El Brinco in Zapata in 1992 most closely resembled a "Brewster's Warbler" (Blanco Rodríguez et al. 1995). This is the third report of a Blue-winged × Golden-winged hybrid in Cuba (González Alonso et al. 1992; Sánchez et al., unpubl. data). One female Blackburnian Warbler (*Dendroica fusca*) was observed during a point count at Dorada on Cayo Coco 7 February 1993. Whereas this species is considered a locally common transient (Garrido and Kirkconnell 1993), this record is among the few winter reports. One Blue Grosbeak (*Guiraca caerulea*) was observed at Coloradas on Cayo Coco in 1994. It is considered a very rare winter visitor (Garrido and García Montaña 1975), and is known only as a transient from Cayo Coco (Kirkconnell, in press). Two Painted Buntings (*Passerina ciris*) were observed and one captured at Coloradas on Cayo Coco in 1994. This species is considered a very rare winter resident on Cayo Coco (Kirkconnell, in press), and a fairly rare winter resident in Cuba in general (Garrido and García Montaña 1975), although locally it may be more common (A. Mitchell, pers. comm.). Other species detected in low numbers included Cedar Waxwing (*Bombycilla cedrorum*) from three sites in Mil Cumbres and one in Zapata, Yellow-rumped Warbler (*Dendroica coronata*) from one site on Cayo Coco, Yellow-throated Warbler (*Dendroica dominica*) from one site in Mil Cumbres and two on Cayo Coco, and Baltimore Oriole (*Icterus galbula*) from one site on Cayo Coco.

Residents. We collected relative abundance data for 39 resident species during the surveys. The following species were ubiquitous, and often abundant, with no clear habitat preference: White-crowned Pigeon (*Columba leucocephala*), Great Lizard-Cuckoo (*Saurothera merlini*), Cuban Emerald (*Chlorostilbon ricordii*), Cuban Tody (*Todus multicolor*), Cuban Pewee (*Contopus caribaeus*), La Sagra's Flycatcher (*Myiarchus sagrae*), Loggerhead Kingbird (*Tyrannus caudifasciatus*), Red-legged Thrush (*Turdus plumbeus*), and Cuban Vireo (*Vireo gundlachii*). Two species were widespread but exhibited clear habitat preferences within regions. Cuban Green Woodpecker (*Xiphidiopicus percussus*) was significantly more abundant in mesic, semideciduous forest in Zapata (point count: $t_4 = 2.70$, $P = 0.05$). In Mil Cumbres, Cuban Bullfinch (*Melopyrrha ni-

gra) was significantly more common in pine than in semideciduous forest (banding: $t_4 = 6.57$, $P = 0.003$; point count: $t_4 = 2.91$, $P = 0.04$). In Zapata, Cuban Bullfinch was significantly more common in xeric, semideciduous forest than in mesic, semideciduous forest (point count: $t_4 = 3.22$, $P = 0.03$, square root transformation). Cuban Bullfinch was significantly more abundant in mangrove than in scrub or semideciduous forest on Cayo Coco (banding: $F_{2,3} = 9.34$, $P = 0.05$).

Several common species exhibited range and/or habitat specificity. Cuban Parrots (*Amazona leucocephala*) were detected by point counts at all areas in Zapata, a known population stronghold (González-Alonso et al. 1987). Cuban Pygmy-Owls were found only in Zapata and Mil Cumbres and are not confirmed from Cayo Coco, although they are common on neighboring Cayo Romano (A. Kirkconnell, pers. comm.). Cuban Trogon (*Priotelus temnurus*) has not been recorded from Cayo Coco (Kirkconnell, in press). Yellow-headed Warblers (*Teretistris fernandinae*) were common in Zapata and Mil Cumbres. In Mil Cumbres they were significantly more common in pine than semideciduous (banding: $t_4 = 3.77$, $P = 0.02$). In eastern Cuba, and thus on Cayo Coco, Yellow-headed Warbler is replaced by Oriente Warbler (*Teretistris fornsi*). Yellow-faced Grassquit (*Tiaris olivacea*) was significantly more abundant in pine than semideciduous in Mil Cumbres (banding: $U = 9$, $P = 0.05$) and significantly more abundant in scrub than in other habitats on Cayo Coco (point count: $F_{2,3} = 132.25$, $P = 0.001$). Scaly-naped Pigeon (*Columba squamosa*), White-winged Dove (*Zenaida asiatica*), Cuban Solitaire (*Myadestes elisabeth*), Olive-capped Warbler (*Dendroica pityophila*), Red-legged Honeycreeper (*Cyanerpes cyaneus*), Cuban Grassquit (*Tiaris canora*), and Cuban Blackbird (*Dives atroviolacea*) were found predominantly or exclusively in Mil Cumbres, where Olive-capped Warbler was significantly more abundant in pine than semideciduous (banding: $t_4 = 3.92$, $P = 0.02$; point count: $t_4 = 3.49$, $P = 0.03$) and Cuban Grassquit was found only in pine. One of the three subspecies of Zapata Sparrow (*Torreornis inexpectata*) is endemic to Cayo Coco (ssp. *varonai,* Regalado Ruíz 1981) where we found them in moderate numbers in all forest types but coastal scrub. Common Ground-Dove (*Columbina passerina*) and Key West Quail-Dove (*Geotrygon chrysia*) were encountered primarily on Cayo Coco, although the ground-dove was fairly common at a previous study site in Zapata (González Alonso et al. 1990).

In Cuba, Gray-headed Quail-Dove (*Geotrygon caniceps*) is considered rare (Rodríguez and Sánchez 1993) and "near-threatened" (Collar et al. 1992), and is known from Zapata and from low humid mountains (Garrido and García Montaña 1975). In this study, we encountered it only in Mil Cumbres, although it was less common in Mil Cumbres than at Los Sábalos, Zapata in 1988 and 1989 (González Alonso et al. 1990, Sirois et al. 1990). Blue-headed Quail-Dove (*Starnoenas cyanocephala*) is considered rare in Cuba (Rodríguez and Sánchez 1993), and quite possibly in danger of extinction (Garrido 1985, Collar et al. 1992). We encountered them in low numbers at a total of three sites in Zapata and Mil Cumbres.

An additional 11 species were detected by banding and/or point counts, or were observed incidentally, at less than four areas. Among rare species, we encountered Gundlach's Hawk (*Accipiter gundlachi*) in Mil Cumbres and Zapata, two of the five regions from which populations are known (Collar et al. 1992). Both regions are among the three "main population nuclei" (Wotzkow 1985). Plain Pigeon (*Columba inornata*) is considered to be at extreme risk of extirpation in Cuba where approximately 100 pairs are believed to survive (Collar et al. 1992), making the sighting of one at Salvador in 1994 especially noteworthy. A Bare-legged Owl (*Gymnoglaux lawrencii*) banded in 1994 at Sitio Viejo on Cayo Coco provided the first confirmed occurrence for Cayo Coco and was the first ever banded in Cuba. A Bananaquit (*Coereba flaveola*) banded at Dorada, Cayo Coco in 1993 was the first record of the species in Cuba in over 20 years (Garrido and García Montaña 1975, Garrido and Kirkconnell, unpubl. data). Other species detected in low numbers included Broad-winged Hawk (*Buteo platypterus*), Mangrove Cuckoo (*Coccyzus minor*), and Greater Antillean Nightjar (*Caprimulgus cubanensis*) each from one site on Cayo Coco, Bee Hummingbird (*Mellisuga helenae*) from one site in Mil Cumbres and one site in Zapata, Cuban Gnatcatcher (*Polioptila lembeyei*) from three sites on Cayo Coco, Bahama Mockingbird (*Mimus gundlachii*) from one site on Cayo Coco, and Yellow Warbler (*Dendroica petechia*) from two sites on Cayo Coco.

Detailed relative abundance data based on mist netting and point count results for each species at each of the 18 sites are available directly from the first author.

RELATIONSHIP OF MIGRANTS TO RESIDENTS

The results from banding and point counts differ in their portrayal of the relationships between the relative abundance and numbers of species of migrants and residents. The numbers of migrant and resident individuals captured/100 net-hr were significantly correlated ($r_s = 0.73$, $P = 0.003$), suggesting that sites that contained large numbers of residents also contained large numbers of migrants. Likewise, the numbers of migrant and resident species captured were significantly correlated ($r = 0.84$, $P < 0.001$), suggesting that sites that supported greater numbers of resident species supported greater numbers of migrant species. However, based on point counts, the numbers of residents and migrants detected within ≤ 25 m were uncorrelated ($r_s = 0.27$, $P = 0.25$), as were the numbers of resident and migrant species detected ($r = -0.14$, $P = 0.57$).

MIST NETS VERSUS POINT COUNTS

As the results above suggest, mist nets and point counts provide differing assessments of the relative abundance of Neotropical migrants and residents, in absolute terms and relative to each other. For Neotropical migrants as a group, point counts detected uniformly lower numbers of migrant individuals than mist nets, often failing to show differences in relative abundance that were suggested by mist netting (e.g., Cayo Coco, Fig. 2a,e). Conversely, relative abundance of residents as a group was underestimated by mist nets, particularly in Mil Cumbres (Fig. 2a,e). Overall, the relative abundance estimates for migrants and residents derived from mist nets and point counts were uncorrelated (migrants, $r_s = 0.389$, $P = 0.11$; residents, $r_s = -0.082$, $P = 0.74$). Estimates of the proportion of migrant individuals from mist nets were significantly greater than from point counts ($t_{34} = 4.33$, $P < 0.001$) and the two estimates were significantly correlated ($r_s = 0.723$, $P = 0.003$). Similarly, a comparison of most captured species with species most detected on point counts shows marked differences (McNicholl et al., unpubl. data).

Mist nets detected significantly more species of migrants than point counts ($t_{34} = 2.48$, $P < 0.02$) whereas point counts detected significantly more species of residents ($t_{34} = 5.32$, $P < 0.001$). The numbers of species of migrants and residents detected by mist nets and point counts were uncorrelated (migrants, $r = 0.318$, $P = 0.20$; resident, $r = 0.068$, $P = 0.79$). Mist nets provided a significantly greater estimate of the proportion of migrant species than point counts ($t_{34} = 6.44$, $P < 0.001$).

More satisfactory estimates of the numbers of migrant and resident species present in an area are obtained from the combined results of banding and point counts (Fig. 3). Based on this analysis, differences in numbers of resident species among regions matched the original point count results. The differences in numbers of migrant species and proportion of migrant species among regions matched the original banding results. However, both banding and point counts underestimated the "actual" number of migrant and resident species present, banding more severely for residents and point counts more severely for migrants. Point counts underestimated the numbers of migrants and residents by 41.3% and 7.8% respectively, whereas banding underestimated the numbers of migrants and residents by 22.9% and 36.0% respectively. The proportion of migrant species was underestimated 53.3% by point counts and 26.3% by banding.

Differences in detectability of migrants and residents by the two methods was further evaluated by regressing the mean number of individuals of a species detected within 25 m on point counts against the mean number of birds of that species captured per 100 net-hours (Fig. 4). Both regressions were significant with resident species having greater detectability on point counts relative to banding. The reverse was true for migrants. The slopes of the regression lines were significantly different ($t_{69} = 2.64$, $P < 0.02$). Individual species correlations of mist net and point count results are available directly from the first author. Only three species had significant positive correlations between their banding and point count results, Gray Catbird, Black-and-white Warbler, and Cuban Bullfinch. Of these, only Gray Catbird exhibited a strong correlation and is an example of a species that frequents the understory where it is easily caught in nets and a species that is vocal during winter and easily detected by point counts. Significant negative correlations occurred among uncommon species for which the likelihood of being detected by either method was probably due to chance. Vocal, high canopy residents such as Scaly-naped

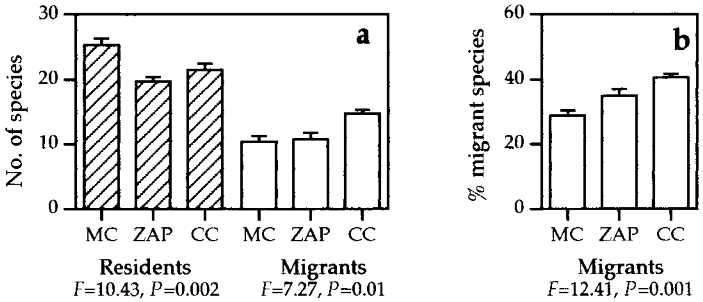

FIGURE 3. Comparison of species richness of Neotropical migrants and residents among three regions in Cuba using the total species censused by banding and point counts combined. MC—Mil Cumbres, ZAP—Ciénaga de Zapata, CC—Cayo Coco. Error bars equal one standard error. Statistics are for ANOVAs among regions.

Pigeon and Cuban Parrot would not have been detected by netting, whereas quiet, largely terrestrial migrants such as Worm-eating Warbler would have been detected only rarely without mist nets.

RELATION OF MIGRANT AND RESIDENT SPECIES ASSEMBLAGES TO VEGETATION STRUCTURE

We used PCA to combine 12 vegetation structure variables into simpler linear combinations of variables with which capture data for selected migrant and resident species could be correlated. We used tree species richness as a structural variable, assuming that it is positively related to structural heterogeneity. The first three principal components accounted for 54.0% of the total variation among the vegetation structure variables (PC-1 = 26.0%, PC-2 = 17.6%, PC-3 = 10.4%). Correlations of each variable with the three principal components are presented in Table 4. PC-1 is most correlated with characteristics of mature forest vegetation with high positive loadings for large tree-size class dominance values and canopy height and negative loadings for small tree-size classes and shrub stem density.

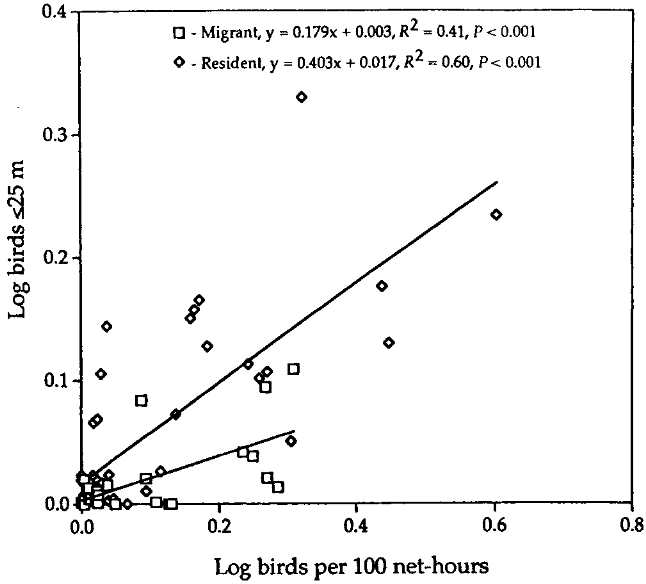

FIGURE 4. Regression of log birds ≤ 25 m against log birds/100 net-hours for 28 species of Neotropical migrants and 45 species of residents for which there were detections by at least one method. Each point represents one species.

TABLE 4. Correlation analysis of 12 vegetation structural variables with PC-I, II, and III.

Habitat variable	PC-I	PC-II	PC-III
Total tree density	−0.327***	0.891***	−0.036
S-class dominance	−0.209**	0.886***	−0.250***
A-class dominance	−0.616***	0.250***	0.333***
B-class dominance	−0.072	−0.002	0.736***
C-class dominance	0.491***	−0.071	0.552***
D-class dominance	0.655***	−0.130	0.187*
E-class dominance	0.621***	−0.085	−0.078
Shrub stem density	−0.494***	−0.203**	−0.030
Canopy cover	0.054	0.377***	0.353***
Ground cover	−0.186*	−0.609***	−0.327***
Mean canopy height	0.694***	−0.166*	0.471***
Tree species richness	0.023	0.055	0.606***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

PC-2 is most correlated with characteristics of lower stature, second-growth forest vegetation with high positive loadings for total tree density, S-class (the smallest tree size class) tree dominance, and canopy cover. PC-3 is most correlated with characteristics of mid-successional forest structure with high loadings for medium stature vegetation, canopy cover and height, and species richness.

Resident and migrant species exhibited different patterns of correlation with the principal components (Fig. 5a,b). Migrant relative abundance tended to be negatively correlated with mature forest structure variables (PC-1), positively correlated with secondary forest variables (PC-2),with little or no correlation with tree species richness and medium stature trees (PC-3). American Redstart and Black-and-white Warbler exhibit a negative correlation with PC-3 largely because of their high capture rates at semideciduous and mangrove net sites on Cayo Coco where species richness was low. Palm Warbler's negative correlation with PC-1, positive correlation with PC-2, and negative correlation with PC-3 is accounted for by high capture rates for the species at pine sites in Mil Cumbres and at the mangrove site on Cayo Coco where trees were widely spaced, canopy cover was only intermediate and tree species richness was relatively low.

Resident species exhibited a broader range of correlations with the principal components. Similar to Palm Warbler, the correlation pattern for Yellow-headed Warbler is best explained by its high capture rate in pine in Mil Cumbres. Cuban Emerald was also captured in greater numbers in Mil Cumbres than other areas and Cuban Solitaire was captured only there. Yellow-faced Grassquit's correlation with PC-2 is best explained by high capture rates in the open-structured pine forest, but its weak negative correlation with PC-1 suggests that its habitat use is also influenced by canopy height which was lower in the coastal scrub sites on Cayo Coco. The Cuban Bullfinch correlation was influenced strongly by high capture rates in pine, but low correlation with PC-3 suggests that their relative abundance is greater in sites with lower species richness and, hence, simpler structure, such as Vereda and Petrolera on Cayo Coco. The Stripe-headed Tanager (*Spindalis zena*) pattern is more difficult to explain since captures occurred mainly in two radically different forest types, sub-montane pine and coastal scrub, which have few structural characteristics in common, and one semideciduous forest site, Vereda, on Cayo Coco. The correlation pattern reflects this in the weaker negative correlation with PC-2 and lack of correlation with PC-1. We suspect that the phenology of fruiting trees is more important in affecting habitat use by this species based on the observation that 15.5% of trees, particularly *Metopium brownii* and *Coccoloba diversifolia,* were in fruit during sampling periods in coastal scrub. Cuban Pewee, Cuban Vireo, Loggerhead Kingbird, Cuban Tody, and Cuban Green Woodpecker represent a group of ubiquitous resident species found in a wide variety of habitats. None show strong correlations with any of the principal components, suggesting that capture rates were distributed evenly across gradients of vegetation structure. La Sagra's Flycatcher lies on the outside of this cluster of species and exhibits slightly higher correlation with forest structure associated with early successional and mid-successional forests, characteristics shared by all of the semideciduous forests. Red-legged Thrush capture

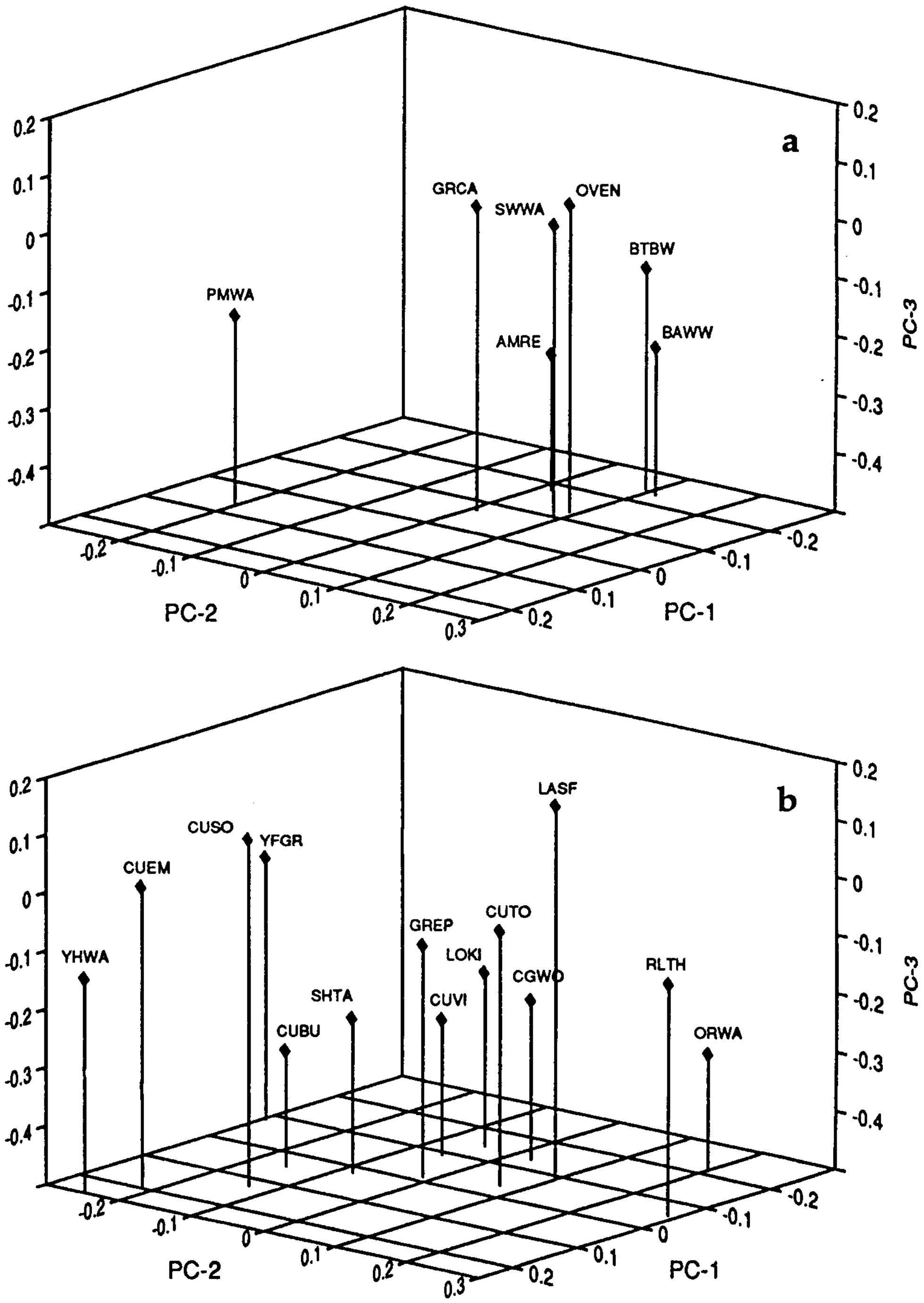

FIGURE 5. Correlation of capture rate (birds/100 net-hour) with three principal components (derived from 12 vegetation structure variables) for seven species of Neotropical migrants and 14 residents at 179 net sites. Part a: migrants; AMRE—American Redstart, BAWW—Black-and-white Warbler, BTBW—Black-throated Blue Warbler, GRCA—Gray Catbird, OVEN—Ovenbird, PMWA—Palm Warbler, SWWA—Swainson's Warbler. Part b: residents; CGWO—Cuban Green Woodpecker, CUBU—Cuban Bullfinch, CUEM—Cuban Emerald, CUSO—Cuban Solitaire, CUTO—Cuban Tody, CUVI—Cuban Vireo, GREP—Cuban Pewee, LASF—La Sagra's Flycatcher, LOKI—Loggerhead Kingbird, ORWA—Oriente Warbler, RLTH—Red-legged Thrush, SHTA—Stripe-headed Tanager, YFGR—Yellow-faced Grassquit, YHWA—Yellow-headed Warbler.

rates showed a strong positive correlation with PC-2 and, hence, forest vegetation with high tree density and a high S-class tree dominance, typical of semideciduous forests and coastal scrub. Oriente Warbler occurred only on Cayo Coco and had highest capture rates in sites with high tree density, low canopy, and low tree species richness.

EVIDENCE FOR SEXUAL SEGREGATION AMONG FOREST TYPES

An analysis of heterogeneity of sex ratios among forest types for eight species of migrants and six species of residents is presented in Table 5. We did not combine mesic, semideciduous forests in Zapata and Cayo Coco because of regional differences exposed by the analyses described above. Sample sizes for some species are low, but the data suggest that sexes of some migrants segregate by forest type. There were three statistically significant examples of sex segregation among habitats by migrants and three by residents.

Among migrants, the majority of Black-throated Blue Warblers captured in sub-montane pine were male. Elsewhere, they showed nearly equal proportions of males and females in mesic, semideciduous forest in Zapata, yet were female-biased in the same forest type on Cayo Coco and in more xeric habitats. Black-and-white Warbler was female-biased in all but xeric, semideciduous forest, where it was male-biased, and mangrove, where the sex ratio was approximately even. American Redstart was male-biased in sub-montane pine and in mesic, semideciduous forest in Zapata, but even or female-biased in all other forest types.

Evidence for sexual segregation was not expected for residents. The strong female bias in Cuban Emeralds in sub-montane pine and semideciduous, and mesic, sub-coastal semideciduous forest on Cayo Coco was indicative of breeding phenology. Emeralds at these sites were part way through their breeding seasons and female activity was high apparently because of frequent foraging to provision young. We also noted evidence of breeding activity among Stripe-headed Tanagers on Cayo Coco (i.e., cloacal protuberances in males, brood patches in females, recently fledged young). On Cayo Coco, we observed that males reacted strongly to the distress calls of other birds, particularly other tanagers, captured in mist nets, often resulting in additional captures. This phenomenon may have been accentuated by male territorial behavior. However, both sexes exhibited this behavior at Mil Cumbres. The male-biased sex ratio of Cuban Bullfinch in sub-montane pine may also be due to breeding phenology and territorial behavior, but the female-biased sex ratio in mangrove has no clear explanation.

DISCUSSION

This study is the most extensive quantitative survey of Neotropical migrant and resident birds undertaken to date in Cuban forest habitats and improves our ability to discuss the status and distribution of Neotropical migrants in Cuba and to compare Cuba with other wintering regions, particularly in the West Indies and adjacent Mexico and Central America. We found that Cuban forests supported large numbers of Neotropical migrant individuals and species, further substantiating that Cuba is an important wintering area. The surveys provided a number of new records for species on a regional and national scale, and increased our understanding of the winter status of several Neotropical migrants, notably Swainson's Warbler (Kirkconnell et al. 1996).

Many of the 23 forest types identified in Cuba are distributed locally, but our surveys included forest habitats that account for a large proportion of the forest cover in the regions surveyed and remaining in Cuba today. Lowland seasonally dry semideciduous forest was historically the most widespread forest type in Cuba (Instituto de Geografía de la Academia de Ciencias y Instituto Cubano de Geodesia y Cartografía 1989), and in the West Indies in general. Our surveys indicate that today it constitutes an important habitat for wintering migrants and residents. Like Wunderle and Waide (1993), we found that xeric habitats supported lower numbers of migrant individuals than other forest types, but also that these differences apparently hold within regions and not beyond. Pine forests were identified as supporting greater numbers of migrants and residents than semideciduous in Mil Cumbres. Other studies have identified mangrove as a forest type highly favored by certain species of overwintering Neotropical migrants (Lynch 1989, 1992, Lefebvre et al. 1992, Wunderle and Waide 1993). Although we were able to survey only one mangrove site, we found it to be the single most productive site for both residents and migrants. We did not survey second growth, pastures, or other

TABLE 5. Male : female sex ratios of dichromatic species in six forest types in three regions of Cuba, based on mistnet captures. Forest types: A—mesic, sub-montane, pine; B—mesic, sub-montane, semideciduous; C—mesic, sub-coastal, semideciduous; D—xeric, sub-coastal, semideciduous; E—xeric, coastal scrub; F—sub-coastal mangrove.

Species	Region	Mil Cumbres		Zapata		Cayo Coco					
	Forest type	A	B	C	D	C	E	F	χ^2	df	*P*
Neotropical migrants											
Northern Parula		1:3	—	—	5:4	3:0	6:2	2:2	5.06	4	0.28
Cape May Warbler		—	—	—	—	—	4:8	—	—	—	—
Black-throated Blue Warbler		5:1	—	13:10	1:7	3:20	14:19	1:3	17.43	5	0.004
Prairie Warbler		—	—	—	2:2	1:1	5:6	8:6	0.34	3	0.95
Black-and-white Warbler		2:3	2:1	4:8	10:3	4:28	7:12	12:10	20.76	6	0.002
American Redstart		11:3	2:0	10:4	5:5	27:30	3:9	9:14	13.36	6	0.04
Common Yellowthroat		4:0	—	—	1:0	—	0:1	5:4	5.00	3	0.17
Hooded Warbler		—	3:0	0:1	—	1:2	—	—	4.28	2	0.12
Residents											
Common Ground-Dove		—	—	—	—	0:2	10:7	1:1	2.49	2	0.29
Cuban Emerald		3:17	0:10	0:1	6:3	1:5	5:4	1:0	18.73	6	0.005
Cuban Green Woodpecker		1:0	1:1	6:3	2:2	9:12	10:9	4:2	2.81	6	0.82
Stripe-headed Tanager		46:27	6:5	—	—	20:18	68:20	9:2	10.19	4	0.04
Cuban Bullfinch		44:21	—	—	2:2	19:17	21:21	23:40	12.55	4	0.01
Yellow-faced Grassquit		47:27	3:2	—	—	6:6	13:13	2:0	3.28	4	0.51

agricultural habitats as have others (e.g., Lynch 1989, 1992, Greenberg 1992, Robbins et al. 1992).

Until recently, all work during winter in Cuba has focused on western Cuba, mainly Zapata and Pinar del Río Province, because of its relatively easy access from La Habana. Our surveys extended coverage far to the east by including Cayo Coco and showed that strong regional differences exist within Cuba. Nonetheless, nearly two-thirds of the country remains largely unstudied during winter. For that reason, we plan to conduct surveys in eastern Cuba in coming years.

Our surveys expanded on preliminary surveys conducted in Los Sábalos, a mesic, semideciduous forest in Zapata, during winter 1988 and 1989 (González Alonso et al. 1990, 1992). Similar to our results, mist nets and point counts provided different estimates of the relative contribution of Neotropical migrants to the winter bird community. Approximately 55% of individuals captured and 10% detected on counts were migrants while our mesic, semideciduous sites in Zapata ranged from 27.8–53.0% and from 11.6–35.9%, respectively. A total of 20 migrant landbird species was recorded by banding and/or point counts at Los Sábalos (41.7% of total), whereas our surveys detected 8–15 species (28.6–42.9% of total) among the six sites, a disparity probably due to differences in sampling effort. Whereas we netted for four mornings and used 10-min point counts, netting at Los Sábalos spanned eight to nine days, sunrise to sunset, and point counts lasted 20 min.

Wunderle and Waide (1993) conducted the only other quantitative study with winter data from Cuba to which our results can be compared. Their surveys covered five sites, one in each of five habitats, four of which were forest habitats. Two habitats corresponded to types we surveyed, montane broadleaf forest (our mesic, sub-montane semideciduous) and mangrove (our sub-coastal mangrove). They emphasized point counts in their surveys, doing 30–31 counts per site, which was approximately twice the number of counts and 3.75 times the number of point count locations per site that we used. They ran nets 221–367.9 net-hours at each site (adjusted to match our use of 9 m nets), approximately half our netting effort. By counting all species detected by both methods and species observed incidentally, Wunderle and Waide found the proportion of migrant species to be 35.8% (19/53). Using the same method, we found 39.0% migrant species (32/82). Acknowledging that Wunderle and Waide's study sites were all in Pinar del Río Province, and that our surveys showed considerable inter-region variation, our Mil Cumbres migrant species proportion is more fairly used as a basis of comparison and was 53.7% (22/41). Greater point count effort may well have resulted in the greater number of resident species detected by Wunderle and Waide.

Species comparisons must be made with caution given the differences in habitats covered. However, the results from both studies were similar in the one shared forest type in Mil Cumbres, although Wunderle and Waide's frequencies of detection were slightly higher, probably due to greater spatial coverage. American Redstart was the most frequently detected migrant on point counts. Black-throated Green Warbler was encountered only twice by us, whereas Wunderle and Waide detected them on approximately 15% of counts. The Tennessee Warblers (*Vermivora peregrina*) and Wilson's Warbler (*Wilsonia pusilla*) detected by Wunderle and Waide were probably migrants, given the numbers they encountered, the timing of their surveys, and the fact that neither is a regularly wintering species in Cuba (Garrido and García Montaña 1975, Garrido and Kirkconnell 1993). Mangrove on Cayo Coco apparently holds greater numbers of Palm and Prairie Warblers than mangrove in Pinar del Río.

Acknowledging that other studies have emphasized surveying a successional continuum (Lynch 1989) or altitudinal and moisture gradients (Wunderle and Waide 1993), several general comparisons can be made to closely neighboring West Indian islands, the Yucatán Peninsula of Mexico, and Belize. We detected 32 species of migrants (39.0% of total) overall. Within habitats a mean of 35.5% of species (range: 28.2–40.6%) were migrants. The proportion of migrant individuals within habitats averaged 32.4% (range: 20.6–50%) using mist nets and 25.1% (range: 18.1–33.4%) using counts. Our surveys detected more species of migrants than in either the Bahamas or on other of the Greater Antilles surveyed by Wunderle and Waide (1993) (range: 12, St. John − 21, Andros). A greater proportion of migrant species were detected by Wunderle and Waide (1993) on New Providence, St. John, Great Inagua, and Andros (range: 41.9–46.6%) where the numbers of resident species were lower than in Cuba. In the Bahamas and Greater Antilles taken together, 35 species of migrants were detected (23% of total). Within habitats, a mean of 32% (range: 6–50%) were migrant species and 25% (range: 1–71%) of individuals were migrants (Wunderle and Waide 1993). In the Cayman Islands, 20 migrant species regularly winter accounting for 42.6% of all species (Johnston 1975). In Jamaican forest and coffee and citrus plantations, Robbins et al. (1992) recorded a mean of 10 migrant species using mist nets (range: 6–16), for a mean of 28.4% migrant species (range: 16.7–44.4%); 17.8% of birds captured were migrants (range: 10–24%). Mist net surveys by Terborgh and Faaborg (1980) on Hispaniola detected a mean of 5 migrant species (range: 1–8) accounting for a mean of 29.6% (range: 8.3–44.4%) of all species. A mean of 30.9% of individuals captured were migrants (range: 3–66%). Also on Hispaniola, Robbins et al. (1992) recorded a mean of 8.5 species using mist nets (range: 6–11) for a mean of 41.7% (range: 33.3–50%) of all species.

Mexico's Yucatán Peninsula and adjacent Belize support a greater number of migrant species than any of the Caribbean islands. Lynch (1989) encountered 43 species on point counts (21% of total) and 38 with nets (26.4% of total). Within habitats, migrants accounted for a mean of 37% of all species (range: 29.2–54.2%) and 41% of individuals. Waide (1980) provided comparable results for the Yucatán, although Waide et al. (1980), in a broader Yucatán survey, found a similar proportion of migrant species ($\bar{x} = 26.8\%$, range: 0–52%), but found a lower proportion of migrant individuals ($\bar{x} = 28.7\%$, range: 0–56%) than Lynch (1989). In Belize, Robbins et al. (1992) encountered a mean of 13.8 migrant species using mist nets (range: 3–28) for a mean of 33.6% (range: 10.7–46.7%) of all species. Overall, it appears that the sites we surveyed in Cuba supported fewer migrant species, but they accounted for a greater proportion of species present in the community than in the Yucatán and Belize and a lower proportion of the total individual birds present than in the Yucatán.

Our banding results suggest that sites that support large numbers and many species of residents also support large numbers and many species of migrants, but our point count results indicated the opposite. Positive correlation of resident and migrant species and individual abundance has been reported from western Mexico (Hutto 1980) and the Yucatán (Waide 1980, Lynch 1992). In the Caribbean, this trend was supported by surveys from the Bahamas, but not from the Greater Antilles (Wunderle and Waide 1993), or Jamaica (Gochfeld 1985). Our results leave the issue without clear support for either trend. PCA correlation of capture rates and vegetation structure in our study sites suggests that residents occupy a broader spectrum of vegetation structure types than migrants. Certain residents (e.g., Cuban Emerald, Cuban Solitaire, Yellow-headed Warbler, and Yellow-faced Grassquit) are apparently specialized in their use of mature, high canopy, montane forest, particularly pine. Red-legged Thrush may be an example of a successional forest specialist. Of the migrant species for which we had sufficient data, only the Palm Warbler was an example of an open habitat specialist, as suggested by Wunderle and Waide (1993). Although we could not apply the PCA analysis to Northern Waterthrush, it was clearly an example of a mangrove forest specialist, as also noted by Lack and Lack (1972), Emlen (1977), Lynch (1989, 1992), and Wunderle and Waide (1993). Our data suggest that more residents are specialists than migrants, a finding supported by Lynch (1989).

Data for sex ratios among habitats suggest that some wintering dichromatic warblers segregate by sex among habitats. Other studies have detected this phenomenon among wintering warblers in the Yucatán (Lynch et al. 1985, Lopez Ornat and Greenberg 1990), Jamaica (Parrish and Sherry 1994), and Puerto Rico (Faaborg and Arendt 1984, Wunderle 1992). Our results indicate different patterns of sexual distribution not only among forest types, but also among regions within the same forest type (e.g., Black-throated Blue Warbler and American Redstart). Just as habitat segregation by sex within a region complicates conservation efforts for a species and necessitates protection of two or more habitats (Petit et al. 1993), segregation across regions poses additional management challenges and deserves further study.

Finally, like others before us, we feel compelled to comment on the efficacy of using mist nets and point counts in surveys of Neotropical migrants and residents. The potential for mist nets to under-sample canopy species has long been known (Karr 1981). Mist nets may inflate the estimate of the ratio of migrant to resident species (Waide 1980, Waide et al. 1980). Wunderle and Waide (1993:929) commented that "only small, secretive, non-flocking species that inhabit dense low-stature vegetation are likely to be best censused by netting." Mist net mesh size may also influence the ratio of migrant to resident species because smaller species, such as migrant warblers, are captured more effectively in small mesh nets, whereas larger species, such as many Neotropical residents, are captured more effectively by larger mesh nets (Pardieck and Waide 1992, Robbins et al., unpubl. data). Petit et al. (1993) view mist-netting as a method potentially supplementary to visual/aural methods, such as point counts, to collect survival information from recaptures. However, because of bias, mist netting is not apparently considered a primary method in surveys of migrant habitat use. We hasten to point out that the methodology chosen by researchers will vary depending on the vegetation structure, the species targeted by the surveys, and the time available. Our results suggest that both mist nets and point counts have inherent biases. Surveys of the regions we sampled in Cuba would have been grossly lacking without the use of both methods, since each method critically underestimated the species composition of the regions when examined singly. In our surveys, both were primary techniques of assessing migrant and resident birds *and* understory and canopy species. We encourage others to use both techniques *intensively and in concert with each other* to obtain the best results.

ACKNOWLEDGMENTS

This project was supported by the Institute of Ecology and Systematics of the Cuban Ministry of Science, Technology, and Environment, the Canadian Wildlife Service Latin American Program, the Long Point Bird Observatory, and the Canadian Nature Federation. Graeme Gibson brought us together and provided the impetus to initiate the work. Kathy Freemark assisted in development of the project design. We would like to thank the following people for their participation in the field: Martín Acosta, Eduardo Alfonso, Vincente Berovides, Pedro Blanco, Jane Bowles, Tania Chataloín, Bev Collier, Ronel Concepción, Enrique del Risco, Donald Fillman, Xiomara Gálvez, María Elena García, Esteban Godinez, Raúl Gómez, Alberto González, Colleen Hyslop, Judith Kennedy, Frank Loyola, Miriam Martinez, Jon McCracken, Beatrice Mulkay, Lourdes Mugica, Carlos Peña, Alina Pérez, Ramon Pérez, Margarita Pimental, Ron Ridout, Rodolfo Sánchez, Eliser Socarrás, Steve Wendt, and Daily Zuñiga. Travel arrangements were facilitated by the Cuban Embassy, the Cuban Consulate General, and Nancy Hovendon of Magna Holidays and the Canada-Cuba Sports and Cultural Festivals. Statistical assistance was provided by Terrie Donovan, Charles Francis, Jim Fultz, and Raymond Semlitsch. Joe Walter produced the map. The manuscript benefitted greatly from the editorial comments of Jane Bowles, John Faaborg, Walter Koenig, Jon McCracken, Chandler Robbins, Frank Thompson, and an anonymous reviewer. This is a publication of Bird Studies Canada and the Long Point Bird Observatory.

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