

DISTRIBUTION OF OVERWINTERING NEARCTIC MIGRANTS IN THE BAHAMAS AND GREATER ANTILLES¹

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Abstract. Point counts and mist nets were used to survey the distribution of nearctic migrant landbirds wintering in 15 habitat types on the islands of Andros, New Providence, and Great Inagua in the Bahamas, and in western Cuba, Jamaica, Dominican Republic, Puerto Rico, and St. John in the Greater Antilles. Of 150 species detected, 23% were overwintering nearctic migrants. Migrants were found at 1-71% of the points in natural or disturbed habitat (mean = 25%). Distance from North America and island size contributed only 9% of the variation in total migrant abundance among all habitats, reflecting the fact that habitats on the same island often differed substantially in suitability. However, distance and island size contributed 48% of the variation in total migrant abundance in xeric habitats, indicating that these factors may be important in contributing to migrant abundance within a habitat. Generally, geographically-restricted species were not abundant while most geographically-widespread species were abundant in a wide range of habitats.

No consistent relationships were found between the abundance and distribution of migrants and residents, but the two groups did not differ in their degree of habitat specialization. Habitat specialization by migrants was rare, with one species restricted primarily to mangroves and another to pine. As found in Yucatan, migrant species that breed in mature temperate-zone forest occurred in both mature forest and second-growth habitats in the winter. However, migrants that breed in early second-growth or edge habitats mostly avoided closed-canopy forests in the Caribbean.

Key words: Bahamas; Caribbean; distribution; habitat use; migratory birds; Parulinae.

INTRODUCTION

Declining populations in some nearctic migrant landbirds may be associated with deforestation on either the northern breeding grounds or on the tropical wintering grounds (reviewed in Askins et al. 1990). Although recent local population declines are attributed mostly to forest fragmentation on the breeding grounds, the high rate of deforestation in Middle America and the Caribbean (Lanly 1982) is likely to have a greater effect in the future (Rappole and Powell 1986). Already, forest cover is estimated at only about 21 percent of the island land area in the Bahamas and Caribbean (Wunderle and Waide, in press), and declines in wintering migrants have recently been documented at one Caribbean site (Faaborg

and Arendt 1990). Caribbean and Bahamian land use changes, as well as those in Mexico and Central America, could be especially detrimental to migrants because most winter in close proximity to the southern U.S. (Keast 1980).

Several studies have demonstrated that nearctic migrant landbirds commonly winter in a diversity of habitats in the Bahamas and Caribbean. Previous investigators described foraging ecology and habitat use on a single island (i.e., Jamaica, Lack and Lack 1972) or compared population biology on pairs of nearby islands (i.e., Grand Bahama and Andros, Emlen 1980; St. Thomas and St. John, Askins et al. 1992). Surveys of local observers throughout the Caribbean documented the distribution and status of migrants (Arendt 1992). Other studies have been broad geographic surveys of migrants on numerous Caribbean islands based on specimens (Pashley 1988a, 1988b, 1990) or censuses in a variety of habitats (Terborgh and Faaborg 1980). The latter study suggested that the proportion of

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wintering migrants, relative to residents, declines with distance from the continental United States. This distribution pattern, which may reflect combined effects of area and distance, was believed to be the major factor controlling migrant abundance in the region. Effects of climate, habitat quality, and local density of resident species were found to be less important (Terborgh and Faaborg 1980).

We surveyed the distribution of wintering nearctic landbird migrants on the islands of Andros, New Providence, and Great Inagua in the Bahamas, and in western Cuba, Jamaica, Dominican Republic, Puerto Rico, and St. John in the Greater Antilles. Our surveys were designed to answer the following questions. (1) What is the pattern of distribution and abundance of individual migrant species among the islands of the Bahamas and Greater Antilles? (2) What is the relative abundance of individual migrant species in the most common natural and disturbed habitats in the Bahamas and Greater Antilles? Answers to these questions will permit comparisons with similar studies in southern Mexico (e.g., Lynch 1989, 1992), and enhance our understanding of migrant winter distribution, facilitating conservation efforts.

METHODS

We surveyed common and widespread habitats representative of both disturbed and undisturbed vegetation in the Bahamas and Greater Antilles. These habitats are broadly classified as: (1) mangrove, (2) dry scrub, (3) dry limestone forest, (4) brushy old field, (5) shaded pasture, (6) mixed, dry limestone scrub and pine overstory, (7) mature pine forest, (8) residential with ornamental plantings, (9) lowland moist second growth, (10) moist/mesic forest, (11) wet limestone forest, (12) shade coffee plantation, (13) sun coffee plantation, (14) montane broadleaf forest, (15) montane second growth. Habitat and locations are described in Wunderle et al. (1992) for Jamaica, and the remainder can be obtained by writing the Library, The International Institute of Tropical Forestry, U.S.D.A. Forest Service, Call Box 25000, Rio Piedras, Puerto Rico 00928-2500, U.S.A. We did not attempt to systematically analyze local variation in bird populations or vegetation within a given habitat type on an island. Instead we pooled samples from different geographic sites on an island for each habitat type.

VEGETATION

We used two to four 16-m diameter circular plots (0.02 ha) to quantify vegetation in all habitats except Bahamian mangroves, brushy old fields, shaded pastures, residential habitats, and the two habitats on St. John. Two plots were placed in vegetation representative of areas in which bird point counts were made. Additional plots were occasionally located near the mist nets or in areas representing the extremes of vegetation structure in variable habitats.

Stems of all standing trees and saplings ≥ 3 cm DBH were measured 1.3 m above the base (DBH) and were recorded within the following diameter classes: 3–8 cm, >8–15 cm, >15–23 cm, >23–38 cm, and >38 cm DBH. Trees were classified as broadleaf, conifer, palm, or standing dead.

Shrub density at breast height was estimated along four 8-m transects running in the cardinal directions centered within the 0.02 ha circle. Density was determined by an observer walking along the transects and counting all woody stems (<3 cm) touching the observer's body and outstretched arms at breast height. The contribution of broadleaf shrubs, coniferous saplings, and palms was recorded separately.

Foliage height profiles were determined at 20 points located at 1.6 m intervals along the north, south, east and west radii of the circular plot (after Schemske and Brokaw, 1991). A 3-m tall pole (2.0 cm diameter) marked at 0.5 m intervals was placed vertically at each sample point. We recorded the presence or absence of foliage touching the pole within each height class. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following estimated height intervals: 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, 20–25, and 25–30 m. For each height interval, percent cover was calculated by dividing the number of points in which foliage was present in that height interval by the total number of sample points ($n = 20$) and multiplying by 100. Heights of ten canopy trees in the plot were measured with optical range finders.

BIRD CENSUSES

Migrant and resident birds were censused with point counts during the winters of 1986–1989, and 1992, as follows: Puerto Rico (21 Nov. 1986–15 Mar 1987); Andros (10–16 Dec. 1986); Great Inagua (17–23 Dec. 1986); New Providence (25–

TABLE 1. Number of point counts and netting effort in 15 habitats in the Bahamas and Greater Antilles, Dec.–Feb., 1986–1989, except Puerto Rico mist netting and St. John point counts (see text). Numbers after island name refer to different geographic sites where same habitat type was sampled. Number in parentheses indicates net hours.

Habitat Island	Stature of Vegetation				Total
	Low (< 3 m)	Medium (4–10 m)	Tall (11–20 m)	Very Tall (> 20 m)	
Mangrove					205 (548)
Andros	30				
Great Inagua	29	(192)			
Cuba			30 (170)		
Jamaica			30 (121)		
Dom. Republic			30 (65)		
Puerto Rico 1			26		
Puerto Rico 2			30		
Dry Scrub					437 (809)
Andros 1		32 (108)			
Andros 2		(109)			
Andros 3		(44)			
New Providence		15 (66)			
Great Inagua 1	30				
Great Inagua 2	30 (58)				
Great Inagua 3	30				
Great Inagua 4	30 (100)				
Jamaica		30			
Dom. Republic 1	30				
Dom. Republic 2		30 (110)			
Dom. Republic 3	45				
Dom. Republic 4		30 (119)			
Dom. Republic 5		45			
Dom. Republic 6	30 (95)				
St. John		30			
Dry Limestone Forest					60 (283)
Jamaica			30 (283)		
Puerto Rico			30		
Brushy Old Field					35
Andros	35				
Shaded Pasture					181
Cuba		31			
Jamaica		30			
Dom. Republic 1		30			
Dom. Republic 2		30			
Dom. Republic 3		30			
Puerto Rico		30			
Mixed Dry Limestone Scrub & Pine Overstory					30
Andros		30			
Mature Pine Forest					205 (346)
Andros 1		30 (110)			
Andros 2		30			
New Providence		30			
Jamaica			30		
Dom. Republic 1			60 (144)		
Dom. Republic 2			25 (92)		
Residential With Ornamental Plantings					49 (32)
Great Inagua		30 (32)			
Puerto Rico			19		

TABLE 1. Continued.

Habitat Island	Stature of Vegetation				Total
	Low (< 3 m)	Medium (4–10 m)	Tall (11–20 m)	Very Tall (> 20 m)	
Lowland Mesic Second Growth					60 (316)
Jamaica		30 (193)			
Dom. Republic		30 (123)			
Mesic/Moist Forest					60 (98)
Dom. Republic			30 (98)		
St. John			30		
Wet Limestone Forest					90 (171)
Jamaica				30 (171)	
Dom. Republic			30		
Puerto Rico			30		
Shade Coffee Plantation					138 (527)
Cuba			30 (283)		
Jamaica			28		
Dom. Republic 1			20 (48)		
Dom. Republic 2			30 (196)		
Puerto Rico			30		
Sun Coffee Plantation					33 (178)
Jamaica		33 (178)			
Montane Broadleaf Forest					194 (3,305)
Cuba			30 (185)		
Jamaica			43 (196)		
Dom. Republic 1			31 (218)		
Dom. Republic 2			30		
Puerto Rico (Low)			30 (1,103)		
Puerto Rico (High)			30 (1,603)		
Montane Second Growth					61 (1,323)
Cuba		31 (234)			
Puerto Rico		30 (1,089)			
Grand Total					1,838 (7,936)

28 Dec. 1986); Dominican Republic (4–29 Jan. 1987); Jamaica (2–23 Dec. 1987); Cuba (21 Feb.–2 Mar. 1989); and St. John (8–11 Jan. 1992). These counts occurred after the fall migration and before the spring migration, and all sampled birds were assumed to be winter residents.

We modified the fixed-radius point count method of Hutto et al. (1986) after running preliminary counts to determine the effectiveness of the technique in three different habitats in Puerto Rico. A single observer recorded all birds seen and heard during a ten-minute period at each point. Counts were initiated at sunrise and terminated before 11:30, with most counts completed before 10:30. Each point was at least 100 m from all others and not closer than 25 m from a habitat edge. We attempted to complete 30 point counts per habitat patch, but frequently

the size of the habitat limited the number of point counts (Table 1). In dense habitats, we sampled from trails or roads and frequently used trails to travel through a habitat. In open habitats, we used a compass to follow a transect.

For each bird observed during a point count, we estimated the minimum distance from the observer. Those birds that were heard but not seen were tallied in one of two categories: ≤ 25 m from the observer or > 25 m from the observer. Before sampling, we chose 25 m as the radius within which we could detect all individuals in all but the most dense habitats. For each habitat sampled on an island, we calculated both the mean number of detections for each species per 25 m radius plot and the percentage of points with at least one detection within 25 m.

We used mist netting as a supplement to point

counts in 33 of 60 sites (Table 1) to help detect secretive species that might otherwise be missed. We used 12 m nets with 30 mm mesh and four shelves, set to a height of 2.5 m, usually in a continuous line. The procedure for all islands, except Puerto Rico, was to set 15 to 20 nets during an afternoon and then open them at sunrise on the following day; nets were kept open until late afternoon. In this way, morning netting was simultaneous with point counts in the same habitat. We clipped off a small piece of the outer primary feather from each captured bird for identification of recaptures.

In Puerto Rico, mist netting was not done simultaneously with point counts. Rather, we present capture results from other years (15 Jan.–29 Feb. 1984, in low montane broadleaf forest and montane second growth). Also, because the Puerto Rican netting involved many more net-hours than at other sites (Table 1), the Puerto Rican data were excluded from quantitative analyses and should be interpreted primarily as an indication of the presence or absence of migrant species.

ANALYSIS

We characterized migrant abundance and species richness at each site with several different measures. The percentage of individuals that were migrants and the percentage of species that were migrants were computed. Migrant species richness was determined by the technique of rarefaction (Simberloff 1972, 1978) to compare species richness in different sites obtained from point count samples of different sizes (15 and 20 individuals). Measures of total migrant abundance include the percentage of point counts with migrants within 25 m and the average number of migrants per point (within 25 m). We calculated a similarity coefficient (S.C.) to compare migrant assemblages between two habitats using the equation $S.C. = 2W/(a + b)$ from Cox and Ricklefs (1977). Here W is the sum of the lesser abundance values for each species common to the two habitats, where the abundance value is the percentage of points with the particular species. The values a and b are the sum of the abundance values (i.e., percentage of points) for all migrant species in the two habitats. The coefficient varies from 0 to 1, with 1 representing complete overlap of migrant assemblages.

Multiple regression (Tabachnick and Fidell 1983) was used to determine the contribution of

certain independent variables to the observed variance in migrant abundance and species richness. Initially multiple regression was used to test the hypothesis that migrant species richness and total abundance at 60 sites sampled by point counts on the seven islands varied with distance from the mainland and with island size. Separate analyses were performed for the Bahamas and the Greater Antilles and for individual migrant species. We report the multiple R^2 values and significance level, as well as the squared semi-partial correlations (and their significance levels), which represent the unique contribution of each independent variable to the R^2 given that other independent variables are constant (Tabachnick and Fidell 1983).

Two different measures were used to quantify the association between two variables. If the association was linear, as established by visual inspection of the graphed data, we used a Pearson correlation coefficient. However, if the association was non-linear or involved a variable measured as a percentage, we used the Spearman rank correlation coefficient. Bonferroni-adjusted probabilities are provided for all multiple comparisons of Pearson or Spearman correlations (see Wilkinson 1989).

For each species, we used a row \times column test of independence (corrected for small cell size) with a G -statistic (Sokal and Rohlf 1981) to test for significant heterogeneity among occupied habitats on the same island. The nonparametric Mann-Whitney U -test was used in cases where the sample distributions were apparently non-normal, based on skewness and kurtosis; the parametric paired t -test was used when the sample distributions were not different from normal. In all statistical analyses a probability of type I error of 0.05 or less was accepted as significant, but we report higher value for descriptive purposes. Throughout the text we use standard errors to describe variation around the mean and provide 95% confidence intervals for percentages.

We used a principal component analysis (PCA) to summarize the distribution of the 16 most abundant migrant species and relate them to potential environmental gradients. We used migrant occurrences in 60 island sites in the Bahamas and Greater Antilles, including the point count results from major sample sites on Andros ($n = 6$), New Providence ($n = 2$), Great Inagua ($n = 6$), Cuba ($n = 5$), Jamaica ($n = 10$), Do-

minican Republic ($n = 19$), Puerto Rico ($n = 10$), and St. John ($n = 2$). The PCA was generated with Systat (Wilkinson 1989) using a correlation matrix and four factors. A varimax rotation was selected because it provided better separation than either equamax or quadramax rotations (Harman 1976). To interpret the underlying environmental gradient represented by each principal component, the habitat variables (weighted for species abundance) were correlated with each PC using Pearson product-moment correlation. Weighting was accomplished by multiplying each bird species' maximum frequency of occurrence by the average habitat variable measurement obtained at the site of the species' maximum occurrence.

RESULTS

DIVERSITY AND ABUNDANCE OF MIGRANTS ON THE EIGHT ISLANDS

We detected a total of 150 species of landbirds (excluding aerial foragers), of which 35 (23%) were overwintering nearctic migrants (see Appendix 1 for scientific names). Migrants constituted the highest percentage of species on Andros (47%; 21/45), followed in descending order by Great Inagua (45%; 15/33), St. John (43%; 12/28), New Providence (42%; 13/31), Cuba (36%; 19/53), Puerto Rico (34%; 18/53), Dominican Republic (31%; 17/55), and Jamaica (30%; 20/67). Of the migrants, a Wilson's Warbler (Cuba) was observed only between point counts. Of the remaining 34 migrant species, 18 were recorded in both point counts and nets, 11 only in point counts, and five only in nets. The majority of wintering migrant species (74%) were wood warblers (subfamily Parulinae in Emberizidae).

We conducted 1,838 point counts at 60 sites in 15 habitats on the eight islands (Table 1). Point counts were not distributed evenly among islands: Andros and Great Inagua received the best coverage in terms of the representation of the major habitats, while the very high diversity of Cuban habitats was poorly represented by our limited samples.

The mean number of migrants per point (abundance) and the percentage of points with migrants at the same site (frequency) are highly correlated (Spearman $r = 0.90$, $df = 58$, $P < 0.0001$), and either measure is an adequate descriptor of overall migrant numbers. In addition, even the most common migrant species, when present at a point, was usually represented by no

more than one individual per point ($\bar{x} = 1.12$; range = 1.00–1.29; $n = 16$ species). Therefore it is reasonable to use frequency or percentage as an indication of abundance. This enables comparison with similar studies in the Yucatan Peninsula (Lynch 1989, 1992).

GEOGRAPHIC DISTRIBUTION PATTERNS

We used multiple regression to examine the possibility that migrant species richness and abundance decreases with distance from the continental U.S. and with island size, as observed by Terborgh and Faaborg (1980). We accomplished this by examining the effect of two independent variables (island size and distance from the closest point on Florida to each census site) on the measures of migrant species richness and total abundance. The eight islands showed considerable differences in both area (St. John, 50 km²–Cuba, 114,524 km²) and distance from Florida (Andros, 205 km–St. John, 1,790 km). These two variables were not significantly correlated (Pearson $r = -0.31$, $df = 6$, $P = 0.46$).

Multiple regression indicates statistically significant variation in the percentages of migrant species and individuals and frequency, which was explained by both island size and distance (Table 2). However, the two independent variables together never accounted for more than 15% of the variation in any of the migrant measures. Distance alone accounted for 9–14% of the total variation. The percentage of migrant species and individuals and frequency (Fig. 1) all declined with distance. The effect of island size was negligible. Variation in rarefaction estimates of species richness ($n = 15$ or 20 individuals) was not significantly related to either island area or isolation. The relatively small amount of variation in migrant prevalence attributable to island size and distance from Florida suggest that other environmental factors are more important.

Island size and distance from the mainland account for considerably more variation in migrant abundance when the analysis is restricted to a specific habitat type. For example, dry scrub or dry forest was sampled at sixteen different sites on all islands except Cuba (Table 1). Multiple regression of the sixteen dry sites indicates that a statistically significant amount of variation in the percentage of migrant species ($R^2 = 0.69$, $P < 0.001$) and frequency ($R^2 = 0.48$, $P = 0.02$) was explained by both island size and distance. In both cases, distance was the only variable

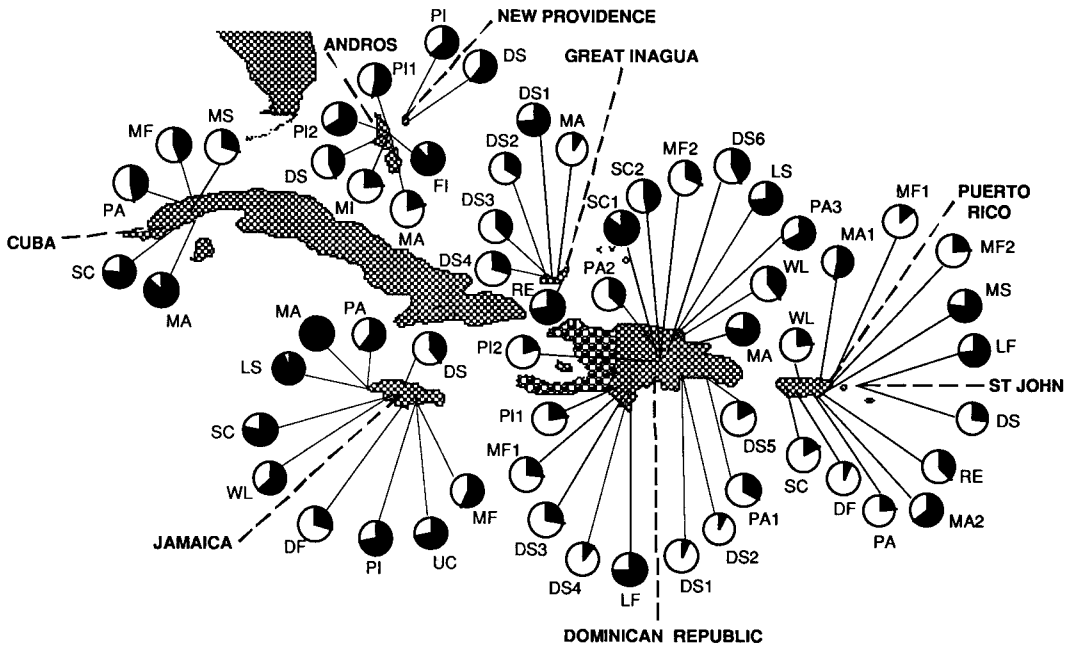


FIGURE 1. Percentage of 25-m radius point counts in which wintering nearctic migrant landbirds were detected in the Bahamas (Andros, New Providence, Great Inagua) and Greater Antilles (Cuba, Jamaica, Dominican Republic, Puerto Rico, St. John) during November–March 1986–1992. The black portion of the circles indicate the percentage of points with migrants in habitats designated by a two letter code: DS, dry scrub; DF, dry limestone forest; FI, brushy field; LF, mesic/moist forest; LS, lowland second growth; MA, mangrove; MI, mixed pine and scrub; MF, montane broadleaf forest; MS, montane second growth; PA, pasture; PI, pine; RE, residential; SC, shade coffee; UC, sun coffee; WL, wet limestone forest. If the same habitat was sampled in more than one location on an island, the number of each location is indicated after the habitat code. Number of point counts in each habitat are summarized in Table 1.

which contributed significantly to variation in the percentage of migrant species ($sr^2 = 0.51$, $t = -4.63$, $P < 0.001$) and frequency ($sr^2 = 0.22$, $t = -2.33$, $P = 0.04$). Thus, migrants constituted a smaller proportion of the species and were less frequently encountered in dry habitats on islands further away from the continent.

Similarly, within the Greater Antilles, migrant frequency in mangroves declined with distance from Florida ($t = 3.43$, $P = 0.04$; $y = -0.05x + 111.18$, $R^2 = 0.80$). This trend was not found in shade coffee or pasture, although the trend in montane broadleaf forests was suggestive ($t = 2.64$, $P = 0.06$; $y = -0.04x + 63.9$, $R^2 = 0.64$).

We also examined the relationship between migrant frequency and distance and island size for individual migrant species with adequate sample sizes (Table 2). Distance and island size together accounted for significant variation in the frequency of six species, and in another three species the contribution was suggestive ($P < 0.10$).

In the species in which distance accounted for a statistically significant or suggestive amount of variation in frequency, the sign of the relationship was always negative. However, the contribution of island size to variation in frequency was not as consistent. For instance, island size provided a negative contribution to variation in frequency in Yellow-throated Warblers and a positive contribution in Blue-gray Gnatcatchers. However, the high counts of Blue-gray Gnatcatchers from the Bahamas were excluded from the analysis because of our inability to distinguish winter residents from permanent residents. Most of the species listed in Table 2 were most abundant in the Bahamas with the exception of the Black-throated Green Warbler.

Other patterns of geographic distribution were apparent in some migrant species, but a relationship with island distance or size was not evident. For example, Black-throated Green Warblers (and possibly Blue-gray Gnatcatchers) were

TABLE 2. Contribution of distance and island size to measures of within habitat migrant abundance on eight islands in the Bahamas and Greater Antilles. *n* refers to number of sites sampled. The squared semipartial correlation is shown which represents the unique contribution of the independent variable to the R^2 .

Measures	<i>n</i>	Multiple r^2	sr^2	
			Distance	Size
Percentage of species which are migrants	60	0.15**	0.14--	0.006
Percentage of individuals which are migrants	60	0.12**	0.09--	0.03
Percentage of points with migrants	60	0.09*	0.09-	0.004
Estimated migrant species richness (15 individuals)	33	0.09	0.08	0.005
Estimated migrant species richness (20 individuals)	29	0.10	0.09	0.007
Individual species				
Palm Warbler	60	0.26***	0.24---	0.03
Yellow-throated Warbler	60	0.23***	0.17---	0.06--
Blue-Gray Gnatcatcher	60	0.17***	0.05-	0.13+++
Prairie Warbler	60	0.14**	0.12---	0.03
Gray Catbird	60	0.14**	0.11---	0.02
Yellow-bellied Sapsucker	60	0.12**	0.09--	0.01
Common Yellowthroat	60	0.09*	0.08--	0.01
Yellow-rumped Warbler	60	0.09*	0.08--	0.01
Black-throated Green Warbler	60	0.08*	0.06-	0.02

* $P < 0.10$; ** $P \leq 0.05$; *** $P < 0.01$; - negative relation, $P \leq 0.10$; -- negative relation, $P < 0.05$; --- negative relation, $P < 0.01$; +++ positive relation, $P < 0.01$.

most abundant in the western Caribbean (Cuba and Jamaica, Figs. 2–6). Cape May Warbler abundance was greatest in southern Bahamas and Dominican Republic, and they are also common in eastern Cuba (Daisy Rodríguez, pers. comm.). Northern Parula Warblers were absent from the northern Bahamas, but common in the Greater Antilles. Finally, American Redstarts, Ovenbirds, Black-and-white Warblers, and Northern Waterthrushes were detected on all islands with no discernable geographic pattern of abundance, although counts were frequently lowest in Puerto Rico (Figs. 2–6).

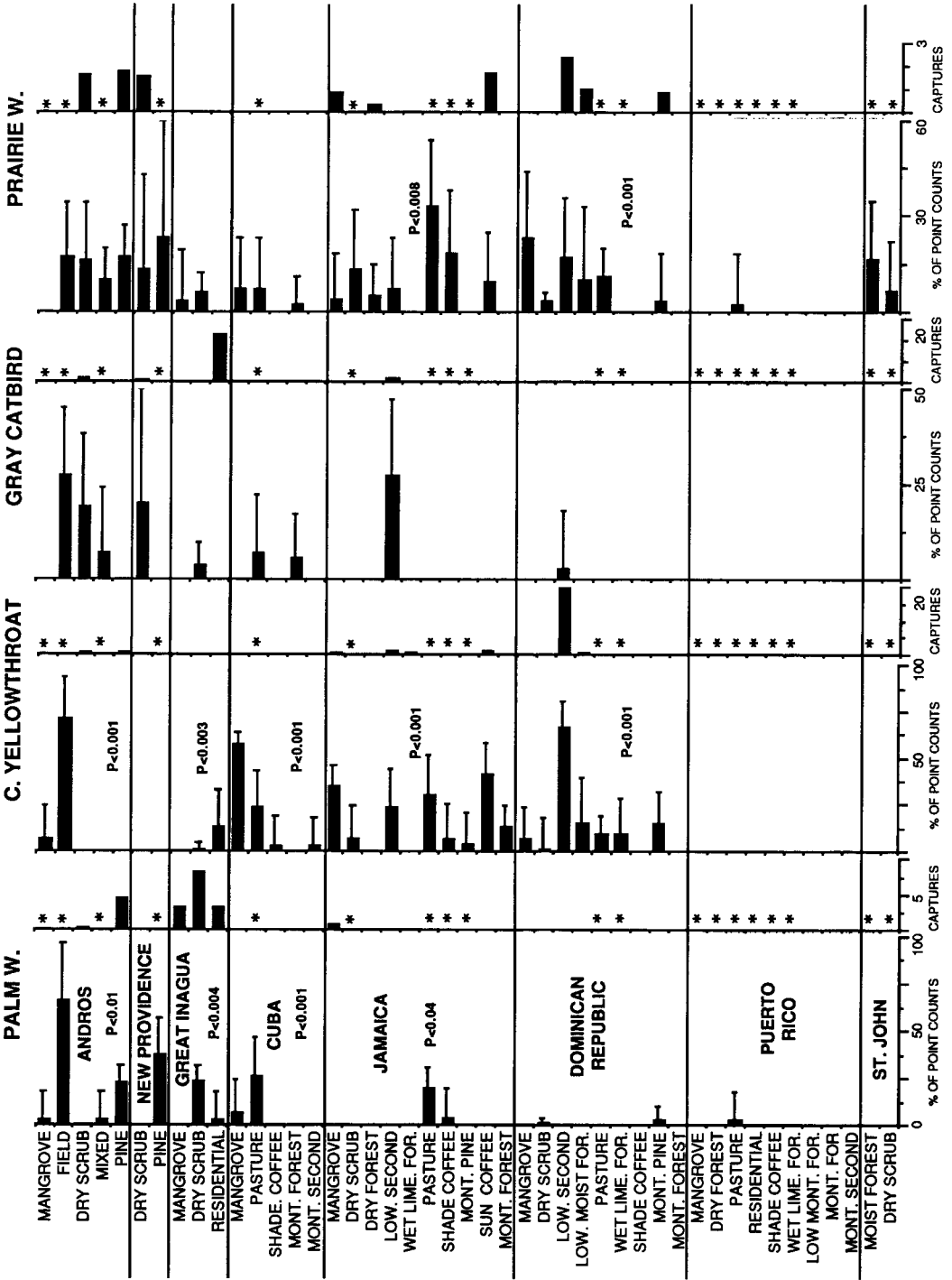
GEOGRAPHIC DISTRIBUTION, HABITAT DISTRIBUTION & ABUNDANCE

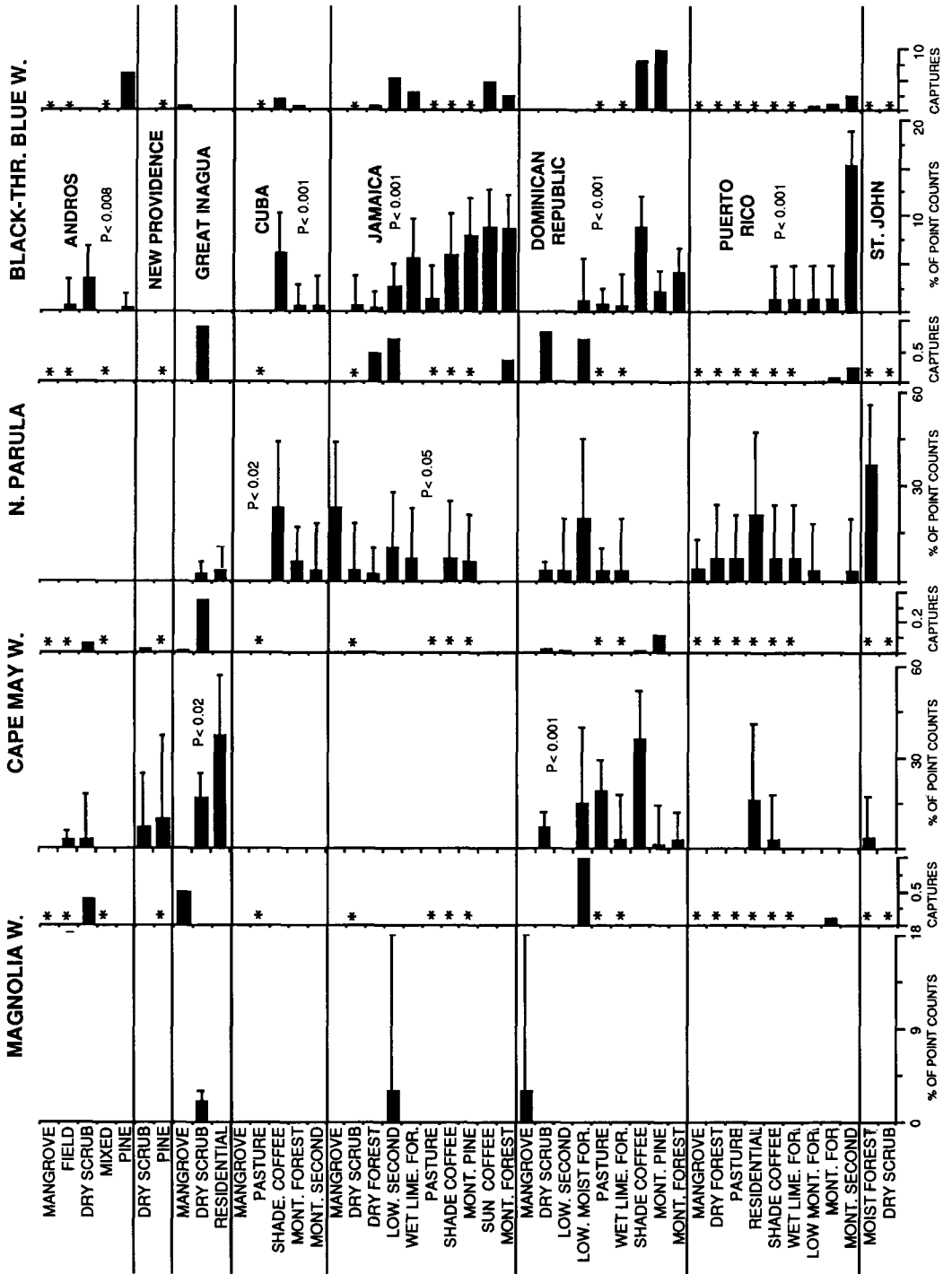
Migrant species with widespread geographic distributions also tend to be widely distributed among different habitats within an island; conversely, species with limited geographic distri-

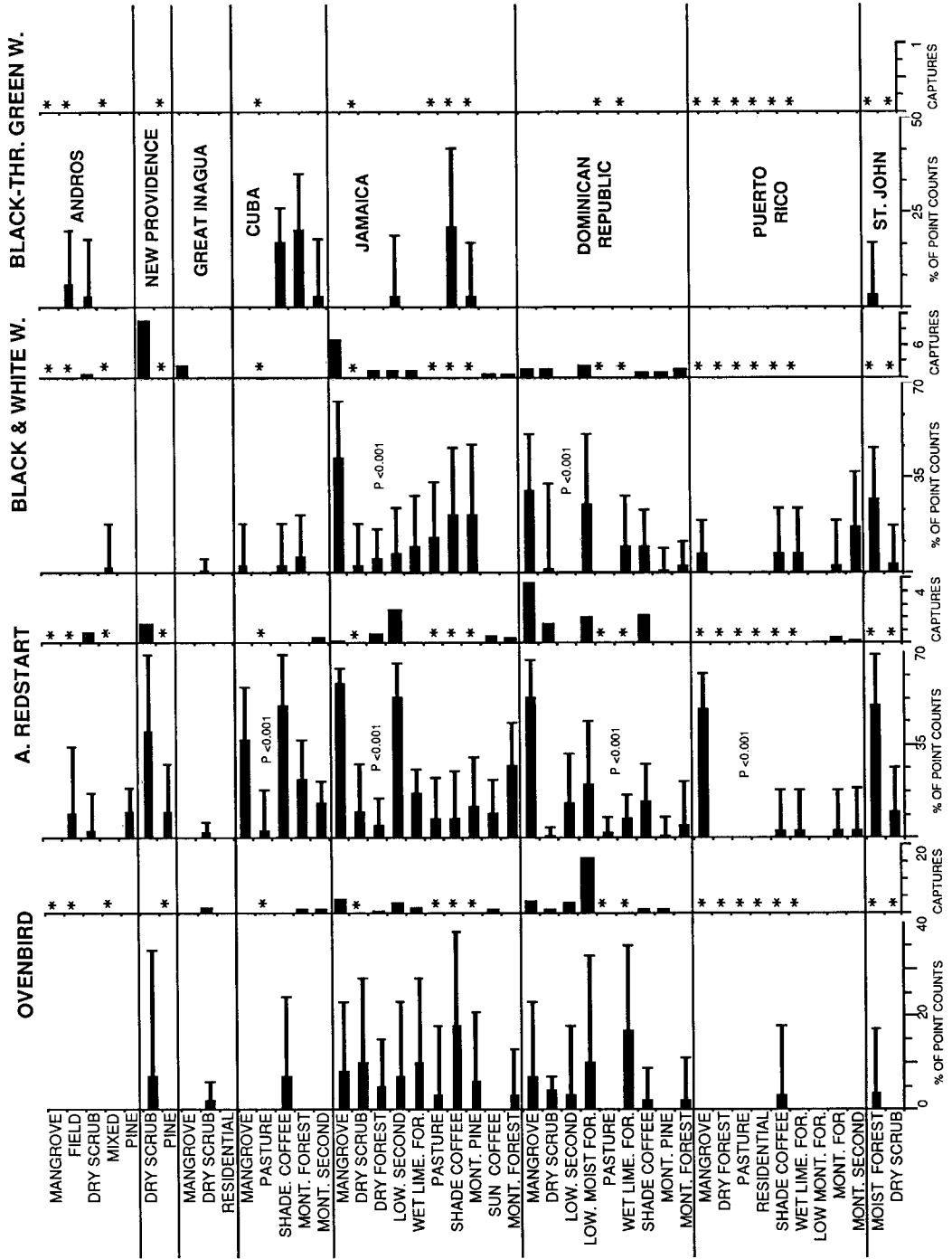
butions tend to have limited distributions among habitats within the occupied islands. The number of islands on which a species was found was positively correlated with the maximum number of occupied habitats expressed as a percentage of the total number of available habitats on an island (Spearman $r = 0.87$, $df = 28$, $P < 0.0001$). This relationship exists even when species occupying only a single island are eliminated from the analysis (Spearman $r = 0.77$, $df = 21$, $P = 0.001$). Northern Waterthrushes are a notable exception to this trend, as discussed below.

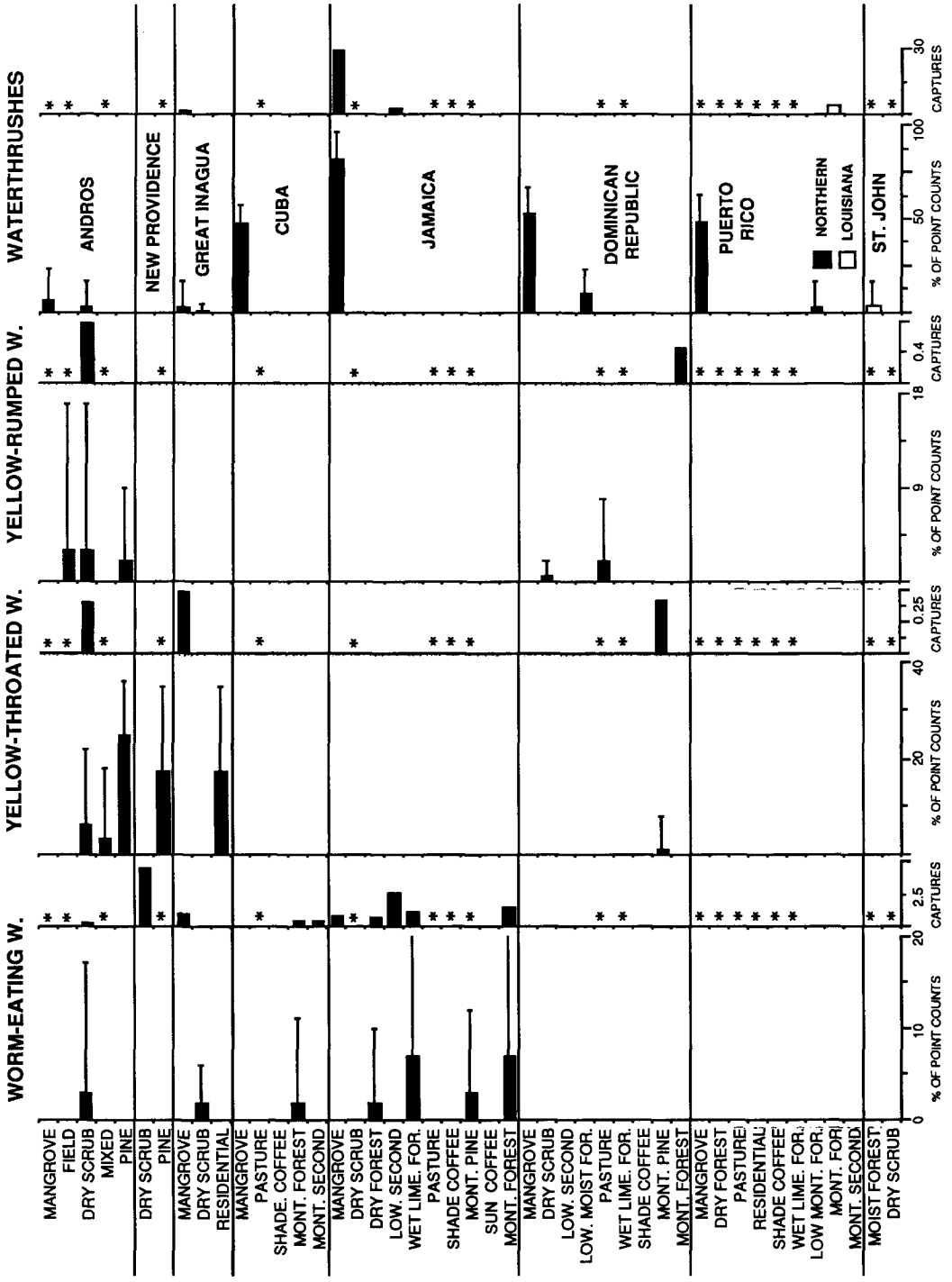
The number of islands on which a migrant species was detected was positively correlated with the maximum count within a habitat (Spearman $r = 0.79$, $df = 28$, $P < 0.001$) as well as the mean count within a habitat (Spearman $r = 0.81$, $df = 28$, $P < 0.001$). Thus, migrants with widespread geographic distributions tend to achieve higher maximum or mean abundances

FIGURES 2–6. Percentage (and 95% confidence interval) of point counts and mist net captures per 100 net hr for different nearctic migrant species, which winter in the Bahamas and Greater Antilles. Note that scales are not the same in all graphs. P values indicate level of significant heterogeneity among point count samples in different habitats on an island. Asterisks indicate habitats which were not sampled by mist nets.

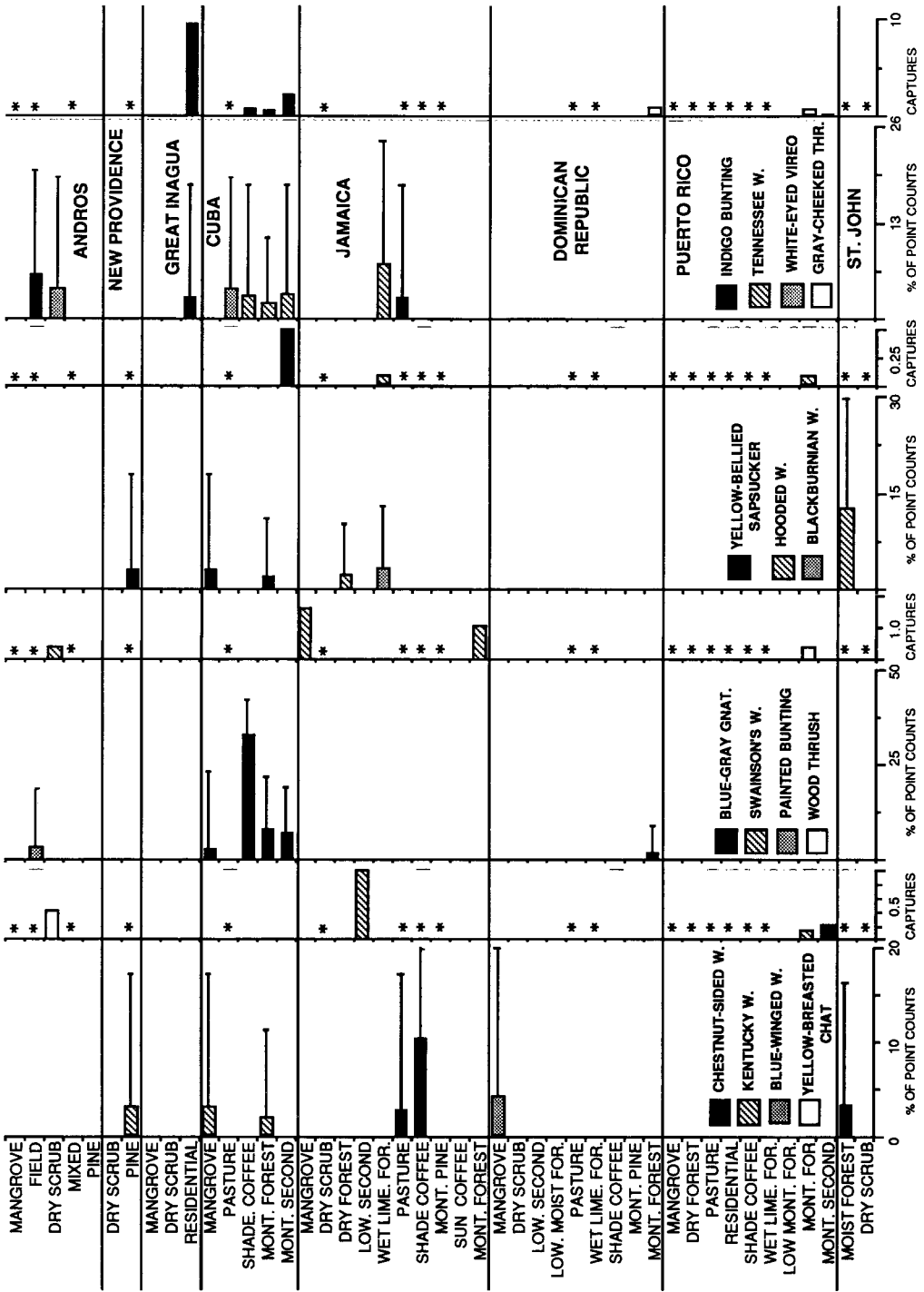








UNCOMMON - RARE SPECIES



in the habitats they occupy than do species with limited geographic distribution. Some of this relationship may be attributable to sampling error (less abundant species are more likely to be missed on an island and hence recorded from fewer islands), but the results suggest that geographically restricted species are rarely abundant and that geographically widespread species are often common.

FACTORS ASSOCIATED WITH MIGRANT ABUNDANCE IN ISLAND HABITATS

Three Bahamian islands. The number of height intervals with foliage and the height of the interval with maximum amount of foliage together accounted for 73% of the variation (multiple regression, $F = 6.71$, $df = 2$, $P = 0.04$) in migrant frequency at 9 sites in the Bahamas. The height interval with maximum foliage accounted for 33.1% ($t = 2.47$, $P = 0.057$) of the total variation, indicating that migrant occurrences increased with height of the interval with the greatest cover. The contribution of number of foliage height intervals was inconsequential ($sr^2 = 0.007$, $t = 0.12$, $P = 0.91$). Not included were sites without vegetation measurements: two mangrove sites, brushy field, residential, and 1 scrub site on Great Inagua. Migrant frequency was lowest in the low-stature mangroves (most < 2 m) on Andros and Great Inagua (Fig. 1). The highest migrant frequencies occurred in two sites heavily disturbed by people—a brushy field on Andros, and the residential section of Mathewtown, G.I.

Greater Antilles. Multiple regression was also used to examine the effect of several environmental factors on migrant frequency and species richness in Jamaica and the Dominican Republic. The analysis was restricted to these two islands because of the broad spectrum of habitats available and sampled, and the relative abundance of migrants. Four environmental characteristics of each sample site were used: elevation, average annual rainfall, number of foliage height intervals, and height interval with maximum foliage cover.

Together, these four variables accounted for a statistically significant amount of variation (multiple $R^2 = 0.53$, $F = 4.58$, $P = 0.01$) in migrant frequency in these two countries ($n = 21$ sites). Of the environmental variables, average annual rainfall was most important ($sr^2 = 0.27$, $t = 2.34$, $P = 0.03$), indicating that total migrant occurrences increased with annual rainfall. Of less im-

portance was the height interval with the maximum amount of foliage ($sr^2 = 0.16$, $t = 2.34$, $P = 0.03$); migrant occurrences increased with height of the interval with the greatest cover.

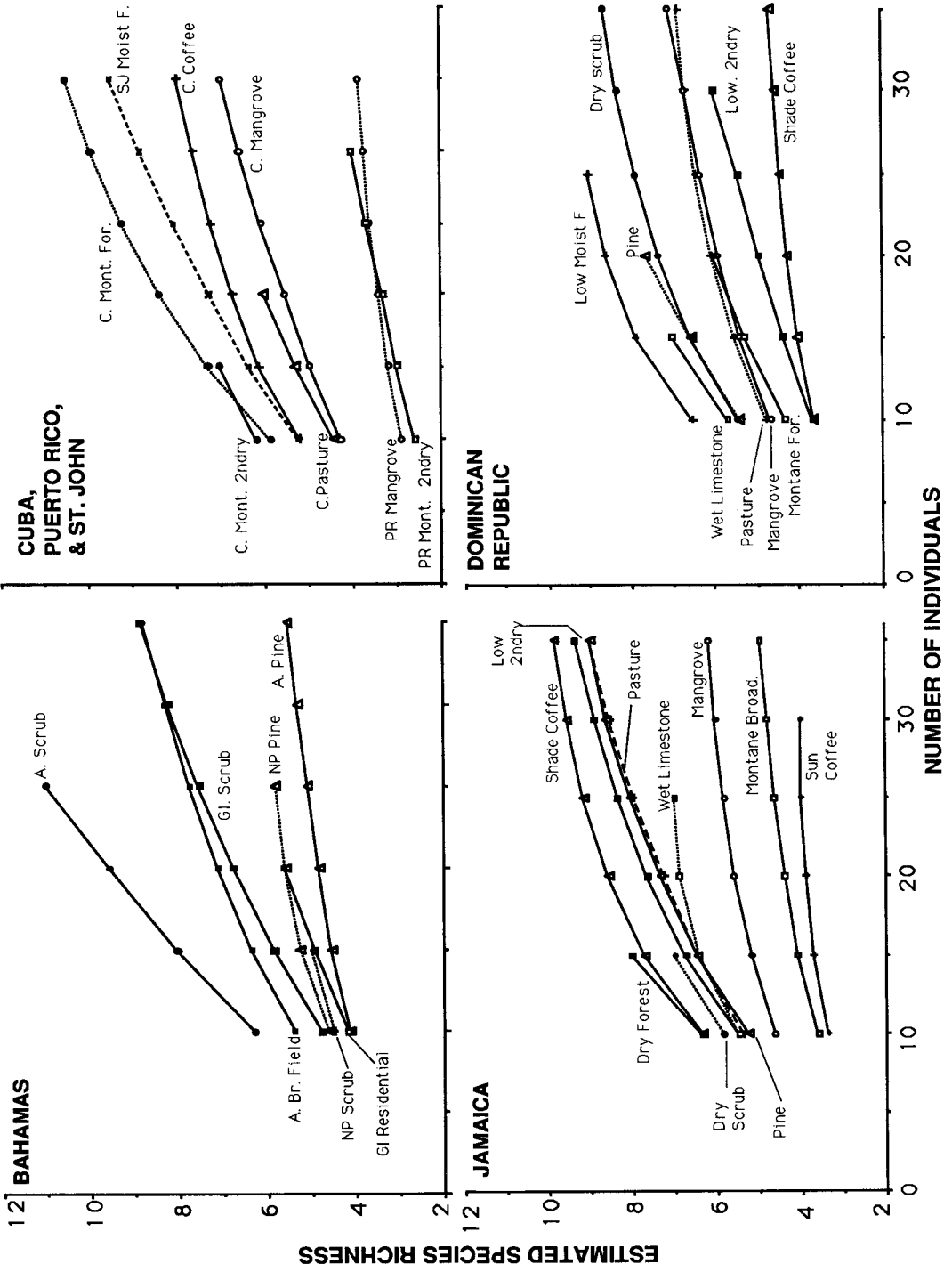
Migrant frequency was consistently high in mangroves in the Greater Antilles (in contrast to the Bahamas), and represented the highest counts on three of the four islands (excluding St. John, where mangroves were not sampled). Other Greater Antillean habitats with high migrant frequencies include moist lowland forests, shade coffee, and most moist secondary woodlands, but not dry habitats which were consistently low as previously indicated by multiple regression (Fig. 1).

MIGRANT SPECIES RICHNESS

Given the differences in winter ranges of migrant species it is not surprising that consistent patterns in species richness were rarely found among habitats on the different islands (Fig. 7). Although Puerto Rican habitats were characterized by relatively low species richness, the other islands showed similar ranges in species richness among habitats, even though the species richness of specific habitat types sometimes varied among islands. Dry scrub habitats were characterized by moderate to high levels of species richness, although migrant frequencies were usually low. In contrast, mangroves were characterized by moderate to low levels of species richness, but with high migrant frequencies. Pastures consistently had moderate levels of species richness. Shade coffee habitats varied most in species richness, being one of the richest habitats for migrant species on Jamaica yet having the lowest species richness in the Dominican Republic (comparable to Jamaican sun coffee). Montane broadleaf forests also varied in species richness among islands.

MIGRANT ASSEMBLAGES

Because the floristic and structural variety of terrestrial habitat types within a given Bahamian island is much less than on a Greater Antillean island, we expected that there would be greater differences in migrant assemblages among habitats within Greater Antillean islands. However, a comparison of mean similarity coefficients (henceforth S.C.) of pairs of migrant assemblages within different habitats on the same island indicates that the average S.C. for migrant assemblages on islands in the Bahamas (0.22 ± 0.04 ,



$n = 14$) was significantly less (Mann-Whitney $U = 525.5$, $P = 0.03$) than the corresponding value in the Greater Antilles (0.33 ± 0.02 , $n = 116$). We attribute the low average similarity of Bahama migrant assemblages primarily to the low-stature mangrove habitat sampled on Andros and Great Inagua. This habitat contained very few migrants (or residents), and constituted an assemblage very different from any other habitat (mean S.C. = 0.08 ± 0.02) on the same island. Elimination of S.C.s involving comparisons with mangroves results in a mean S.C. of 0.32 ± 0.04 for the Bahamas, which was not significantly different from the Greater Antilles value (Mann-Whitney $U = 453.00$, $P = 0.91$).

Mangroves in the Greater Antilles were the only habitat in which the migrant assemblages were consistently similar among islands, despite differences in migrant frequency and species richness. In fact, this was the only habitat type in which migrant assemblages were significantly more similar to each other within a habitat than within an island (Mann-Whitney $U = 162$, $P < 0.001$). Migrant assemblages in mangroves on the four islands had a mean S.C. of 0.65 ± 0.02 ($n = 6$ pairwise comparisons) in contrast to a mean of 0.23 ± 0.03 ($n = 27$ pairwise comparisons) for all mangrove assemblages compared to all other habitats on the same island. The very abundant Northern Waterthrush, restricted primarily to mangroves, accounted for much of the distinctiveness of the mangrove assemblages across all islands, although Black-and-white Warblers, American Redstarts, and Common Yellowthroats were usually also more abundant in mangroves than in other habitats.

In the one instance where we could compare assemblages within a habitat type to other assemblages on the same island, we found that the migrant assemblage was not unique to the specific habitat type. This was evident in the dry scrub habitat in the Dominican Republic, which was sampled in six different sites. Analysis of mean similarity coefficients for migrant assemblages in scrub ($\bar{x} = 0.23 \pm 0.04$, $n = 15$) with the mean similarity coefficient for scrub compared with non-scrub habitats ($\bar{x} = 0.27 \pm 0.4$,

$n = 8$) in the Dominican Republic, indicated no significant difference (Mann-Whitney $U = 49.00$, $P = 0.48$). The similarity of migrant assemblages in scrub and non-scrub habitats is largely attributed to Ovenbirds, Cape May Warblers and Prairie Warblers, which were common and widespread in different habitats in the Dominican Republic.

ORDINATION OF MIGRANT ASSEMBLAGES

Migrant abundances in the sample sites were ordinated using PCA to determine the migrant assemblages in the Bahamas and Greater Antilles. The first four principal components accounted for 56.3% of the variation in the species correlation matrix, with PC-1 accounting for 18.7%, PC-2 contributing 14.3%, and PC-3 contributing 12.2% (Fig. 8). Correlation analysis of the available habitat variables with the PCs suggests that PC-1 represents a gradient in vegetation structure (Table 3). The species with low scores (i.e., on the left of PC-1 in Fig. 8) occurred mainly in habitats with few broadleaf foliage height zones, small DBH broadleaf trees, and low stature (e.g., in some Bahamian woodlands). In contrast, the species with high PC-1 scores were found in relatively tall stature forests, with larger DBH trees (e.g., in mangroves in the Greater Antilles). Correlation analysis with PC-2 and the available habitat variables failed to reveal any significant correlations (Table 3), possibly because vegetation measurements were not made in open (pasture) or shrubby (brushy field) habitats. The PC-2 axis indicates that the species on the right side of the axis are common in open or shrubby habitats (e.g., Andros brushy field) while the species on the left side are common in habitats with fewer, but larger stems, and generally greater canopy height (e.g., Greater Antillean forests-wet limestone, shade coffee, mangrove, montane broadleaf). Species with high positive loadings on PC-3 were found in forests with a high closed canopy (e.g., Cuban shade coffee) in contrast to species with negative loadings usually found in habitats with lower mean canopy heights (e.g., Bahamas dry scrub, mangroves).

←

FIGURE 7. Rarefaction curves from point counts showing the rate at which estimated migrant species richness increases as a function of the number of individuals censused in major habitats in the Bahamas and Greater Antilles. Sample sites and number of point counts are summarized in Table 1.

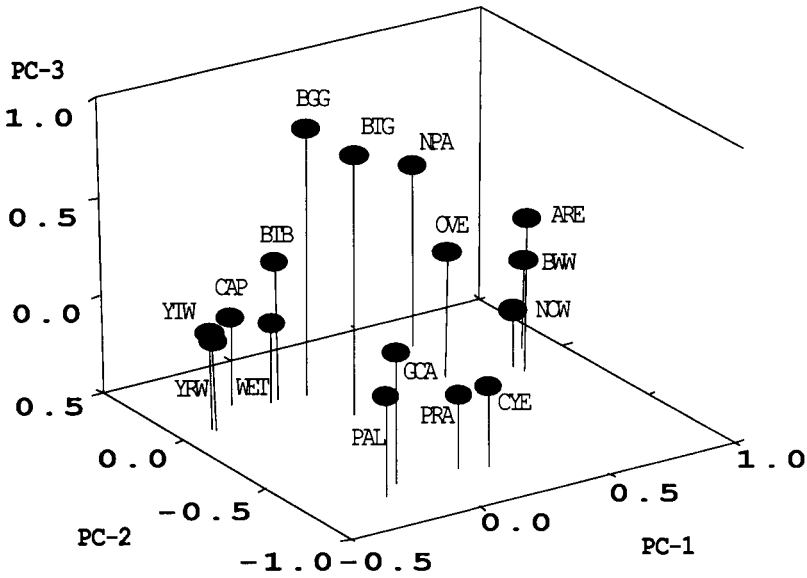


FIGURE 8. Principal components ordination of 16 common nearctic migrants according to the first three principle components of their winter habitat relationships based on point counts conducted in the Bahamas and Greater Antilles. The first component accounts for 18.7% of the total variance, the second component 14.3%, and the third component 12.2%. Symbols for the species are: ARE, American Redstart; BGG, Blue Gray Gnatcatcher; BTG, Black-throated Green Warbler; BTB, Black-throated Blue Warbler; BWW, Black-and-white Warbler; CAP, Cape May Warbler; CYE, Common Yellowthroat; GCA, Gray Catbird; NPA, Northern Parula; NOW, Northern Waterthrush; OVE, Ovenbird; PAL, Palm Warbler; PRA, Prairie Warbler; YRW, Yellow-rumped Warbler; YTW, Yellow-throated Warbler.

DEGREE OF HABITAT SPECIALIZATION

To quantify the degree of habitat specialization (“ecological amplitude” of Emlen 1977, 1980) for each species we used the exponential of the Shannon-Weiner diversity index (H') calculated from the relative rates of occurrence in habitats on an island (Table 4). Because of their diversity of habitat types and high migrant abundance, Jamaica and the Dominican Republic were used to calculate the mean of the percentage of the maximum $\exp(H')$ for each of the most abundant migrant species. This enabled us to rank migrants

in relation to the degree of habitat specialization from the most generalized (Ovenbird) to the most specialized (Northern Waterthrush). A weakness of this approach was that the two most abundant species in the Bahamas (Prairie Warbler and Palm Warbler) were relatively generalized in habitat use there, but were relatively specialized in their habitat use in the Greater Antilles. The opposite pattern occurred in the Common Yellowthroat, which was ecologically more generalized in the Greater Antilles. Therefore, this ranking scheme and classification is specific to the Greater An-

TABLE 3. Correlation analysis of six habitat variables with PC-I, II, and III.

Habitat variable	PC-I	PC-II	PC-III
Height interval with maximum foliage	0.633**	-0.328	0.507**
Number of height intervals with foliage	0.705***	-0.099	-0.020
Mean canopy height	0.457*	-0.204	0.510**
Mean DBH	0.480*	-0.091	0.189
Total stems	0.053	0.342	-0.023
Shrub density	0.023	0.407	-0.117

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

TABLE 4. Degree of habitat specialization, based upon the most abundant migrants in point counts in the Bahamas and Greater Antilles. Degree of specialization is based on the exponential of the Shannon-Weiner diversity statistic (H') calculated from the relative rates of occurrence in the different habitats on an island. Each species' $\exp(H')$ was calculated separately for every island in which 10 or more individuals were detected. The value can vary from 1 (complete specialization on one habitat type) to a maximum value (equal use of all available habitats) depending upon the largest number of habitats sampled on an island (Andros, 5; Cuba, 5; Jamaica, 10; Dominican Republic, 9; Puerto Rico, 9). To make comparisons among islands we divided a species' $\exp(H')$ by the maximum $\exp(H')$ for the island and multiplied by 100 to provide percentage of the maximum $\exp(H')$. Because of the diversity of habitat types and high migrant abundance, Jamaica and the Dominican Republic were used to calculate a mean value of the percentage of the maximum $\exp(H')$, as indicated by the degree of specialization below.

Degree of specialization	Species	Percentage of maximum $\exp(H')$				
		Andros	Cuba	Jamaica	Dom. Rep.	Puerto Rico
Generalist Species						
70%	Ovenbird	—	—	79	61	—
61%	American Redstart	54	78	70	53	31
58%	Black-and-white Warbler	—	58	68	48	38
*	Blue-gray Gnatcatcher	—	56	—	—	—
Moderate Specialist Species						
51%	Prairie Warbler	62	54	55	47	—
51%	Common Yellowthroat	26	48	66	37	—
51%	Black-throated Blue Warbler	44	38	67	34	29
50%	Cape May Warbler	40	—	—	50	—
*	Yellow-throated Warbler	50	—	—	—	—
*	Gray Catbird	50	40	—	—	—
46%	Northern Parula	—	44	54	37	54
Specialist Species						
20%	Black-throated Green Warbler	—	50	20	—	—
15%	Palm Warbler	44	34	16	14	—
14%	Northern Waterthrush	—	20	10	18	1

* The degree of specialization was not calculated for these species due to their scarcity in Jamaica and the Dominican Republic.

tilles, and its applicability may decrease outside that region.

PATTERNS OF HABITAT DISTRIBUTION

We recognized several patterns of habitat distribution in the Bahamas and Greater Antilles based upon the degree of habitat specialization (Table 4), the habitat types occupied and the degree of heterogeneity among occupied habitats on the same island (Figs. 4–8). Below we summarize the patterns of migrant habitat distribution we observed and relate them to previous habitat studies on Grand Bahama (Emlen 1977), Jamaica (Lack and Lack 1972) and the Yucatan peninsula of Mexico (Lynch 1989, 1992).

1. *Early-mid-successional species.* These species were detected most frequently in open areas, areas of early succession, or forest edge, usually sites with substantial human disturbance (Fig. 4).

Palm Warblers displayed the most habitat specialization of the group, and showed significant

heterogeneity in occurrences among occupied habitats on four islands with maximum detections in a brushy field, pine forest, dry scrub, and pastures. Even in the pine forest and dry scrub, the species was observed primarily in open areas along roads (in dry scrub) or in the relatively open understory of burned pine stands. Similarly, others have found them commonly in coastal sand habitat with tall grasses and dense scrub (Emlen 1977), man-modified grasslands in the lowlands (Lack and Lack 1972), and in coastal dune scrub, grasslands, and burned areas (Lynch 1989, 1992).

Common Yellowthroats were moderately specialized in habitat occurrence, and showed significant heterogeneity in occurrences among occupied habitats on five islands. Yellowthroats were most common where herbs and small shrubs contributed to a "brushy" understory: brushy field, lowland second growth, mangrove, pasture, and sun coffee. Others found them abundant in marsh, old field and coastal sand habitats (Emlen

1977), in areas with lush herb layers at the edges of swamps and some forests including montane forest (Lack and Lack 1972), and in brushy pastures, recently abandoned agricultural plots, and coastal scrub (Lynch 1989, 1992).

Gray Catbirds were also moderately specialized in habitat occurrence, being most abundant where woody shrubs produced a brushy understory such as in the brushy field, lowland second growth, and dry scrub habitats, as documented elsewhere (Emlen 1977; Lynch 1989, 1992).

Prairie Warblers were also moderately specialized in habitat occupancy, with significant heterogeneity in occurrence among occupied habitats in two Greater Antilles islands. The species was common in early second growth to mature forest edge habitats with maximum counts in pine, pastures, lowland second growth, and brushy field. Prairie Warblers were sometimes found in forest edges, but never under or in closed canopy forests of tall stature. Elsewhere, the species was most abundant in coppice (Emlen 1977), or in various lowland forest types, especially where scrubby mimosaceous trees predominate (Lack and Lack 1972).

Although uncommon in these islands, White-eyed Vireos, Yellow-rumped Warblers, Yellow-breasted Chat, and Painted and Indigo buntings might be included in this group as suggested by our observations and those of others (Lack and Lack 1972, Emlen 1977, Lynch 1989).

2. *Mid-successional to mature forest species.* These species were found across a broad spectrum of disturbed sites, as well as early successional stages up to and including several different mature forest types. Whereas these species were found in a variety of habitats, their abundances varied significantly among occupied habitats on the same island and their $\exp(H')$ values suggest moderate levels of habitat specialization.

Cape May Warblers were the most opportunistic of this group, with significant heterogeneity in occurrence in occupied habitats on two islands. Maximum detections occurred in montane coffee, residential, and pasture habitats, and only rarely detected in mature forest. Often their abundance was related to flower abundance, as previously observed by others in a variety of habitats including mature pine stands (Kale 1967, Emlen 1973), parkland and woodland edges at all altitudes (Lack and Lack 1972), and coastal scrub (Lynch, pers. comm.).

Northern Parula Warblers were observed across

a wide range of habitats (particularly on Puerto Rico), with significant heterogeneity of occurrences in occupied habitats on two islands in the Greater Antilles. Maximum detections occurred in montane coffee, mangroves, lowland moist forest and edge, and residential habitats in the Greater Antilles. Parulas were less frequently encountered in closed canopy forest, but appeared most frequently in areas with broken canopy or forest edge. Elsewhere, the species has been found commonly in coppice (Emlen 1977), mesic lowland second growth woodland (Lack and Lack 1972), moist forests (Askins and Ewert 1992), and across almost the entire successional continuum (Lynch 1989, 1992).

Black-throated Blue Warblers were found in both closed canopy forests and second growth with significant heterogeneity in occurrences among occupied habitats on the four Greater Antillean islands and Andros. Four independent variables (elevation, rainfall, height of the maximum foliage interval, and number of foliage height intervals) measured at 21 sample sites in Jamaica and the Dominican Republic accounted for 58% of the variation in Black-throated Blue Warbler abundance on these two islands (multiple regression, $F = 5.56$, $P = 0.005$). Elevation contributed 37% of this variation ($t = 3.76$, $P = 0.002$), indicating that abundance increased with elevation, while height of the maximum foliage interval contributed 16% of this variation, indicating that abundance increased with the height interval with the greatest cover ($t = 2.48$, $P = 0.03$). Maximum detections occurred in montane habitats including second growth, montane forest, coffee, and pine (with broadleaf understory). Elsewhere, the species was found exclusively in coppice (Emlen 1977), or in closed-canopy semi-evergreen tropical forest (J. Lynch, pers. comm.).

Rarer species, such as Chestnut-sided Warbler and Kentucky Warbler, might be placed in this group. Elsewhere this latter species is restricted to moist tropical forest and its later successional stages (Lynch 1989, 1992).

3. *Forest generalists.* These are a group of migrant species with relatively high $\exp(H')$ values, found across an array of different forest types, including some second growth forests. Ovenbirds were the most generalized of the group, with no significant heterogeneity in detections among habitats within the two islands with adequate samples. Four independent variables (el-

evation, rainfall, height of the maximum foliage interval, and number of foliage height intervals) measured at 21 sample sites accounted for 53% of the variation in Ovenbird abundance on Jamaica and the Dominican Republic (multiple regression, $F = 4.53$, $P = 0.01$). Height of the maximum foliage interval contributed 21% of this variation ($t = 2.67$, $P = 0.02$), indicating that Ovenbird abundance increased with height of the maximum foliage interval, while elevation contributed 18% of the variation ($t = -2.51$, $P = 0.02$), indicating that abundance decreased with altitude on the two islands. Maximum Ovenbirds counts occurred in shade coffee and wet limestone forest, both habitats with a closed canopy. Similarly, others have noted the widespread distribution of Ovenbirds among all types of natural forests (Lack and Lack 1972) and across virtually the entire successional and moisture continua (Lynch 1989, 1992), although the species is most abundant in coppice elsewhere (Emlen 1977).

American Redstarts were widespread among a variety of forest types, although significant heterogeneity in detections occurred among occupied habitats on each of the Greater Antillean islands. Redstarts were particularly abundant in mangroves (Greater Antilles only) with high occurrences also in shade coffee, lowland second growth, and dry scrub on New Providence. Others have found the species most commonly in coppice (Emlen 1977); in all types of natural woodland, particularly mangroves, sea-level forest, and lowland riverine forest, although scarce in the mountains (Lack and Lack 1972); and across a wide spectrum of wooded habitats, regardless of stature or moisture regime (Lynch 1989).

Black-and-white Warblers displayed significant between-habitat heterogeneity in detection rates on both Jamaica and the Dominican Republic where maximum occurrences were found in mangroves and lowland forest and edge (D.R. only). Four habitat variables (elevation, rainfall, height of the maximum foliage interval, and number of foliage height intervals) measured at 21 sample sites in Jamaica and the Dominican Republic accounted for 48% of the variation in Black-and-white Warbler abundance in these two islands (multiple regression, $F = 3.75$, $P = 0.03$). Height of the foliage interval with the maximum cover accounted for 17% of the variation in Black-and-white Warbler abundance ($t = 2.14$, $P =$

0.05), indicating that abundance increased with height of the foliage interval with the maximum cover. Others have noted its abundance in coppice (Emlen 1977), in a variety of natural forest, from mangroves and dry scrub to the wettest and higher montane forest, including cultivated forests such as pine plantations (Lack and Lack 1972), and in mid-late successional stages of all forest types (Lynch 1989, 1992).

Black-throated Green Warblers were commonly detected in a variety of "mature" and secondary habitats including brushy field in the Bahamas. Others have found it abundant in coppice (Emlen 1977), woodlands (broadleaf, pine or juniper) at all altitudes (Lack and Lack 1972), and mid- to late successional semi-evergreen and semi-deciduous forest in the Yucatan Peninsula where it also occurs in scattered trees and shrubs in pastures and fields (Lynch 1989, 1992).

Blue-gray Gnatcatchers showed significant heterogeneity in detections among habitats in Cuba. There, maximum detections were found in shade coffee.

Several additional species (e.g., Yellow-bellied Sapsucker, Magnolia Warbler, and Tennessee Warbler) also may belong in this group.

4. *Forest specialists.* Forest specialists represent a group of species found mostly in mature forest or shade coffee and only rarely in second-growth habitats.

Worm-eating Warblers were found in a variety of forest types in the Greater Antilles including montane pine and broadleaf forests, wet limestone forest and dry forest, and in dry scrub and residential habitats in the Bahamas. Others have noted its presence in mature pine stands (Emlen 1977), all natural forest types (except mangroves) including cultivated forest with thick cover (Lack and Lack 1972), and moist forest where it occurs sparingly in mid-stage successional growth (Lynch 1989, 1992, pers. comm.).

Yellow-throated Warblers were pine specialists where pines occurred, as illustrated on Andros, where they showed significant heterogeneity in detections among habitats. Others have noted its pine specialization in the Caribbean (Lack and Lack 1972, Emlen 1977, Terborgh and Faaborg 1980). Elsewhere, in the absence of pines, the species is characteristic of native coastal scrub with emergent palms, pasture and fields with scattered remnant trees, and towns (Lynch 1989, 1992).

Rare species that might be included in this

group include Louisiana Waterthrush, Hooded Warbler, Swainson's Warbler, Blue-winged Warbler, Blackburnian Warbler, Wood Thrush, and Gray-cheeked Thrush.

5. *Extreme forest specialist.* Finally, Northern Waterthrushes represent the most extreme forest specialist. They were found almost exclusively in mangroves, as observed by others (Lack and Lack 1972; Emlen 1977; Terborgh and Faaborg 1980; Lynch 1989, 1992).

MIGRANTS COMPARED WITH RESIDENTS

No consistent relationships were found between the abundance and distribution of migrants and residents within sites in the Bahamas or Greater Antilles. For example, in the Bahamas a significant positive correlation was found between the number of migrant and resident species detected in a habitat (Pearson $r = 0.73$, $df = 12$, $P = 0.05$), indicating that the Bahamian habitats rich in resident species are also rich in migrant species. Yet, there was no significant correlation between the total number of migrant individuals and total number of resident individuals detected in a Bahamian habitat (Pearson $r = 0.11$, $df = 12$, $P > 0.50$). Also, the frequency of migrant detections was not significantly correlated with the percentage of individuals that were migrants (Spearman $r = 0.65$, $df = 12$, $P = 0.41$), in contrast to the Greater Antilles (see below). Nor did we find that habitats that support a large absolute number of all species or all individuals also support a greater proportion of migrants, as found in Mexico (Hutto 1980). The total number of species and proportion of migrant species in a habitat were not correlated (Spearman $r = 0.20$, $df = 12$, $P > 0.50$). Similarly, the total number of individuals and the proportion of individuals that were migrants were not correlated (Spearman $r = 0.15$, $df = 12$, $P > 0.50$).

Similarly to the Bahamas, no consistent relationships were found between the abundance and distribution of migrants and residents among sites in the Greater Antilles. In contrast to the positive correlation found in the Bahamas, no correlation existed between the number of migrant and resident species detected in a habitat in the Greater Antilles (Pearson $r = 0.38$, $df = 44$, $P = 0.26$). Moreover, no significant correlation was found between the total number of migrant and resident individuals detected at a site (Pearson $r = 0.06$, $df = 44$, $P > 0.5$). However, in contrast to the Bahamas, the frequency of migrant detections was significantly correlated with the per-

centage of individuals that were migrants (Spearman $r = 0.86$, $df = 44$, $P < 0.001$). Habitats that support a large number of species do not necessarily support a greater proportion of migrant species (Spearman $r = 0.17$, $df = 44$, $P > 0.5$), nor do habitats that support a large total number of individuals support a higher proportion of migrant individuals (Spearman $r = 0.13$, $df = 44$, $P > 0.50$).

Previous studies in the Bahamas (Emlen 1980) indicated that overwintering migrants and residents display equivalent levels of habitat generalization, in contrast to Mexico where migrants are more generalized than residents in habitat use (Lynch 1989). To examine migrant and resident habitat distributions we compared the $\exp(H')$ values for resident and migrant species that had an adequate sample size ($n \geq 10$) within the same island (Table 5). The average $\exp(H')$ values for migrants and residents do not differ for any of the islands, suggesting that migrants do not differ from island residents in the degree of habitat specialization.

MIST-NETTING COMPARED WITH POINT COUNTS

Total migrant net capture rates were only weakly correlated with total migrant occurrences in point counts in the same habitat (Pearson $r = 0.47$, $df = 27$, $P < 0.05$). The maximum migrant capture rate (68.5 migrants per 100 net hr) occurred in a Jamaican mangrove site with other high capture rates in residential habitat (G.I.), dry scrub habitats in the Bahamas, and lowland second growth habitats in Jamaica and the Dominican Republic. The percentage of migrant individuals in net captures was positively, but weakly, correlated with the corresponding percentage in point counts (Spearman $r = 0.55$, $df = 27$, $P = 0.002$). Migrants constituted an especially high percentage of the individuals captured in lowland second growth in the Dominican Republic (73%), and in mangroves on Cuba (67%) and in the Dominican Republic (70%).

The percentage of migrant species in point counts was weakly correlated with the percentage of migrants in mist net samples in the same habitats (Spearman $r = 0.56$, $df = 27$, $P = 0.003$). Migrant species constituted a significantly higher percentage of the species sampled by mist nets ($\bar{x} = 41.0\% \pm 2.7$) than by point counts ($\bar{x} = 31.5\% \pm 1.9$) in the same habitat (paired t -test, $t = 3.91$, $df = 27$, $P = 0.001$). No correlation was found between the rarefaction ($n = 15$ individ-

TABLE 5. Degree of habitat specialization of residents and migrants on five islands. Degree of specialization is based on the exponential of the Shannon-Weiner diversity statistic (H') as explained in Table 4. n refers to number of species. P refers to significance of difference between residents and migrants on the same island as determined by Mann Whitney U Test.

Island	Mean exp(H') \pm SE		P
	Residents (n)	Migrants (n)	
Andros	2.8 \pm 0.2 (13)	2.4 \pm 0.3 (7)	0.23
Cuba	2.9 \pm 0.2 (22)	2.4 \pm 0.2 (11)	0.06
Jamaica	4.0 \pm 0.3 (32)	4.4 \pm 0.8 (12)	0.57
Dom. Republic	3.6 \pm 0.3 (32)	3.8 \pm 0.4 (9)	0.47
Puerto Rico	3.3 \pm 0.3 (27)	2.9 \pm 0.6 (5)	0.86

uals) estimates of migrant species richness derived from point counts and those from netting in the same habitats (Pearson $r = 0.14$, $df = 10$, $P = 0.67$).

There was no significant correlation between the rank order of occurrence rates of individual migrant species as estimated by mist net surveys and point counts in 23 of the 26 sites where both methods were used. At the remaining three sites, the correlation was negative—dry scrub, New Providence (Spearman $r = -0.79$, $df = 5$, $P = 0.03$); montane broadleaf forest, Cuba (Spearman $r = -0.63$, $df = 10$, $P = 0.03$); montane second growth, Cuba (Spearman $r = -0.65$, $df = 8$, $P = 0.04$). Thus, estimates of relative species abundances based on mist net samples of migrants did not resemble estimates based on point counts in the same habitat.

The following individual migrant species occurrence rates in mist net samples were significantly correlated with the number of point count occurrences in the same habitat: Prairie Warbler (Spearman $r = 0.70$, $df = 27$, $P < 0.001$), Black-throated Blue Warbler (Spearman $r = 0.65$, $df = 27$, $P < 0.001$), Gray Catbird (Spearman $r = 0.64$, $df = 27$, $P < 0.001$), Northern Waterthrush (Spearman $r = 0.55$, $df = 27$, $P = 0.003$), Ovenbird (Spearman $r = 0.54$, $df = 27$, $P = 0.005$), Palm Warbler (Spearman $r = 0.56$, $df = 27$, $P = 0.003$), Cape May Warbler (Spearman $r = 0.51$, $df = 27$, $P = 0.008$), Indigo Bunting (Spearman $r = 0.48$, $df = 27$, $P = 0.012$), Yellow-throated Warbler (Spearman $r = 0.43$, $df = 27$, $P = 0.03$), and Yellow-rumped Warbler (Spearman $r = 0.40$, $df = 27$, $P = 0.04$). Not surprisingly, the correlation between occurrence rates in mist net samples and point counts appeared to be strongest for species that forage close to the ground, and weakest for those restricted primarily to the canopy.

DISCUSSION

OVERALL PATTERNS IN THE CARIBBEAN

Our surveys demonstrate that the decrease in migrant abundance with distance from North America is more complex than originally described by Terborgh and Faaborg (1980). They could not separate area from distance effects because of the strong negative correlation between island area and distance from the mainland in the Greater and Lesser Antilles. Therefore, they concluded that the combined effects of island size and distance were major factors controlling migrant distribution in the Greater and Lesser Antilles, as migrants were faced with diminishing returns by flying farther and farther to smaller and smaller targets. No doubt area/distance effects are important in the Lesser Antilles, where migrant abundance is very low and declines southward (Terborgh and Faaborg 1980; Wunderle, unpubl. data). However, closer to the continent, total migrant density and species richness does not strongly decline from the Bahamas through the Greater Antilles, suggesting that factors other than distance and island size determine the abundance of wintering migrants in this region.

It is not surprising that the expected decrease in total migrant abundance with distance from North America was only weakly supported given that migrant abundance was often highly variable among different habitat types on the same island. The range in migrant abundance on an island was often substantial, indicating that different habitats on an island varied considerably in their attractiveness to wintering migrants. However, the effect of distance became more apparent when the analysis was restricted to a single habitat type (i.e., xeric habitats or mangroves), indicating that distance may influence total mi-

grant abundance within some habitats. Finally, distance did have an important effect on the abundance of certain species that wintered mostly in the Bahamas.

Contrary to the island size and distance predictions, censuses in the moist forest on St. John, the smallest and most distant island studied, indicate relatively high densities and species richness of wintering migrants. Askins et al. (1992) also found high migrant densities and species richness in moist forest on St. John, but not in moist forest on nearby St. Thomas. They attributed the abundance of migrants on St. John to the presence of extensive tracts of moist forest (only 12% of the island is developed), in contrast to St. Thomas, where the remaining moist forest is highly fragmented (62% of the island is residential or urban). Thus, in this case, relatively extensive forest tracts may harbor a higher abundance and diversity of species than small forest remnants, a finding consistent with previous studies in temperate-zone deciduous forests and tropical rain forest (e.g., Ambuel and Temple 1983, Lovejoy et al. 1984).

Although our study was not designed to examine the effect of habitat fragmentation on wintering migrant abundance and diversity, several findings suggest that migrant abundance is not always positively correlated with fragment size. At some sites, migrants are very abundant in small isolated habitat patches. We did not detect differences in migrant density or species richness between the large, relatively undeveloped island of Andros and the nearby small, highly developed (and densely populated) island of New Providence. The highly degraded and fragmented pine forest on New Providence had migrant counts comparable to those in the more extensive and less degraded pine forest on Andros. Within dry scrub, migrant densities were similar on the two islands, although total migrant species richness was greater in Andros scrub. The absence of an area effect may be partially attributed to the relatively high abundance on both islands of early successional species such as Palm Warblers and Prairie Warblers. However, even some of the forest generalist species such as American Redstart and Ovenbird were more abundant in the fragmented forests of New Providence.

Robbins et al. (1987) also found that most species of winter residents had comparable densities in small and large forest tracts in Puerto Rico, the Dominican Republic, Jamaica, Costa Rica, and Venezuela. In some of our sites, mi-

grants were very abundant in small habitat patches. For example, migrants were often abundant and diverse in small (1–5 ha) coffee plantations isolated in pastures in the Dominican Republic. These observations suggest that wintering migrant abundances are not invariably lower in small habitat fragments than in large tracts. As suggested by Askins et al. (1992), the effect of fragmentation may depend upon habitat type, the degree of habitat isolation, and the species of migrant under consideration.

One of the largest continuous forest patches sampled in our study was the Luquillo Experimental Forest (113 km²) in eastern Puerto Rico. At this site we surveyed birds in both low and mid-elevation montane broadleaf forest and found that migrant densities and species richness were among the lowest of any forest habitats sampled in our entire study. Migrant counts were 4–6 times higher in moist forest on St. John, despite the fact that the entire island is only half the size of the Luquillo Forest. In this case, food supply might be a major contributing factor to these differences in migrant abundance. For example, the Luquillo Forest is characterized by high densities of lizards and frogs (e.g., Drewry 1970, Reagan 1986), which might depress foliage insect densities (Pacala and Roughgarden 1985), thereby limiting populations of insectivorous birds. In moist forests on some small islands, the very abundant Pearly-eyed Thrasher (*Margarops fuscatus*) may limit lizard populations (McLaughlin and Roughgarden 1989), which might result in higher insect densities. This may occur on St. John where thrasher populations are very high (Askins and Ewert 1991), but obviously, direct sampling of insect populations will be necessary to determine some of the causes for habitat differences in wintering migrant abundance.

XERIC HABITATS

Xeric scrub and forest consistently had the lowest total counts of migrants of any habitats we sampled in the Greater Antilles. This pattern has been previously observed in the Caribbean (Lack and Lack 1972, Terborgh and Faaborg 1980, Askins et al. 1992) in contrast to the abundance of migrants in xeric vegetation in parts of Mexico (Hutto 1980, Waide 1980, Waide et al. 1980, Lynch 1989). These differences may be attributed partly to the fact that the migrants wintering in the Caribbean breed in the mesic eastern forests of North America, whereas some sections of Mexico (particularly the Pacific drainage) are vis-

ited by migrants that breed in xeric sites in the western United States (Terborgh 1989). However, migrants that breed in the mesic forests of eastern North America are common in winter bird communities associated with dry forest in the Yucatan Peninsula (Waide 1980, Lynch 1989). The low density of migrants in dry insular habitats is somewhat surprising, given that seasonally dry habitats predominated in the Caribbean region during the Pleistocene (Pregill and Olson 1981), and often contain the greatest abundance and diversity of resident species on an island (Kepler and Kepler 1970). Yet no migrant species was restricted to dry habitats, nor did any migrants reach their maximum abundance in dry habitats.

In the Caribbean, xeric habitats are highly seasonal. Distinct wet and dry seasons cause fluctuations in food resources, as found elsewhere in the tropics for insects (Wolda 1978, Hespenheide 1980) and fruit (Morton 1980). A winter (i.e., dry season) decline in food availability in xeric habitats may make it difficult for some species to obtain adequate fat reserves for spring migration (Orejuela et al. 1980, Bosque and Lentino 1987). Such habitats are also characterized by periodic severe droughts, during which both resident and migrant populations of some species may decline (Orejuela et al. 1980, Faaborg et al. 1984). Drought on the tropical wintering grounds has been demonstrated to cause population declines on the temperate breeding grounds in at least one European bird species (Winstanley et al. 1974, Batten and Marchant 1977). The likelihood that winter food supplies will decline faster in xeric than mesic or moist habitats may make dry habitats less suitable for species that establish stable winter territories (Bosque and Lentino 1987). Individuals that do occur in xeric habitats may be subordinates who have been excluded from more "desirable" moist habitats by dominant individuals occupying more mesic sites (Parrish and Sherry 1991, Marra et al. 1991). Opportunistic species, such as Cape May Warbler and Prothonotary Warbler (*Protonotaria citrearia*), may take advantage of drought-induced declines in resident insectivores to move into dry forest (Faaborg et al. 1984).

SECOND GROWTH HABITATS

As previously observed (e.g., Willis 1966, Tramer and Kemp 1980, Waide 1980, Lynch 1989, Lynch 1992), both total migrant occurrences and occurrences of some species are often high in

second growth or disturbed habitats. This is consistent with findings that food resources such as insects (e.g., Janzen 1973) and flowers and fruit (e.g., Levy 1988, Loiselle and Blake 1990) are frequently more abundant in second-growth than in mature tropical forests. Second growth may be more suitable for some migrants because it is often more resistant to hurricane damage, as it suffers less structural damage and has a higher recovery rate than mature forest (Wunderle et al. 1992). However, higher migrant abundance in second growth may reflect unstable territories and high population turnover in contrast to mature habitats characterized by lower migrant densities, more stable territories and lower population turnover (Rappole and Warner 1980).

MIGRANTS AND RESIDENTS

Many early workers believed that overwintering migrants could "fit in" to the species-rich tropical communities by occupying highly disturbed, marginal, or ephemeral habitats where permanent residents were mostly absent (e.g., Slud 1960, Willis 1966, Fitzpatrick 1980). This view predicts that a negative correlation should occur between the abundance of migrants and residents across a variety of habitats. In contrast to these predictions, studies in the Yucatan Peninsula and western Mexico have found a positive correlation between the occurrence rates of migrants and residents (Waide 1980, Hutto 1980, Lynch 1992). These studies demonstrate that habitats favorable for migrants as a group are also favorable for residents as a group. Therefore, even though migrants were often abundant in disturbed Mexican habitats, so were residents. Although our positive correlation between the number of migrant and resident species in habitats in the Bahamas is consistent with the findings in Mexico, we found no consistent relationship between the abundance and distribution of migrants and residents among different Caribbean habitats. Thus, we found habitats that were rich in residents and migrants (e.g., brushy field), rich in migrants but poor in residents (e.g., mangroves, Greater Antilles), poor in migrants but rich in residents (e.g., dry scrub/forest, Greater Antilles), and poor in migrants and residents (e.g., pine, D.R.).

MIGRANTS IN THE CARIBBEAN VERSUS THE YUCATAN PENINSULA

The migrant surveys by Lynch (1989, 1992) in the Yucatan Peninsula provide another example

of migrant abundance and habitat distribution across a broad geographic area. However, comparison of the Yucatan and Caribbean data should be made cautiously because our methods differed slightly. For instance, sampling effort differed: our study involved 1,838 point counts (7,936 net hr) in 15 habitats; Lynch conducted 976 point counts (11,562 net hr) in 11 major habitat types. Lynch's point counts varied in duration from 10–12 min each, compared with our 10 min counts, and Lynch used tape-recorded playback (including chip notes of two migrant species, distress squeaks, and owl whistles) in contrast to our silent counts. Lynch (1989) emphasized a successional continuum from early (field/pasture), mid-("acahual"), to late succession (mature semievergreen forest). In contrast, we took advantage of available altitudinal and moisture gradients to sample a diversity of habitat types, without obtaining full representation of the successional continuum. Despite these differences, the similarity of our overall procedures allows some general comparisons of migrant abundance and habitat distribution between island and continental wintering grounds.

The percentage of nearctic migrant species was similar in the two regions (21% Yucatan versus 23% Caribbean), although the total number of migrant species in Yucatan was higher (43 species Yucatan versus 35 species Caribbean). Within a habitat, the average percentage of migrant species was also similar (Yucatan \bar{x} = 37%, range 29–54%; Caribbean \bar{x} = 32%, range 6–50%). However, a major difference occurred in the average percentage of migrant individuals within a habitat, which was higher in the Yucatan (\bar{x} = 41%, range 30–58%; Caribbean \bar{x} = 25%, range 1–71%).

Migrants constituted the highest percentage of individuals in mangroves in both the Yucatan (58%) and Greater Antilles (\bar{x} = 60%; range 53–71%), partially due to the high densities of Northern Waterthrushes. In Yucatan, only the Northern Waterthrush had its maximum rate of occurrence in mangrove forest, although other species were also abundant there. In contrast, five species had their maximum rate of occurrence in Greater Antillean mangroves (American Redstart, Black-and-white Warbler, Northern Waterthrush, Magnolia Warbler, Yellow-bellied Sapsucker).

Lynch's use of playback during point counts

undoubtedly increased the detectability of many migrant species, thereby contributing, in part, to the substantially higher average of migrant individuals per point count in Yucatan (\bar{x} = 3.3, range 2.6–4.1; Caribbean, \bar{x} = 0.8, range 0.1–3.1). However, even with the use of playback in the Yucatan counts, the maximum occurrence for some geographically widespread species was actually higher in some Caribbean habitats than in Yucatan. For instance, occurrences were highest in Caribbean habitats for Common Yellowthroat, American Redstart, Black-and-white Warbler, Gray Catbird, Yellow-throated Warbler, Black-throated Green Warbler, Ovenbird, and Worm-eating Warbler. In Yucatan, several species that winter primarily in the Caribbean (e.g., Cape May Warbler, Palm Warbler, Yellow-throated Warbler, Yellow-rumped Warbler and Blue Grosbeak) had their highest occurrences in coastal scrub, although most (except Cape May Warbler) were also found far from the coast in milpas and pastures in northern Yucatan (Lynch 1989). Another migrant confined mostly to the Caribbean, the Black-throated Blue Warbler, was detected in Yucatan by mist netting in mature semievergreen forest.

For other geographically widespread species, maximum frequencies were highest in Yucatan habitats: Hooded Warbler, Magnolia Warbler, White-eyed Vireo, Indigo Bunting, and Kentucky Warbler. Swainson's Warblers were detected by mist net in both acahual and mature semievergreen forest in Yucatan and only by mist netting in the Caribbean.

Many migrant species wintering in both regions tend to use the same habitat types or habitats at the same state of succession. For instance, the migrants found in early successional stages in both regions include Common Yellowthroat, Palm Warbler, Yellow-rumped Warbler, and Indigo Bunting; species found across the entire successional spectrum include the Northern Parula; forest generalist species found in a variety of broadleaf forests include American Redstart, Black-throated Green Warbler, and Ovenbird; species specialized on mature broadleaf forests include Hooded and Kentucky Warbler; and a highly specialized species, the Northern Waterthrush, that is largely restricted primarily to mangroves. However, not all species were consistent in their habitat use in the two regions. The Yellow-throated Warbler was restricted al-

most solely to pine forests in the Caribbean, but was restricted to early successional broadleaf communities in Yucatan. The presence of Yellow-throated Warblers in early successional stages in Yucatan could simply result from the absence of pine in the region, as on Great Inagua where the species was found in a residential area. However, it is conceivable that the Yellow-throated Warblers wintering in the Caribbean come from populations which breed in temperate pine forests (e.g., Delmarva Peninsula or northwestern Florida, Morse 1989), in contrast to the Mexican populations, which may breed in temperate broadleaf forests of the southern and central United States.

In Yucatan, Lynch (1989) noted that most migrants that bred in mature temperate-zone forests also occurred both in forest and second growth. In contrast, migrants which bred in second-growth habitats in the temperate zone tended to avoid mature forest in Yucatan. Our work confirms this observation and, for two species common to both regions, the habitat breadth pattern was more evident in the Caribbean. For example, Gray Catbirds were restricted to shrubby second growth in the Caribbean, in contrast to a "generalist" distribution (including some closed-canopy forest) in Yucatan. Black-and-white Warblers were found throughout an array of second-growth and mature forests in the Caribbean (designated as forest generalists) in contrast to the Yucatan where they were found primarily in mature forests (forest specialist). In the Caribbean, Common Yellowthroat, Prairie Warbler, Palm Warbler, Yellow-rumped Warbler, Gray Catbird, and Indigo Bunting were restricted to forest edge or early successional habitats, and rarely found in closed-canopy broadleaf forests. However, Palm and Prairie Warblers were also found in closed-canopy pine forests where the understory was destroyed by fire. In contrast to the absence of second growth species in closed-canopy forests, the species common in closed-canopy forests (forest generalists) were found in a variety of Caribbean second growth habitats, even in pastures with widely scattered shade trees.

Finally, both Yucatan and Caribbean migrant surveys indicated that mist-nets under-sampled canopy dwellers and consequently mist-net results were rarely correlated with point count results. In both studies, few migrant species were detected by mist-nets that were not also detected

by point counts, whereas the reverse was not true. Only small, secretive, non-flocking species that inhabit dense low-stature vegetation are likely to be best censused by netting.

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LITERATURE CITED

- AMBUEL, B., AND S. A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64: 1057-1068.
- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds, 6th ed. American Ornithologists Union, Washington, DC.
- ARENDT, W. J. 1992. Status of North American migrant landbirds in the Caribbean: a summary. *In* J. Hagan and D. Johnston [eds.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Press, Washington, DC.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America, p. 1-57. *In* D. M. Power [ed.], *Current ornithology*. Plenum Press, New York.
- ASKINS, R. A., AND D. N. EWERT. 1991. Impact of

- Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. *Biotropica* 23:481-487.
- ASKINS, R. A., D. N. EWERT, AND R. L. NORTON. 1992. Abundance of wintering migrants in fragmented and continuous forests in the US Virgin Islands. *In* J. Hagan and D. Johnston [eds.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- BATTEN, L. A., AND J. H. MARCHANT. 1977. Bird population changes for the years 1974-75. *Bird Study* 24:55-61.
- BOSQUE, C., AND M. LENTINO. 1987. The passage of North American migratory landbirds through xerophytic habitats on the western coast of Venezuela. *Biotropica* 19:267-273.
- COX, G. W., AND R. E. RICKLEFS. 1977. Species diversity and ecological release in Caribbean land bird faunas. *Oikos* 28:113-122.
- DREWRY, G. E. 1970. The role of amphibians in the ecology of a Puerto Rican rain forest, p. 16-54. *In* R. G. Clements, G. E. Drewry, and R. J. Lavigne [eds.], *The Rain Forest Project Annual Report*, No. 147. Puerto Rico Nuclear Center, San Juan.
- EMLÉN, J. T. 1973. Territorial aggression in wintering warblers at Bahama agave blossoms. *Wilson Bull.* 85:71-74.
- EMLÉN, J. T. 1977. Land bird communities of Grand Bahama Island: the structure and dynamics of an avifauna. *Ornithological Monograph* 24.
- EMLÉN, J. T. 1980. Interactions of migrants and resident land birds in Florida and Bahama pinelands, p. 133-143. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- FAABORG, J. R., AND W. J. ARENDT. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. *J. of Field Ornithol.* 55:376-378.
- FAABORG, J. R., W. J. ARENDT, AND M. S. KAISER. 1984. Rainfall correlates of bird population fluctuations in a Puerto Rican dry forest: a nine year study. *Wilson Bull.* 96:575-593.
- FAABORG, J. R., AND W. J. ARENDT. 1990. Long-term declines in winter resident warblers in a Puerto Rican dry forest. *Amer. Birds* 43:1226-1230.
- FAABORG, J. R., AND J. W. TERBORGH. 1980. Patterns of migration in the West Indies, p. 157-163. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- FITZPATRICK, J. W. 1980. Wintering North American tyrant flycatchers in the neotropics, p. 67-78. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- HESPENHEIDE, H. A. 1980. Bird community structure in two Panama forests: residents, migrants, and seasonality during the nonbreeding season, p. 227-237. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- HUTTO, R. L. 1980. Winter habitat distribution of migratory land birds in western Mexico, with special reference to small foliage-gleaning insectivores, p. 181-203. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics*. Smithsonian Institution Press, Washington, DC.
- HUTTO, R. L., S. M. PLETSCHE, AND P. HENDRICKS. 1986. A fixed-radius point count method for non-breeding and breeding season use. *Auk* 103:593-602.
- JANZEN, D. H. 1973. Sweep samples of tropical foliage insects, description of study sites, with data on species abundances and size distributions. *Ecology* 54:659-686.
- KALE, H. 1967. Aggressive behavior by a migrating Cape May Warbler. *Auk* 84:120-121.
- KEAST, A. 1980. Synthesis: ecological basis and evolution of the nearctic-neotropical bird migration system, p. 559-576. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics*. Smithsonian Institution Press, Washington, DC.
- KEPLER, C. B., AND A. K. KEPLER. 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guanica forests, p. E 183-191. *In* H. T. Odum and R. F. Pigeon [eds.], *A tropical rain forest*. N.T.I.S., Springfield, VA.
- LACK, D., AND P. LACK. 1972. Wintering warblers in Jamaica. *Living Bird* 11:129-153.
- LANLY, J. P. 1982. Tropical forest resources. Food and Agriculture Organization, United Nations, Rome, Italy.
- LOISELLE, B. A., AND J. G. BLAKE. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. 13:91-103.
- LOVEJOY, T. E., J. M. RANKIN, R. O. BIERREGAARD, JR., K. S. BROWN, JR., L. H. EMMONS, AND M. E. VAN DE VOORT. 1984. Ecosystem decay of Amazon forest remnants, p. 295-325. *In* M. H. Nitecki [ed.], *University of Chicago Press*, Chicago.
- LYNCH, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. *Condor* 91:515-544.
- LYNCH, J. F. 1992. Distribution of overwintering nearctic migrants in the Yucatan Peninsula, II: Use of natural and human-modified vegetation. *In* J. Hagan and D. Johnston [eds.], *Smithsonian Institution Press*, Washington, DC.
- MARRA, P. P., T. W. SHERRY, AND R. T. HOLMES. 1991. Territorial exclusion by older males in a neotropical migrant in winter removal experiments in American Redstarts. Abstract, American Ornithologists Union meeting, Montreal.
- MC Laughlin, J. F., AND J. ROUGHGARDEN. 1989. Avian predation on *Anolis* lizards in the north-eastern Caribbean: an interisland contrast. *Ecology* 70:617-628.
- MORSE, D. H. 1989. American warblers: an ecological and behavioral perspective. Harvard Univ. Press, Cambridge, MA.
- MORTON, E. S. 1980. Adaptations to seasonal changes by migrant land birds in Panama Canal Zone, p. 437-453. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics*. Smithsonian Institution Press, Washington, DC.

- OREJUELA, J. E., R. J. RAITT, AND H. ALVAREZ. 1980. Differential use by North American migrants of three types of Colombian forests, p. 253–264. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- PACALA, S., AND J. ROUGHGARDEN. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). *Oecologia* 64:160–162.
- PARRISH, J. D., AND T. W. SHERRY. 1991. Sexual habitat segregation in American Redstarts wintering in Jamaica. Abstract, Wilson and Cooper Ornithol. Soc. Joint Meeting, Norman, OK.
- PASHLEY, D. N. 1988a. Warblers of the West Indies. I. The Virgin Islands, Caribb. J. of Sci. 24:11–22.
- PASHLEY, D. N. 1988b. Warblers of the West Indies II. The western Caribbean. Caribb. J. Sci. 24:112–126.
- PASHLEY, D. N. 1990. Warblers of the West Indies. III. The Lesser Antilles. Caribb. J. Sci. 26:75–97.
- PREGILL, G. K., AND S. L. OLSON. 1981. Zoogeography of West Indian vertebrates in relation to pleistocene climatic cycles. *Ann. Rev. Ecol. Syst.* 12:75–98.
- RAPPOLE, J. H., AND D. W. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico, p. 353–393. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- RAPPOLE, J. H., AND G. POWELL. 1986. The Hooded warbler, p. 827–853. *In* R.L.D. Silvestro [ed.], *Audubon Wildlife Report*. National Audubon Society, New York.
- REAGAN, D. P. 1986. Foraging behavior of *Anolis stratulus* in a Puerto Rican rain forest. *Biotropica* 18:157–160.
- ROBBINS, C. S., B. A. DOWELL, D. K. DAWSON, J. COLON, F. ESPINOZA, J. RODRIGUEZ, R. SUTTON, AND T. VARGAS. 1987. Comparison of neotropical winter bird populations in isolated patches versus extensive forest. *Acta. Oecol. Gen.* 8:285–292.
- SCHEMSKE, D. W., AND N. BROKAW. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62:938–945.
- SIMBERLOFF, D. S. 1972. Properties of the rarefaction diversity measurement. *Am. Nat.* 106:414–418.
- SIMBERLOFF, D. S. 1978. Use of rarefaction and related methods in ecology, p. 150–165. *In* J. Cairns, R. J. Livingston, and K. I. Dickson [eds.], *Biological data in water pollution assessment: quantitative and statistical analyses*. Am. Soc. Testing and Materials Spec. Tech. Publ. No. 652.
- SLUD, P. R. 1960. The birds of finca “La Selva”: a tropical wet forest locality. *Bull. Amer. Mus. Nat. Hist.* 121:49–148.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, New York.
- TABACHNICK, B. G., AND L. S. FIDELL. 1983. *Using multivariate statistics*. Harper and Row, Publ., New York.
- TERBORGH, J. W. 1989. *Where have all the birds gone?* Princeton Univ. Press, Princeton, NJ.
- TERBORGH, J. W., AND J. R. FAABORG. 1980. Factors affecting the distribution and abundance of North American migrants in the eastern Caribbean region, p. 145–155. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- TRAMER, E. J., AND T. R. KEMP. 1980. Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica, p. 285–296. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- WAIDE, R. B. 1980. Resource partitioning between migrant and resident birds: the use of irregular resources, p. 337–352. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- WAIDE, R. B., J. T. EMLÉN, AND E. J. TRAMER. 1980. Distribution of migrant birds in the Yucatan Peninsula: a survey, p. 165–171. *In* A. Keast and E. S. Morton [eds.], *Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, DC.
- WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187–231.
- WILKINSON, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.
- WINSTANLEY, D., R. SPENCER, AND K. WILLIAMSON. 1974. Where have all the Whitethroats gone? *Bird Study* 21:1–14.
- WOLDA, H. 1978. Fluctuations in abundance of tropical insects. *Amer. Naturalist* 112:1017–1045.
- WUNDERLE, J. M., D. J. LODGE, AND R. B. WAIDE. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *Auk* 109: 148–166.
- WUNDERLE, J. M., AND R. B. WAIDE. In press. Future prospects for nearctic migrants wintering in Caribbean forests. Growing points in the knowledge of bird migration in the Neotropics. ICBP Technical Publ., Cambridge, U.K.

APPENDIX I. List of nearctic migrants detected in the Bahamas and Greater Antilles during winter surveys in the period 1984–1991. Both the scientific and common names and sequence follow the AOU (1983) checklist. Island names have the following abbreviations: A., Andros; N.P., New Providence; G.I., Great Inagua; C., Cuba; J., Jamaica; D.R., Dominica Republic; P.R., Puerto Rico; S.J., St. John. Method of detection was either by point count (P) or mist netting (N). * Indicates that the species was detected in a small mesic woods in Nassua, where sample includes only 10 points. ** Indicates that the species was detected outside of point counts.

Species	Island							
	A.	N.P.	G.I.	C.	J.	D.R.	P.R.	S.J.
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	0	P	0	PN	0	0	0	0
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	0	0	0	P	0	P	0	0
Gray-cheeked Thrush (<i>Catharus minimus</i>)	0	0	0	0	N	0	N	0
Wood Thrush (<i>Hylocichla mustelina</i>)	0	0	0	0	0	0	N	0
Gray Catbird (<i>Dumetella carolinensis</i>)	PN	PN	PN	P	PN	P	0	0
White-eyed Vireo (<i>Vireo griseus</i>)	P	0	0	P	0	0	0	0
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	0	0	0	0	0	0	0	P
Blue-winged Warbler (<i>Vermivora pinus</i>)	0	0	0	0	0	P	0	0
Tennessee Warbler (<i>Vermivora peregrina</i>)	0	0	0	P	P	0	0	0
Virginia's Warbler (<i>Vermivora virginiae</i>)	0	0	0	P	0	0	0	0
Northern Parula (<i>Parula americana</i>)	0	0	PN	P	PN	PN	PN	P
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	0	0	0	0	P	0	N	P
Magnolia Warbler (<i>Dendroica magnolia</i>)	N	0	PN	0	P	PN	N	**
Cape May Warbler (<i>Dendroica tigrina</i>)	P	P	PN	0	0	PN	P	P
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	PN	0	N	PN	PN	PN	PN	**
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	PN	0	0	0	0	PN	0	0
Black-throated Green Warbler (<i>Dendroica virens</i>)	P	0	0	P	P	0	0	P
Blackburnian Warbler (<i>Dendroica fusca</i>)	0	0	0	0	P	0	0	0
Yellow-throated Warbler (<i>Dendroica dominica</i>)	PN	P	PN	0	0	P	0	0
Prairie Warbler (<i>Dendroica discolor</i>)	PN	PN	P	P	PN	PN	P	P
Palm Warbler (<i>Dendroica palmarum</i>)	PN	P	PN	P	PN	PN	P	0
Black-and-white Warbler (<i>Mniotilta varia</i>)	PN	N	PN	P	PN	PN	PN	P
American Redstart (<i>Setophaga ruticilla</i>)	PN	PN	P	PN	PN	PN	PN	P
Worm-eating Warbler (<i>Helminthos vermivorus</i>)	PN	N	PN	PN	PN	0	0	0
Swainson's Warbler (<i>Limnothlypis swainsonii</i>)	N	0	0	0	N	0	0	0
Ovenbird (<i>Seiurus aurocapillus</i>)	N	P	PN	PN	PN	PN	PN	P
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	P	*	P	P	PN	P	P	P

APPENDIX I. Continued.

Species	Island							
	A.	N.P.	G.I.	C.	J.	D.R.	P.R.	S.J.
Louisiana Waterthrush (<i>Seiurus motacilla</i>)	0	0	0	0	0	0	PN	0
Kentucky Warbler (<i>Oporonis formosus</i>)	0	0	0	0	N	0	N	P
Common Yellowthroat (<i>Geothlypis trichas</i>)	PN	*	P	PN	PN	PN	N	0
Hooded Warbler (<i>Wilsonia citrina</i>)	0	*	0	0	PN	0	N	P
Wilson's Warbler (<i>Wilsonia pusilla</i>)	0	0	0	**	0	0	0	0
Yellow-breasted Chat (<i>Icteria virens</i>)	N	0	0	0	0	0	0	0
Indigo Bunting (<i>Passerina cyanea</i>)	P	0	PN	N	P	0	0	0
Painted Bunting (<i>Passerina ciris</i>)	P	0	0	0	0	0	0	0