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The Assemblage of Birds Foraging in Native West Indian Pine (*Pinus occidentalis*) Forests of the Dominican Republic during the Nonbreeding Season[1]

Steven C. Latta[2] and **Joseph M. Wunderle, Jr.**
International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 490, Palmer, Puerto Rico 00721

ABSTRACT

We studied avian resource use in a native West Indian pine (*Pinus occidentalis*) forest in the Cordillera Central of the Dominican Republic during the nonbreeding season. The forest is characterized by a fairly open pine canopy and a dense mixed-broadleaf and pine understory. We used a principal components analysis of 23 foraging characters for 23 bird species, including foraging height, the proportional use of 5 different foraging methods, 3 horizontal positions and foliage densities, and 11 foraging substrates. Five principal components accounted for 74 percent of the total variance of the assemblage variables and resulted in the delineation of at least 5 foraging guilds. 78 percent of bird species had mean foraging heights of 5.0–10.0 m, corresponding to the region of overlap of pine and broadleaf vegetation. As a result, the diversity of foraging substrates and maneuvers used by birds, rather than foraging height, appears to be the primary means by which birds that exploit this habitat separate ecologically. Migrant wood warblers (Parulinae) are probably able to integrate into the community because of little diet overlap between residents and migrants, and the fairly specialized nature of their largely insectivorous foraging habits. Avian foraging in this habitat may reflect the effects of frequent disturbance such as hurricanes.

RESUMEN

Estudiamos el uso de recursos por aves en un bosque de pino nativo (*Pinus occidentalis*) en la Cordillera Central de la República Dominicana durante la época de no-reproducción. El bosque se caracteriza por un dosel de pino bastante abierto, con pinos y arbustos mixtos y densos en las clases de vegetación de alturas más bajas. Utilizamos un análisis de componentes principales de 23 caracteres de comportamientos alimenticios para 23 especies, incluyendo la altura de alimentación, el uso proporcional de cinco métodos de comportamientos alimenticios, tres posiciones horizontales y clases de densidades de los arbustos, y once substratos de alimentos. Cinco componentes principales explicaban 74 por ciento de la variación total entre las 23 especies y delineaban por lo menos cinco guildas de alimentaciones. 78 por ciento de las especies de aves tenían una altura media de alimentacion de 5.0–10.0 m, coincidiendo con la región de traslapo de pinos y arbustos. Como consecuencia, la diversidad de substratos de alimentos y métodos de comportamientos alimenticios utilizados por las aves, en vez de la altura de comportamientos alimenticios, es la manera principal en que las aves utilizando este hábitat separaban los nichos ecológicos. Aves migratorias (Parulinae) probablamente pueden integrarse en la comunidad porque hay poco traslapo de alimentaciones entre los residentes y migrantes, y sus comportamientos alimenticios estan bastante especializado. Es posible que el comportamiento alimenticio de aves en este hábitat refleja los efectos de perturbaciones frecuentes como huracánes.

Key words: *Dominican Republic; foraging behavior; foraging guilds; Hispaniola; hurricanes; migratory birds;* Pinus occidentalis.

PINE FOREST, OFTEN WITH A BROADLEAF UNDERSTORY, is a significant component of the vegetation in the Caribbean basin (Lugo *et al.* 1981, FAO 1991). Caribbean pine (*Pinus caribaea*) is native to the northern Bahama Islands, Cuba, and Central America where it grows from 0–1000 m elevation, and has been widely planted elsewhere (Liegel 1991). West Indian pine (*P. occidentalis*) is native only to Hispaniola and Cuba. Pine makes up 21 percent of the forest area on Hispaniola and 36 percent of the forest area in Cuba (FAO 1991); 19 percent of the land area of the Bahamas is in pine (FAO 1991). Native pine forests in the Caribbean are declining under severe disturbance from wildfire, agriculture, grazing, and cutting for fuelwood, charcoal production, and building materials (Hartshorn *et al.* 1981, Lugo *et al.* 1981) and this has impacted adversely a number of bird populations (Arendt 1992). Natural disturbances, primarily hurricanes, also affect Caribbean forests (Brokaw & Walker 1991) and their bird communities (Wiley & Wunderle 1994).

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[2] Current address: University of Missouri, Division of Biological Sciences, 110 Tucker Hall, Columbia, Missouri 65211, U.S.A.

The structure of West Indian bird communities has been the focus of many studies (Ricklefs & Cox 1972, Lack 1976, Terborgh & Faaborg 1980, Case *et al.* 1983, Faaborg 1985), although none has detailed avian communities in pine forests. Several surveys have reported that pine forests in the West Indies harbor a diverse avifauna (Arendt 1992, Wunderle & Waide 1993), but these surveys focused on the presence or absence of species. Terborgh and Faaborg (1980) described the general foraging behavior of birds comprising the migrant warbler complex in Hispaniolan pine forests and suggested that seven species separate by vertical stratification and foraging tactics, resulting in a tightly-structured, pinewoods-warbler complex. Latta and Wunderle (1996a) analyzed foraging behavior of migrants and residents in mixed-species foraging flocks, also in Hispaniolan pine, but focused on flock composition, flocking propensity, and modifications of foraging behavior while in flocks. Others have focused on bird use of managed forests of exotic pine. Falkenberg *et al.* (1983) found fewer birds in *P. caribaea* plantations than in native broadleaf forest in Jamaica, and Cruz (1988) described resource use, niche structure, and avian assemblage patterns in an introduced Caribbean pine plantation in Puerto Rico.

Despite the apparent value of pine forests to migratory and resident birds, quantitative analyses of the avian assemblages or avian resource use in pine forests are lacking. Therefore, the objectives of this study were to quantify where and how birds forage in *P. occidentalis* pine forests in the Cordillera Central of the Dominican Republic, and determine the food resources used by birds in these forests. These observations enabled us to describe the assemblage of birds in native pine forest, assess the integration of migrants and permanent residents into the winter bird community, and evaluate the importance of the pine and broadleaf components of the forest to birds in the nonbreeding season. We conclude by speculating on how disturbance to the vegetation could affect the bird community.

STUDY SITE AND METHODS

Study site.—Pine forests were sampled at six sites on slopes 905–1050 m elevation near Manabao (16°6′N, 70°48′W) and at six sites 643–779 m elevation near Jarabacoa (19°9′N, 70°39′W) in La Vega Province in the Cordillera Central of the Dominican Republic from October-April, 1993–95. Native pine forests, some of which have been selectively logged, remain on the steeper slopes and ridgetops, with small numbers of introduced *P. caribaea* and variable amounts of broadleaf understory that may be affected by fire, cutting, or cattle grazing. Sites were chosen on the basis of availability, proximity (no site was > 20 km from the farthest site), and similarity in structure. Although the area of our study sites was not measured, the remnant patches were all estimated to be > 100 ha. Sites were visited in sequence so that approximately equal search time was spent at each site.

We used eight 16-m diameter circular plots (0.02 ha) on four sites to quantify vegetational distribution. Plots were nonrandomly selected to represent the full range of vegetational variation in which avian foraging observations were made. Foliage heights were determined at 20 points located at 1.6 m intervals along the north, south, east, and west radii of each circular plot. A 3-m tall pole marked at 0.5 m intervals was placed vertically at each sampling point. We recorded the presence or absence of foliage touching the pole within each height class and identified the foliage as either pine or broadleaf. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following height intervals: 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, and 20–25 m. This was facilitated by the relatively sparse canopy, but height estimations were also checked with a range finder. We used the midpoint of each height category to calculate the median and mean pine and broadleaf tree heights for all plots combined.

Foraging behavior.—Foraging observations were made from 0700–1800 h by walking slowly through the habitat until a foraging bird was located. The first foraging event 5 sec after an individual was initially detected was recorded to avoid a bias toward more conspicuous feeding techniques. Only a single foraging event was recorded per individual per day to reduce the problem of autocorrelation inherent in sequence data (Wagner 1981).

We used the terminology of Remsen and Robinson (1990) to describe foraging maneuvers and foraging-site classifications. Foraging maneuvers included glean, hang, reach-up, reach-out, reach-under, jump-up (leap), sally-strike, sally-stall, sally-hover, sally-pounce, and probe. In all statistical analyses, foraging methods were combined into five categories. We used the term "glean" to designate all near-perch maneuvers in which the forager remained on a perch and picked a food item from the substrate surface. This category included all forms of reaching, hanging, and gleaning. The term "jump" was used for any lunging or jumping from the substrate to obtain a food item. We used the term "probe" for any maneuver in which the forager obtained a food item from the subsurface by probing or pecking. This included maneuvers by birds probing flowers for nectar, as well as probing into lichens, bark, or wood. Finally, aerial foraging was divided between maneuvers to forage in the air ("sally-air") and aerial maneuvers to forage on the surface of substrates ("sally-surface"). Any form of sally or hover was placed in one of these two categories.

The location of the food item, or the "substrate type" was assigned to 1 of 11 categories: needles, wood, or cones (pines); leaves, wood, flowers, fruit or seed (broadleaf shrubs); and epiphyte, air, herbaceous or vines, and ground. Foraging site was also characterized with respect to: (1) estimated height of the bird above the ground, (2) horizontal position of the bird (inner ⅓ of tree, middle ⅓ of tree, outer ⅓ of tree), and (3) foliage density (the amount of light passing through an imaginary 2.0 m diameter sphere surrounding the foraging site; 1 = 75–100% of light passes through, 2 = 25–74%, 3 = 0–24%). Height estimates were checked daily with a range finder to assure accuracy.

Most species included in these analyses are sexually monomorphic so that data from the sexes could not be distinguished. Dimorphic species with large sample sizes (Black-throated Blue Warbler, Black-and-white Warbler, American Redstart; scientific names in Table 1) were analyzed for sexual differences in foraging heights and methods to determine if separation of the sexes was justified.

In Dominican pine forests most species of birds participate in mixed-species foraging flocks (Latta & Wunderle 1996a). Although flocking may alter the foraging behavior of some bird species (Latta & Wunderle 1996a, b), flocking and solitary birds were lumped together for this analysis. This is justified because of the high flocking propensity of most flock participants and the relatively few changes in foraging behavior displayed by flocking birds (Latta & Wunderle 1996a).

Statistical analyses.—The software package SYSTAT Version 5.2 (Wilkinson 1992) was used to perform various statistical tests described in Sokal and Rohlf (1981). A probability of type I error ≤ 0.05 was accepted as significant, but greater values are shown for descriptive purposes. Data presented are means ± 1 SD. When data were not normally distributed, nonparametric statistics were used. An independent samples *t*-test was used to test for intraspecific differences in the mean foraging heights of males and females of sexually dimorphic species. A 2 × 2 Test of Independence with a X^2 statistic or a Row × Column Test of Independence with a *G* statistic was used to compare percent use of various feeding locations of males and females within a species, and to test for the independence of species' foraging location within pine, broadleaf, or other substrates.

We used SAS (SAS 1990) and the methods of Holmes *et al.* (1979) to perform a principal component analysis (PCA) on foraging data. For each of 23 of the most frequently observed avian species, we considered 23 foraging characters: mean foraging height, and the proportional uses of 5 different foraging methods, 3 horizontal positions, 3 foliage densities, and 11 foraging substrates. PCA transformed the original variables into a linear combination of uncorrelated variables known as principal components, which additively partition the variance for the set of variables. Five components were retained based on the Kaiser criterion (Kaiser 1960) and a scree test. We then used a Varimax rotation (Kaiser 1960) of the components to facilitate interpretation of the resulting factors by reducing split-loadings. For the purpose of visualizing relationships between the 23 bird species in the pine forest based on the 23 foraging characters, the species were plotted in the three-dimensional space dictated by the first three factors of the PCA.

RESULTS

Vegetation profile.—A foliage height profile (Fig. 1) was determined for representative pine habitat which shows a fairly open canopy, a denser mixed-broadleaf understory, and a sparse intermediate layer. Pine foliage predominated in the canopy with greatest cover in the 10–20 m height categories, and a maximum pine height of 22.5 m. Mean and median pine heights were 13.9 m (±5.1 m) and 13.5 m, respectively. Broadleaf tree and shrub species were not sampled but included *Ribes* sp., *Inga vera*, *Mangifera indica*, *Citrus* sp., *Cecropia* sp., *Syzygium jambos*, *Clusia* sp., *Lyonia* sp., and *Miconia* sp., as well as numerous unidentified shrubs. Mean broadleaf height was 3.2 m (±3.5 m) and median broadleaf height was 1.75 m. The broadleaf trees and shrubs primarily formed a dense ground cover, but scattered broad-

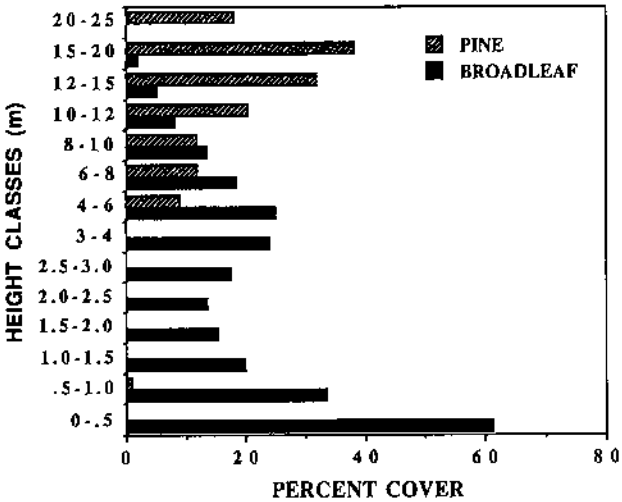

FIGURE 1. The percent cover of pine, broadleaf trees, and shrubs in each of 14 height classes in pine forest of the Cordillera Central, Dominican Republic.

leaf trees extended into the canopy as the maximum broadleaf height was 17.5 m.

AVIAN COMMUNITY MEMBERS.—We observed a total of 63 bird species in pine forest (see Wunderle & Latta 1996 for a complete list), but restricted our analysis to 23 species with feeding observation sample sizes >15 (Table 1). However, these 23 species nearly represented the entire winter-avian community. Of the 63 species observed, only 32 oc-

TABLE 1. *Bird species; species code; foraging behavior sample size; mean foraging height (x̄; SD); and percent use of three substrates (pine, broadleaf, other) for each of 23 species of birds observed in pine forest in the Cordillera Central of the Dominican Republic. An (*) indicates a migratory species.*

Species		Code	*N*	Height	Pine percent	BL percent	Other percent	*P*
Antillean Mango	*Anthracothorax dominicus*	AM	20	5.7 (3.4)	20	50	30	0.032
Hispaniolan Emerald	*Chlorostilbon swainsonii*	HE	22	5.0 (3.9)	28	57	15	0.001
Vervain Hummingbird	*Mellisuga mimima*	VH	18	5.7 (4.4)	28	45	27	0.239
Narrow-billed Tody	*Todus angustirostris*	NB	62	3.9 (2.5)	5	83	12	0.000
Broad-billed Tody	*Todus subulatus*	BB	58	6.0 (3.4)	17	83	0	0.000
Hispaniolan Woodpecker	*Melanerpes striatus*	HW	39	8.6 (3.5)	61	32	7	0.000
Hispaniolan Pewee	*Contopus hispaniolensis*	PE	102	5.9 (3.9)	14	8	78	0.000
Greater Antillean Elaenia	*Elaenia fallux*	EL	64	8.7 (4.1)	32	23	45	0.161
Cape May Warbler*	*Dendroica tigrina*	CM	30	6.7 (3.1)	20	70	10	0.000
Black-thr. Blue Warbler (M)*	*Dendroica caerulescens*	BM	133	6.3 (3.9)	40	47	13	0.002
Black-thr. Blue Warbler (F)*	*Dendroica caerulescens*	BF	80	4.3 (2.8)	19	70	11	0.000
Yellow-rumped Warbler*	*Dendroica coronata*	YR	45	8.3 (3.8)	69	16	15	0.000
Yellow-throated Warbler*	*Dendroica dominica*	YT	48	11.9 (3.7)	92	4	4	0.000
Pine Warbler	*Dendroica pinus*	PI	79	9.7 (3.5)	93	1	6	0.000
Prairie Warbler*	*Dendroica discolor*	PR	38	5.3 (3.8)	40	57	3	0.000
Palm Warbler*	*Dendroica palmarum*	PA	32	5.4 (4.5)	69	9	22	0.000
Black-and-white Warbler*	*Mniotilta varia*	BW	89	9.1 (3.3)	84	8	8	0.000
American Redstart*	*Setophaga ruticilla*	AR	82	8.5 (3.8)	44	22	34	0.149
Ground Warbler	*Microligia palustris*	GW	53	3.7 (2.2)	29	58	13	0.000
Bananaquit	*Coereba flaveola*	BQ	36	7.3 (2.8)	9	88	3	0.000
Stripe-headed Tanager	*Spindalis dominicensis*	ST	59	5.6 (2.3)	0	98	2	0.000
Black-crowned Palm Tanager	*Phaenicophilus palmarum*	PT	46	6.5 (3.3)	39	50	11	0.000
Rufous-collared Sparrow	*Zonotrichia capensis*	RS	20	2.3 (2.4)	16	36	48	0.011

curred frequently enough to be recorded in point counts by Wunderle & Latta (1996). The mean number of detections of each species per point (×100) ranged from 2.2–95.6, with an overall mean of 20.8 birds/point for these 32 species, and a mean of 28.3 birds/point for the 23 species in this study. The only excluded birds with detection rates near the mean were the Hispaniolan Parrot (48.9), Rufous-throated Solitaire (42.2), and Mourning Dove (11.1). All other excluded species were recorded < 3 times on point counts and can be considered ecologically insignificant in the pine community. Of the 23 species included, 14 were permanent residents and 9 were migratory winter residents.

Preliminary analyses of the sexually dimorphic Black-and-white Warbler and American Redstart revealed no differences in foraging heights ($t = 0.3$, df = 87, $P = 0.766$; $t = 0.2$, df = 80, $P = 0.876$) or foraging methods ($G = 2.8$, df = 1, $P = 0.091$; $G = 6.4$, df = 3, $P = 0.095$) and so the sex data were pooled. Because significant differences were found in foraging heights ($t = -4.0$, df = 213, $P < 0.000$) but not foraging methods ($G = 2.5$, df = 3, $P = 0.471$) for Black-throated Blue Warblers, the sexes were treated separately in all further analyses.

Foraging heights and substrates.—Mean foraging heights by species (Table 1) ranged from 2.3 m (±2.4 m) to 11.9 m (±3.7 m), but 78 percent of species ($N = 18$) had mean foraging heights from 5.0–10.0 m, corresponding to the region of overlap of pine and broadleaf vegetation (Fig. 1). Four species had mean foraging heights < 5.0 m, including Narrow-billed Tody, female Black-throated Blue Warbler, Ground Warbler, and Rufous-collared Sparrow. Only the Yellow-throated Warbler had a mean foraging height > 10.0 m.

All bird species used both pine and broadleaf substrates for foraging, but nearly all species showed a significant difference in percent use of foraging substrates when substrates were broadly classified as either pine, broadleaf, or "other" substrate types (Table 1). Only the Vervain Hummingbird ($G = 0.0$, df = 2, $P = 0.239$), Greater Antillean Elaenia ($G = 0.0$, df = 2, $P = 0.161$), and American Redstart ($G = 0.0$, df = 2, $P = 0.149$) did not differ statistically in use of substrate categories. In contrast, species with the most restricted use of foraging substrates were the Yellow-throated Warbler and Pine Warbler, for which > 90 percent of foraging observations were on pine substrates, and the Stripe-headed Tanager, for which > 90 percent of observations involved broadleaf substrates. Four other species foraged primarily (>50%) on pine substrates, including Hispaniolan Woodpecker, Yellow-rumped Warbler, Palm Warbler, and Black-and-white Warbler. Eight species foraged primarily (>50%) on broadleaf substrates: Hispaniolan Emerald; Narrow- and Broad-billed Todies; Cape May, female Black-throated Blue, Prairie, and Ground Warblers; and Bananaquit.

Within the conifers, pine needles were the most commonly used foraging substrate, on which 87 percent of the species ($N = 20$) foraged at least part of the time (Table 2). For many species, 10–25 percent of foraging maneuvers were directed at pine needles, but only the Pine Warbler used needles for > 50 percent of foraging maneuvers. Pine trunks, limbs, and branches (pine wood) were also used for foraging by 87 percent of the species ($N = 20$), but wood comprised < 10 percent of the subtrates used by eight of these species. Pine wood was the primary substrate used by the Hispaniolan Woodpecker, and the Yellow-rumped, Palm, and Black-and-white Warblers. Pinecones were the primary substrate used by the Yellow-throated Warbler.

Within the broadleaf component of the forest, leaves were the most commonly used foraging substrate, on which 91 percent of the species ($N = 21$) foraged at least part of the time (Table 2). Both Broad- and Narrow-billed Todies fed nearly exclusively on broadleaf substrates; male and female Black-throated Blue Warblers, Prairie Warblers, and Ground Warblers made the highest use of this substrate. Broadleaf trunks, limbs, and branches were used by 78 percent of the species ($N = 18$), but only three species (Rufous-collared Sparrow, Hispaniolan Woodpecker, Ground Warbler) used wood for > 10 percent of their feeding maneuvers; no species made wood its primary foraging substrate. The fruit and seeds of broadleaf species were used by 61 percent of avian species ($N = 14$), but the Stripe-headed Tanager was the most frugivorous species in the community having made 80 percent of all feeding maneuvers on this substrate. Flowers of broadleaf trees were an important feeding substrate for four species (Antillean Mango, Hispaniolan Emerald, Cape May Warbler, Bananaquit), but 52 percent of the species ($N = 12$) made some use of flowers.

Substrates other than pines and broadleafed trees also were used and contributed to the diversity of foraging niches. Epiphytes, most commonly pine mistletoe, lichens, and bromeliads, were used by 61

TABLE 2. *Percent use of foraging categories by 23 bird species in pine forest of the Cordillera Central, Dominican Republic. Species codes are found in Table 1. See text for complete descriptions of foraging categories.*

Foraging categories	Species																						
	AM	HE	VH	NB	BB	HW	PE	EL	CM	BM	BF	YR	YT	PI	PR	PA	BW	AR	GW	BQ	ST	PT	RS
Foraging method																							
Glean	5					28	2	19	57	70	78	80	84	81	66	72	90	32	79	28	95	63	90
Jump				23	9		1	17		6	6	2	4		10			5	2		2	7	
Probe	50	50	22			72			33	1	1		4	8		3	8		4	69		24	5
Sally-air	10		11	1			69	23	7	5	2	11	4	2		3	1	33	2	3		4	
Sally-surface	35	50	67	76	91		28	41	3	18	13	7	4	9	24	22	1	30	13		3	2	5
Horizontal position																							
Inner		5	6	2		59	19	6	3	4	10	11	4	2		10	50	6	8	6	2	14	30
Middle	7	21	19	52	50	33	39	52	38	48	53	55	44	24	49	65	43	52	57	28	58	40	50
Outer	93	74	75	46	50	8	42	42	59	48	37	34	52	74	51	25	7	42	35	66	40	46	20
Foliage density																							
Light	90	64	89	26	33	49	86	64	48	55	38	78	65	86	68	78	73	71	43	55	54	67	55
Moderate	10	23	11	42	50	44	13	28	41	31	36	16	35	12	29	22	21	28	36	17	37	26	25
Dense		13		32	17	7	1	8	10	14	26	6		2	3		6	1	21	28	9	7	20
Substrate—pine																							
Needles	15	23	28	5	14		9	23	10	21	8	29	38	75	26	25	3	22	25	3		17	
Wood	5	5			3	61	5	9	7	18	11	38	23	13	11	44	81	21	4	3		22	16
Cones									3	1		2	31	5	3			1		3			
Substrate—broadleaf																							
Leaves		12	23	75	76	3	5	9	23	27	45	2	4		45	3	1	21	32	16	3	24	5
Wood	5		5	5	7	23	1		10	8	8	8			4	6	7	1	15	3		4	26
Flowers	45	45	17					3	34	7	8	2			8					66	15	2	
Fruit/seeds				3		6	2	11	3	5	9	4		1					11	3	80	20	5
Substrate—other																							
Epiphytes		5	5	5		7		22		3	4	4		4			7		2		2	7	11
Air	20	5	17	2			70	23	7	5	2	11	4	2		3	1	34	2	3		4	
Herbs/vines	10	5	5	5			7		3	4	5				3	6			9				32
Ground							1			1						13							5

percent of species (N = 14; Table 2). The Greater Antillean Elaenia was the most common consumer of mistletoe fruits. Lichens on tree trunks and limbs were most often searched by Black-and-white, Black-throated Blue, and Yellow-throated Warblers, and Black-crowned Palm Tanagers. Many of these species, as well as the Rufous-collared Sparrow, also foraged in the long, hanging lichens common in these high elevation sites. Bromeliads were frequently probed for invertebrates by Black-crowned Palm Tanagers and Hispaniolan Woodpeckers. The Rufous-collared Sparrow fed 32 percent of the time on the herbaceous ground cover, but 52 percent of species (N = 12) also made some use of this substrate. The forest floor was seldom used by feeding birds (17% of species, N = 4), although 13 percent of Palm Warbler observations were on the ground. Finally, 78 percent of the species foraged aerially (N = 18), but only the Hispaniolan Pewee, Greater Antillean Elaenia, and the American Redstart foraged mainly in the air.

Foraging maneuvers.—Gleaning and aerial sallies to substrate surfaces were the most common foraging maneuvers used by birds in the pine community, with 87 percent of species (N = 20) using each maneuver. Gleaning made up > 50 percent of all foraging maneuvers for 56 percent of the species (N = 13), including all of the warblers except the American Redstart, as well as Stripe-headed Tanager, Black-crowned Palm Tanager, and Rufous-collared Sparrow. Sallying or hovering to feed on the substrate surface was the most common foraging method used by the Hispaniolan Emerald, Vervain Hummingbird, Broad-billed and Narrow-billed Todies, and the Greater Antillean Elaenia. Aerial maneuvers to forage in the air were used by 74 percent of the species (N = 17), but only the Hispaniolan Pewee and the American Redstart used aerial sallies more than any other foraging maneuver. Subsurface probing was used by 65 percent of species (N = 15), including the nectarivorous Antillean Mango, Hispaniolan Emerald, and Bananaquit, as well as the Hispaniolan Woodpecker. Jumping was the most infrequently used foraging maneuver. Although 56 percent of the species (N = 13) used jumps or leaps, no species appeared to favor this maneuver.

Multivariate analysis.—Five principal components accounted for 74 percent of the total variance for the assemblage variables (Table 3). The first eigenvalue accounted for 22 percent of the variance in the 23 variables. The second eigenvalue accounted for another 19 percent of the variance, and the third, fourth, and fifth eigenvalues accounted for 13, 11, and 9 percent of the variance, respectively.

Each of the factors were bipolar in that they included both high positive and negative loadings (Table 3). Factor 1 had high positive loadings for jumping and sallies to surfaces, high foliage density, and use of leaf substrates, combined with high negative loadings for low foliage density. This factor separated out the todies as unique in foraging on leaf substrates in areas of high foliage density (Fig. 2). The importance of foliage density in this first principal component probably was also related to the type of substrate most often used by the species, as broadleaf sites often occurred at higher density than pine substrates. Factor 2 had high positive loadings for use of pine and broadleaf wood and for foraging in horizontal positions near the tree trunk, and high negative loadings for foraging in outer horizontal positions and on pine needles. Factor 2 clearly distinguished the woodpecker and the Black-and-white Warbler from all other community members. The third factor had high positive loadings for probing and feeding on flowers, and negative loadings for gleaning and intermediate horizontal positions. This factor separated the nectarivores (the three hummingbirds, Bananaquit, and Cape May Warbler) from other foragers. Factor 4 separated the sallying species (especially Greater Antillean Elaenia and American Redstart, but also the Black-throated Blue Warbler) with high positive loadings for sallying to the air or other substrate, and a high negative loading for gleaning. Finally, the fifth factor had high positive loadings for height and use of pinecones and needles, and high negative loadings for the use of wood, the ground, and the herbaceous understory. This factor distinguished the Pine, Yellow-rumped, and Yellow-throated Warblers, and the Hispaniolan Pewee.

Figure 2 plots all 23 bird species along the first three principal component axes. This figure indicates the five foraging guilds, described above, as well as the position of four ground and foliage gleaners (Prairie, Ground, and Palm Warblers, and Rufous-collared Sparrow) and three omnivores (Black-crowned, Palm, and Stripe-headed Tanagers) that fall outside these guilds in this analysis.

DISCUSSION

Avian guild traits.—The bird assemblage in the Hispaniolan pine forest is dominated by permanent residents (76% of point count detections) as op-

TABLE 3. *The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of the 23 characters.*

	Factors				
	I	II	III	IV	V
Eigen root	4.979	4.366	3.063	2.616	2.009
Factor contribution to total variance	0.22	0.19	0.13	0.11	0.09
Cumulative variance explained	0.22	0.41	0.54	0.65	0.74
Foraging categories					
Foraging method					
Glean			−0.492	−0.684	
Jump	0.777				
Probe			0.926		
Sally-air				0.853	
Sally-surface	0.593			0.472	
Height					0.901
Horizontal position					
Inner		0.943			
Middle			−0.836		
Outer		−0.819	−0.500		
Foliage density					
Light	−0.811				
Moderate	0.713				
Dense	0.662				
Substrate—pine					
Needles		−0.491			0.458
Wood		0.780			
Cones					0.582
Substrate—broadleaf					
Leaves	0.874				
Wood		0.594			−0.543
Flowers			0.817		
Fruit/seeds					
Substrate—other					
Epiphytes					
Air				0.889	
Herbs/vines					−0.839
Ground					−0.459

posed to migrants (24%), and by insectivores (49%) as opposed to nectarivores (25%) and fruit and seedeaters (26%; Wunderle & Latta 1996). The dominance by permanent residents is not surprising, as Terborgh (1980) stated that 20–40 percent of winter birds in Hispaniola are migrants, and Lack (1976) and Emlen (1977) found very similar proportions of migrants and residents in Jamaican and Grand Bahaman pine forests, respectively. However, the dominance of insectivores in the pine forest is inconsistent with previous Caribbean studies which show that the frugivore guild is the most complex guild in the West Indies (Faaborg 1985), and frugivores or omnivores dominate in other Caribbean habitats (Lack 1976, Faaborg *et al.* 1984). The paucity of frugivores or frugivory in the Dominican pine forests undoubtedly relates to the relatively low fruit abundance present during our study. Had fruit been more abundant in the understory, it is likely that we would have observed numerous instances of primarily insectivorous species feeding opportunistically on fruit.

Birds in this study used a wide variety of foraging substrates. Nearly all species foraged in both pine and broadleaf, but the predominance of foraging on broadleaf substrates by most species suggests the importance of the understory to these birds, and the importance of nonpine leaves to the

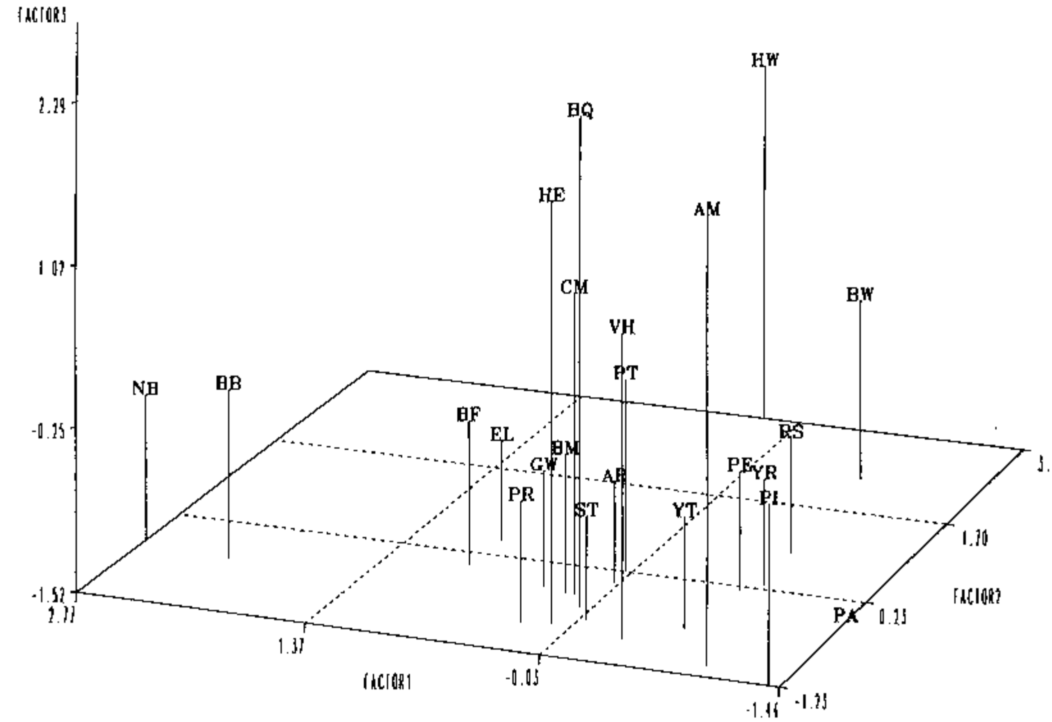

FIGURE 2. Projection of 23 bird species along the first three principal component axes. Axes 1, 2, and 3 account for 22, 19, and 13 percent of total variance, respectively. Species codes are provided in Table 1.

invertebrate fauna supporting the birds. Although Emlen (1977) showed that insect populations reach higher densities in pine crown tops than in upper or lower portions of trunks, we know of no comparison of potential prey abundance between pine canopy and broadleaf understory. In general, however, insect densities in the West Indies appear to be lower than in comparable mainland sites (Janzen 1973a, b), and to be particularly low in pine forest. Standardized leaf inspections showed a diversity (but not abundance) of invertebrates including grasshoppers, leafhoppers, lepidopteran larvae, beetles, and spiders in the understory of this forest (Wunderle & Latta 1996); however, counts of arthropods per leaf in pine forest understory were lower than those in nearby sun and shade coffee plantations (Wunderle & Latta 1996), and lower than found in a variety of habitats on the U.S. Virgin Islands (Askins & Ewert 1994). A low abundance and diversity of insect prey on longleaf pine (*P. palustris*) trees in the southeastern U.S. was attributed to natural pine products such as turpentine (Wahlenberg 1946), also present in *P. occidentalis* (Zanoni *et al.* 1990). In the broadleaf understory, xerophytic plants with tough and aromatic leaves also may be poisonous or distasteful to many invertebrates. Nevertheless, insects appear to be a sufficiently reliable resource to assure migrant survival until the next breeding season; and they are perhaps more reliable than fruit and seeds which may be subject to relatively marked and unpredictable fluctuations in abundance (Terborgh & Faaborg 1980).

The majority of foraging maneuvers used by birds in the pine community are consistent with a high degree of insectivory, and particularly with the gleaning of insects from substrate surfaces. With the exception of the todies, birds from each of the identified guilds frequently gleaned. However, because of the high frequency of gleaning by many species, gleaning was not a positive factor in defining any of the guilds in the PCA.

Despite the predominance of gleaning insectivores, we observed a wide variety of foraging maneuvers, even within guilds. For example, all members of the nectarivore guild foraged not only by probing for nectar, but also by hovering or gleaning insects from leaves, pine needles, spider webs, and other substrates; members of the aerial insectivore guild used sallies as their primary foraging maneuver, but also gleaned substrates; even congeneric species such as the two todies used diverse foraging maneuvers, the Narrow-billed Tody having relied more heavily on near-surface jumping than the Broad-billed Tody.

The diversity of foraging substrates and maneuvers used by members of this avian community appears to be the primary means by which birds that exploit this habitat separate ecologically. This is surprising because studies in other habitats showed foraging height to be the primary factor in subdividing the winter bird community (Terborgh & Faaborg 1980, Hutto 1981). In Hispaniolan pine, most of the species foraged in a narrow strata of the forest 5–10 m high. Our PCA indicates that height was heavily weighted as a factor in only the fifth principal component, and that subdivision of the community is achieved by other means, such as the density of foliage occupied, foraging substrate, or foraging maneuver. The narrowness of the feeding zone used by birds in this habitat may be in part a result of birds foraging primarily in mixed-species flocks, and the tendency of flock members to converge with the foraging behavior of the nuclear species of the flock (Moynihan 1962). In our previous study in this Dominican site, a common tendency of species that altered their foraging behavior in mixed-species flocks was to move up or down in the foliage so that foraging height tended to converge on that of the nuclear species (Latta & Wunderle 1996a, b).

Our results suggest that the structural substrate diversity associated with a combined pine overstory and a broadleaf understory appears to contribute to avian biodiversity by offering a variety of foraging sites. This is consistent with several studies in diverse habitats, in which the diversity of vegetation and the structural complexity of the habitat appear to enhance bird diversity and use by affecting the ways birds can find food resources and coexist within a site (MacArthur & MacArthur 1961, Karr & Roth 1971, Holmes *et al.* 1979). Cruz (1988) found similar results when comparing bird use in pine plantations of Puerto Rico. He showed that complex habitat conditions, understory vegetation, vine thickets, and shrubs were important in determining the presence and abundance of some bird species. Wunderle and Waide (1994) also noted that pine forests in the Dominican Republic that lacked a broadleaf understory were "relatively sterile" in terms of migrants, and the data presented here make clear why the understory is of such importance.

Integration of seasonal migrants into the resident bird community.—The vegetational diversity of the pine forest also may contribute to the integration of migrants into the winter community. Because variation in the foraging methods and microhabitats used by a bird species influences the range of prey available to that species (Lack 1971, Cody 1974, Robinson & Holmes 1982), and presumably the diversity of prey taken (Poulin & Lefebvre 1996), our results support the hypothesis that migrants complement resident species by filling unused niches (Hespenheide 1980, Rappole & Warner 1980). This is supported by Poulin and Lefebvre's (1996) observation of little diet overlap between migrants and residents using similar foraging substrates, suggesting that in their Panamanian site, migrants were well integrated into a much larger avian community. Dietary analyses would be useful to further test this hypothesis.

In addition, migratory winter residents may be able to integrate into the pine forest community because few species of permanent residents are present, most permanent residents are primarily fruit and seedeaters, and the migrant insectivores are fairly specialized in their foraging habits. In pine forests of the Cordillera Central we found only 14 winter resident species making up the avian community, so that the diet of migrants was less likely to overlap that of the residents. Terborgh and Faaborg (1980) found that resident frugivores, omnivores, and nectarivores overlapped in foraging height distributions, but were distinguished by size relationships as in this study, such that small (Vervain), medium (Hispaniolan Emerald), and large (Antillean Mango) hummingbirds, and the still larger nectarivorous Bananaquit were all sympatric. In contrast, members of the migratory pine–woods warbler complex differ from one another not by size, but by relatively subtle quantitative differences in their foraging tactics (MacArthur 1958). In fact, wintering migrants in the West Indies are a nonrandom subset of all North American species that migrate to the tropics, with small, gleaning insectivores strikingly overrepresented (Faaborg & Terborgh 1980). Our results differ from those of Terborgh and Faaborg (1980), however, in that the more subtle foraging differences we observed among migrants were not related to vertical stratification but to foraging tactics and foraging maneuvers.

Potential impact of disturbance on the bird community.—Some of the patterns of avian organization observed in the pine forest community may be the result of hurricane disturbance. Caribbean hurricanes are a major factor in shaping forest vegetation structure, often resulting in patchy damage that affects forest stand structure and dynamics for decades (Brokaw & Grear 1991, Brokaw & Walker 1991). Although cultivated *P. caribaea* from native seed sources are quite wind-resistant in environments having high hurricane incidence (Liegel 1991), several studies of *Pinus* species have proven it to be more susceptible to hurricane damage than hardwoods (Brokaw & Walker 1991). However, topographic location, variation in tree morphology, and stand physiognomy also may affect tree damage (Brokaw & Walker 1991). Hurricane damage may result in defoliation and changes in abundance of certain food resources, but more severe structural damage to the forest also may make it difficult for forest-dwelling species to segregate on the basis of foraging height (Waide 1991, Wunderle *et al.* 1992). The apparent unimportance of height in separating community members and the flexibility we observed in foraging, particularly among the permanent residents, suggest that these species could shift among foraging sites and food resources and still coexist. This may be particularly important among montane nectarivores and fruit and seedeaters in the Caribbean, which face high risks of hurricane-induced losses due to indirect effects occurring after the passage of the hurricane (Wiley & Wunderle 1994). Hurricanes may also contribute to the character of the avifaunal community by reducing the number of bird species surviving in montane habitats to those capable of using a broad range of microhabitats (Wunderle *et al.* 1992).

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