

THE COMPOSITION AND FORAGING ECOLOGY OF MIXED-SPECIES FLOCKS IN PINE FORESTS OF HISPANIOLA¹

STEVEN C. LATTA^{2,3} AND JOSEPH M. WUNDERLE, JR.

International Institute of Tropical Forestry, U.S.D.A. Forest Service, P.O. Box 490
Palmer, Puerto Rico 00721

Abstract. We determined the flocking propensity of 48 species of birds occurring in native pine forest in the Cordillera Central of the Dominican Republic, and the species composition of 180 mixed-species flocks. Flocks were unusually ubiquitous, with 46 species occurring in at least one flock, 11 species regularly present, and all insectivorous species and all migrant species participating. Most birds encountered were permanent residents, but winter residents (Nearctic migrants) were an important component of the flocks and, as a group, had the highest flocking propensity. Flocks were cohesive and the resident insectivore, the Black-crowned Palm Tanager (*Phaenicophilus palmarum*) often served as the nuclear species. Censuses suggest species richness within flocks reflects the species present in the habitat, but agonistic interactions indicate that intraspecific aggression may limit the number of individuals of a species in these flocks. Species co-occurrence data indicate that species do not occur independently of one another in flocks. Positive associations were far more common than negative co-occurrences, suggesting mutual habitat dependencies or species interactions within flocks. A non-random association of nearest neighbors also indicated that species may be gaining feeding benefits from flocking by associating as close neighbors with an individual of another species, but we were not able to rule out the possibility that predation is an important selective agent.

Intraspecific comparisons of foraging behavior between flocking and solitary birds provides some evidence that individuals modify foraging locations and foraging tactics upon joining mixed-species flocks, and that their foraging behavior tends to converge with the feeding behavior of the nuclear species. An increase in the feeding rate was recorded for one species. These data suggest that at least some species may accrue feeding advantages as flock participants.

Key words: mixed-species flocks; pine forest; Hispaniola; foraging behavior; Nearctic migratory birds; nuclear species.

Sinopsis. Determinamos la tendencia para hacer bandadas para 48 especies de aves en los bosques de pinos nativos de la Cordillera Central de la República Dominicana, y la composición de 180 bandadas de especies mixtas. Las bandadas son bien común, con 46 especies que se encontraban en por lo menos una bandada, 11 especies que se encontraban regularmente en bandadas, y todas las especies insectívoras y las especies migratorias participandose. Las mayorías de las aves son residentes permanentes, pero residentes del invierno (aves migratorias) son una parte importante de las bandadas, y como un grupo tienen una alta propensión para hacer bandadas. Las bandadas son cohesiva, y el residente insectívoro, *Phaenicophilus palmarum*, es la especie nuclear. Datos del censo indican que la abundancia de las especies dentro de las bandadas refleja las especies que están en el hábitat, pero datos sobre interacciones indican que agresión intra-especie limita el número de individuos de una especie en las bandadas. Datos sobre el co-ocurrencia de especies indican que las especies no ocurren independiente en las bandadas. Asociaciones positivas están más común que co-ocurrencias negativas, indicando dependencias mutúal del hábitat o interacciones entre especies en las bandadas. Una distribución no al azar de "vecinos cerca" también indica que las especies están ganando más comida cuando están asociada con "vecinos cerca" de otras especies, pero no pudimos excluir la posibilidad que predación es un agente selectiva importante.

Comparaciones intra-especies del comportamiento alimenticio entre aves en bandadas y aves solitarias provienen evidencia que individuos modifican localizaciones de alimentaciones y métodos alimenticios cuando están en bandadas, y que su comportamiento ali-

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² Current Address: University of Missouri, Division of Biological Sciences, 110 Tucker Hall, Columbia, Missouri, 65211.

³ Corresponding author.

menticio hace converger con el comportamiento alimenticio del especie nuclear. La razone de alimentacion subi6 para una especie en bandadas. La informaci6n indican que algunas especies ganan ventajas de alimentaciones como miembros de bandadas.

INTRODUCTION

Many species of birds commonly associate in mixed-species flocks during the non-breeding season (Rand 1954, Powell 1985). Hypothesized selective advantages of flocking have been summarized by Powell (1985), but the favored hypotheses are decreased predation and increased foraging efficiency. The predation hypothesis suggests that the cost of vigilance is reduced for each individual participating in flocks because more individuals are available to detect approaching predators (Elgar 1989). The protection afforded flock participants may also allow the birds to forage in more exposed sites and use riskier behavior—foraging faster with less vigilance (Buskirk et al. 1972, Pulliam 1973). A bird that enjoys the protection of a flock may also suffer a cost through increased interspecific competition or interference in food acquisition, or because of the need to adjust movement rates and other behaviors in order to stay with the flock (Hutto 1988, Petit and Bildstein 1987). The foraging facilitation hypothesis suggests that birds benefit from group foraging through the flushing of insects by the activity of flock members (Belt 1874 cited in Powell 1985); locating or allowing the use of new types of food, foraging locations, or foraging tactics (Valburg 1992); or facilitating a reduction of niche overlap (Morse 1967). Support for the foraging facilitation hypothesis does not exclude the possibility that a species benefits from predator avoidance as well.

Powell (1985) and Hutto (1988, 1994) have suggested that before distinguishing between competing hypotheses to explain the evolution of mixed-species flocking behavior, we first need more descriptive studies, particularly from the tropics, to determine whether foraging efficiency increases or decreases as a result of flocking, and to assess whether flock members accrue any feeding advantages at all. Information on group membership, patterns of movement and association, and foraging behavior of individuals in many kinds of mixed-species flocks can help us to better understand the costs and benefits associated with participation in such flocks.

Here we present data describing mixed-species foraging flocks occurring in native pine forests of the Dominican Republic. Our goals are to describe flock composition, the flocking propen-

sity of permanent-resident and winter-resident bird species, and flock organization in order to determine whether there are non-random patterns of association within flocks. In order to understand some of the costs and benefits associated with participation in mixed-species flocks, we also tested whether a species modifies foraging locations, foraging tactics, or foraging rates in the presence of a mixed-species flock.

STUDY SITE AND METHODS

STUDY SITE

Mixed-species flocks were observed in pine forest at six sites on slopes near Manabao (905–1,050 m) and six sites near Jarabacoa (643–779 m) in La Vega province in the Cordillera Central of the Dominican Republic from Oct. to Apr., 1993–95. Native pine forests (*Pinus occidentalis*), many of which have been selectively logged, remain on the steeper mountain slopes and ridgetops, with variable amounts of broadleaf understory which may be affected by fire, cutting, or grazing. A foliage height profile was determined for representative pine habitat in an area where feeding observations were collected and it shows a fairly open canopy, a denser mixed-broadleaf understory, and very little in the way of an intermediate layer (Wunderle and Latta, in press). Pine foliage predominated in the canopy with greatest cover in the 15–20 m height category, although scattered broadleaf trees also extended into the canopy. Broadleaf species were not sampled but included *Ribes* sp., *Inga vera*, mango (*Mangifera indica*), citrus (*Citrus* sp.), *Cecropia* sp., *Syzygium jambos*, *Clusia* sp., *Miconia* sp., as well as numerous unidentified shrubs. Although the exact area of the pine forest is unknown, the remnant patches were all large enough that trails could be followed for five or more hours without leaving the pine or returning to previously censused habitat.

POINT COUNTS

Point count data were used to estimate abundances of all species. A total of 44 fixed-radius point counts (Hutto et al. 1986) were conducted from 11 Jan.–9 Feb. 1994, in which an observer recorded all birds seen and heard during a ten-minute period at each point. Each point was at

least 100 m from all others. Counts were initiated at sunrise and terminated before 11:00, with most counts completed before 10:30. All counts were made by the same observer who estimated the minimum distance to each bird detected during a count within a 25 m radius. We calculated the mean number of detections for each species per 25 m radius plot. To verify the independence of samples from each point we compared mean detections per 25 m radius plot at ≥ 200 m intervals with those at 100 m intervals and found no significant differences. These data are presented in Wunderle and Latta (in press).

FLOCKING BEHAVIOR

Flocking observations were made from 07:00–18:00 hrs in pine forests where feeding activity occurred all day. To reduce the possibility of encountering a given individual or flock more than once, habitat was never censused more frequently than once a week. Observations were made by walking slowly through the habitat until a bird was encountered. In all cases the bird was identified and categorized as either solitary or a member of a mixed-species flock. A flock was defined as comprising at least three conspecifics or two heterospecifics within 25 m of one another and moving together for at least five min. Flocks were followed for as long as possible but the maximum time was 60 min. Generally, flocks were not followed for more than 150 m, which reduced the possibility of accumulating species through turnover as the flock moved through adjoining territories. For each mixed-species flock we recorded the number of individuals of each species, the nearest neighbor (< 10 m) of focal individuals, agonistic interactions between birds, and the linear distance moved by the flock. Single-species flocks occurred but were small and unusual. These flocks were not included in our analyses. Only the Cattle Egret occurred exclusively in single species flocks and so was excluded from our analyses. We also excluded all raptors and hummingbirds.

FORAGING BEHAVIOR

Foraging observations were made as often as possible for both solitary birds and flock participants. The first foraging event five seconds after an individual was initially detected was recorded to avoid a bias toward the more conspicuous feeding techniques. We sought to record only a single foraging event from an individual each day to reduce the problem of autocorrelation inher-

ent in sequence data (Wagner 1981). This was facilitated by the frequent presence of only one individual of each sex of each species in flocks.

Terminology for foraging maneuvers and foraging site classifications was derived from Remsen and Robinson (1990). Foraging maneuvers included glean, hang, reach-up, reach-out, reach-under, jump-up (leap), sally-strike, sally-stall, sally-hover, sally-pounce, and probe.

The location of a food item when attacked by the bird was identified as the foraging site and the following were noted: (1) estimated height of the bird above the ground; (2) estimated height of the tallest tree within 15 m (canopy height); (3) horizontal position of the bird (inner 1/3 of tree, middle 1/3 of tree, outer 1/3 of tree); (4) the amount of light passing through an imaginary 2.0 m diameter sphere surrounding the foraging site (0 = 100% of light passes through, 1 = 95%–99%, 2 = 75%–94%, 3 = 25%–74%, 4 = 5%–24%, and 5 = 0–4%); (5) the location of the prey item, or the “primary substrate type” (for example a tree species or air); (6) the “secondary substrate” or the location of the food item within or on the primary substrate (for example leaf, twig, trunk, fruit, flower); and (7) substrate condition (live or dead). Height estimates were checked daily with a rangefinder.

Because canopy heights varied somewhat between sites, bird height relative to canopy height was calculated and used in further analyses. In all statistical analyses, sample sizes within a cell were increased with the following condensations: (1) horizontal positions 1 and 2 were combined; (2) foliage density scores of 0–2 and 4–5 were combined; (3) foraging methods were combined into three categories: surface moves (glean, hang, probe), near-surface moves (reach, jump-up), and aerial moves (all sallies); and (4) primary substrates and secondary substrates were re-classified into five categories: woody material (trunk, branch, twig); leaves (including pine needles, epiphytes, lichen, and mistletoe); fruit, seeds, and pine cones; flowers; and air, ground, or herbaceous ground cover. For most species cells were further condensed by summing sparse cells (< 5) in an “other” category prior to statistical analysis.

Feeding rates were determined by following insectivores and recording the time of each feeding attempt with a cassette recorder. Birds were followed for up to 10 min or as long as consecutive feeding attempts could be observed. Rates were calculated as the average time between feed-

ing attempts, but no rates were determined unless there were at least four consecutive attempts.

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 of 0.05 or less was accepted as significant, but greater values are shown for descriptive purposes. Data presented are means \pm SE. When data were not normally distributed, nonparametric statistics were used.

Independent samples *t*-test (with pooled variances) or a Mann-Whitney *U*-test was used to test for intraspecific differences in the means of foraging heights and feeding rates. Regression was used to relate the occurrence of a species in a flock to log transformed relative abundance from point counts. A 2×2 Test of Independence with a χ^2 -statistic or a Row \times Column Test of Independence with a *G*-statistic was used to test for the independence of species co-occurrences within flocks, and to compare various feeding behaviors and feeding site characteristics of solitary individuals and flocking individuals within a species. A Bonferroni correction for multiple comparisons was not used in these comparisons but the number of significant results expected by chance alone is noted. In tests where cells were sparse (< 5) we used a χ^2 -test with Yates' correction for continuity, or a *G*-test with Williams' correction.

RESULTS

SPECIES ABUNDANCE AND FLOCK COMPOSITION

We detected 2,667 birds representing 48 species in our surveys (Table 1, includes scientific names). The most numerous species overall were Bananaquit, Black-crowned Palm Tanager, Black-throated Blue Warbler, Pine Warbler, Stripe-headed Tanager, Greater Antillean Elaenia, and Greater Antillean Pewee. Most birds encountered were permanent residents (33 species and 1,953 individuals; Table 2), but migratory winter residents were common (15 species and 714 individuals). Insectivores (25 species and 1643 individuals) and omnivores (16 species and 527 individuals) predominated over granivores (5 species and 205 individuals) and nectarivores (2 species and 292 individuals; Table 2).

We detected 180 mixed-species flocks, which contained 77% of all individuals observed. Flocks averaged 7.1 ± 0.2 species and 11.3 ± 0.5 individuals. Of the 48 species observed, 46 species were present in at least one flock, and eleven species were recorded as occurring regularly (present in $> 25\%$ of the flocks; Table 3). The species occurring in the greatest number of flocks (Table 3) were Black-throated Blue Warbler (78% of flocks), Black-crowned Palm Tanager (60%), Greater Antillean Pewee (60%), Black-and-white Warbler (53%), Pine Warbler (52%), and Bananaquit (49%). Of the eleven regularly occurring species, the Stripe-headed Tanager, Black-crowned Palm Tanager, and the Bananaquit were the most intraspecifically gregarious, averaging the highest number of individuals per flock (Table 1).

Flocking propensity, or the proportion of encounters with a species during which the bird was associated with a flock, was calculated for each species (Table 1) and for each guild (Table 2). Of the 23 species with more than 20 observations, flocking propensity ranged from 0.59 to 1.00. Flocking propensity was highest for Antillean Siskin (1.00), Prairie Warbler (1.00), Yellow-throated Warbler (0.97), Black-and-white Warbler (0.96), American Redstart (0.95), Yellow-rumped Warbler (0.92), and Greater Antillean Pewee (0.91). Insectivores and granivores had similarly high flocking propensities (0.81). Omnivores had a moderately high flocking propensity (0.75), but nectarivores had a low propensity (0.61). As a group, though, migrants had the highest propensity for joining flocks (0.87) and this differed significantly from that of permanent residents ($\chi^2 = 51.8$, $df = 1$, $P < 0.001$).

When analyzed by diet type, the proportionate abundance of individual insectivores and granivores participating in flocks was greater than proportionate abundances derived from point count data ($\chi^2 = 23.8$, $df = 1$, $P < 0.001$ and $\chi^2 = 7.8$, $df = 1$, $P = 0.005$, respectively). In contrast, the proportionate abundances of individual omnivores and nectarivores in flocks was significantly less than proportionate abundances derived from point count data ($\chi^2 = 19.9$, $df = 1$, $P < 0.001$ and $\chi^2 = 14.3$, $df = 1$, $P < 0.001$, respectively). The proportionate abundance of migratory individuals participating in mixed-species flocks was significantly higher than proportionate abundances derived from point count data ($\chi^2 = 11.8$, $df = 1$, $P < 0.001$). The prob-

TABLE 1. The diet, resident status, abundance, flocking propensity, intraspecific gregariousness, number of agonistic interactions, and number of times each of 48 species of landbirds were observed in pine forest in the Cordillera Central of the Dominican Republic.

Species		Diet ¹	Res ²	Abd ³	% ⁴	\bar{x} n ⁵	Ag ⁶	n ⁷
Common Bobwhite	<i>Colinus virginianus</i>	O	PR	0.0	1.00	6.0	0/0	6
Scaley-naped Pigeon	<i>Columba squamosa</i>	O	PR	2.2	0.60	1.5	0/0	5
Mourning Dove	<i>Zenaida macroura</i>	O	PR	11.1	0.35	1.4	0/0	20
Zenaida Dove	<i>Zenaida aurita</i>	O	PR	0.0	0.00	0.0	0/0	9
White-winged Dove	<i>Zenaida asiatica</i>	O	PR	0.0	0.00	0.0	0/0	1
Common Ground Dove	<i>Columbina passerina</i>	O	PR	0.0	0.50	1.0	0/0	2
Hispaniolan Parrot	<i>Amazona ventralis</i>	O	PR	48.9	1.00	2.0	0/0	2
Hispaniolan Lizard Cuckoo	<i>Saurothera longirostris</i>	I	PR	6.7	0.30	1.0	0/0	10
Smooth-billed Ani	<i>Crotophaga ani</i>	I	PR	2.2	1.00	2.0	0/0	2
Hispaniolan Trogon	<i>Temnotrogon roseigaster</i>	O	PR	0.0	1.00	1.0	0/0	2
Narrow-billed Tody	<i>Todus angustirostris</i>	I	PR	13.3	0.71	1.3	0/3	142
Broad-billed Tody	<i>Todus subulatus</i>	I	PR	15.6	0.61	1.3	0/0	28
Hispaniolan Woodpecker	<i>Melanerpes striatus</i>	I	PR	42.2	0.76	1.4	0/0	94
Grey Kingbird	<i>Tyrannus dominicensis</i>	I	PR	0.0	0.50	1.0	0/0	2
Loggerhead Kingbird	<i>Tyrannus caudifasciatus</i>	I	PR	2.2	0.56	1.0	0/0	9
Stolid Flycatcher	<i>Myiarchus stolidus</i>	I	PR	2.2	0.80	1.0	0/0	5
Greater Antillean Pewee	<i>Cotopus caribaeus</i>	I	PR	22.2	0.91	1.3	1/4	151
Greater Antillean Elaenia	<i>Elaenia fallax</i>	O	PR	37.8	0.85	1.7	11/7	161
Red-legged Thrush	<i>Mimocichla plumbea</i>	O	PR	2.2	0.59	1.5	1/0	34
Rufous-throated Solitaire	<i>Myodestes genibarbis</i>	O	PR	42.2	0.40	1.0	0/0	15
Palmchat	<i>Dulus dominicus</i>	O	PR	4.4	0.73	9.5	0/0	52
Black-whiskered Vireo	<i>Vireo altiloquus</i>	I	M	0.0	0.67	1.3	0/0	6
Blue-winged Warbler	<i>Vermivora pinus</i>	I	M	0.0	1.00	1.0	0/0	1
Northern Parula	<i>Parula americana</i>	I	M	0.0	1.00	1.0	0/0	1
Cape May Warbler	<i>Dendroica tigrina</i>	N	M	8.9	0.72	1.5	0/2	25
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	I	M	46.7	0.79	1.3	3/2	233
Yellow-rumped Warbler	<i>Dendroica coronata</i>	I	M	37.8	0.92	3.5	1/0	100
Black-throated Green Warbler	<i>Dendroica virens</i>	I	M	0.0	1.00	1.0	0/0	1
Yellow-throated Warbler	<i>Dendroica dominica</i>	I	M	2.2	0.97	1.6	0/2	63
Pine Warbler	<i>Dendroica pinus</i>	I	PR	44.4	0.74	1.5	3/1	195
Prairie Warbler	<i>Dendroica discolor</i>	I	M	2.2	1.00	1.1	0/0	21
Palm Warbler	<i>Dendroica palmarum</i>	I	M	0.0	0.79	2.1	0/0	42
Black-and-white Warbler	<i>Mniotilta varia</i>	I	M	20.0	0.96	1.1	0/0	110
American Redstart	<i>Setophaga ruticilla</i>	I	M	11.1	0.95	1.1	0/0	76
Ovenbird	<i>Seiurus auricapula</i>	I	M	0.0	0.73	1.1	0/0	11
Common Yellowthroat	<i>Geothlypis trichas</i>	I	M	4.4	0.56	1.0	0/0	16
Ground Warbler	<i>Micrologia palustris</i>	I	PR	13.3	0.67	1.8	3/1	81
Bananaquit	<i>Coereba flaveola</i>	N	PR	95.6	0.60	1.8	6/0	267
Blue-hooded Euphonia	<i>Euphonia musica</i>	O	PR	2.2	0.50	1.0	0/0	6
Stripe-headed Tanager	<i>Spindalis zena</i>	O	PR	46.7	0.80	2.9	3/1	192
Black-crowned Palm Tanager	<i>Phaenicophilus palmarum</i>	I	PR	31.1	0.79	1.8	8/0	243
Black-cowled Oriole	<i>Icterus dominicensis</i>	O	PR	0.0	1.00	1.0	0/0	1
Antillean Siskin	<i>Carduelis dominicensis</i>	G	PR	0.0	1.00	2.4	0/0	26
Greater Antillean Bullfinch	<i>Loxigilla violacea</i>	O	PR	2.2	0.74	1.3	0/0	19
Yellow-faced Grassquit	<i>Tiaris olivacea</i>	G	PR	2.2	0.82	2.5	0/0	71
Black-faced Grassquit	<i>Tiaris bicolor</i>	G	PR	0.0	0.50	1.0	1/0	2
Indigo Bunting	<i>Passerina cyanea</i>	G	M	0.0	0.75	3.0	0/0	8
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	G	PR	22.2	0.76	1.7	0/0	98

¹ Diet based on foraging observations (this study) and Wunderle and Latta (in press): G = granivore, I = insectivore, N = nectarivore, O = omnivore.

² Resident status: PR = permanent resident, M = migratory winter resident.

³ Mean number of birds per point count ($\times 100$) from Wunderle and Latta (in press).

⁴ Proportion of (n) encounters with a species during which the individual was observed foraging with a mixed-species flock.

⁵ Mean number of individuals of this species in a flock, given that at least one was detected.

⁶ Number of intraspecific and interspecific agonistic interactions observed in mixed-species flocks.

⁷ Number of individuals encountered either alone or in a mixed-species flock.

TABLE 2. The abundance, flocking propensity, and number of times birds of various diet types or residency statuses were encountered in pine forests of the Cordillera Central of the Dominican Republic.

	Spp ¹	n ²	Flock ³	% ⁴	A ⁵	P ⁶
All species	48	2,667	2,061	0.77	292	—
Insectivores	25	1,643	1,325	0.81	144	<0.001
Granivores	5	205	165	0.81	11	0.005
Omnivores	16	527	393	0.75	90	<0.001
Nectarivores	2	292	178	0.61	47	<0.001
Migrants	15	714	618	0.87	60	<0.001
Residents	33	1,953	1,443	0.74	232	<0.001

¹ Number of species in a given diet type or residency status.

² Number of individuals encountered either alone or in a mixed-species flock.

³ Number of individuals encountered in a mixed-species flock.

⁴ Proportion of individuals observed foraging with a mixed-species flock.

⁵ Abundance (number of individuals encountered either alone or in a mixed-species flock) derived from point count data (Wunderle and Latta, in press).

⁶ Probability of no difference between the observed proportions within flocks (%) and proportions observed in point count samples.

ability of occurrence of a species in a flock could, however, be predicted from log transformed point count abundance data ($r = 0.93$, $df = 1$, $P < 0.001$).

Of those flocks that were followed for > 10 min, rate of movement was determined for 82 flocks. The average rate at which flocks moved was $2.1 \pm 0.1 \text{ m} \cdot \text{min}^{-1}$.

Potential avian predators were occasionally observed in the pine forest. These included Red-tailed Hawk (*Buteo jamaicensis*), American Kestrel (*Falco sparverius*), Sharp-shinned Hawk (*Accipiter striatus*), and Barn Owl (*Tyto alba*). We once observed an accipiter make an unsuccessful pass on a mixed-species flock, and we suspect that this is the most effective predator of small birds in the area.

FLOCK ORGANIZATION AND AGONISTIC BEHAVIOR

Species co-occurrences were calculated for the 26 species that occurred in more than 5 flocks (Table 3). Of 325 possible pairwise comparisons, 48 were significantly different than the expected number of co-occurrences. Forty-four of these significant comparisons were positive, indicating that these pairs of species occurred together more frequently than expected. Four pairwise combinations were negative suggesting that these species pairs may be avoiding one another. Three of these negative pairwise combinations involved the nectarivorous Bananaquit. Because only 16 comparisons are expected to be positive based on chance alone at the $P = 0.05$ level, these data indicate that not all birds are joining flocks independently of one another.

Nearest neighbors were recorded for eight frequently encountered species in mixed-species flocks (Table 4). The distribution of nearest

neighbors overall was found to be independent of focal species ($G = 190.2$, $df = 49$, $P < 0.001$), and for each focal species the identity of nearest neighbors differed significantly from expected proportions derived from point count abundances (Table 4).

We noted 64 agonistic interactions among 17 species (Table 1). We found a significant difference in the number of intraspecific and interspecific agonistic interactions ($\chi^2 = 52.5$, $df = 1$, $P < 0.001$; Table 1); intraspecific interactions were far more frequent, and interspecific interactions less frequent, than would be expected if birds were interacting at random with one another.

FORAGING BEHAVIOR

We analyzed six aspects of feeding behavior for ten commonly-occurring species that were present both as flock members and as solitary individuals to determine if changes in foraging behavior occurred in the presence of mixed-species flocks. These ten species (and sample sizes for foraging observations as flock members and as solitary birds) included: Bananaquit (17/19), Black-throated Blue Warbler (142/71), Cape May Warbler (12/18), Greater Antillean Pewee (68/33), Greater Antillean Elaenia (46/18), Hispaniola Woodpecker (22/17), Ground Warbler (17/31), Prairie Warbler (25/13), Black-crowned Palm Tanager (33/13), and Stripe-headed Tanager (36/23). Adequate sample sizes of the sexually dimorphic Black-throated Blue Warbler allowed us to test the sexes separately. Only three of these comparisons are expected to be positive based on chance alone at the $P = 0.05$ level.

We examined several variables to determine whether a species shifted foraging locations in the presence of mixed-species flocks. Intraspe-

TABLE 3. The number of 180 mixed-species flocks in which each species was recorded, and the number of those occasions in which each of the other species was also recorded. Numbers of positive co-occurrences that are significantly greater than expected are underlined (as determined from Yate's corrected chi-square tests; $P < 0.05$), the number of significant negative co-occurrences are italicized and underlined.

Focal species	n	Co-occurring species																								
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Black-throated Blue Warbler	141	<u>92</u>	87	81	81	71	68	<u>69</u>	59	48	39	39	30	28	20	17	14	12	11	13	9	7	8	3	6	6
2 Black-crowned Palm Tanager	108	71	68	<u>61</u>	58	47	44	44	38	40	33	29	24	22	16	11	9	10	10	11	8	9	8	7	6	6
3 Greater Antillean Pewee	108	<u>70</u>	<u>62</u>	<u>44</u>	52	42	44	44	40	34	35	<u>20</u>	16	17	12	14	11	8	9	5	6	7	6	5	5	5
4 Black-and-white Warbler	96	61	46	48	41	42	33	<u>37</u>	30	<u>29</u>	15	16	14	13	14	10	8	9	6	8	4	5	5	5	5	5
5 Pine Warbler	94	47	<u>54</u>	44	32	35	25	29	28	19	10	12	6	11	5	4	5	7	6	3	6	4	4	4	4	4
6 Bananaquit	89	42	44	32	26	20	13	11	7	9	5	2	5	6	9	3	5	3	5	3	5	4	4	4	4	4
7 Greater Antillean Elaenia	82	39	29	31	22	24	16	<u>20</u>	7	8	8	6	4	2	4	3	6	2	4	2	4	2	4	2	4	2
8 Narrow-billed Tody	78	35	31	23	18	11	9	10	8	8	4	4	2	4	1	3	2	5	4	2	4	1	3	2	5	4
9 American Redstart	67	23	22	15	<u>22</u>	7	11	7	10	6	4	6	4	0	4	0	4	1	2	2	2	2	2	2	2	2
10 Stripe-headed Tanager	53	15	14	11	11	4	8	3	2	5	2	5	2	5	3	4	0	2	5	2	5	3	4	0	2	5
11 Hispaniolan Woodpecker	50	16	<u>20</u>	10	12	12	10	5	10	4	6	3	3	6	4	3	6	4	3	4	6	3	3	6	4	3
12 Rufous-collared Sparrow	44	11	17	5	7	2	5	4	0	3	2	6	2	2	1	1	1	1	1	1	1	1	1	1	1	1
13 Yellow-throated Warbler	39	3	11	10	10	10	9	8	5	8	1	2	2	0	1	0	5	0	1	1	1	1	1	1	1	1
14 Ground Warbler	30	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
15 Yellow-rumped Warbler	26	6	8	1	5	6	3	4	4	6	4	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16 Yellow-faced Grassquit	23	7	3	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
17 Prairie Warbler	20	4	3	5	3	5	3	1	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18 Palm Warbler	16	3	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19 Red-legged Thrush	13	4	1	4	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	0
20 Broad-billed Tody	13	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	0
21 Cape May Warbler	12	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0	1	2	0
22 Antillean Siskin	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23 Greater Antillean Bullfinch	11	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
24 Common Yellowthroat	9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25 Ovenbird	7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
26 Rufous-throated Solitaire	6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TABLE 4. The occurrence of pairs of nearest neighbors in mixed-species flocks. Values indicate the number of times a particular species was observed as the near neighbor of the focal species on the left. The identity of near neighbors differs significantly among species ($G = 190.2$, $df = 49$, $P < 0.001$).

Focal species	Neighboring species								P^1
	1	2	3	4	5	6	7	8	
1 Black-throated Blue Warbler	4	10	10	10	8	4	0	9	0.049
2 Black-crowned Palm Tanager	10	10	5	6	3	0	2	3	0.026
3 Greater Antillean Pewee	10	5	10	7	0	7	4	2	0.003
4 Black-and-white Warbler	10	6	7	0	8	0	10	9	<0.001
5 Pine Warbler	8	3	0	8	9	2	5	4	0.014
6 Greater Antillean Elaenia	4	0	7	0	2	17	0	2	<0.001
7 Yellow-throated Warbler	0	2	4	10	5	0	7	4	<0.001
8 American Redstart	9	3	2	9	4	2	4	0	0.042

¹ From G -test, with expected numbers based on proportions derived from point count data.

cific comparisons of relative foraging heights and horizontal positions of flocking and solitary individuals were non-significant for all species. Nearly significant differences were found, however, in the relative foraging height of the insectivorous Ground Warbler with a mean height of 0.21 ± 0.02 m for solitary birds, but 0.32 ± 0.05 for flocking birds ($t = 1.8$, $df = 46$, $P = 0.064$). The normally skulking Ground Warblers tended to forage higher in the foliage in the presence of interspecific flocks. Opposite trends were found for the two nectarivores—the Bananaquit and the Cape May Warbler. These two species foraged higher in the canopy (relative foraging heights of 0.47 ± 0.04 and 0.51 ± 0.05 , respectively) as solitary birds, but in the company of mixed-species flocks the Bananaquit foraged at a mean relative height of 0.36 ± 0.04 , and the Cape May Warbler at 0.36 ± 0.06 . These trends towards lower relative foraging heights for the nectarivores in the presence of flocks were also nearly significant ($t = -1.9$, $df = 34$, $P = 0.065$ and $t = -1.8$, $df = 27$, $P = 0.071$).

Intraspecific differences in foraging location of solitary and flocking birds of each species were further analyzed with respect to the type of foraging substrate, the use of live or dead substrates, and the foliage density surrounding the foraging location. Flocking Hispaniolan Woodpeckers occurred significantly ($\chi^2 = 13.5$, $df = 1$, $P < 0.001$) more often on tree trunks or branches than did solitary birds (90% vs 35%), which were observed foraging on leaves, epiphytes, or fruit 65% of the time. Nearly-significant differences in substrate use were found for Bananaquits ($\chi^2 = 2.8$, $df = 1$, $P = 0.096$), where the proportion of flow-

ers used (as opposed to all other substrate types) decreased in the presence of mixed-species flocks from 79% to 53% of observations. Both the Prairie Warbler and the Black-crowned Palm Tanager showed a near-significant trend towards the use of more leaf and pine needle substrates (as opposed to all other substrate types) as members of mixed-species flocks ($\chi^2 = 3.1$, $df = 1$, $P = 0.078$; $\chi^2 = 2.7$, $df = 1$, $P = 0.098$). Prairie Warblers and Palm Tanagers increased leaf and needle use from 46% to 80%, and 69% to 74%, respectively. We were unable to reject the null hypothesis of no intraspecific differences in the use of live or dead substrates for any species, but significant differences were found in foliage density scores surrounding foraging sites for male Black-throated Blue Warblers ($G = 13.2$, $df = 2$, $P = 0.001$), Greater Antillean Elaenia ($G = 7.5$, $df = 2$, $P = 0.024$), Ground Warbler ($G = 6.8$, $df = 2$, $P = 0.033$), and Stripe-headed Tanager ($G = 7.1$, $df = 2$, $P = 0.029$). The two insectivorous warbler species were observed significantly more often on substrates with a more open foliage density as interspecific flock members ($G = 13.2$, $df = 2$, $P = 0.001$ for Black-throated Blue Warbler; $G = 6.8$, $df = 2$, $P = 0.033$ for Ground Warbler). For Black-throated Blue Warblers, use of the most open category of foliage density rose from 37% for solitary birds to 62% for flock members; corresponding proportions for the Ground Warbler were 23% and 59%. The omnivorous species showed an opposite trend. Flocking Greater Antillean Elaenia and Stripe-headed Tanagers decreased use of substrates with more exposed foliage density scores ($G = 7.5$, $df = 2$, $P = 0.024$; $G = 7.1$, $df = 2$, $P = 0.029$), with

percent usage dropping from 83% to 56% of all foraging observations and from 70% to 43%, respectively.

Shifts in foraging methods were observed for two species in the presence of mixed-species flocks. Ground Warblers shifted from primarily near-surface reaches and jumps (55% of observations) as solitary birds to gleaning behavior as flock members (65% of observations; $G = 6.9$, $df = 2$, $P = 0.033$). Black-crowned Palm Tanagers also shifted from near-surface maneuvers (77%) outside of flocks to gleaning (61%) within flocks ($G = 8.1$, $df = 2$, $P = 0.019$). A near-significant trend towards the use of fewer non-surface (aerial) maneuvers by the Greater Antillean Elaenia was observed ($G = 5.7$, $df = 2$, $P = 0.058$); outside of flocks 78% of feeding attempts were non-surface maneuvers, while only 56% of maneuvers within flocks were aerial sallies.

The scarcity of individuals apart from mixed-species flocks limited the analysis of feeding rates, but adequate sample sizes to compare within-species foraging rates were obtained for two insectivores, the Greater Antillean Pewee ($n = 37$), and the Black-throated Blue Warbler ($n = 63$). The pewee fed significantly faster in the presence of mixed-species flocks ($t = -3.1$, $df = 35$, $P = 0.004$); the mean time between feeding attempts was 38.5 ± 3.8 sec outside of flocks, but decreased to 23.0 ± 3.2 sec within flocks. Foraging rates did not differ between male and female Black-throated Blue Warblers in flocks ($U = 259.5$, $P = 0.83$), or as solitary birds ($U = 15.0$, $P = 0.68$), so the two sexes were combined. Foraging rates of flocking Black-throated Blues ($\bar{x} = 9.8 \pm 1.2$ sec.) were not significantly different from those of non-flocking birds ($\bar{x} = 7.9 \pm 1.4$ sec.; $U = 380.5$, $P = 0.19$).

DISCUSSION

Mixed-species flocks have not been previously described from Hispaniola; in fact, very little work has been done on the behavior and ecology of birds on the island (Dod 1981). We found mixed-species flocks, however, to be ubiquitous in the pine forests of the Cordillera Central, even though many of the same flock constituents were territorial and did not form flocks in nearby shade coffee plantations and riparian habitat (pers. observ.). Pine forest differs from shade coffee in the Cordillera Central in being relatively open habitat and in containing significantly fewer invertebrates in the understory (Wunderle and Latta,

in press). Birds appear to be generally conspicuous and more exposed in pine compared to broadleaf habitats.

FLOCK ORGANIZATION AND AGONISTIC BEHAVIOR

The high number of regularly occurring species in mixed-species flocks is unusual (Powell 1985) and indicates that there are many commonly occurring species with a high flocking propensity in this habitat. Nearly all bird species occurring in the pine forest participated to some degree in flocks. Even species that foraged on the ground or in dense understory vegetation appeared to join flocks, at least when the flock passed through their presumed territory, but more detailed observations on joining and following are needed to assess the participation of ground-foraging birds in flocks with canopy birds. Species such as Palm Warbler, Rufous-collared Sparrow, and Yellow-faced Grassquit were regularly seen in flocks, while Ground Warblers and Narrow-billed Todies also participated and were two species that most clearly adjusted their foraging behavior in the presence of flocks. The only non-participating species were the three species of hummingbirds, Cattle Egret, and the birds of prey. Some species were often seen in monospecific flocks, but at times associated (perhaps coincidentally) with mixed-species flocks. These species included Common Bobwhite, several doves, Hispaniolan Parrot, Smooth-billed Ani, Palmchat, Stripe-headed Tanager, and Antillean Siskin.

The most numerous participants in mixed-species flocks were permanent residents, but migrants formed an important component of all flocks and, as a group, had the highest flocking propensity. Most studies of mixed-species flocks report migrants as only a minor component of the flocks (Powell 1985), but in western Mexico Hutto (1994) found half the participants and half the species were migrants. Migrants and residents were also reported in mixed-species flocks in Cuba (Eaton 1953) and Jamaica (Lack and Lack 1972), and in both the U.S. Virgin Islands (Ewert and Askins 1991) and Puerto Rico (Staiicer 1992) flocks were described that consisted almost entirely of migrants. Most species participating in mixed-species flocks in the Cordillera Central were insectivores, and all of the insectivorous species occurring in the pine habitat were recorded in mixed-species flocks.

The mean flock size of 7.1 species and 11.3

individuals in the Cordillera Central is comparable to other studies, falling within the range of flock sizes reported by Powell (1985). The mean rate of movement was similar to that recorded from the U.S. Virgin Islands, where Ewert and Askins (1991) found mixed-species flocks moving at 1.6 m min^{-1} , nearly the same rate as reported here. Results from studies of understory flocks in the Neotropics, however, show flocks moving much faster, with an average movement rate of 5.0 m min^{-1} (Powell 1985).

Although most individuals were not color-banded, our impression was that most flock participants remained with the flock as it moved through the pine forest and that there was very little turnover in species or individuals. This is the same pattern described by Hutto (1987) and Munn and Terborgh (1979). A few species appeared to join mixed-species flocks for only short periods of time. This was particularly true of those species that also tended to flock monospecifically. In these cases monospecific and mixed-species flocks may have had overlapping territories or ranges and periodically foraged together. Other species that participated in mixed-species flocks may have maintained smaller, individual territories, and joined the flock only when the flock passed through their territory. These species generally appeared very active in the presence of mixed-species flocks, but did not appear to move long distances. We suspect that Broad-billed and Narrow-billed todies, Greater Antillean Pewees, Ground Warblers, Rufous-collared Sparrows, and some Black-throated Blue Warblers may have maintained such territories.

Agonistic interactions have not been frequently recorded in mixed-species flocks in the West Indies (Ewert and Askins 1991, Staicer 1992), but aggression has been commonly reported in flocks in other regions and may regulate the abundance of individuals or species within the flock (Morse 1970, Munn and Terborgh 1979, Powell 1985). Our data, showing a higher than expected incidence of intraspecific interactions, suggest that aggression may be used to limit the number of individuals per species in these flocks. However, the highly significant correlation we found between point count census data and flock composition indicate that flock composition is a reflection of the pool of species present in the habitat. This suggests that species richness within the flock is limited primarily by the number of species occurring in the habitat, and that the fre-

quency of occurrence of a species in flocks reflects its relative abundance in the habitat as indicated by point counts.

Flocks in the Cordillera Central appear to be cohesive, unlike mixed-species flocks or aggregations reported from Puerto Rico (Post 1978, Staicer 1992) and Jamaica (Lack and Lack 1972). We were often able to follow flocks for thirty minutes or more. Elsewhere in the West Indies, Eaton (1953) found cohesive flocks in Cuba, as did Ewert and Askins (1991) in the Virgin Islands, but care must be taken in such comparisons because of differences in methodologies and definitions.

Nuclear species (*sensu* Moynihan 1962) may be important in maintaining the cohesion of mixed-species flocks (Hutto 1994). Hutto characterized nuclear species (after Moynihan 1962) as: (1) occurring more often in the forefront of flocks, as they are joined and followed by other species more often than they themselves join and follow; (2) intraspecifically gregarious with a high flocking propensity and a relatively greater number of individuals per flock than other species; (3) regular participants of mixed-species flocks; and (4) generally conspicuous in their plumage, calls, and behavior. A single species is generally viewed as the nuclear species (Powell 1985), but Hutto (1994) found two nuclear species in western Mexico, and Powell reports as many as six species contributing to the maintenance of group cohesion in the Amazon. Resident species are most often reported as the nuclear species (Powell 1985; but see Greenberg 1984, Hutto 1994).

Our data suggest that the permanent resident Black-crowned Palm Tanager is often a nuclear species in these flocks. The palm tanager was the second most frequently encountered species in the pine forest, is unusually gregarious and vocal, has a relatively high flocking propensity, and is conspicuously colored. Although the Bananaquit was more common, it is not insectivorous and had a much lower flocking propensity. Several other species had a higher flocking propensity than the palm tanager, but were less common and less intraspecifically gregarious, or did not appear to be conspicuous. The Greater Antillean Pewee may also serve as a weak nuclear species in some instances, as it often appeared as a vocal component at the forefront of flocks, but the species is neither visually conspicuous nor intraspecifically gregarious.

Species co-occurrence data indicate that spe-

cies do not occur independently of one another in flocks. Negative co-occurrences, suggesting that species may be avoiding one another, were recorded for four pairs of species. Although exploitative competition or differences in microhabitat requirements between species may explain these negative co-occurrences, the most likely explanation is that they are a statistical artifact of multiple pairwise comparisons.

Positive associations between pairs of species which occurred in numbers higher than expected, were far more common. While these associations may also reflect a statistical artifact, the high number of associations suggest biological mechanisms are required to explain at least some of the results. Positive associations may reflect mutual microhabitat dependencies which, though difficult to recognize, may explain the co-occurrence of species pairs such as Yellow-throated and Yellow-rumped warblers, both of which forage in the higher reaches of pine trees, and the association of Ground Warblers and Rufous-collared Sparrows, which forage in low, broadleaf thickets.

The presence of so many positive associations may, however, result from species interactions (Hutto 1994). Evidence from our nearest neighbor analysis supports the species interaction hypothesis, suggesting that a non-random spatial organization exists within the flock. First, the close neighbors of each of the most common species were significantly different than those expected on the basis of the relative abundance of species, and the distribution of nearest neighbors differed significantly among these species. In addition, some of the same species-pairs that occurred together more often than expected on the basis of census data (such as Black-throated Blue Warbler and palm tanager; Black-and-white Warbler and Pine Warbler; Black-and-white Warbler and Yellow-throated Warbler; Table 3), are the same species-pairs found in close association within flocks (Table 4).

The benefit of associating with another species may be related to food acquisition or to increased protection from predators. If the primary benefit of group protection (auditory warnings), however, is afforded a flock member regardless of position within the flock, as Hutto (1994) suggests, then flock participants may instead accrue feeding benefits from species associations within the flock. While this explanation may apply to tightly cohesive flocks, it is more difficult to apply

to the sometimes widespread and dispersed Hispaniolan pine flocks. In these flocks, mutual predator protection is a likely possibility for some species pairs which share similar feeding behaviors and foraging rates, and feeding facilitation may still explain other positive species co-occurrences.

FORAGING BEHAVIOR

Most measures of the impact of interspecific flocking behavior on niche overlap indicate that flocking results in a reduction in foraging niche diversity, or the convergence of feeding behaviors (Powell 1985). Several studies have reported changes in avian feeding behavior resulting from association with mixed-species flocks (Morse 1970, Valburg 1992), including the convergence of the foraging behavior of individuals within the flock with that of the nuclear species (Buskirk 1976, Valburg 1992), but only Buskirk (1972, cited in Powell 1985) has recorded convergence of foraging methods by insectivores. Intraspecific comparisons of flocking and solitary birds in this study provide some evidence that individuals modify foraging locations or foraging tactics upon joining a mixed-species flock, and that these changes tend to converge with the feeding behavior of the nuclear species. Caution must be taken in interpreting these results as environmental conditions were uncontrolled and may have differed independently of flocking behavior.

Changes in the relative height of feeding activity were the most frequently recorded modification among flocking birds, and these changes supported the hypothesis of niche convergence. While the two nectarivorous species, the Bananaquit and the Cape May Warbler, which normally feed relatively high in the vegetation, moved lower in the vegetation in the presence of flocks, the Black-throated Blue Warbler and the Ground Warbler moved from low and dense foliage to relatively higher foraging sites. This was also the pattern exhibited by both the Broad-billed and Narrow-billed tody (Latta and Wunderle, in press).

For the nuclear species, as well as flock members as a whole, gleaning was the most common foraging method, and leaves and pine needles were the most common substrate. The observed shifts in foraging method and substrate use by flocking species supports the reduction of niche diversity towards the gleaning of leaves and needles. The Bananaquit, for example, appeared to

be acting more insectivorous by using fewer flowers for foraging sites, while the Prairie Warbler and the Black-crowned Palm Tanager both used a higher percentage of leaves when foraging in flocks. Only the Hispaniolan Woodpecker appeared to feed in more specialized locations, with more foraging on trunks and limbs. The significant shift towards more gleaning by both the Ground Warbler and the palm tanager, and the nearly significant use of less aerial maneuvers by the Greater Antillean Pewee, are further indications of niche reduction in the mixed-species flocks.

The shift to gleaning in the presence of mixed-species flocks may be assumed to be less risky behavior, as birds remain in the vegetation while foraging. But birds may also be using riskier behavior by foraging in more exposed locations. This was observed in Black-throated Blue Warblers and Ground Warblers, as well as in Broad-billed and Narrow-billed todies (Latta and Wunderle, in press) which both foraged in sites with a lower foliage density in the presence of mixed-species flocks. Only the Greater Antillean Elaenia and the Stripe-headed Tanager were found to forage in significantly denser vegetation when in flocks. Feeding in more exposed locations may be the result of individuals benefitting from the protection offered by the flock through mutual vigilance or confusion of predators (Powell 1985). Under the predation hypothesis, the protection afforded by the flock may allow birds to forage faster with less vigilance (Sullivan 1984). The increased feeding rates we have recorded for the Greater Antillean Pewee may indicate that the foraging behavior of this species is constrained by predators.

Feeding advantages may be expected to accrue individuals in flocks under the food facilitation hypothesis as well. In addition, the high number of positive associations of species-pairs, and the convergence of some spatial parameters and foraging behaviors by flocking species, suggest that some birds are finding enhanced foraging opportunities amidst flocks. Support for the food facilitation hypothesis does not exclude the possibility that birds benefit from predator avoidance as well (Powell 1985). In order to completely understand the evolutionary significance of flocking behavior, we need more complete descriptions of the structure and dynamics of mixed-species flocks from many habitats and geographic areas. Studies of color-banded birds would en-

able one to follow individual birds both within and apart from flocks to accurately assess feeding benefits accruing to the individual.

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