

# WINTER FLOCKING OF INSECTIVOROUS BIRDS IN MONTANE PINE-OAK FORESTS IN MIDDLE AMERICA<sup>1</sup>

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**Abstract.** We studied mixed-species insectivorous bird flocks in pine-oak forests in Middle America during three winter seasons to determine whether patterns of flock structure and dynamics were similar to those reported from other tropical sites. We also analyzed patterns of association among bird species, as well as their foraging behavior and the vegetation characteristics associated with birds in flocks. We encountered 333 flocks containing 144 species, of which 26 species had adequate sample sizes for analyses. The size and rate of movement of the flocks were similar to those reported from other Neotropical sites, however, the species richness of our flocks was lower than reported in most other studies, perhaps due to simpler vegetation structure or higher latitude. Only 3 of 50 significant correlations between species pairs were negative, indicating that species generally were not restricted in their participation in mixed-species flocks by other species. In only one instance did we observe correspondence between the association of species-pairs in flocks and their foraging behavior. For most species there was no relationship between association between species-pairs in flocks and vegetation parameters with which they were associated. Thus, additional factors besides foraging facilitation and mutual association with particular vegetation characteristics must be responsible for many of the positive correlations among species pairs. We suggest that non-random association among species within flocks may result in part from enhanced vigilance for predator detection afforded by flock members using similar parts of the environment at the same time.

**Key words:** *foraging, mixed-species flocks, Neotropics, vegetation characteristics.*

## INTRODUCTION

Participation by birds in mixed-species flocks is widespread in the Neotropics, and numerous studies have been directed at determining the adaptive significance of this behavior (Powell 1985). Explanations for the phenomenon fall into two principal categories: reduced predation and enhanced foraging success.

The “predation reduction” category of flocking benefits includes the following explanations: (1) enhanced detection of a potential predator through monitoring behavior of co-participants (Moynihan 1962, Pulliam 1973, Powell 1985), (2) reduced exposure to predation by being part of a group (“distraction” hypothesis of Miller 1922 and Moynihan 1962; “selfish herd” of Hamilton 1971 and Vine 1971), (3) capitalization by some members on superior familiarity of other flock members with the flock’s home range, thereby avoiding dangerous areas (Moynihan 1962), and (4) “strength in numbers” re-

sulting in intimidation or deterrence of some predators by mobbing (Moynihan 1962). “Foraging enhancement” hypotheses include (1) “information transfer” in which flock members benefit from clues provided by flock mates about the location of resources (Moynihan 1962, Ward and Zahavi 1973, Valburg 1992), (2) the “beater” effect in which flock members exploit prey flushed by the activity of the flock (Moynihan 1962, King and Rappole, in press), and (3) reduction in foraging niche overlap among flock participants (Morse 1970).

In addition to benefits, several researchers have proposed that there are costs involved with participation in mixed-species foraging flocks as well. For instance, increased competition for food, or reduced foraging efficiency as a result of the necessity to modify foraging behavior to match the speed or location of the flock could have negative effects on flock members, forcing them to make choices in terms of participating in flocks or foraging as solitary individuals (Jones 1977, Hutto 1988).

The study of the costs and benefits of flock

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participation and their effect on flock composition is complicated by the fact that flock participants may benefit simultaneously from enhanced predator detection and enhanced foraging efficiency (Moynihan 1962, Powell 1985). For example, flocking could improve foraging efficiency because flock members spend less time scanning for predators (Sullivan 1984, Elgar 1989). Also, it is probable that different kinds of flocks may provide different benefits to their members (Moynihan 1962). Clearly, additional information is needed on patterns of association of species within and among flocks that allow us to test hypotheses about the costs and benefits of flocking (Powell 1985, Hutto 1994, Latta and Wunderle 1996).

Previous studies of mixed-species foraging flocks in the Neotropics indicate that there is substantial regional variation in the composition and dynamics of mixed-species flocks. In the humid tropics, resident species tend to predominate, and many individuals occur outside of flocks (Powell 1985). These characteristics contrast with those observed for flocks in highland pine and pine-oak forests in Mexico (Hutto 1987, Gram 1998) and the Caribbean (Latta and Wunderle 1996) in which Neotropical-Nearctic migrants play a much greater role, and fewer individuals occur away from flocks. We studied mixed species flocks in southern Mexico, Guatemala, and Honduras to determine whether patterns of flock structure and dynamics in this little studied habitat were similar to those reported from other parts of the tropics. In addition, we tested whether bird species were nonrandomly associated with other species, whether positive or negative relationships among species were associated with similarities or differences in foraging behavior, and whether there was evidence of intraspecific interactions or sex-specific differences in foraging behavior within flocks. Finally, because previous studies have cited the possible confounding effects of the association of species with specific vegetation characteristics in analyses of mixed-species flocking (Hutto 1994, Latta and Wunderle 1996), we also quantified vegetation variables to test whether associations of species with particular vegetation characteristics might be responsible for positive or negative relationships between bird species.

#### METHODS

Field work was conducted over three winter seasons (1 December 1995–1 February 1996; 10

January–15 February 1997; 10 January–23 February 1998) primarily in the central and western highlands of Honduras and the eastern highlands of Guatemala. We also include data from four days of fieldwork in Chiapas, Mexico (28 February–3 March 1998). We concentrated our field efforts in pine and pine-oak habitat above 1,000 m elevation. Other major habitat types in the highlands are broadleaf forest (including cloud forest), pasture, agricultural fields (sun coffee, beans, corn), tree crops (bananas, shade coffee, citrus), and various early successional stages of forest regrowth. The bird species we included in our analyses are widespread and abundant in pine and pine-oak forest across the study area (Howell and Webb 1995), thus we are confident that our results were not significantly affected by regional variation in bird distribution and abundance.

Flocks were located by walking through forested habitats searching visually for individual birds and listening for vocal members of mixed-species flocks, such as the Greater Pewee, Dusky-capped Flycatcher, and Painted Redstart (scientific names of bird species are listed in Table 1). A flock was defined as  $> 2$  individuals within 25 m of each other and moving in concert (Hutto 1987). When a flock was located, the observer stayed with it until no further bird species were detected. Average time required to record all species in a mixed-species flock was about 1.5 hr, although it ranged up to 4 hr, depending on flock size and habitat conditions. Although birds were not individually marked, we are confident few species joined or left the flocks as they progressed because few of the species included in our analyses occurred out of flocks on a regular basis (see below). We tested for non-random association among species by scoring species as present (1) or absent (0) in each flock and analyzed the association among species using Pearson correlation, which, when applied to 0, 1 data, yields a correlation coefficient, the  $P$ -value of which corresponds to that of a Chi-square test of independence (Sokal and Rohlf 1995). Significance values were Bonferroni-corrected to account for multiple tests. These analyses were restricted to species that occurred in  $\geq 15\%$  of flocks, plus the Red-faced Warbler because sufficient foraging data were available for this species (see below).

We tested whether species were represented in flocks as solitary individuals more often than

TABLE 1. Frequency and average ( $\pm$  SE) number of individuals per flock for bird species occurring in  $\geq 15\%$  of flocks, or species for which  $\geq 10$  foraging maneuvers were recorded, in Central America and Mexico, 1995–1998. Average numbers of individuals per flock was calculated for flocks in which the species occurred.

	Frequency of occurrence	Mean number of individuals
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	81.7	1.41 $\pm$ 0.05
Black-throated Green Warbler ( <i>Dendroica virens</i> )	77.5	3.10 $\pm$ 0.15
Blue-headed Vireo ( <i>Vireo solitarius</i> )	63.1	1.22 $\pm$ 0.04
Hermit Warbler ( <i>Dendroica occidentalis</i> )	61.3	2.50 $\pm$ 0.11
Black-and-white Warbler ( <i>Mniotilta varia</i> )	56.5	1.11 $\pm$ 0.03
Townsend's Warbler ( <i>Dendroica townsendi</i> )	54.4	1.62 $\pm$ 0.07
Painted Redstart ( <i>Myioborus pictus</i> )	53.5	1.34 $\pm$ 0.04
Grace's Warbler ( <i>Dendroica gracia</i> )	49.9	1.36 $\pm$ 0.05
Slate-throated Redstart ( <i>Myioborus miniatus</i> )	47.5	1.30 $\pm$ 0.04
Olive Warbler ( <i>Peucedramus taeniatus</i> )	42.9	1.35 $\pm$ 0.04
Golden-cheeked Warbler ( <i>Dendroica chrysoparia</i> )	39.9	1.14 $\pm$ 0.03
Crescent-chested Warbler ( <i>Vermivora superciliosa</i> )	39.6	1.67 $\pm$ 0.06
Greater Pewee ( <i>Contopus pertinax</i> )	39.0	1.18 $\pm$ 0.04
Hammond's Flycatcher ( <i>Empidonax hammondii</i> )	27.9	1.01 $\pm$ 0.03
Dusky-capped Flycatcher ( <i>Myiarchus tuberculifer</i> )	26.4	1.23 $\pm$ 0.03
Brown Creeper ( <i>Certhia americana</i> )	24.9	1.23 $\pm$ 0.03
Streak-headed Woodcreeper ( <i>Lepidocolaptes affinis</i> )	24.6	1.23 $\pm$ 0.03
Hepatic Tanager ( <i>Piranga flava</i> )	23.7	1.34 $\pm$ 0.04
Tufted Flycatcher ( <i>Mitrephanes phaeocercus</i> )	20.4	1.24 $\pm$ 0.03
Acorn Woodpecker ( <i>Melanerpes formicivorus</i> )	18.6	2.08 $\pm$ 0.06
Mountain Trogon ( <i>Trogon mexicanus</i> )	17.7	1.31 $\pm$ 0.03
Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	17.7	1.00 $\pm$ 0.02
Common Bush Tanager ( <i>Chlorospingus ophthalmicus</i> )	16.5	5.02 $\pm$ 0.17
Black-headed Siskin ( <i>Carduelis notata</i> )	16.2	2.50 $\pm$ 0.10
Hairy Woodpecker ( <i>Picoides villosus</i> )	15.3	0.96 $\pm$ 0.02
Red-faced Warbler ( <i>Cardellina rubrifrons</i> )	12.0	0.98 $\pm$ 0.02

expected by chance by comparing the frequency of flocks that contained only a single individual of a species with the expected frequency calculated using a Poisson distribution. In addition, we tested whether more flocks containing two or more individuals had individuals of both sexes (based on plumage type) more than expected by chance using sign tests.

Foraging behavior was sampled by observing focal individuals, and recording the first foraging maneuver observed. Although the use of initial foraging observations may bias results towards conspicuous foraging maneuvers, these biases appear to be minor in most cases (Wagner 1981, Morrison 1984, Hejl et al. 1990). Only one foraging maneuver for each species per flock per individual was recorded to ensure independence of observations. We classified foraging behaviors into three categories: (1) near perch foraging maneuvers (foraging maneuvers directed at food that can be reached from the bird's perch) in the inner half of the plant, (2) near perch foraging maneuver in the outer half of the plant, and (3) aerial maneuver (foraging

maneuvers in which a bird must leave its perch to reach food). Few aerial maneuvers were directed at the inner portion of the plant, so only one category of aerial maneuver was considered. We analyzed the distribution of foraging maneuvers by each species, and the distribution of foraging maneuvers between sexes for dimorphic species, among the three categories using Chi-square tests of independence. Although analyses of foraging behavior were restricted to species for which we recorded  $> 10$  foraging maneuvers, the average number of foraging maneuvers/species was much higher than this (see below).

In addition, vegetation data were collected at five randomly-located points along 42 1-km transects on which flock species composition and bird foraging behavior also were recorded. Vegetation parameters measured included canopy height, number and size (dbh) of trees by species, shrub density, canopy cover, and ground cover (James and Shugart 1970). These variables were averaged for each transect, tested for normality using Shapiro-Wilk tests, and log-

transformed where necessary to improve normality and equality of variances. We calculated correlation coefficients between the number of individuals of each bird species on each transect and vegetation variables measured on each transect using Pearson correlation. Only bird species for which we analyzed foraging behavior were included in this analyses. We reduced the dimensions of the vegetation variables using principal components analysis (PCA), rotated the resulting PCA axes using Varimax rotation, and ordinated all bird species on the first two rotated vegetation factors. Statistical tests are considered significant at  $P < 0.05$  unless stated otherwise, and were Bonferroni-corrected where necessary to account for multiple tests. Means are presented  $\pm$  SE.

## RESULTS

We detected 6,695 individual birds of 144 species in 333 flocks during the course of the study. Flock size averaged  $20.4 \pm 0.6$  individuals, and on average  $12.6 \pm 0.5$  species were represented. Twenty-five species occurred in  $> 15\%$  of flocks, and were included in the analyses (Table 1). In addition to these, we included a 26th species, the Red-faced Warbler, which occurred in 12% of the flocks that we observed, because we had sufficient foraging data ( $> 10$  maneuvers).

### FLOCK STRUCTURE AND DYNAMICS

Few individuals of any insectivorous bird species were observed out of flocks, except for the dawn (to 30 min after sunrise) and dusk (30 min before sunset) periods during which flocks were assembling or breaking up for the night, respectively. Generally, flocks appeared to be cohesive, and moved within a restricted area corresponding to a home range. Straight-line distances traveled were used to calculate approximate size of the home range for four flocks. Assuming that home ranges were roughly circular, estimates were 1.8, 3.1, 7.1, and 9.6 ha. Because flocks rarely were followed for more than a few hours before a full count of species was obtained, these likely represent minimum home range size estimates.

Flocks appear to form shortly after dawn, and on several occasions, Painted Redstarts, a conspicuously-colored, noisy bird that exhibited the characteristics of a nuclear species (*sensu* Moynihan 1962), were observed alone calling loudly and flashing their wing and tail patches shortly

after dawn in a manner consistent with behavior directed at assembling the flock for the day's activities. Flock members apparently do not roost together. In one instance, a Painted Redstart was found calling loudly alone, evidently preparing to roost on a horizontal root sticking out from an overhanging road cut just before dusk. A pile of droppings below the spot indicated that this roost had been in use for some time. In another instance, two Tufted Flycatchers, also frequent nuclear species, were found calling loudly just before dusk with no other flock members evident. On one occasion, we observed the pre-dusk movement of an entire flock to a water source for bathing. On several occasions, flocks approaching from different directions were observed to merge together. No evidence of overt aggressive or territorial behavior, e.g., chases or supplantings, were observed, although these occurrences often were accompanied by evident increased levels of vocalization.

### RELATIONSHIPS AMONG SPECIES

The correlation analyses revealed 47 significant positive correlations out of 338 possible combinations of species pairs. Wilson's Warbler was correlated with Slate-throated Redstart. Black-throated Green Warbler was correlated with Blue-headed Vireo, Black-and-white Warbler, Painted Redstart, and Grace's Warbler. Blue-headed Vireo was correlated with Townsend's Warbler. Hermit Warbler was correlated with Townsend's Warbler, Painted Redstart, Olive, Golden-cheeked and Crescent-chested Warbler, Greater Pewee, and Brown Creeper. Black-and-white Warbler was correlated with Townsend's and Crescent-chested Warblers and Greater Pewee. Townsend's Warbler was correlated with Slate-throated Redstart, Golden-cheeked and Crescent-chested Warbler, Greater Pewee, Tufted Flycatcher, Mountain Trogon, and Red-faced Warbler. Painted Redstart was correlated with Grace's Warbler, Greater Pewee, Acorn Woodpecker, and Black-headed Siskin. Grace's Warbler was correlated with Greater Pewee and Hepatic Tanager. Slate-throated Redstart was correlated with Golden-cheeked and Crescent-chested Warbler, Spot-crowned Woodcreeper, and Common Bush-Tanager. Olive Warbler was correlated with Golden-cheeked and Crescent-chested Warbler, Greater Pewee, Hammond's Flycatcher, Brown Creeper, and Tufted Flycatcher. Golden-cheeked Warbler was correlated with

TABLE 2. Foraging behavior of 12 bird species in mixed-species foraging flocks in Central America and Mexico, 1995–1998. Values that differ significantly from expected values are in bold print. Foraging maneuvers are defined in the text.

Bird species	Foraging maneuver			$\chi^2$	<i>P</i>	<i>n</i>
	Aerial	Near perch inner	Near perch outer			
Wilson's Warbler	<b>15</b>	8	5	7.3	0.03	28
Black-throated Green Warbler	11	11	11	0.0	1.00	33
Blue-headed Vireo	8	6	6	0.0	0.99	20
Hermit Warbler	8	11	15	1.2	0.56	34
Black-and-white Warbler	<b>1</b>	<b>21</b>	4	61.1	<0.001	26
Townsend's Warbler	5	7	12	2.5	0.29	24
Grace's Warbler	3	2	<b>14</b>	43.8	<0.001	19
Slate-throated Redstart	<b>17</b>	3	<b>0</b>	120.0	<0.001	20
Olive Warbler	3	2	<b>11</b>	18.7	<0.001	16
Golden-cheeked Warbler	16	<b>0</b>	14	21.8	<0.001	30
Crescent-chested Warbler	<b>0</b>	6	<b>13</b>	44.6	<0.001	19
Red-faced Warbler	<b>9</b>	2	1	16.3	<0.001	12

Crescent-chested Warbler. Crescent-chested Warbler was correlated with Spot-crowned Woodcreeper, Tufted Flycatcher, and Red-faced Warbler. Greater Pewee was correlated with Hepatic Tanager. Spot-crowned Woodcreeper was correlated with Common Bush-Tanager. Tufted Flycatcher was correlated with Red-faced Warbler. Acorn Woodpecker was correlated with Hairy Woodpecker. We also observed three species pairs that were negatively correlated: Tufted Flycatcher and Black-throated Green Warbler, Common Bush-Tanager and Greater Pewee, and Hepatic Tanager and Slate-throated Redstart. The ratio of positive to negative correlations was significantly different than that expected by chance (sign test;  $P < 0.001$ ).

Twenty-three of the 26 bird species that occurred in  $\geq 15\%$  of flocks were represented within flocks by a single individual significantly more often than expected by chance based on the Bonferroni corrected  $P$ -value ( $P = 0.002$ ). The frequency with which Hermit Warblers, Common Bush-Tanagers, and Black-headed Siskins occurred in flocks as sole representatives of their species did not differ from random. The two sexually dimorphic species for which we have data (Golden-cheeked Warbler and Black-and-white Warbler) were represented by members of both sexes (based on plumage type) more often than expected in cases in which a flock was observed to contain more than one individual (sign test  $P < 0.05$ ).

We recorded an average of  $23.4 \pm 2.0$  foraging maneuvers for 12 species (Table 2). Bird

foraging maneuvers were significantly nonrandomly distributed among foraging categories ( $\chi^2_{24} = 149.3$ ,  $P < 0.001$ ). Black-and-white and Crescent-chested Warblers used aerial maneuvers significantly less than expected by chance. Wilson's Warblers, Slate-throated Redstarts, and Red-faced Warblers used aerial maneuvers more than expected by chance. Black-and-white Warblers used near-perch maneuvers directed at the inner portion of the plant significantly more than expected by chance, and Golden-cheeked Warblers used near-perch maneuvers directed at the inner portion of the plant significantly less than expected by chance. Grace's, Olive and Crescent-chested Warblers used near-perch maneuvers directed at the outer portion of the plant significantly more than expected by chance, and Slate-throated Redstarts used near-perch maneuvers directed at the outer portion of the plant significantly less than expected by chance. The foraging maneuvers of Black-throated Green Warblers, Blue-headed Vireos, Hermit Warblers, and Townsend's Warblers did not differ among foraging categories ( $P \geq 0.12$ ). Foraging behavior did not differ between male and female Black-and-white and Golden-cheeked Warblers ( $P > 0.30$ ), the two sexually dimorphic species for which we have sufficient foraging data.

Several of the vegetation variables were highly correlated ( $P < 0.001$ ). Thus, we reduced the number of variables included in the analyses to tree height, percent canopy cover, basal area of pines and deciduous trees to avoid colinearity of variables. The first two rotated factors from the

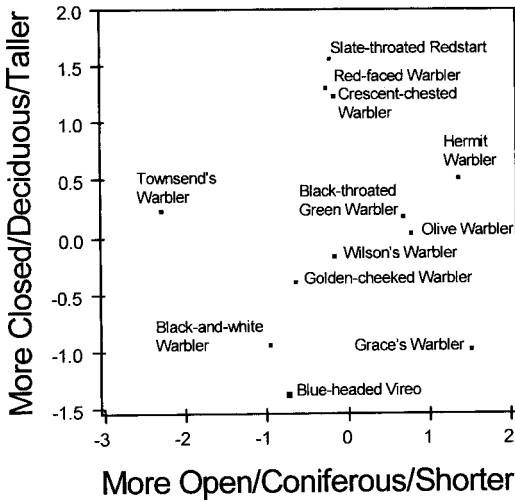


FIGURE 1. Principle components ordination of bird species occurring in  $\geq 15\%$  of flocks, and Red-faced Warbler, and axes derived from habitat variables measured at random points on 42 1-km transects, 1995–1998.

principal components analysis accounted for 88% of the variability in abundance of bird species among transects. There was substantial variability among species in patterns of vegetation use (Fig. 1). Townsend's Warblers were most abundant on transects with moderately closed, moderately tall-stature mixed forest, Hermit, Black-throated Green, Olive, and Grace's Warblers were most abundant on transects with short to medium-stature, open-canopy pine forest, Slate-throated Redstarts, Red-faced and Crescent-chested Warblers were most abundant on transects with relatively open, tall, mostly deciduous forest, and Golden-cheeked, Wilson's and Black-and-white Warblers, and Blue-headed Vireos used mixed forest of intermediate characteristics.

## DISCUSSION

### FLOCK STRUCTURE AND DYNAMICS

The size of our flocks falls within the range of 6–40 individuals typical of Middle and South American mixed-species flocks (Powell 1985). The number of species we found per flock is similar to those reported by Latta and Wunderle (1996) in pine forests on Hispaniola (7 species), and Hutto (1987) and Gram (1998) in Mexican pine-oak forests (18.3 and 9.93 species, respectively), which is low compared to most studies

of Middle and South American mixed-species flocks (10–48 species; Powell 1985). Fewer species in pine and pine-oak dominated forest flocks may reflect the simpler habitat structure or increased latitude of these sites relative to moist tropical forests where most research on mixed species flocks has been conducted.

Other studies have cited the restriction of flock activities to a discrete home range, and our estimates of home range sizes fall within the range described in other studies of mixed-species foraging flocks in the Neotropics (0.8–14.3 ha) (Buskirk et al. 1972, Munn and Terborgh 1979, Jullien and Thiollay 1998). Furthermore, other accounts report that flocks make pre-dusk movements toward water to bathe (Munn and Terborgh 1979, Powell 1979) and do not appear to roost together at night (Davis 1946, Buskirk et al. 1972, Munn and Terborgh 1979). We did not observe vigorous chases or supplantings between members of different flocks at flock home range boundaries (Jones 1977, Munn and Terborgh 1979, Gradwohl and Greenberg 1980), although we did observe increased amounts of vocalization when different flocks came into contact that might be associated with inter-flock aggression (Buskirk et al. 1972).

### POTENTIAL COSTS OF FLOCKING

Flock attendance might involve a cost in terms of foraging efficiency if birds have to compromise their optimal foraging speed to match the speed of the flock (Jones 1977, Hutto 1988), or if their territory boundaries do not coincide with the territory boundaries of the flock (Munn and Terborgh 1979, Powell 1979). We do not have information on species-specific flock participation in relation to flock speed; however, if certain species were associated with slow flocks and others with fast-moving flocks, we would expect to see negative correlations between species characteristic of slow versus fast-moving flocks. In contrast to this prediction, we observed far fewer negative correlations among species than expected by chance. Similarly, we found little evidence to support the assertion that the occurrence of some species is limited to flocks whose territories coincide with their territories because few species occurred out of flocks.

An additional cost of flock attendance could be increased competition for food, a factor which could potentially restrict the participation

in flocks by species which use similar resources (Jones 1977, Munn and Terborgh 1979, Hutto 1988). However, the vast majority (94%) of significant correlations among species occurrences in our flocks were positive, and the foraging behavior of two of the three species pairs that were negatively correlated, and for which we have foraging data (Tufted Flycatcher and Black-throated Green Warbler, Common Bush-Tanager and Greater Pewee) were dissimilar. Tufted Flycatchers ( $n = 9$ ) foraged entirely on airborne prey, whereas Black-throated Green Warblers only took 11% of airborne prey (unpubl. data). Similarly, Common Bush-Tanagers ( $n = 6$ ) foraged entirely on prey on vegetation, whereas Greater Pewees ( $n = 6$ ) foraged entirely on airborne prey. Thus, it appears that if competition exists among species for food, it is not mitigated by selective avoidance by species of flocks containing potential competitors (Hutto 1994). It is possible that the differences in foraging behavior we observed among species within flocks is a form of character displacement, which could explain the lack of evidence of exclusion of species from flocks by competing species (Jones 1977). However, if this were the case, we would expect to observe negative correlations among species with similar foraging behavior, a pattern that was not apparent in our study.

#### RELATIONSHIPS AMONG SPECIES

*Foraging enhancement.* Flocking behavior may confer advantages to flock members by enhancing foraging efficiency. For instance, birds may benefit from the presence of flock mates who flush concealed prey (Moynihan 1962, Munn and Terborgh 1979, King and Rappole, in press). Although we did not observe any cases in which a bird captured a prey item flushed by another bird during our study, flocking birds could cause subtle evasive movements by prey that might be sufficient to reveal the prey items to foraging birds yet still be beyond the ability of human observers to detect (Powell 1985). Thus we are unable to rule out the potential importance of the "beater effect" to flock members.

Flock members also could benefit from flock mates by using information to exploit patchily distributed resources (Ward and Zahavi 1973), or by copying modes of exploitation of certain food items or microhabitats (Valburg 1992). However, if flock members benefited from shared information about food resources, we

would predict that species that are positively associated among flocks would exhibit similar foraging behavior (Hutto 1994). In contrast to this prediction, we only observed one case in which a species pair (Wilson's Warbler and Slate-throated Redstart) was both positively correlated in flocks and exhibited similar patterns of foraging behavior. Conversely, species pairs that exhibited similar foraging behavior (Slate-throated Redstart and Red-faced Warbler, Grace's and Olive Warbler) were not positively correlated in flocks. Finally, the flocks we observed occupied relatively small home ranges and traversed them regularly, and therefore, probably had a substantial amount of familiarity with the location of food resources that would decrease the importance of information gained from flock mates (Moynihan 1962, Powell 1985).

*Mutual association with vegetation characteristics.* An alternative explanation for the preponderance of positive correlations among bird species pairs in flocks considered by Hutto (1994) and Latta and Wunderle (1996) is that positive correlations among species result from similar association with particular vegetation characteristics. Our observation that Slate-throated Redstarts, Crescent-chested Warblers, and Red-faced Warblers were positively associated in flocks and also similar to each other in vegetation use provides some support for this explanation. However, other species that were similar in vegetation use (Black-throated Green, Olive, and Hermit Warblers) were not positively associated within flocks. Furthermore, Townsend's Warblers were consistently associated in flocks with Blue-headed Vireos, Hermit Warblers, Black-and-white Warblers, Slate-throated Redstarts, Golden-cheeked Warblers, Crescent-chested Warblers, and Red-faced Warblers, but do not exhibit close similarities with any of these species in terms of vegetation use.

*Anti-predator benefits.* Although the potential for flocking to decrease the vulnerability of flock members to predation is widely cited (Hutto 1988, Thiollay and Jullien 1998), previous discussions have dismissed predation as an important influence on the species composition of flocks, maintaining that information about approaching predators is transmitted by auditory cues, and therefore, flock mates are equally suitable as sentinels regardless of where they forage within the flock (Hutto 1994, Latta and Wun-

derle 1996). However, Davis (1975) found that alarm signals in pigeons (*Columba livia*) could be transmitted by subtle behavioral cues that would presumably be more easily detected at close proximity. Furthermore, flock mates also decrease the probability of an individual being selected as prey during an attack on the flock, a benefit that should also be best realized when flock mates are in close proximity (Hamilton 1971, Vine 1971).

If birds benefit from associating with flocks because other flock members serve as sentinels or alternative targets to predators, and if this benefit is greater for birds that forage in close proximity to each other, then it follows that conspecifics would be the most likely candidates, since they are most similar in foraging behavior. However, conspecifics also would compete most closely for resources. These suggestions lead to some interesting predictions. First, flock members should exhibit territoriality towards other conspecifics because they are least able to reduce competition through character displacement (Jones 1977). Second, in instances where a conspecific flock member is tolerated, the two should be of different sexes, because this will maximize the potential for partitioning resources through intersexual differences in foraging. Our observation that most bird species in our study were represented within flocks by a single individual more often than expected, and that in cases in which a flock was observed to contain more than one individual, the species was represented by members of both sexes more often than expected, are consistent with these predictions. Although we observed no sex-specific differences in foraging behavior between male and female Black-and-white or Golden-cheeked Warblers, males of both of these species foraged higher than females, although this difference was significant only for Golden-cheeked Warblers ( $t_{28} = 2.13$ ,  $P = 0.04$ ). Others have observed the co-occurrence in flocks of members of the opposite sex for transient or wintering migrants (Zahavi 1971, Leck 1972, Gradwohl and Greenberg 1980). Because it is extremely unlikely that any reproductive factors are involved in these occurrences, the best explanation would seem to be that birds are exploiting conspecifics for protection from predators while minimizing the costs of competition for food by preferentially flocking with conspecifics of slightly variant foraging behavior and/or morphology.

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