

FLOCKING AND FORAGING BEHAVIOR OF WINTERING PROTHONOTARY WARBLERS

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ABSTRACT.—We quantified flocking behavior and examined the impact of social context (solitary, single-species flocks, and mixed-species flocks) on the foraging behavior of Prothonotary Warblers (*Protonotaria citrea*) wintering in a Costa Rican mangrove forest and surrounding habitats. Based on observations collected over two winters during 70 visits to four sites, 87% (483) of the 555 Prothonotary Warblers encountered moved in flocks and over 48% (271) of these individuals were in single-species flocks. Although the propensity to join flocks was 6% higher for Prothonotary Warblers in the second winter of the study, neither the average size of single-species flocks nor the average number of individuals or species in mixed-species flocks differed between years. Twenty-seven different species were identified in mixed-species flocks that had at least one Prothonotary Warbler, but Nearctic migrants dominated these flocks. Analyses of focal observations on 57 females and 93 males indicated that Prothonotary Warbler foraging behavior was largely independent of flock type and size. Foraging maneuver, substrate, and location did not differ significantly for individuals of either sex foraging alone, in single-species, or mixed-species flocks. The species is almost strictly insectivorous, gleaning made up 70% of 150 prey capture attempts observed and about half of all attempts (76 of 150) were directed towards leaf surfaces. Foraging generally occurred in the outer third of the tree, on branches less than 1 cm in diameter, in the bottom half of the canopy. Agonistic interactions among flock members that involved Prothonotary Warblers were uncommon and neither flock type nor size were useful predictors for rates of foraging, movement, preening, or vigilance. Received 14 May 1999, accepted 14 Oct. 1999.

Various costs and benefits have been hypothesized for individuals that associate with foraging flocks (see reviews by Moynihan 1962, Morse 1977, Powell 1985). Compared to solitary foragers, members of such groups gain increased protection from predation through greater overall vigilance and predator detection by the group (Pulliam 1973, Kenward 1978) and lessened individual probability of predation (Hamilton 1971, Lazarus 1979). Similarly, group members may benefit from enhanced foraging opportunities as a result of a decreased requirement for individual vigilance (Powell 1974, Popp 1988) and through copying the foraging behavior of more successful individuals in the group (Krebs et al. 1972, Morse 1978, Waite and Grubb 1988). However, it also has been suggested that the benefits of predator protection within flocks may come at the cost of de-

creased feeding efficiency (Rabenold and Christensen 1979, Hutto 1988). Competition among flock members for resources, as well as the potential need to adjust foraging behavior to match the movement patterns of other members in the flock, could hinder foraging effectiveness (Austin and Smith 1972, Alatalo 1981, Petit and Bildstein 1987).

In addition to flock size, species composition may influence foraging behavior and thus alter the relative costs and benefits of membership in a group. Mixed-species flocks may have less inter-individual competition for food than similarly sized flocks of conspecifics (Fretwell 1972, Barnard and Thompson 1985, Hogstad 1988). Some species substantially alter their foraging behavior when in flocks of differing compositions (Valburg 1992, Latta and Wunderle 1996). However, there have been relatively few studies to compare the foraging behavior of individuals in a population where they may forage as single individuals, in single-species flocks, and in mixed-species flocks. We present data describing the foraging behavior of Prothonotary Warblers (*Protonotaria citrea*) wintering in Costa Rica. Our goals were to describe the composition of foraging flocks which include Prothonotary Warblers, assess differences in the propensity of Prothonotary Warblers to form flocks across

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years, and compare the foraging behavior of individual Prothonotary Warblers in flocks of different composition. We examined these data to determine if there were any differences within the sexes and between males and females in their foraging tactics, locations, and rates of foraging behavior while associated with flocks of different composition and size.

STUDY SITE AND METHODS

We conducted field work from November through January during the boreal winters of 1990–1991 and 1991–1992 at Tivives, Puntarenas, Costa Rica ($9^{\circ} 52'$

N, $84^{\circ} 42' W$; Fig. 1). We used narrow foot trails along the edge of coastal mangrove forest and in the adjacent hillside woods to survey study sites. Inland edges of the mangrove were dominated by black mangroves (*Avicennia germinans* and *A. bicolor*) with canopy heights ranging from 3–10 m; pure stands of red mangrove trees (*Rhizophora racemosa*), covering about 60% of the entire mangrove, occupied the central portion with canopy heights ranging from 25–30 m (see Jiménez 1988 for details). Soil in the black mangrove sections of the forest remained damp throughout the two study periods; only during the monthly inundation associated with spring tides was there standing water in these areas. Adjacent hillsides were covered in sec-

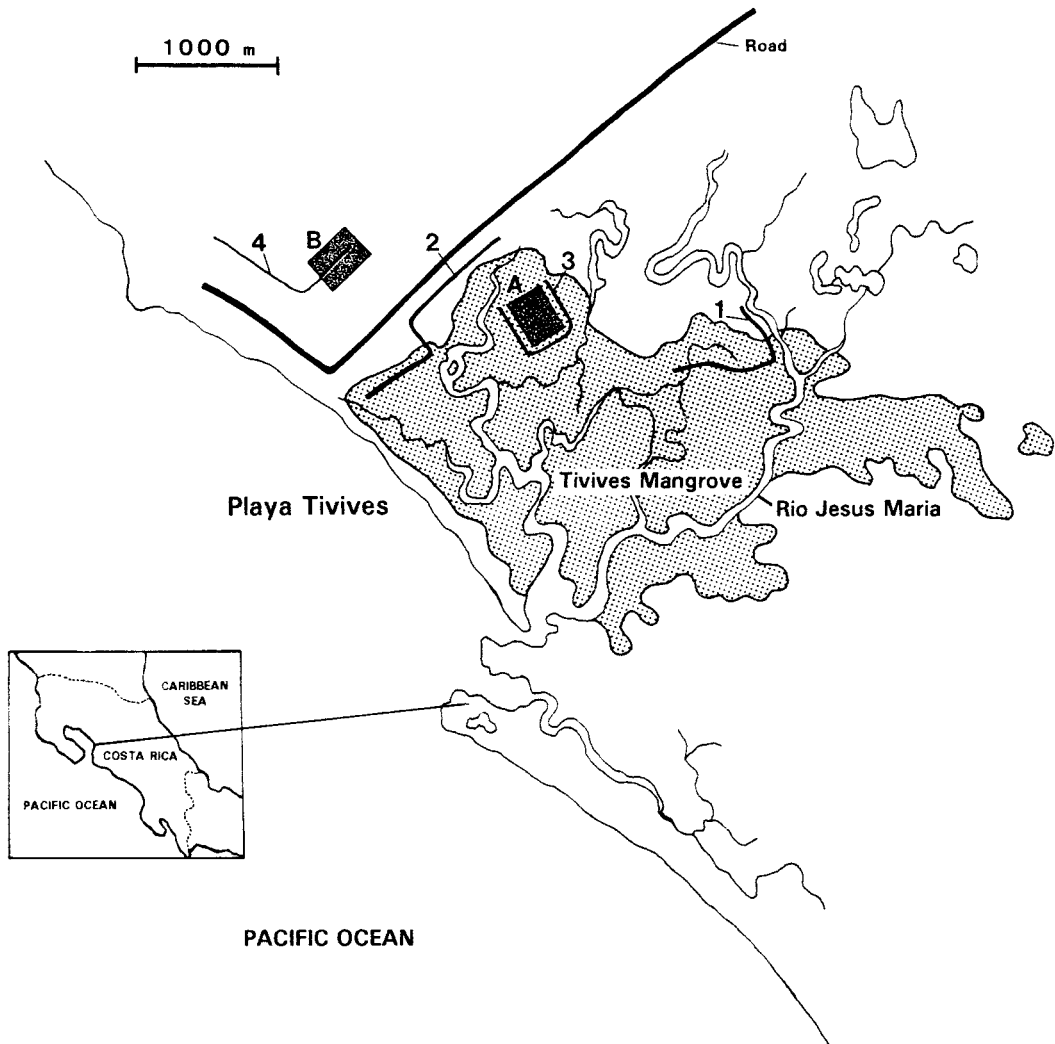


FIG. 1. Map of Tivives mangrove and surroundings showing the two trapping areas (A = Mangrove Trap Area, B = Hillside Trap Area) and four trails used for behavioral observations (1 = Turnaround Road, 2 = Access Road Mangrove, 3 = Trap Area, and 4 = Hillside Trail).

ond-growth forest dominated by guacimo (*Guazuma ulmifolia*), cecropia (*Cecropia peltata*), and poro-poro (*Cochlospermum vitifolium*), creating a canopy 7–10 m high, with emergent Guanacaste trees (*Enterolobium cyclocarpum*) up to 30 m tall.

Four transects (indicated on Fig. 1) were established to make foraging observations of Prothonotary Warblers: (1) Turnaround Road, 250 m along a 5-m wide strip of gallery forest on the river bank flanked by rice fields and cattle pastures, then 750 m running along the northern edge of the mangrove in a 10–50 m wide band of *Avicennia*; (2) Access Road Mangrove, 500 m in a 3–15 m wide band of *Avicennia* on the western edge of the mangrove, then 1000 m of roadway parallel to the western edge of the mangrove at the base of the adjacent hillside; (3) Trap Area, a perimeter trail along mist-net lanes in the 4.8 ha area of *Avicennia* in the northwestern corner of the mangrove with a total length of just over 1000 m; (4) Hillside Trail, 600 m in second-growth forest along net lanes, then 400 m up a ravine with a small permanent creek (1 m wide) which runs perpendicular to the mangrove.

We surveyed the four transects nine times each year with the exception of the Access Road Mangrove and Turnaround Road transects which had eight visits in winter 1991–1992. To reduce the possibility of encountering and recording data for the same individual or flock, each transect was surveyed no more frequently than once every seven days from November through January each year. One transect was completed each day between 05:30 and 10:30 local time by walking slowly along the trails listening for call notes and watching for activity. Progress along the trail was interrupted to observe individual Prothonotary Warblers and flocks of two or more birds that included at least one Prothonotary Warbler. For the purposes of this paper, we followed Powell (1985) who defined flocks as cohesive units that form through contact with other individuals in the group and move together. We considered all individuals within 10 m of one another, which appeared to be joining or following one another (regardless of species), to be members of the flock. Prothonotary Warblers were classed as members of a single-species flock if all potential flockmates were of the same species. Prothonotary Warblers in any flock that included, on the basis of the criteria listed above, individuals of at least one other species were considered to be members of a mixed-species flock.

For each Prothonotary Warbler encountered we recorded age and/or sex, bands and color bands, the number, age and/or sex of associated conspecifics within 10 m of each other, the species and number of other associated birds within 10 m, time, and location. The maximum distance that we followed any individual or flock was approximately 50 m, so the chance that a species “joined” a flock simply by having that flock move into its territory was reduced. We compared the flocking propensity (Hutto 1994) of Prothonotary Warblers between years, as well as the relative proportions of migrants and residents in mixed-species flocks, using χ^2 analyses (all analyses were conducted

using SAS version 6.03 on a Unix platform; SAS Institute Inc. 1988). The number of Prothonotary Warblers in single-species flocks and the number of Prothonotary Warblers and individuals of other species in mixed-species flocks, as well as the number of species in those flocks, were compared between years based on Mann-Whitney *U*-tests where parametric test assumptions were violated. A *t*-test was used to compare the mean number of Prothonotary Warblers in single-species flocks versus mixed-species flocks with data from both years pooled.

Once social context was ascertained, focal observations were made of individual Prothonotary Warblers to characterize and compare general foraging behavior for males and females in each flock type (solitary, single-species flock, and mixed-species flock). This analysis was based on the collection of data for one foraging maneuver for a single male and female in each flock. Circumstances did not always allow for each of these data points to be collected for all flocks encountered because of flock composition or movements. In related research, 164 Prothonotary Warblers were captured at two locations on the study site (see Fig. 1) and individually marked with a combination of colored, plastic leg bands and U.S. Fish and Wildlife Service numbered aluminum leg bands (see Warkentin and Hernández 1995 for details). Although fewer than 8% (42) of the 555 Prothonotary Warblers we encountered during these transects were color banded, we made every effort not to record behavior for the same individual more than once per transect to reduce the potential for producing autocorrelated data (Wagner 1981). To avoid bias for more conspicuous foraging behaviors, such as sallies that might draw attention to a particular individual or type of maneuver, we based our assessment on the first foraging maneuver seen 10 s after beginning observations on the individual. For each focal individual we recorded the following information based on the location of the bird, rather than its potential prey, because only a small percentage of foraging attempts were aerial: (1) height of the foraging bird estimated to the nearest 1 m; (2) canopy height estimated to the nearest 1 m below 10 m and to the nearest 2.5 m above 10 m; (3) perch diameter estimated to be ≤ 0.5 , 1, 2, or 3+ cm; (4) horizontal position in the canopy of the perch tree relative to the trunk was categorized as inner $\frac{1}{3}$, middle $\frac{1}{3}$, or outer $\frac{1}{3}$; (5) foraging substrate was classified as leaf, bark, ground, dead leaf, or air; (6) prey type where visible; and (7) foraging maneuver. We classified foraging maneuvers into three major categories based on the descriptions of Remsen and Robinson (1990). Accuracy of categorization was high as these observations were made from distances of less than 5 m using close-focusing binoculars. All behavioral data were collected by the senior author. Gleans were those near-perch maneuvers where the bird picked prey items from a substrate surface without leaving the perch. Gleaning included reaches, hangs, and lunges as well as foraging from surfaces when no acrobatic movements were required. Probes also were classified as near perch ma-

TABLE 1. Flocking behavior of Prothonotary Warblers during two boreal winters in forested habitats of Tivives, Costa Rica. Values presented include the number of encounters with each type of social grouping plus, where appropriate, the mean number \pm SE and range (all in parentheses) of Prothonotary Warblers seen in single-species and mixed-species flocks, and the mean number of individuals of other species in mixed-species flocks.

	1990–1991	1991–1992
Solitary Prothonotary Warblers	45	27
Single-species flocks	32	28
	(4.5 \pm 0.5, 2–13)	(4.5 \pm 0.6, 2–13)
Mixed-species flocks	24	30
Prothonotary Warblers	(3.7 \pm 0.6, 1–11)	(4.1 \pm 1.0, 1–32)
Other species	(4.1 \pm 0.7, 1–14)	(4.4 \pm 0.6, 1–13)

neuers but entailed an insertion of the bill into a substrate to extract hidden prey items. Sallies were wing-powered aerial maneuvers where the bird flew from a perch to attack the prey and then returned to a perch. Differences in foraging behavior (i.e., foraging maneuver, substrate, perch diameter, and position in the tree) for male and female Prothonotary Warblers in each flock type and between the sexes were compared using χ^2 analyses. Where necessary, cells were collapsed to ensure adequate sample size (following the criteria described by Zar 1996). We examined data on foraging height and foraging height as a function of canopy height using a general linear model (PROC GLM, SAS Institute Inc. 1988). Because of the strong correlation between height of perch and canopy height ($r^2 = 0.68$, $n = 150$, $P < 0.001$), only the analysis of perch height is included.

We also were interested in how rates of behavior might change with the composition or size of the flock. To assess variation in behavior between individuals in groups of different composition (solitary individuals, single-species, or mixed-species flocks) and size (1, 2–5, 6–9, and 10+ individuals), sequential observations were collected from members of the same flocks discussed above and transformed into rates of behavior (observations per 100 s). Observations of a single focal individual were continued as long as possible to a maximum of 10 minutes, although the average length of contact was 96 s. In addition to the data on position and foraging maneuver listed above, we recorded the pace of movement by focal individuals through the habitat (hops and flights of all lengths), preening activity (cleaning feathers, bill wiping, and scratching), social interactions (intra- and interspecific), and vigilance (scanning the environment for potential predators or competitors, which was indicated by positioning the head such that the bird obviously was not looking at near-perch surfaces for prey). Recorded observations were timed during transcription to determine the rates of occurrence for each of these behaviors. We used a general linear model (PROC GLM, SAS Institute Inc. 1988) to analyze log-transformed data (of the variable value itself plus the minimum non-zero value for that variable) for foraging rates (all maneuver types combined), preening, scanning, and movement between

perches. This treatment of the data provided a better distribution pattern than the typical transformations recommended for proportions (e.g., arcsine; Zar 1996).

RESULTS

Flocking behavior.—During the 36 transects completed in the 1990–1991 season, we encountered 279 Prothonotary Warblers; 34 transect visits in the 1991–1992 season resulted in the sighting of 276 Prothonotary Warblers. These encounters included sighting solitary individuals, as well as birds in single-species flocks, and mixed-species flocks (Table 1). The propensity for Prothonotary Warblers to join flocks varied between years with 83.9% (234) of 279 individuals seen participating in flocks during the 1990–1991 season and 90.2% (249) of 276 individuals seen in flocks during the 1991–1992 season ($\chi^2 = 4.396$, $df = 1$, $P < 0.05$). However, there were no significant differences between years in the median number of Prothonotary Warblers found in single-species flocks and mixed-species flocks, or the median number of individuals of other species in mixed-species flocks (Mann-Whitney U -tests: respectively, $U = 462.5$, $U = 389$, $U = 384$; $P > 0.05$ in all cases; see Table 1 for sample sizes). Nor was there a significant difference between the mean number of Prothonotary Warblers in single-species flocks (mean \pm SE reported throughout: 4.5 \pm 0.4, $n = 60$) and mixed-species flocks (3.9 \pm 0.6, $n = 54$) when both years were combined (t -test: $t = 0.813$, $df = 112$, $P > 0.05$). There were no significant differences between years in the number of species involved in mixed-species flocks (1990–1991: 3.9 \pm 0.4 species, 1991–1992: 3.2 \pm 0.2 species; $U = 442.0$, $P > 0.05$).

The list of species observed with Prothonotary Warblers in the 54 mixed-species flocks seen over both years contains 11 migrants and 15 residents (Table 2) with an average of 3.5 species per mixed-species flock (range: 2–8 species). Tennessee Warblers (*Vermivora peregrina*) were the most common other member of mixed-species flocks containing Prothonotary Warblers and made up 40% (92) of 230 individuals in 31 of these mixed-species flocks. Overall in mixed-species flocks containing at least one Prothonotary Warbler, migrants outnumbered residents by about 5 to 3 (144 versus 86).

Foraging behavior.—Based on observations of 57 females and 93 males made during the transects in both years, foraging maneuver was independent of flock type for both females ($\chi^2 = 1.57$, $df = 4$, $P > 0.05$; Fig. 2a) and males ($\chi^2 = 2.82$, $df = 4$, $P > 0.05$; Fig. 2b). The proportional use of foraging maneuvers, pooled across flocking types, was not significantly different between females and males ($\chi^2 = 2.57$, $df = 2$, $P > 0.05$). Likewise, foraging substrate was independent of flock type for females ($\chi^2 = 6.99$, $df = 4$, $P > 0.05$; collapsed to leaf, bark and others because of sample size; Fig. 3a) and males ($\chi^2 = 4.33$, $df = 6$, $P > 0.05$; based on leaf, dead leaf, bark, and others; Fig. 3b), with no significant difference between females and males in substrate use pooled across flock types ($\chi^2 = 6.23$, $df = 3$, $P > 0.05$; based on leaf, dead leaf, bark, and other) in their use of foraging substrates. In general, gleaning made up 70% (105) of 150 prey capture attempts by females and males, with about half of all attempts (76 of 150) directed towards leaf surfaces. Of the 150 foraging events observed, only 2 were directed towards non-arthropod targets, one involved eating berries and the second taking nectar.

Data on the location of these foraging individuals within the canopy or tree also suggest no differences on the basis of social structure or sex. Perch diameter was independent of flock type among females ($\chi^2 = 0.48$, $df = 4$, $P > 0.05$; collapsed to ≤ 0.5 , 1 and 2+ cm because of sample size; Fig. 4a) and males ($\chi^2 = 9.64$, $df = 6$, $P > 0.05$; Fig. 4b), with no association between sex and perch diameter pooled across flock types ($\chi^2 = 3.65$, $df = 3$, $P > 0.05$). Similar results were ob-

tained when we examined the association between position in the canopy and flock type (females: $\chi^2 = 4.51$, $df = 4$, $P > 0.05$, Fig. 5a; males: $\chi^2 = 6.87$, $df = 4$, $P > 0.05$, Fig. 5b; sex vs perch position: $\chi^2 = 1.85$, $df = 2$, $P > 0.05$). Likewise, perch height was not influenced by either sex or flock type (GLM: $F_{3,144} = 0.35$, $P > 0.05$). In general, most observed perches were in the outer third of the tree (116 of 150), primarily on branches smaller than 1 cm diameter (89 of 150), frequently in the bottom half of the canopy (mean of perch height/canopy height = 0.33), and averaged 3.0 ± 0.2 m above ground (range: ground to 10 m with 66% of observations 3 m or lower).

With the exception of female scanning behavior, for which flock type was a useful predictor of scan rate (GLM: $F_{1,71} = 4.86$, $P < 0.05$), flock type and flock size had no influence on rates of behavior (scanning, foraging maneuver, movement, and preening events per minute) during foraging, as we measured it (Tables 3, 4). There were no significant interaction effects between flock type and size for any of the variables examined. Agonistic interactions (supplanting from perches or chasing) between members of flocks were not common. Of the 7 occasions when such interactions were observed, 5 involved Prothonotary Warblers in mixed-species flocks (2 intraspecific interactions and 3 interspecific interactions) and the other 2 were in single-species flocks (extended chases by adult males of an adult male in one case and an adult female in the other). These rates of occurrence were not significantly different ($\chi^2 = 0.85$, $df = 1$, $P > 0.05$).

DISCUSSION

Knowledge of Prothonotary Warbler ecology on its nonbreeding grounds is limited. Although several studies have provided information of a largely qualitative nature on foraging (e.g., Post 1978, Hespeneide 1980, Morton 1980), detailed quantitative data on flocking and foraging behavior for wintering Prothonotary Warblers are only available from one study in Venezuela (Lefebvre et al. 1992, 1994). In addition, this species is of interest as one of a group of migrant (both Nearctic and Neotropical) and resident birds dependent upon mangrove habitats in Latin America

TABLE 2. The number of mixed-species flocks containing Prothonotary Warblers observed in forested habitats of Tivives, Costa Rica, and the number of occasions on which each of the other species listed below was recorded in those flocks.

Species	Co-occurring species																											
	n	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	27	
1 <i>Protonotaria citrea</i>	54	31	13	12	11	7	6	6	5	5	4	3	3	3	3	3	2	2	2	2	1	1	1	1	1	1	1	1
2 <i>Vermivora peregrina</i>	31		7	6	5	5	4	2	3	2	4	1	1	1	3	2	2	1	2	2	1	1	0	0	1	1	0	0
3 <i>Dendroica petechia erithachoroides</i>	13			0	0	3	2	4	1	3	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0
4 <i>Polioptila albilorus</i>	12				0	0	0	0	2	0	4	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0
5 <i>Setophaga ruticilla</i>	11					1	3	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 <i>Lepidocolaptes soutleyetti</i>	7						1	1	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	0	1
7 <i>Mniotilta varia</i>	6							1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
8 <i>Seiurus noveboracensis</i>	6							0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
9 <i>Dendroica petechia</i>	5							1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
10 <i>Todirostrum cinereum</i>	5							0	0	0	0	0	0	2	2	0	0	1	2	0	0	0	0	0	0	0	0	0
11 <i>Icterus galbula</i>	4									0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
12 <i>Vireo flavifrons</i>	3										0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	
13 <i>Tityra inquisitor</i>	3												0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
14 <i>Thryothorus pleurostictus</i>	3													0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15 <i>Pachyrhamphus aglaiae</i>	3														1	0	0	2	2	1	0	0	0	0	0	0	0	0
16 <i>Vermivora pinus</i>	3																0	0	1	2	0	0	0	0	0	0	0	0
17 <i>Piranga rubra</i>	2																	0	0	0	0	0	0	0	0	0	0	0
18 <i>Helmintheros vermivorus</i>	2																	0	0	0	0	0	0	0	0	0	0	0
19 <i>Hylophilus decurtatus</i>	2																		0	0	0	0	0	0	0	0	0	0
20 <i>Sittasomus griseicapillus</i>	2																			2	0	0	0	0	0	0	0	0
21 <i>Euphonia luteicapilla</i>	2																				0	0	0	0	0	0	0	0
22 <i>Arremonops rufivirgatus</i>	1																				0	0	0	0	0	0	0	0
23 <i>Tolmomyias sulphurescens</i>	1																					0	0	0	0	0	0	0
24 <i>Trogon melanocephalus</i>	1																						0	0	0	0	0	0
25 <i>Seiurus auricapillus</i>	1																							1	0	0	0	0
26 <i>Dendrocolaptes certhia</i>	1																								0	0	0	0
27 <i>Troglodytes aedon</i>	1																									0	0	0

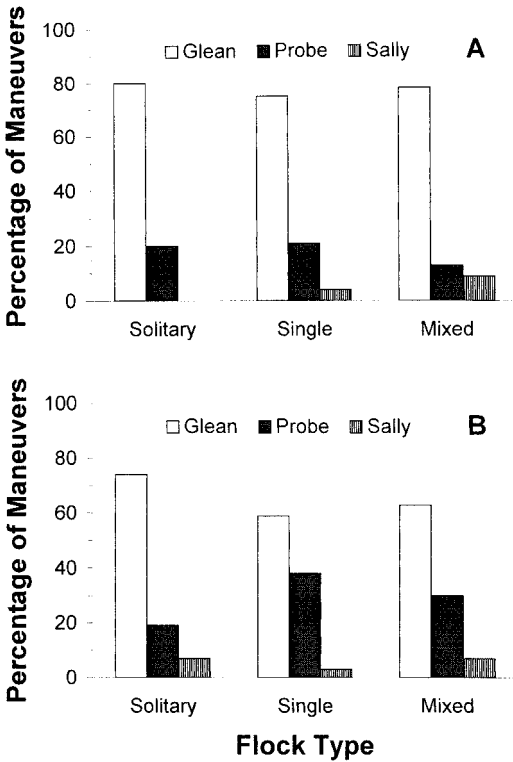


FIG. 2. Foraging maneuvers by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 24$, mixed-species flocks (Mixed) $n = 23$] and (B) males (Solitary $n = 31$, Single $n = 32$, Mixed $n = 30$).

(French 1966, Hutto 1980, Russell 1980, Lynch 1989, Styles and Skutch 1989, Lefebvre et al. 1992, Warkentin and Hernández 1995). Such species face an uncertain future as mangrove forests continue to be degraded or lost through timber harvest, coastal development and pollution, and the expanding aquaculture industry (Leonard 1987, Terborgh 1989, Olson et al. 1996).

A large proportion of the Prothonotary Warblers we encountered during this study moved in flocks and almost half of the birds seen over both years were in single-species flocks (Table 1). The tendency for this species to form single-species flocks during winter has been noted previously on a qualitative basis for Panama (Hespenheide 1980, Morton 1980). However, Post (1978) never observed single-species Prothonotary Warbler flocks in a limited sample from Puerto Rico, nor did Lefebvre and coworkers (1994) during their

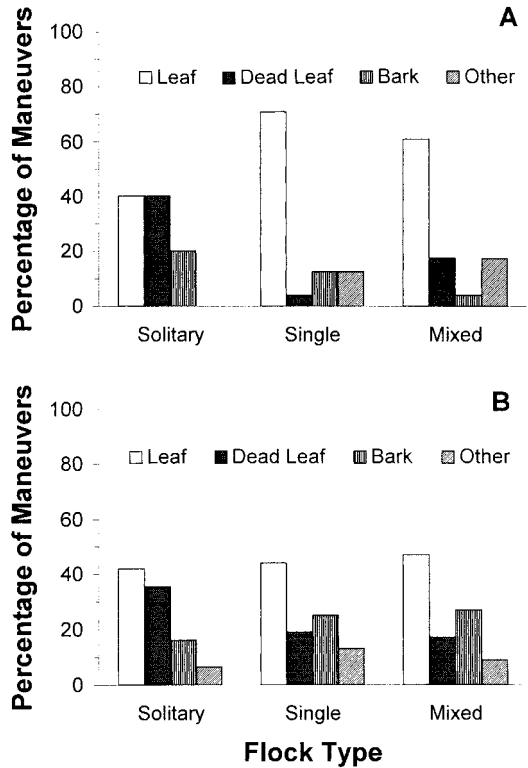


FIG. 3. Foraging substrate use by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 24$, mixed-species flocks (Mixed) $n = 23$] and (B) males (Solitary $n = 31$, Single $n = 32$, Mixed $n = 30$). Other category includes soil surfaces, aerial sallys, nectar sources and fruit.

more extensive work in Venezuelan mangroves. In both cases, Prothonotary Warblers were seen foraging only in mixed-species flocks or alone (Post 1978, Lefebvre et al. 1994). The propensity for Prothonotary Warblers in this study to join flocks increased from winter 1990–1991 to winter 1991–1992. But each of the three social groupings was well represented in both years, and within flock types (mixed-species flock and single-species flock) there were no significant differences between years in the sizes of the flocks or the average number of member species in mixed-species groups.

Hutto (1994) suggested that insectivorous mixed-species flocks in western Mexico are often chance associations whose membership can be predicted on the basis of species abundance in the area. Across the Neotropics, mi-

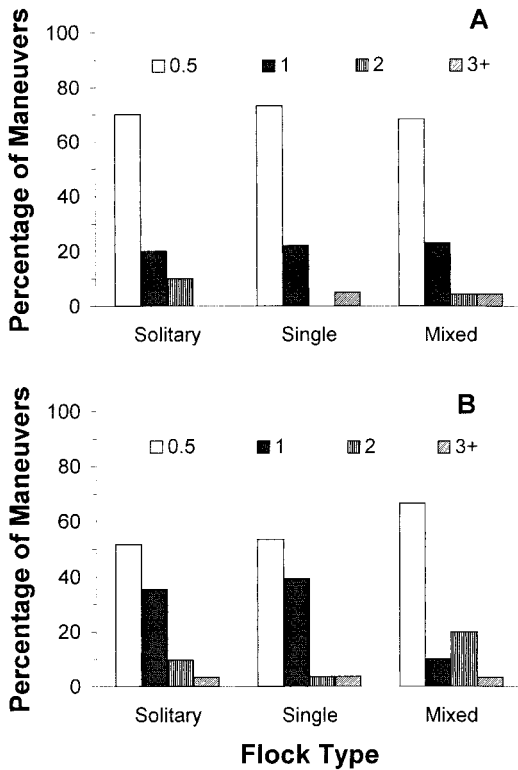


FIG. 4. Foraging perch diameter by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 22$, mixed-species flocks (Mixed) $n = 22$] and (B) males (Solitary $n = 31$, Single $n = 28$, Mixed $n = 30$). Diameter categories are in cm.

grants often take part in these mixed-species flocks but typically constitute only a minor component (Powell 1985). An exception to this is within mangrove forest where migrants are more numerous than residents when compared with the surrounding habitats (Hutto 1980, Lynch 1989), and numerically dominate mixed-species flocks (this study). Among

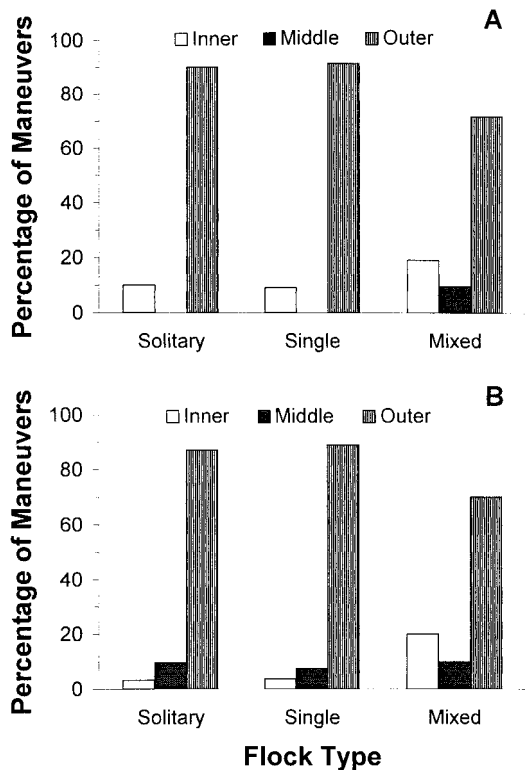


FIG. 5. Foraging location within the canopy by flock type for (A) females [Solitary $n = 10$, single-species flocks (Single) $n = 22$, mixed-species flocks (Mixed) $n = 21$] and (B) males (Solitary $n = 31$, Single $n = 27$, Mixed $n = 30$). Canopy positions were inner $\frac{1}{3}$, middle $\frac{1}{3}$, and outer $\frac{1}{3}$.

mixed-species flocks at Tivives containing at least one Prothonotary Warbler, the most consistent flockmate for Prothonotary Warblers was the Tennessee Warbler (Table 2). The dominance of migrants, such as Prothonotary and Tennessee warblers, in these flocks may simply reflect the high percentage of Nearctic

TABLE 3. Rates (mean \pm SE per 100 s) of scanning, foraging, moves between perches, and preening by Prothonotary Warblers in single-species flocks (Single), mixed-species flock (Mixed), or foraging alone (Alone) in forested habitats of Tivives, Costa Rica during two boreal winters.

Sex	Flock	n	Scan	Forage	Move	Preen
Male	Alone	32	1.8 \pm 0.4	7.1 \pm 1.1	15.3 \pm 1.7	2.2 \pm 1.0
	Single	40	1.5 \pm 0.4	6.1 \pm 0.8	14.9 \pm 1.3	1.3 \pm 0.5
	Mixed	35	1.4 \pm 0.5	5.9 \pm 0.9	14.3 \pm 0.9	2.0 \pm 0.7
Female	Alone	8	2.7 \pm 1.2	8.0 \pm 1.7	13.6 \pm 2.3	2.0 \pm 2.0
	Single	43	1.4 \pm 0.4	4.8 \pm 0.7	16.0 \pm 0.9	2.0 \pm 0.7
	Mixed	25	0.4 \pm 0.3	8.9 \pm 2.0	16.0 \pm 1.7	0.5 \pm 0.2

TABLE 4. Rates (mean \pm SE per 100 s) of scanning, foraging, moves between perches, and preening by Prothonotary Warblers for flocks of varying sizes in forested habitats of Tivivies, Costa Rica during two boreal winters.

Sex	Flock size	<i>n</i>	Scan	Forage	Move	Preen
Male	1	32	1.8 \pm 0.4	7.1 \pm 1.1	15.3 \pm 1.7	2.2 \pm 1.0
	2–5	52	1.2 \pm 0.3	5.5 \pm 0.6	15.4 \pm 1.0	1.6 \pm 0.5
	6–9	16	1.8 \pm 0.6	7.5 \pm 1.6	13.6 \pm 1.2	1.3 \pm 0.7
	10+	7	2.3 \pm 2.0	6.8 \pm 2.0	11.2 \pm 2.5	2.4 \pm 1.8
Female	1	8	2.7 \pm 1.2	8.0 \pm 1.7	13.6 \pm 2.3	2.0 \pm 2.0
	2–5	35	0.8 \pm 0.2	6.3 \pm 1.0	16.2 \pm 1.2	0.5 \pm 0.2
	6–9	20	1.4 \pm 0.7	4.7 \pm 1.7	15.2 \pm 1.3	2.8 \pm 1.1
	10+	13	1.1 \pm 0.6	9.1 \pm 2.5	16.8 \pm 2.3	1.9 \pm 1.1

migrants that occupy this mangrove forest during the boreal winter (Warkentin and Hernández 1995). Prothonotary Warblers constituted 30% (216) of the 708 migrants captured at Tivivies during mist-netting over two winters (Warkentin and Hernández 1995), and the only other species caught in large numbers were Mangrove Warblers (*Dendroica petechia erithachorides*) and Northern Waterthrush (*Seiurus noveboracensis*); both of which are territorial and unlikely to join a foraging flock (Schwartz 1964, Wiedenfeld 1992). Thus chance associations may explain not only the high percentage of migrants in the mixed-species flocks of mangroves, but also the large proportion of single-species Prothonotary Warbler flocks we encountered at this site. Overall, there were few other migrants or residents for Prothonotary Warblers to join with that foraged in a similar niche.

Joining a mixed-species flock has been suggested to have costs in terms of a reduced foraging niche (Powell 1985), changes in foraging behavior (Valburg 1992, Latta and Wunderle 1996), or convergence among members on the foraging behavior of the nuclear species (Morse 1970, Valburg 1992; but only Buskirk 1972, cited from Powell 1985, recorded convergence of foraging maneuvers by insectivores). Given our limited sample size for some of these comparisons, we may not have been able to detect subtle changes in behavior between individuals foraging alone, in single-species flocks, or in mixed-species flocks. But neither were there any substantive changes evident in our comparisons of maneuver type (Fig. 2), foraging substrate (Fig. 3), perch diameter (Fig. 4) and position (Fig. 5), or rates of movement and preening (Tables

3, 4) that could be related to flock composition or size. Even vigilance and foraging rates, two elements hypothesized to change in response to foraging context (Morse 1977, Powell 1985), were largely unaffected by flock composition or size, with the notable exception that females were less vigilant in mixed-species flocks.

Increased intra- and interspecific competition and reduced risk of predation are two factors that individuals must balance in assessing the relative costs and benefits of flock membership. We found that the average number of Prothonotary Warblers in single-species flocks and mixed-species flocks was not significantly different (respectively, 4.5 and 3.9; Table 1). In terms of competition, this suggests that intraspecific competition among Prothonotary Warblers would remain consistent for individuals pursuing either flocking strategy, but those who join mixed-species flocks face the added interspecific competition of mixed-species flocks from an average 4.2 other individuals (Table 1). In contrast to reports that indicate that aggressive interactions are a common feature of mixed-species flock foraging (Morse 1970, Munn and Terborgh 1979, Powell 1985), we rarely observed such encounters. A limited sample of seven observations, based on 54 mixed-species flocks with 2 intraspecific interactions and 3 interspecific interactions versus 60 single-species flocks with 2 intraspecific interactions, makes it difficult to detect broad tendencies, but we found no significant increase in agonistic encounters for Prothonotary Warblers in mixed-species flocks. Although we did not examine food availability, it could be that the relatively moist conditions present in the mangrove over

the winter supported sufficiently large arthropod populations so that food was not limiting. In terms of predation risk, all individuals in a mixed-species flock should benefit from auditory predator warnings regardless of species (Hutto 1994), and thus the larger mixed-species flocks we observed should be afforded greater predator protection. Yet mixed-species flocks were not the most common foraging association involving Prothonotary Warblers that we encountered. Perhaps predation is not a strong selective pressure in the region. Although Ferruginous Pigmy-Owls (*Glaucidium brasilianum*), Sharp-shinned Hawks (*Accipiter striatus*), and Peregrine Falcons (*Falco peregrinus*) were seen at Tivives, we have no detailed data on the survivorship of wintering warblers at this site.

To fully understand the factors influencing foraging decisions for the Prothonotary Warbler and other species that may forage alone, in single-species flocks, or in mixed-species flocks, more detailed studies of marked individuals foraging in each of these three situations are needed. Although we color-marked Prothonotary Warblers, we were unable to collect any significant amount of foraging data for the same individual in different flocking situations. Such data would be invaluable in assessing more effectively the impact which flock composition and size have upon foraging behavior.

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