The Condor 100:44–53

WINTER PARTICIPATION BY NEOTROPICAL MIGRANT AND RESIDENT BIRDS IN MIXED-SPECIES FLOCKS IN NORTHEASTERN MEXICO[1]

WENDY K. GRAM[2]
Division of Biological Sciences, 110 Tucker Hall, University of Missouri–Columbia, Columbia, MO 65211

Abstract. Mixed-species foraging flocks in northeastern Mexico are large, diverse, and include Neotropical migrant and resident species. I characterized the species composition and social organization of mixed-species flocks in four habitats of the El Cielo Biosphere Reserve during the winters of 1993–1995. Thirty-seven percent of all species found in the Reserve participated in mixed-species flocks, including 16 migrant species. Flocks in the dry pine-oak forest had more migrant individuals than flocks in the humid oak-pine/cloud forest or tropical semi-deciduous forest, but flocks in the tropical semi-deciduous forest had more migrant species than resident species. Migrant species rarely have been reported as nuclear species that attract other species to the flock and maintain flock cohesion, yet both Ruby-crowned Kinglet (*Regulus calendula*) in the dry pine-oak forest, and Blue-gray Gnatcatcher (*Polioptila caerulea*) in the tropical semi-deciduous forest, are migrant species that behaved as nuclear flock species. Bridled Titmouse (*Parus wollweberi*) and Crescent-chested Warbler (*Vermivora superciliosa*), Mexican resident species, were nuclear species in the dry pine-oak forest and the humid oak-pine/cloud forest, respectively. I found that Ruby-crowned Kinglet and Crescent-chested Warbler were follower species (species that occurred regularly in flocks but did not behave as nuclear species) in habitats where they were not nuclear species, indicating that the social role of a species within a flock may depend on habitat, resource availability, species density, or the other species present in the mixed-species flock.

Key words: mixed-species flock, Neotropical migrant, Mexico, nonbreeding season, nuclear species, follower species.

Resumen. Las parvadas forrajeras de especies mixtas, que se presentan en el noreste de México son grandes y diversas, e incluyen especies residentes y migratorias neotropicales. Las parvadas de especies mixtas presentes en cuatro habitats diferentes en la Reserva de la Biosfera "El Cielo" fueron estudiadas para determinar su composición específica y su organización social, durante los inviernos de 1993 a 1995. El 37% de todas las especies encontradas en la Reserva forman parte de las parvadas de especies mixtas, incluyendo 16 especies migratorias. Las parvadas en el bosque seco de pino-encino presentaron mayor número de individuos migratorios que las parvadas del bosque húmedo de encino-pino, del bosque mesófilo de montaña o el bosque tropical subcaducifolio, sin embargo las parvadas de este último habitat tuvieron más especies migratorias que residentes. Las especies migratorias han sido raramente reportadas como especies núcleo de las parvadas. El Reyezuelo Sencillo (*Regulus calendula*), en bosque seco de pino-encino, y la Perlita Grisilla (*Polioptila caerulea*), en bosque tropical subcaducifolio, son especies migratorias que se comportan como líderes de las parvadas. El Paro Embridado (*Parus wollweberi*) y el Chipe Cejiblanco (*Vermivora superciliosa*), son especies mexicanas residentes que se comportan como especies núcleo en el bosque seco de pino-encino y en el bosque húmedo de pino-encino/bosque mesófilo de montaña respectivamente. Se encontró que el Reyezuelo Sencillo y el Chipe Cejiblanco se comportaron como especies seguidoras, es decir que son especies que regularmente se presentan en las parvadas pero no se comportan como especies núcleo, en habitats donde no eran especies núcleo, indicando que el papel social de una especie dentro de una parvada puede depender del tipo de habitat, la disponibilidad de recursos, la densidad de la especie, o de otras especies presentes en las parvadas de especies mixtas.

Palabras clave: Parvadas de especies mixtas, migratoria neotropical, M(e)xico, Temporada de no anidación, especies núcleo, especies seguidoras.

---

[1] Received 21 October 1996. Accepted 11 August 1997.

[2] Current address: Department of Biology, University of Missouri - St. Louis, 8001 Natural Bridge Rd., St. Louis, MO 63121, e-mail: wgram@umslvma.umsl.edu

INTRODUCTION

Mixed-species flocks commonly occur in the Neotropics during the nonbreeding season (Powell 1985), but the composition and structure of these flocks vary widely among different regions and habitats. Studies of marked flock members in permanent understory flocks reveal the complex social structure and cohesion possible in heterospecific groups, with some species defending common territories against conspecifics in neighboring flocks in Peru (Munn and Terborgh 1979). Other permanent flocks in Costa Rica have a consistent species composition but include a variety of individuals of each species at different times, depending upon the location of the flock relative to territory boundaries (Powell 1979, Munn 1985). Permanent mixed-species flocks mostly consist of resident species that defend territories and participate in the same flocks throughout the year, although time spent with the flock varies between breeding and nonbreeding seasons. Most members of these permanent, highly organized flocks are insectivores; frugivores tend to form larger, less stable aggregations that are centered around an abundant resource (Powell 1985). In the West Indies and Mexico, flocks consist of both migrant and resident species (Hutto 1987, Ewert and Askins 1991, Latta and Wunderle 1996), but the flocks are not as tightly organized as the permanent mixed-species flocks found in Central and South America.

Although mixed-species flocks are variable in occurrence, composition, and organization in different geographical areas, flocks that remain together usually have one or more nuclear species that act to attract other species to the flock and maintain flock cohesion. Typically, mixed-species flocks have a subset of species that are regular flock members, or core species. The core species are present in most flocks as nuclear or follower species (Buskirk et al. 1972, Munn and Terborgh 1979, Powell 1979). Other species occasionally are seen in flocks and may join flocks only under certain circumstances such as flock presence in a territory; these species are joiner species.

Most flocking species remain nuclear, follower, or joiner species in mixed-species flocks regardless of habitat or geographical area (Munn and Terborgh 1979, Powell 1985). In a classic study of mixed-species flocks in the northeastern United States, Morse (1970) found only one case of a species, the Black-capped Chickadee (*Parus atricapillus*), occupying a different social role within flocks among different geographical areas. Black-capped Chickadees became a "secondary leader" in Maryland because they often followed Tufted Titmouse (*Parus bicolor*), a "true leader," whereas Black-capped Chickadees in Louisiana were classified as "true leaders" with Tufted Titmouse.

To better understand why some species forage in mixed-species flocks and the influence of flock composition on the social roles of species within a flock, I initiated a large-scale study of mixed-species flocks in three habitats in the El Cielo Biosphere Reserve in northeastern Mexico. Within one geographical area, the distribution of migrant and resident species varies among habitats (Gram and Faaborg 1997), providing an opportunity to compare flock size, composition, and the social role of each species within a flock among habitat types. Specifically, I addressed the following questions: (1) Does the size and composition of mixed-species flocks differ among the habitats in the El Cielo Biosphere Reserve, and, if so, why? and (2) Does a species occupy the same social role in mixed-species flocks in different habitats?

METHODS

STUDY AREA

I studied mixed-species flocks in tropical semideciduous forest, humid oak-pine/cloud forest, and dry pine-oak forest in the El Cielo Biosphere Reserve, located in Tamaulipas, Mexico (23°15′N, 99°50′W), along the slopes of the Sierra Madre Oriental mountain range (see Gram and Faaborg 1997 for a detailed description of the study sites). Although I independently collected data on flocks in humid oak-pine forest and cloud forest, I combined data from flocks at these two habitats because the flocks were not different in composition, the habitats were structurally very similar (Gram 1996), and the rough terrain in both habitats prevented large sample sizes from either habitat.

FLOCK COMPOSITION

I studied flocks from December 1993 to February 1994, and during February 1995 in the four primary habitats in El Cielo. Flocks were located by walking a transect through the forest. When a bird was detected, I and my field assistants recorded the social context (alone, species pair, monospecific flock, mixed-species flock) and foraging behavior of each bird. A mixed-species flock was defined as two or more birds of more than one species within 10 m of each other and moving together in the same general direction. Once a mixed-species flock was found, we followed it until we lost the flock, or we collected foraging data on all of the individuals, approximated from the total number of foraging observations per species and the number of individuals per species. Composition of the flock was determined from participant lists, including the species and number of each species present, that we generated every 15 min while following a flock. We kept qualitative notes on species that remained with the flock for short periods of time or appeared to move independently of the flock. On average, we followed flocks for 2–3 hr in the dry pine-oak forest, where there was high visibility, and for 30 min to 2 hr at all other sites where the vegetation and topography limited continuous observation. Although birds in the flocks were not marked, we mapped the flock location as we followed it and we did not collect foraging data from the same areas more than once each winter.

To compare the composition of mixed-species flocks among tropical semi-deciduous forest, humid oak-pine and cloud forest combined, and dry pine-oak forest, I calculated the mean number of species and individuals for each flock from the participant lists. The grand mean numbers of species and individuals per flock for each habitat were then calculated from the flock means. To test for differences among habitats, I compared species and individual means among the three habitat types with analysis of variance (ANOVA) and Duncan's multiple range test, after log-transforming the data to equalize variances. I also compared migrant and resident participation in mixed-species flocks to the overall distribution of individuals and species in each habitat as determined from point-count surveys (see Gram and Faaborg 1997) to evaluate whether flocks were a random assortment of the birds at a site.

SOCIAL ROLES WITHIN THE FLOCK

The role of a species in a flock was determined quantitatively by whether it was intraspecifically gregarious, and its regularity of occurrence, and qualitatively by whether it was followed by other species more often than it followed others, the presence of conspicuous plumage or behavior, and its tendency to remain with and follow a flock continuously. A nuclear species was defined as a species that was intraspecifically gregarious (mean number of individuals per flock > 3; Winterbottom 1943, Greig-Smith 1978), was a regular flock participant (present in $> 50\%$ of flocks; McClure 1967), was followed more often than it followed others (Munn and Terborgh 1979), displayed a conspicuous plumage or behavior (Chipley 1977), and remained with the flock continuously. A follower species was defined as a species that averaged less than three individuals per flock, was a regular flock participant, followed more than it was followed, and remained with the flock continuously (similar to Type I–III core species of Munn and Terborgh 1979). A joiner species was one that did not stay with the flock continuously and was not a regular flock participant (similar to Type IV–V core species of Munn and Terborgh 1979); many of the joiner species appeared to join flocks only when the flock passed through their territory or foraging area.

To determine if species were intraspecifically gregarious, I compared the mean number of individuals of each species per flock among the three habitat types with ANOVA, after log-transforming the data to equalize variances. I also calculated the proportion of flocks in which each species was present in each habitat as a measure of regularity of occurrence (Hutto 1994).

RESULTS

FLOCK COMPOSITION

I detected 66 species (37% of all species seen in the Reserve) participating in mixed-species flocks, including 16 migrant species (39% of all migrants in the Reserve; Gram and Faaborg 1997). The mean number of species and individuals per flock among the three habitats varied significantly; the dry pine-oak forest and humid oak-pine/cloud forest had the greatest number of species per flock, and dry pine-oak forest had the most individuals per flock (Table 1). The mean number of species per flock and individuals per flock were highly correlated (Pearson's $r = 0.83$, $n = 89$, $P < 0.001$).

TABLE 1. Summary of Neotropical migrant and Mexican resident participation in n flocks in El Cielo.

Variable	Tropical semi-deciduous forest $n = 23$	Humid oak-pine/cloud forests $n = 24$	Dry pine-oak forest $n = 42$	F
Mean (± SE) number species per flock	6.48 ± 0.54	9.33 ± 1.03	9.93 ± 0.64	5.5*
migrant species	4.17 ± 0.31	4.29 ± 0.39	4.33 ± 0.31	0.1
resident species	3.12 ± 0.40	5.04 ± 0.72	5.60 ± 0.45	4.4*
Mean (± SE) number individuals per flock	10.65 ± 1.38	19.29 ± 2.09	25.90 ± 2.25	12.4**
migrant individuals	7.00 ± 0.80	6.17 ± 0.65	14.62 ± 1.57	12.9**
resident individuals	4.94 ± 0.91	13.13 ± 1.70	11.23 ± 0.89	9.0**

* $P < 0.01$, ** $P < 0.001$. All comparisons based on ANOVA tests.

Migrants averaged 4.26 species per flock across all habitats with no significant differences in species richness among habitats, whereas residents averaged significantly fewer species per flock in tropical semi-deciduous forest than in dry pine-oak forest or humid oak-pine/cloud forest (Table 1). The mean number of resident species per flock was significantly different than the mean number of migrant species per flock in the tropical semi-deciduous forest ($t_{38} = 2.13$, $P < 0.05$) and the dry pine-oak forest ($t_{73} = 2.32$, $P < 0.05$); we found more resident species in the dry pine-oak forest and more migrant species in the tropical semi-deciduous forest. Conversely, Gram and Faaborg (1997) reported more migrant species in the dry pine-oak forest and more resident species in the tropical semi-deciduous forest when evaluating the general distribution of species (not limited to flocks) in these habitats.

The dry pine-oak forest had significantly more migrant individuals per flock than flocks in the tropical semi-deciduous forest or humid oak-pine/cloud forest, and the tropical semi-deciduous forest had significantly fewer resident individuals per flock than the dry pine-oak forest or humid oak-pine/cloud forest (Table 1). The number of migrant individuals per flock did not differ significantly from the number of resident individuals per flock in the dry pine-oak forest ($t_{82} = 1.84$, $P < 0.10$) and tropical semi-deciduous forest ($t_{44} = 1.83$, $P < 0.10$); the general distributional data indicated that the abundances of migrant and resident individuals differed at these sites (Gram 1996). We detected significantly more resident individuals per flock in the humid oak-pine/cloud forest than migrant individuals ($t_{46} = 3.82$, $P < 0.001$), depicting the same pattern as the general abundance and distributional data for humid oak-pine/cloud forest.

SOCIAL ROLES WITHIN THE FLOCK

I used the regularity of occurrence in flocks and the mean number of individuals per flock (Table 2), in combination with the qualitative criteria, to evaluate the role of a species in a flock. Most core species were seen in at least 50% of the flocks in one habitat, except for Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*), Orange-crowned Warbler (*Vermivora celata*), Nashville Warbler (*V. ruficapilla*), Olive Warbler (*Peucedramus taeniatus*), and Hepatic Tanager (*Piranga flava*); these species only were detected in small numbers in the Reserve, which may explain their absence from many flocks. It is possible that Ivory-billed Woodcreeper and Hepatic Tanager are joiner species, but I have classified them as core follower species because their flocking propensity indices (proportion of total independent observations from point counts that a species was seen in a mixed-species flock) were 0.56 and 0.62, respectively (Gram 1996).

The mean number of individuals of a species per flock varied among habitats for ten core species, including four migrant species (Table 2). Ruby-crowned Kinglet (*Regulus calendula*) in the dry pine-oak forest averaged the greatest number of individuals per flock for all species; Crescent-chested Warbler (*Vermivora superciliosa*) was the most abundant species per flock in the humid oak-pine/cloud forest and Blue-gray Gnatcatcher (*Polioptila caerulea*) was the most abundant species per flock in the tropical semi-deciduous forest. Solitary Vireo (*Vireo solitarius*), Black-and-white Warbler (*Mniotilta varia*), and Spot-crowned Woodcreeper (*Lepidocolaptes affinis*) exhibited the most consistency among habitats, averaging 0.78, 0.58, and 1.15 individuals per flock, respectively (Table 2). The mean number of species in the flocks

TABLE 2. The mean (± SD) number of individuals per flock and percent of n flocks in which each core species participated (regularity of occurrence). Core species include follower and nuclear species as defined in the text.

Species		Mean number of individuals per flock				Regularity of occurrence		
		Tropical semi-deciduous forest $n = 23$	Humid oak-pine/ cloud forests $n = 24$	Dry pine-oak forest $n = 42$	F	Tropical semi-deciduous forest $n = 23$	Humid oak-pine/cloud forests $n = 24$	Dry pine-oak forest $n = 42$
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	0.04 ± 0.21	0.88 ± 0.95	0.02 ± 0.15	23.6**	4%	50%	2%
Ivory-billed Woodcreeper	*Xiphorhynchus flavigaster*	0.13 ± 0.34	0.50 ± 0.88	0.05 ± 0.22	5.1*		25%	5%
Spot-crowned Woodcreeper	*Lepidocolaptes affinis*		1.13 ± 0.95	1.17 ± 0.94	0.1		63%	67%
Bridled titmouse	*Parus wollweberi*			3.95 ± 2.58				83%
Ruby-crowned Kinglet•	*Regulus calendula*	0.96 ± 1.22	1.00 ± 1.06	9.36 ± 6.87	63.9**	52%	63%	100%
Blue-gray Gnatcatcher•	*Polioptila caerulea*	3.09 ± 2.63	0.33 ± 0.56	0.10 ± 0.30	79.7**	100%	29%	10%
Solitary Vireo•	*Vireo solitarius*	0.74 ± 0.54	0.92 ± 0.72	0.69 ± 0.75	1.0	70%	71%	57%
Hutton's Vireo	*Vireo huttoni*		0.13 ± 0.34	0.81 ± 0.74	19.5**		13%	62%
Orange-crowned Warbler•	*Vermivora celata*	0.26 ± 0.26	0.08 ± 0.40		2.9	26%		4%
Nashville Warbler•	*V. ruficapilla*	0.13 ± 0.34		0.02 ± 0.15	3.0	13%	2%	
Crescent-chested Warbler	*V. superciliosa*		5.00 ± 3.80	1.38 ± 1.64	24.9**		83%	64%
Townsend's Warbler•	*Dendroica townsendi*		1.04 ± 0.91	1.57 ± 1.36	1.9		67%	74%
Hermit Warbler•	*D. occidentalis*		0.13 ± 0.45	1.12 ± 1.35	17.8**		8%	60%
Black-throated Green Warbler•	*D. virens*	0.70 ± 0.76	1.50 ± 1.18	0.55 ± 1.02	8.9**	52%	83%	29%
Black-and-white Warbler•	*Mniotilta varia*	0.56 ± 0.50	0.50 ± 0.51	0.69 ± 0.56	0.9	57%	50%	64%
Olive Warbler	*Peucedramus taeniatus*		0.04 ± 0.20	0.45 ± 0.77	6.6*		4%	29%
Hepatic Tanager	*Piranga flava*	0.04 ± 0.21	0.29 ± 0.62	0.55 ± 0.86	4.2*	4%	21%	33%

* $P < 0.05$, ** $P < 0.001$. All comparisons based on ANOVA.
• = Neotropical migrant species.

occupied by a core species and all the flocks in a habitat were not significantly different (all *t*-tests, $t_{22\text{–}82} < 0.82$, all *P*s > 0.40), indicating that species were not attracted to flocks of a particular size.

Both Ruby-crowned Kinglet and Blue-gray Gnatcatcher were seen in 100% of the flocks in dry pine-oak forest and tropical semi-deciduous forest, respectively, and Bridled Titmouse and Crescent-chested Warbler were seen in over 80% of the flocks in dry pine-oak forest and humid oak-pine/cloud forest, respectively (Table 2). A highly regular occurrence in flocks and a mean abundance greater than three individuals per flock were criteria for a nuclear species, indicating that Ruby-crowned Kinglet, Bridled Titmouse, Crescent-chested Warbler, and Blue-gray Gnatcatcher were nuclear species in their respective habitats. These species also were frequently followed by other species, conspicuous in their behavior by constantly chipping, and remained with the flock continuously. Although Black-throated Green Warbler also was a highly regular flock participant in the humid oak-pine/cloud forest (Table 2), it was a follower species because it averaged only 1.5 individuals per flock, was rarely followed, did not exhibit conspicuous chipping behavior or flashy plumage, and remained with the flock continuously.

Ruby-crowned Kinglets also were found in flocks in tropical semi-deciduous and humid oak-pine/cloud forests but in fewer numbers and with less frequency (Table 2); in these habitats, Ruby-crowned Kinglets were follower species. Similarly, Crescent-chested Warblers were found in dry pine-oak forest, but they were follower species in flocks in this habitat. Within one geographical area, both Ruby-crowned Kinglet and Crescent-chested Warbler, a migrant and resident species, respectively, behaved as nuclear species in one habitat and follower species in other habitats.

The joiner species in each habitat were different and their frequencies of participation in flocks also varied (Table 3). Of the 49 joiner species, 7 were migrants, including a woodpecker, a flycatcher, a wren, a thrush, 2 warblers, and a grosbeak (Table 3). The joiner species varied in size, foraging habits, and wintering social systems; Painted Redstart (*Myioborus picta*) and Hermit Thrush (*Catharus guttatus*) probably were individually territorial, whereas Golden-browed Warbler (*Basileuterus belli*), Golden-crowned Warbler (*B. culicivorus*), Green Jay (*Cyanocorax yncas*), Gray-breasted Jay (*Aphelocoma ultramarina*), and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) foraged primarily in monospecific flocks (pers. observ.). The grosbeaks, tanagers, and orioles foraged for fruit and insects, and the finches and sparrows ate seeds and fruits. Joiner species were taxonomically diverse and participated opportunistically in flocks when flocks were nearby.

DISCUSSION

FLOCK COMPOSITION

The mixed-species flocks of El Cielo are larger and more diverse than wintering flocks in temperate North America (Morse 1970, Austin and Smith 1972), Central and South America (Davis 1946, Moynihan 1962, Powell 1979), and in Old World tropical habitats (McClure 1967, Croxall 1976, Bell 1980), but they are similar in structure and composition to the nonbreeding season flocks of western Mexico (Hutto 1987, 1994). Flocks in dry pine-oak forest were the largest in size; these flocks had the most species per flock and large numbers of Ruby-crowned Kinglet and Bridled Titmouse individuals per flock (Table 2). Hutto (1987) also reported high species richness (mean of 18.6 species per flock, $n = 11$ flocks) for flocks in pine-oak woodlands in western Mexico, and those flocks included many of the same species, or the western congeners, as the flocks at El Cielo. The mean number of species per flock in western Mexico is nearly twice that at El Cielo, but this difference may be due to different working definitions of a mixed-species flock, higher elevation (2,000–3,000 m) sites visited in western Mexico than in El Cielo, and different study designs; we studied a large number of flocks in the same geographical area, whereas Hutto studied fewer flocks over a larger geographical region. It is clear, however, that the pine-oak habitats of northern Mexico support unusually large and diverse mixed-species flocks.

What factors influence flock size and composition? Although mixed-species understory flocks in Costa Rica contain over 40 participating species, only 11–13 species are regularly seen in flocks that average less than 10 individuals (Powell 1979, 1985). Territorial constraints influence these permanent flocks by restricting flock composition to the individuals maintaining

TABLE 3. The number of flocks in each habitat in which a joiner species was observed. A joiner species is one that only remains with the flock for a short period of time and does not follow the flock.

Species		Tropical semi-deciduous forest $n = 23$	Humid oak-pine/cloud forests $n = 24$	Dry pine-oak forest $n = 42$
Mountain Trogon	*Trogon mexicanus*		1	
Elegant Trogon	*T. elegans*	1		
Acorn Woodpecker	*Melanerpes formicivorus*			2
Yellow-bellied Sapsucker•	*Sphyrapicus varius*			6
Red-naped Sapsucker•	*S. nuchalis*			1
Ladder-backed Woodpecker	*Dendrocopos scalaris*			1
Hairy Woodpecker	*Picoides villosus*			8
Smoky-brown Woodpecker	*Veniliornis fumigatus*		1	1
Bronze-winged Woodpecker	*Piculus rubiginosus*		4	
Tufted Flycatcher	*Mitrephanes phaeocercus*		5	
Greater Pewee	*Contous pertinax*	1	6	16
Western "Cordilleran" Flycatcher	*Empidonax dificilis*	1		
Eastern Phoebe•	*Sayornis nigricans*			1
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	5	3	5
Great crested Flycatcher	*M. crinitus*		1	
Boat-billed Flycatcher	*Megarynchus pitangua*	1		
Gray-collared Becard	*Pachyramphus major*	1		
Green Jay	*Cyanocorax yncas*		1	
Gray-breasted Jay	*Aphelocoma ultramarina*			3
Tufted "black-crested" Titmouse	*Parus bicolor*	6		
Carolina Wren	*Thryothorus ludovicianus*	1		
House Wren•	*Troglodytes aedon*			2
Brown-backed Solitaire	*Myadestes obscurus*	3		2
Hermit Thrush•	*Catharus guttatus*			3
Clay-colored Robin	*Turdus grayi*	1		
Blue Mockingbird	*Melanotis caerulescens*		1	
White-eyed Vireo	*Vireo griseus*	5		
Warbling Vireo	*V. gilvus*		1	
Rufous-browed Peppershrike	*Cyclarhis gujanensis*		2	
Tropical Parula	*Parula pitiayumi*	7	1	
Yellow-rumped Warbler•	*Dendroica coronata*			3
Wilson's Warbler•	*Wilsonia pusilla*	11	10	
Painted Redstart	*Myioborus picta*		1	17
Golden-crowned Warbler	*Basileuterus culicivorus*	7	1	
Rufous-capped Warbler	*B. rufifrons*		1	2
Golden-browed Warbler	*B. belli*		5	
Yellow-throated Euphonia	*Euphonia hirundinacea*	1		
Striped-backed Tanager	*Piranga bidentata*		1	
White-winged Tanager	*P. leucoptera*		5	
Rose-breasted Grosbeak•	*Pheucticus ludovicianus*		1	
Black-headed Grosbeak	*P. melanocephalus*			4
Blue Bunting	*Cyanocompsa parellina*	1		1
Rufous-sided Towhee	*Pipilo erthrophthalmus*			3
Rufous-capped Brush-finch	*Atlapetes pileatus*		1	1
Olive Sparrow	*Arremonops rufivirgatus*	1		
Melodius Blackbird	*Dives dives*		1	
Audubon's Oriole	*Icterus graduacauda*		6	11
Lesser Goldfinch	*Carduelis psaltria*		1	
Hooded Grosbeak	*Hesperiphona abeillei*			1

• = Neotropical migrant species.

territories in the immediate area of the flock and promoting high turnover in membership as the flock moves to neighboring territories. Environmental, temporal, and breeding patterns throughout the year also contribute to patterns in the structure and composition of mixed-species flocks (Munn and Terborgh 1979, Powell 1979, Hutto 1987).

In Mexico, territoriality is not evident among core flocking species, but some joiner species, such as Hermit Thrush, Painted Redstart, and Greater Pewee (*Contous pertinax*), appear to defend winter territories and occasionally join flocks while the flock is in their territory. It is possible that the core flock species defend a large common territory, as Munn and Terborgh (1979) found with understory mixed-species flocks in Peru, but interactions between flocks were never seen in Mexico, and core flocking species were never observed in a flock area without a mixed-species flock. Flocks in all habitats regularly were seen in the same general area, following a similar path through the forest (pers. observ.), but, because birds were not individually marked, I cannot be certain that the same individuals in the same flocks were in the same place each day. My impression is that each flock has a home range, an area that is used consistently but not actively defended. The high proportion of apparently nonterritorial migrant species in mixed-species flocks in northern Mexico may promote these home ranges, which perhaps are ecologically equivalent to the actively defended territories of permanent understory flocks.

At El Cielo, nuclear species were represented by an average of three to nine individuals per flock (Table 2), and most core flock species did not appear to defend territories. By contrast, the nuclear species in permanent understory flocks averaged two individuals (usually a breeding pair) per flock and all core species defended a territory (Munn and Terborgh 1979, Powell 1979). Migrant species play a minor role, if any, in the permanent understory flocks, with Powell (1979) reporting that Black-throated Green Warblers, Black-and-white Warblers, and Wilson's Warblers only were infrequent joiner species. Conversely, migrant species in Mexico were nuclear species in dry pine-oak forest and tropical semi-deciduous forest, and Black-throated Green Warbler and Black-and-white Warbler were core follower species in several habitats. Flock composition was consistent within a habitat and does not necessarily reflect the overall distribution of species in a habitat, suggesting that flocks are not random collections of species in each habitat. In Mexico, where large numbers of migrants winter (Hutto 1980, Greenberg 1992, Gram and Faaborg 1997), mixed-species flocks may be influenced by the transient characteristics of many migrant species and the subsequent effects of the influx of large numbers of wintering species on the resource base; flocks consist of the available species, both migrant and resident, that probably derive overall winter survival benefits from flock participation (Gram 1996), plus the opportunistic joiner species.

SOCIAL ROLES WITHIN THE FLOCK

The social role of core flock species in each habitat varied with the distribution of species across different habitats and regions. The Ruby-crowned Kinglet was a nuclear species, along with the Bridled Titmouse, in dry pine-oak forest, but in tropical semi-deciduous forest and humid oak-pine/cloud forest, the Ruby-crowned Kinglet was a follower species with fewer individuals per flock and a less regular occurrence in flocks. In western Mexico, the Ruby-crowned Kinglet also is a follower species in pine-oak woodlands (Hutto 1987). Ruby-crowned Kinglets differ in their abundance and foraging behavior among habitats (Gram 1996), and perhaps these factors influence the social role of a species in a heterospecific foraging group. Furthermore, intraspecific competition may limit the number of Ruby-crowned Kinglets that can successfully forage together without frequent aggressive interactions in some habitats, or other species may affect the foraging behavior of Ruby-crowned Kinglet directly through interspecific competition, also limiting the number of Ruby-crowned Kinglets that can efficiently forage in a flock.

The resident Crescent-chested Warbler exhibited a similar change in social roles between humid oak-pine/cloud forest, where it was a nuclear species, and dry pine-oak forest where it was a follower species. In western Mexico, the Crescent-chested Warbler also was found in pine-oak woodland, but it averaged only 1.0 individual per flock when present (Hutto 1987) as opposed to 2.1 individuals per flock when present in El Cielo. In both western Mexico and El Cielo, Blue-gray Gnatcatchers are a nuclear species in tropical semi-deciduous forest; we found more individual Blue-gray Gnatcatcher per flock in El Cielo (3.1) than Hutto reported in western Mexico (1.98), but the Nashville Warbler also is a nuclear species in western Mexico, averaging 2.61 individuals per flock (Hutto 1994).

The role of a species in a flock can change, as demonstrated by the differential roles of

Ruby-crowned Kinglet, Crescent-chested Warbler, Blue-gray Gnatcatcher, and Nashville Warbler in Mexico. Species may not "choose" to be nuclear, follower, or joiner species in a flock, and differences in social roles among sites is probably the result of many factors including species composition and abundance in mixed-species flocks and the distribution of resources at a site (Moynihan 1962, Austin and Smith 1972). The flocking patterns at El Cielo suggest that a nuclear species may maintain flock cohesion simply by its conspicuous foraging behavior and vocalizations that provide a focal point for the other flocking species (Austin and Smith 1972, Hutto 1994). Without a nuclear species, a mixed-species flock may never form, and flocks without nuclear species disintegrate quickly (Vuilleumier 1970). The social role of a species in a flock may be passive, making changing roles feasible among different habitats with different flock mates.

For many species, such as the warblers and Ruby-crowned Kinglet at El Cielo, flocking may be beneficial during the nonbreeding season because these species are rarely observed without a mixed-species flock. The high abundance of wintering migrant species and some resident species may facilitate the formation of large flocks that, in turn, are attractive to a wide range of species in northern Mexico. Two species, a migrant and a resident, occupied different social roles within flocks in different habitats, suggesting that flock composition and the number of individuals per species in a flock may influence the social role of species in mixed-species flocks. The specific role of a species in a flock may be secondary, however, to the primary function of the flock, which may be to facilitate winter survival of participating individuals.

Some species both participate in flocks and forage without flocks at the same site (Ewert and Askins 1991, Stacier 1992, Hutto 1994) or they are regular flock members in one region but do not participate in foraging flocks in a different geographical area, such as the Black-and-white Warbler (Faaborg and Arendt 1984). Few data exist on the survival rates of a species when it participates in a mixed-species foraging flock versus when it does not forage in a flock, either in the same habitat or across habitats and geographical regions. Further studies examining survival rates during the nonbreeding season for species in mixed-species flocks are needed to better understand why many species around the world forage in mixed-species flocks.

ACKNOWLEDGMENTS

I gratefully acknowledge the assistance of the many people who helped me collect data on flocking behavior, including: R. Brito-Aguilar, R. Herrera-Herrera, P. Jones, S. Patlyek, M. and C. Speiss, and J. Tewksbury. Logistical support in Mexico was provided by L. Lof, J. Pérez, G. Aguilar, and S. García of the Rancho del Cielo Department at The University of Texas at Brownsville/Texas Southmost College and the Gorgas Science Foundation, Inc., and G. Sánchez-Ramos and C. Gutierrez-Nuñes at the Instituto de Ecología y Alimentos de la Universidad Autónoma de Tamaulipas. R. Brito-Aguilar translated the abstract to Spanish. This manuscript benefited from the helpful comments of J. Faaborg, C. Galen, M. Ryan, B. Loiselle, and three anonymous reviewers. Funding was provided by a grant from the National Fish and Wildlife Foundation and U.S. AID, and by the Division of Biological Sciences at the University of Missouri-Columbia.

LITERATURE CITED

Austin, G. T., and E. L. Smith. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. Condor 74:17–24.

Bell, H. L. 1980. Composition and seasonality of mixed-species feeding flocks of insectivorous birds in the Australian capital territory. Emu 80: 227–232.

Buskirk, W. H., G. V. N. Powell, J. F. Wittenberger, R. E. Buskirk, and T. U. Powell. 1972. Interspecific bird flocks in tropical highland Panama. Auk 89:612–624.

Chipley, R. M. 1977. The impact of wintering migrant wood warblers on resident insectivorous passerines in a subtropical Colombian oak woods. Living Bird 15:119–141.

Croxall, J. P. 1976. The composition and behavior of some mixed-species bird flocks in Sarawak. Ibis 118:333–346.

Davis, D. E. 1946. A seasonal analysis of mixed flocks of birds in Brazil. Ecology 27:168–181.

Ewert, D. N., and R. A. Askins. 1991. Flocking behavior of migratory warblers in winter in the Virgin Islands. Condor 93:864–868.

Faaborg, J., and W. J. Arendt. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. J. Field Ornithol. 55:376–378.

Gram, W. K. 1996. The social structure of an avian community during the nonbreeding season. Ph.D. diss., Univ. Missouri, Columbia, MO.

Gram, W. K., and J. Faaborg. 1997. The distribution of Neotropical migrant birds wintering in the El Cielo Biosphere Reserve, Tamaulipas, Mexico. Condor 99:658–670.

Greenberg, R. 1992. The nonbreeding season: introduction, p. 175–177. *In* J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

Greig-Smith, P. W. 1978. The formation, structure and function of mixed-species insectivorous bird flocks in West African savanna woodland. Ibis 120:284–295.

HUTTO, R. L. 1980. Winter habitat distribution of migratory land birds in western Mexico, with special reference to small, foliage-gleaning insectivores, p. 181–203. *In* A. Keast and E. S. Morton [eds.], Migrant birds in the Neotropics: ecology, behavior, distribution and conservation. Smithson. Inst. Press, Washington, DC.

HUTTO, R. L. 1987. A description of mixed-species insectivorous bird flocks in western Mexico. Condor 89:282–292.

HUTTO, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. Condor 96: 105–118.

LATTA, S. C., AND J. M. WUNDERLE. 1996. The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. Condor 98: 595–607.

MCCLURE, H. E. 1967. The composition of mixed species flocks in lowland and sub-montane forests of Malaya. Wilson Bull. 79:131–154.

MORSE, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr. 40:119–168.

MOYNIHAN, M. 1962. The organization and probable evolution of some mixed species flocks of Neotropical birds. Smithson. Misc. Collect. 143:1–140.

MUNN, C. A. 1985. Permanent canopy and understory flocks in Amazonia: species composition and population density. Ornithol. Monogr. 36:683–710.

MUNN, C. A., AND J. W. TERBORGH. 1979. Multi-species territoriality in Neotropical foraging flocks. Condor 81:338–347.

POWELL, G. V. N. 1979. Structure and dynamics of interspecific flocks in a Neotropical mid-elevation forest. Auk 96:375–390.

POWELL, G. V. N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. Ornithol. Monogr. 36:713–732.

STACIER, C. A. 1992. Social behavior of the Northern Parula, Cape May Warbler and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico, p. 308–320. *In* J. M. Hagan III and D. W. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithson. Inst. Press, Washington, DC.

VUILLEUMIER, F. 1970. L'organisation sociale des bandes vagabondes d'oiseaux dans les Andes du Perou central. Revue Suisse de Zoologie 77:209–235.

WINTERBOTTOM, J. M. 1943. On woodland bird parties in northern Rhodesia. Ibis 85:437–442.