

FLORIDA FIELD NATURALIST

QUARTERLY PUBLICATION OF THE FLORIDA ORNITHOLOGICAL SOCIETY

VOL. 11, No. 2

MAY 1983

PAGES 25-44

COMPOSITION AND BEHAVIOR OF MIXED-SPECIES FLOCKS OF FOREST BIRDS IN NORTH-CENTRAL FLORIDA

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As in probably all other forested regions of the world, the forest canopy birds of north-central Florida associate in mixed-species flocks during the non-breeding season. These flocks appear to form around intraspecifically-social groups of Carolina Chickadees and Tufted Titmice (scientific names of birds are listed in Table 1). The flocks typically contain several individuals of these two species plus several other attendant individuals from a constantly changing complex of resident and migrant species. Mixed-species flocks with comparable species composition from Louisiana and Maryland have been described by Morse (1970) but have not been described previously for Florida. In this paper I describe the species composition of these flocks, the patterns of aggression within and between flocks, and the patterns of movement for flocks in north-central Florida during the winter of 1977-78.

STUDY AREA

I studied flocks in approximately 50 ha of the 2200-ha San Felasco Hammock State Preserve, 20 km NW of the University of Florida campus, Gainesville, Alachua County, Florida. The site was at least 3 km from the nearest public road.

The study area contained an open stand of long-leaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) which sloped off gradually on three of four sides into denser second growth loblolly pine (*Pinus taeda*) and turkey oak. On the fourth side was a much denser second growth woods of sweetgum (*Liquidamber styraciflua*), southern red oak (*Quercus falcata*), mockernut hickory

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TABLE 1. Bird species participating in mixed-species flocks in north-central Florida.

Species	No. of flocks in which species occurred	No. of ind./flock \pm SD	% of total flocks in which species occurred	% participation ^{1,2}	Date of 1st obs. ³	Date of last obs. ³
Tufted Titmouse						
<i>Parus bicolor</i>	58	3.8 \pm 1.4	96.7	—	—	—
Carolina Chickadee						
<i>Parus carolinensis</i>	49	3.8 \pm 1.2	81.7	—	—	—
Pine Warbler						
<i>Dendroica pinus</i>	39	2.6 \pm 1.8	65	—	—	—
Yellow-rumped Warbler						
<i>Dendroica coronata</i>	36	11.3 \pm 5.6	60	80	10-3	—
Black-and-white Warbler						
<i>Mniotilta varia</i>	35	1.1 \pm 0.3	58.3	71.4	10-3	—
Yellow-throated Warbler						
<i>Dendroica dominica</i>	33	1.1 \pm 0.2	55	—	—	—
Ruby-crowned Kinglet						
<i>Regulus calendula</i>	26	4.3 \pm 1.8	43.3	57.8	10-24	—
Solitary Vireo						
<i>Vireo solitarius</i>	26	1.1 \pm 0.3	43.3	55.3	10-14	—
Downy Woodpecker						
<i>Picoides pubescens</i>	22	1.4 \pm 0.5	36.7	—	—	—
Brown Creeper						
<i>Certhia familiaris</i>	19	1.0 \pm 0	31.7	54.3	12-3	2-24
Red-bellied Woodpecker						
<i>Melanerpes carolinus</i>	18	1.6 \pm 0.6	30	—	—	—
Blue-gray Gnatcatcher						
<i>Poliioptila caerulea</i>	9	1.2 \pm 0.4	15	—	—	—
Northern Parula						
<i>Parula americana</i>	9	1.4 \pm 0.7	15	69.2	—	10-12
American Goldfinch						
<i>Carduelis tristis</i>	8	6.6 \pm 1.9	13.3	30.8	1-3	2-24
White-eyed Vireo						
<i>Vireo griseus</i>	7	1.0 \pm 0	11.7	—	—	—
Orange-crowned Warbler						
<i>Vermivora celata</i>	6	1.3 \pm 0.5	10	13.6	10-3	2-10
American Redstart						
<i>Setophaga ruticilla</i>	3	1.0 \pm 0	5	30	9-11	10-14
Yellow-throated Vireo						
<i>Vireo flavifrons</i>	3	1.0 \pm 0	5	37.5	—	9-13
Eastern Phoebe						
<i>Sayornis phoebe</i>	3	1.0 \pm 0	5	13.04	10-24	1-13

(Table 1. Continued)

Species	No. of flocks in which species occurred	No. of ind./flock \pm SD	% of total flocks in which species occurred	% participation ^{1,2}	Date of 1st obs. ³	Date of last obs. ³
Red-breasted Nuthatch <i>Sitta canadensis</i>	3	1.0 \pm 0	5	50	10-24	12-3
Palm Warbler <i>Dendroica palmarum</i>	2	1.0 \pm 0	3.3	—	—	—
Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	2	1.0 \pm 0	3.3	—	—	—
Eastern Wood-Pewee <i>Contopus virens</i>	1	1.0 \pm 0	1.7	100	10-12	10-12
Blackburnian Warbler <i>Dendroica fusca</i>	1	1.0 \pm 0	1.7	100	10-24	10-24
Cerulean Warbler <i>Dendroica cerulea</i>	1	1.0 \pm 0	1.7	100	11-2	11-2

¹Number of flocks in which species occurred/number of flocks observed during period in which species was present in study area X 100.

²Dash (—) indicates that the species was present throughout the study period.

³Dash (—) indicates that the species was present at beginning or end of the study period, whichever applicable.

(*Carya tomentosa*), and laurel oak (*Quercus hemisphaerica*). This second-growth deciduous woods continued to slope toward a small swamp surrounded by a relatively mature stand of laurel oak, pignut hickory (*Carya glabra*), basket oak (*Quercus michauxii*), and magnolia (*Magnolia grandiflora* and *M. virginiana*). A power line corridor 40 m wide crossed through the study area.

METHODS

From September 1977 through March 1978 I followed mixed-species flocks and began attempting to mark birds for individual identification in December 1977 using mist nets to catch the birds. I marked several chickadees and titmice with colored plastic leg bands and U.S. Fish and Wildlife Service aluminum bands. I censused flocks after 10-15 min of the initial encounter, then followed them for periods of up to 5 h. I recorded the flock's position irregularly at 5 to 30 min intervals and when the flock crossed a notable landmark or changed direction. I later reconstructed the flocks' routes on maps of the study area and then used them to calculate distances and rates of flock movement. I also constructed a composite map to measure flock territory sizes.

RESULTS

FLOCK COMPOSITION

In 60 periods of continuous observation of a mixed-species flock, I observed 25 species that appeared to show some affinity to the flocks (Table 1). The flocks usually contained both Carolina Chickadees and Tufted Titmice. Species associations without these two species lacked cohesiveness and soon disintegrated. Nine species occurred in fewer than five flocks, because they were present in the study area only for brief periods (such as Cerulean Warbler, Blackburnian Warbler, Eastern Wood Pewee, American Redstart, and Red-breasted Nuthatch) or because they had little affinity for the mixed-flocks (such as the Yellow-bellied Sapsucker, Eastern Phoebe, Yellow-throated Vireo, and Palm Warbler).

The flocks contained an average of 6.9 species ($SD = 1.9$, range = 3-11) and an average of 21.7 individuals ($SD = 9.4$, range = 7-40). Several attendant species, the Black-and-white Warbler, Yellow-throated Warbler, Brown Creeper, and Solitary Vireo, typically occurred singly within the flocks. The Ruby-crowned Kinglet and American Goldfinch occurred in intraspecific groups of four to eight individuals that joined and left the flocks together. Pine Warblers usually occurred singly or in pairs, but occasionally up to six individuals occurred with the mixed-flocks. The frequency of occurrence of the White-eyed Vireo in the flocks (Table 1) is almost certainly an underestimation, because it tended to remain in dense thickets and was usually noticed only when the flock crossed a road or clearing.

The study area contained two titmouse flocks with territories of 13.5 and 11.3 ha (Fig. 1). There appeared to be only one chickadee flock in the area of the two titmouse territories. Their border appeared to coincide for the most part with the outer border of the two combined titmouse territories but may have extended past the boundary to the north.

INTRAFLOCK AGGRESSION

I observed 59 acts of intraflock aggression (Table 2). These consisted either of attacks followed by chases or of supplanting attacks, in which the aggressor flew directly at another bird and landed where the victim had been. The two nuclear species accounted for 73.7% of these acts of aggression; 47.5% overall were interspecific.

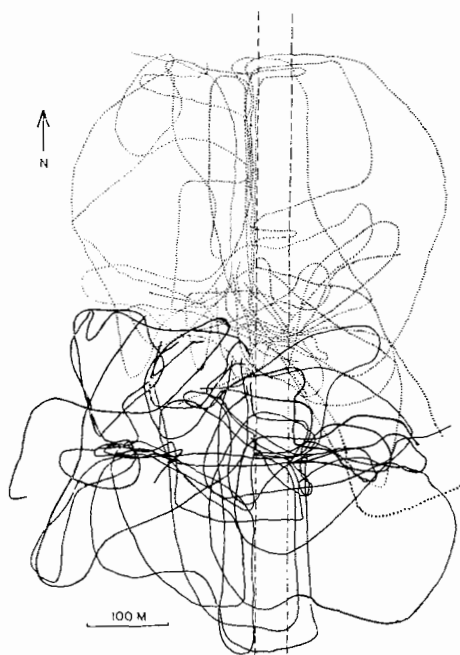


Fig. 1. Composite map of paths taken by mixed species flocks. Solid lines indicate one Tufted Titmouse flock; dotted line indicates the other Tufted Titmouse flock; dashed lines indicate borders of power line corridor.

Aggression became most frequent in February (Fig. 2), reaching a peak of 0.22 aggressions/h of observation. Titmice were the principal antagonists in the flocks, accounting for 67.8% of interspecific aggressions (Table 2). Chickadees were their most frequent victims (40.6% of titmouse aggressions).

In terms of attacks received per sighting (number of attacks received/number of flock censuses containing a given species), the Yellow-throated Warbler was the most frequent victim of aggression. I never observed it showing hostility toward any other bird, but because it typically occurred singly in the flocks, it is possible that it excluded conspecifics. The Pine Warbler was the main aggressor against the Yellow-throated Warbler. This aggression occurred as displacements from long-leaf pine needle tufts. Nevertheless, the Yellow-throated Warbler persistently returned to the needle tufts within several minutes of being displaced.

TABLE 2. Aggressive interactions among flock members.

Victim	RbW	CC	TT	BC	SV	BwW	CW	YtW	PW	Total
Red-bellied Woodpecker										0
Carolina Chickadee		16	13							29
Tufted Titmouse	1		13							14
Brown Creeper						1				1
Solitary Vireo					1					1
Black-and-white Warbler						1				1
Cerulean Warbler										0
Yellow-throated Warbler		1	2				1		5	9
Pine Warbler			4							4
Total	1	17	32	0	1	2	1	0	5	59

MOVEMENT PATTERNS

In the few cases in which flocks were followed for longer than 3 h, and in which they were not exposed to the threat of predation by either Sharp-shinned (*Accipiter striatus*) or Cooper's Hawks (*A. cooperii*), the flocks were regularly saltatory in their movements, tending to drift slowly for an hour to an hour and a half and then to move rapidly to another area and repeat the cycle. When the flocks were exposed to the hawks, however, they showed altered this pattern. When the hawk was sighted by a flock, a high whistle alarm call was given by a titmouse or chickadee, and all birds stopped all activity and waited for one to 10 minutes before resuming activity (mean = 5.5 min) (Gaddis 1980). Upon resumption of activity, the birds usually left the area at a rapid pace and then continued to move erratically. Frequent changes in direction accompanied this erratic movement rate.

The composite map of the movement paths of the two titmouse flocks (Fig. 2) indicates that flock territories were consistently held but also that considerable overlap occurred between them. Certain areas along the border between the two titmouse flocks and along the power line appeared to be more frequently traversed than others, but I observed no overall pattern in the flocks' routes.

The flocks moved at an overall average rate of 324 m/hr throughout the period of study, but large seasonal and daily variations occurred in these rates (Table 3). This table suggests a decrease at midday and an overall increase from January to February to March (differences in total monthly rates as well as daily rates are all significant at $p < .001$, Student's t-test). However, this pattern was not necessarily consistent within subcategories; reversals of the overall

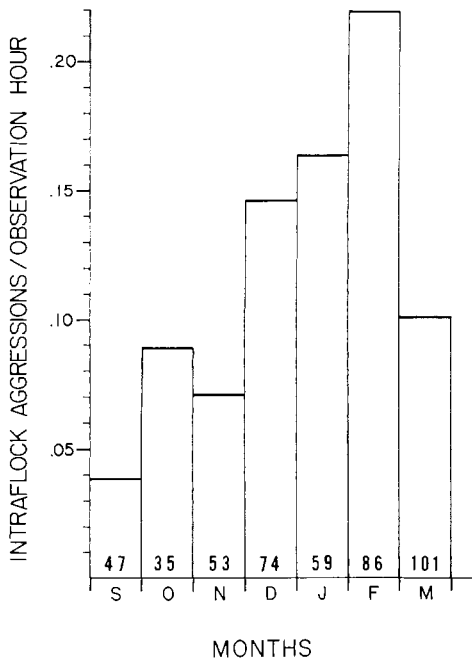


Fig. 2. Monthly rates of intraflock acts of aggression. Number of observation hours for each month is indicated in the bottom of each bar.

daily trend occurred in February and March, and only the 1000-1400 time period showed the overall seasonal trend.

Linear regression of movement rates vs. flock size in terms of both number of individuals/flock and number of species/flock showed no significant correlations. Nor were the correlations improved by separating the data into deciduous and coniferous habitats, i.e. the patterns of flock movement appeared to be equally uninfluenced by flock size in coniferous as well in deciduous woods.

INTERFLOCK AGGRESSION

The titmouse and chickadee flocks trespassed widely in neighboring territories, and interflock fights commonly resulted. When these interflock fights occurred, the fighting was exclusively intraspecific and involved only the nuclear species, i.e. titmice and chickadees. Thus, titmice fought against titmice, chickadees fought against chickadees, and attendant species avoided the conflict. Interflock

TABLE 3. Flock movement rates (m/h) \pm SD by months and by times of day.

Time of day	Dec.-Jan.	February	March	Total
0700-1000	362.5 \pm 118.6 N = 8	267.5 \pm 122.5 N = 11	355.6 \pm 62.2 N = 4	362.03 \pm 179.3 N = 23
1000-1400	273.3 \pm 131.04 N = 17	303.1 \pm 148.01 N = 11	453.7 \pm 191.4 N = 4	311.7 \pm 172.3 N = 32
1400-1800	604.9 \pm 195.3 N = 4	234.7 \pm 166.1 N = 5	280.0 \pm 147.7 N = 3	377.6 \pm 154.1 N = 12
Total	305.9 \pm 121.1 N = 29	319.5 \pm 159.0 N = 26	381.7 \pm N = 11	323.9 \pm 159.2 N = 66

confrontations consisted of excited vocal exchanges among the nuclear species with frequent attacks and chases. Titmice occasionally locked claws and fell to the ground in grappling combat. Vocal exchanges could extend for up to an hour.

DISCUSSION

The patterns of aggressive interactions reported by Morse (1970) for mixed species flocks in Louisiana and Maryland were similar to those I saw in Florida. In Louisiana and Maryland, as in Florida, at least half of all aggressions were made by Carolina Chickadees and Tufted Titmice. The proportion of inter- to intra-specific attacks was much higher for the Tufted Titmouse than for the Carolina Chickadee in the Louisiana and Maryland flocks as it was also in Florida. Furthermore, in Louisiana and Maryland, the Tufted Titmouse accounted for 29.8% of all interspecific aggressions (compared to 67.8% in Florida) and the Carolina Chickadee was its most frequent victim (47.1% of titmouse aggressions, 40.6% in Florida).

In spite of this disproportionately high interspecific aggressiveness of the Tufted Titmouse, Morse (1970:132-134) concluded that flock leaders showed a "low level of interspecific hostility." Morse further suggested that this characteristic of the leaders may contribute to their attractiveness to other species. The idea that nuclear species in mixed-species flocks should show low interspecific aggressiveness has also been suggested by Moynihan (1960), but I believe it appears to be questionable for the case of the Tufted Titmouse in

Morse's data from Louisiana and Maryland flocks and in my own from Florida flocks.

The overall pattern of movement rates shown by the Florida flocks appeared also to be shown by the mixed flocks led by Carolina Chickadees in Tennessee studied by Wallace (1970). Although Wallace's sample sizes were too small for confident interpretation, a rate decrease at midday was suggested. No overall seasonal trend was apparent. Odum (1942) also reported a decrease in movement rate at midday in Black-capped Chickadee (*Parus atricapillus*) flocks in New York, but he presented no data on the seasonality of the phenomenon.

That the midday decrease in movement rate was not expressed in February and March in the Florida flocks probably reflected the decreasing availability of foraging resources during those months. Long-leaf pine seeds had been abundant until late December and early January, and served as a major foraging resource for the nuclear species. While the parids were foraging on these seeds, they would often cease activity entirely for up to an hour during midday. However, when the long-leaf pine seed resource was depleted, not only did aggression rates increase dramatically (Fig. 1) but also the midday rest periods were no longer observed.

Morse (1970:154) reported a general tendency for large flocks to move faster than smaller ones. He further reported differences in the relationships between flock size and rate of movement in coniferous as opposed to deciduous woods, although he did not report the levels of statistical significance for the correlations. My data fail to confirm Morse's conclusion that the relationships between flock size and movement rate are different in the different habitat types, and they also fail to confirm the presence of a significant overall correlation between the two variables. Morse (1970) considered that the suggested correlation was explainable in terms of scarce food reserves, to which large flocks are probably subjected, and the resulting need for individuals in large flocks to forage over larger areas. (The basis for his assumption of scarce food reserves is that larger flocks were found where overall bird densities were low, and, from Gibb (1960), that bird densities in England were low where reserves were low.) Although I found no correlation between flock size and movement rate in the Florida flocks, their increase in movement rate in February and March could possibly have been due to a decrease in availability of food (following the depletion of long-leaf pine seeds), which would be consistent with Morse's suggestion.

SUMMARY

Winter flocks that formed around Carolina Chickadees and Tufted Titmice contained an average of 6.9 species (SD = 1.9, range = 3-11, N = 60) and 21.7 individuals (SD = 9.4, range = 7-40). The flocks moved at an overall rate of 324 m/h (SD = 159.2, N = 66). A composite map of flock movements showed that no regular routes were used.

Fifty-nine acts of aggression were observed, 47.5% of which were interspecific. The Tufted Titmouse, one of the two nuclear species, accounted for 67.8% of the interspecific aggressions. A seasonal increase in aggression was shown with a peak in February of 0.22 aggressions/observation hour.

ACKNOWLEDGMENTS

A Sigma Xi grant-in-aid of research helped to finance this research. Vickie Duncan Tillman assisted with the fieldwork. Helpful comments on the manuscript were provided by J. W. Hardy and Mary LeCroy.

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