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WINTER BEHAVIOR OF TUFTED TITMICE

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Tufted Titmice (*Parus bicolor*) are non-migratory woodland birds widely distributed in the midwestern and eastern United States and are at present expanding their range northward (Gosselin and David 1980). Despite extensive studies of North American (Dixon 1956, Glase 1973) and Eurasian congeners (Perrins 1979), little intensive research has been done on this common species and information concerning behavior outside the breeding season is often contradictory and incomplete. For example, Wilford (1977) reported that, in winter, Tufted Titmice do not form cohesive groups and individual titmice are either transient or local permanent birds; whereas Gillespie (1930) and Condee (1970) found titmice in winter flocks with stable territory boundaries. Furthermore, little work has been done on the nature of social interactions among wintering titmice.

The primary purpose of this study was to investigate winter behavior of Tufted Titmice. The objectives of this study were to determine (1) whether birds formed social groups during the non-breeding season; if so, (2) the sex and age of group members; (3) patterns of social dominance within groups; and (4) fate of group members during the ensuing breeding period.

STUDY AREAS AND METHODS

The study was conducted in central Missouri from October–June 1977–78 and September–May 1978–79 in a 16.5-ha area of mature, undisturbed oak-hickory forest within the Rock Bridge State Park (RB), Boone Co., and in an area similar in size and species composition but intensively managed in the U.S. Forest Service Cedar Creek Management Area (CC), in Callaway County (Fig. 1). White oak (*Quercus alba*), black oak (*Q. velutina*) and hickory (*Carya* spp.) were dominant on upland ridges and American sycamore (*Platanus occidentalis*) and green ash (*Fraxinus pennsylvanica*) on bottomland areas. Scattered honey locust (*Gleditsia triacanthos*) and eastern redcedar (*Juniperus virginiana*) were present in old-field habitat. Both study areas were surrounded by similar habitat, cultivated farmland, pasture, and urban development.

Mark and capture of birds.—Titmice were banded with USFWS numbered bands from late September–January (1978) or February (1979) and all trapped individuals received unique combinations of colored plastic leg bands. In addition we marked the titmice during 1978–79 by painting with model airplane paint the ventral side of retrices with individualized patterns to facilitate identification of birds at a distance (Dixon 1956). Titmice were captured in eight Potter traps baited with sunflower seeds. Traps were moved frequently to avoid influencing movement or behavior of the titmice. The total trapping effort consisted of 270 trap-h on RB and 230 h on CC in 1977–78 and 175 h (RB) and 125 h (CC) in 1978–79. Birds were sexed by length of wing chord (N = 26) or observation of breeding activity (N = 5) and aged by examination of skull ossification and bill color (Condee 1970). Titmice sexed in fall and winter and found in spring proved by wing measurement to have been correctly determined.

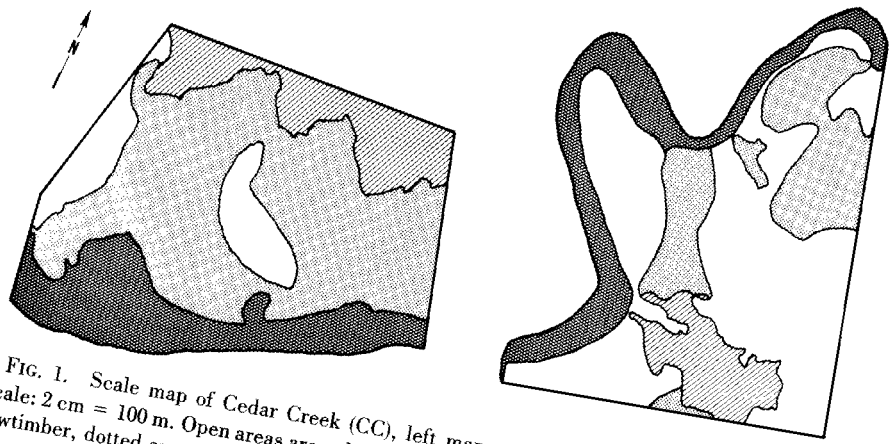

FIG. 1. Scale map of Cedar Creek (CC), left map, and Rock Bridge (RB) study plots. Scale: 2 cm = 100 m. Open areas are upland saw-timber, cross hatched areas are bottomland sawtimber, dotted areas are pole-timber, striped areas are saplings and old-fields.

Distribution of birds in winter and fall.—The study areas were marked with colored marker flags at 40-m intervals; thus, we could map locations of individual titmice. In winter, each study area was surveyed 2–3 times/week during which we recorded the locations and movements of titmice. We devoted particular effort to mapping the locations of aggressive encounters between birds and recording the identity of birds in association with other titmice. Observations were transferred to composite maps for each individual and/or group of birds. Distances travelled and areas occupied during winter were calculated with a planimeter.

We determined the fate of titmice marked in winter by searching the study areas and surrounding areas at least twice weekly from March–June (1978) and May (1979). The location and identity (when possible) of singing males, pairs observed in courtship feeding, and birds involved in inter-male aggression were mapped. The area of an individual breeding territory was delineated by the polygon of outermost points, all of which had been recorded before the end of April.

Determination of dominance hierarchies.—In this study we follow Morse (1970:120) in defining a flock as "Any group of two or more birds, whose formation depends upon positive responses by individuals to members of their own or other species."

Dominance hierarchies within the flocks that we detected were determined by observation of behavioral interaction between titmice on and off bait-sites. Bait-sites consisted of suspended 1-m^2 platforms covered with sunflower seeds. A minimum of 10 observation periods (15 min each) were held at bait-sites within the territory of each flock during which we recorded the number of times each titmouse successfully acquired a seed. Bait-sites were moved frequently and observation periods were held only when all flock members were present. Data from observation periods were analyzed by averaging the number of seeds acquired/bird/period and testing for differences between birds with Kruskal-Wallis and multiple comparisons tests (Conover 1971).

Behavior away from bait-sites was recorded by documenting cues to dominance such as supplanting, chasing, "facing off," and "appeasement" (Dixon 1956, Glase 1973). During

TABLE 1

SIZE, AGE, AND SEX CHARACTERISTICS OF WINTER FLOCKS OF TUFTED TITMICE

	No. of ind./ flock (N = 14)	Adults (N = 8)[a]		Juveniles (N = 8)	
		Males/flock	Females/flock	Males/flock	Females/flock
$\bar{x}$	2.9	1.13	1	0.5	0.38
Range	(2–5)	(1–2)	(1)	(0–2)	(0–1)

[a] Sample size indicates number of flocks in which all members were aged and sexed.

such bouts the birds involved were scored as either winners or losers. Encounters resulting in no apparent winner were scored as a tie (Ketterson 1979). Data obtained on and off bait-sites were then used to rank each titmouse within a flock.

RESULTS

Thirty-five titmice were trapped and marked on the study areas. Nine juveniles either settled on areas off the plots or were not observed subsequent to being marked. Disappearances occurred early in the field seasons (September–October) during periods when there was considerable movement of titmice.

Flock structure.—Titmice which remained on the plots formed 14 flocks. We found, during both winters, four flocks on the RB plot and three on the CC plot. The flocks began to form in September and membership was stable by late October in both years. We were unable to identify the age and/or sex of one or more individuals in six of the flocks. One bird remained unbanded on CC during the 1977–78 winter. Fifteen titmice trapped and marked during the first field season were still present on the study areas during the 1978–79 winter.

The number of birds per flock ranged from 2–5 with two being the modal flock size (Table 1). All flocks consisting of two birds, in which we were able to identify the sex of both individuals, were comprised of one male and one female. Overall, males outnumbered females in the flocks for both the adult and juvenile age classes. In the flocks where all individuals were aged the adult : juvenile ratio was 1.42:1. Only one flock contained more than one adult male and no flocks contained more than one female of either age class.

The composition of the flocks was stable throughout the flocking period. We did not observe any additions to any flock after mid-October, although there may have been movement of unbanded birds. Seven marked birds did disappear from the flocks. We found the remains of three titmice (feathers, but no bands) and it is likely that these birds were preyed upon by Sharp-shinned Hawks (*Accipiter striatus*) that were observed on the

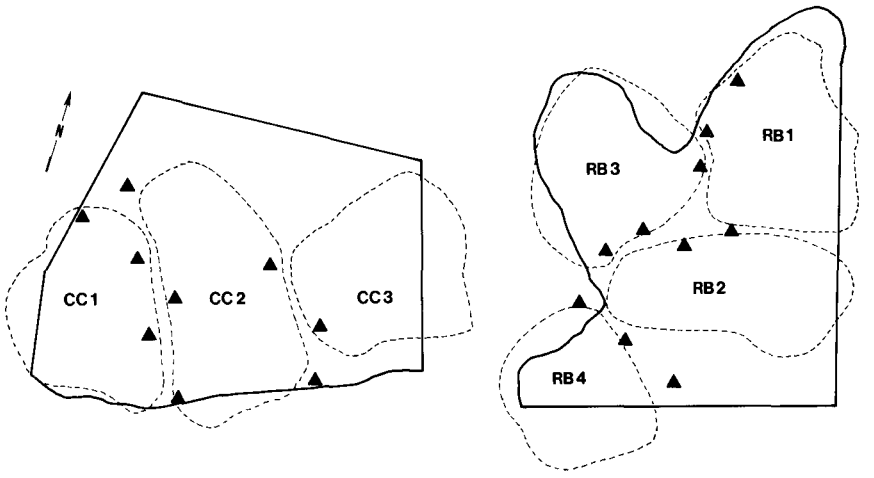

FIG. 2. Configuration of winter flock territories of Tufted Titmice on CC and RB study plots, 1978–79 winter. Triangles denote sites of inter-flock confrontations. Numbers indicate flock labels.

plots during both winters. None of the birds that disappeared were found on nearby areas or elsewhere.

Flock territories and movements.—The average size of the flock territories was 5.4 ha (Fig. 2). The territory boundaries were stable and defined early in the flocking period. The size and configuration of the territories were similar between the two field seasons on both plots (1977–78: $\bar{x}$ = 5.33 ha, N = 7; 1978–79: $\bar{x}$ = 5.47 ha, N = 7, NS, Wilcoxon Signed Rank Test). The size of the flocks and of their territories were not significantly correlated (P = 0.29, N = 14, NS, Spearman's Rho).

Inter-flock aggressive behavior, which was observed 41 times, occurred on or near territory boundaries (Fig. 2). These disputes occurred between males in 38 (93%) of the cases observed and were characterized by loud vocalizations and relatively "excited" behavior. We occasionally saw single birds within a neighboring territory. The intruders, always males, either quietly returned to their own territory or were driven off by residents.

Within their flock territories the titmice travelled singly (20% of all observations), in pairs (65%), or in groups of three or more (15%). The flocks which contained four or five individuals were cohesive early in the day (06:00–09:00) and later fragmented into pairs or single birds. Similar patterns of flock cohesion have been reported by Austin and Smith (1972). All birds were observed throughout their flock's territory. However, it appeared that within the larger flocks (≥3 individuals, N = 8) pairs, com-

TABLE 2
SAMPLE SOCIAL DOMINANCE PATTERNS IN WINTER FLOCKS OF TUFTED TITMICE

Flock number	Position in social hierarchy				
	1	2	3	4	5
CC1:77–78	Adult M	Juv. M	Adult F	Juv. F	—
CC1:78–79	Adult M	Adult M	Adult F	—	—
CC2:78–79	Adult M	Adult F	—	—	—
CC3:78–79	Adult M	Adult F	Juv. M	—	—
RB1:78–79	Adult M	Juv. M	Juv. M	Adult F	Juv. F
RB2:78–79	Adult M	Adult F	—	—	—
RB3:77–78	Adult M	Adult F	Juv. F	—	—
RB4:78–79	Adult M	Adult F	—	—	—

prised of one female and male, preferred certain portions of their flock's territory for winter activity.

The titmouse flocks preferred forested areas to the more open old-field habitat. Mature bottomland habitat appeared to be favored when the titmice were foraging. In addition, during especially windy, cold weather the titmice would habitually seek the riparian areas where vegetation (canopy trees, shrub layers) was particularly thick.

Social dominance within flocks.—The intra-flock dominance hierarchy was linearly peck-right (Table 2); that is, each member of a flock was consistently either dominant or subordinate to its fellow flock members once the hierarchies became established. Dominance patterns were not site specific. Males were generally dominant over females and, within a sex, adults over juveniles. An exception to this was in the CC3:77–78 flock, in which an adult female was dominant over a juvenile male.

Flock members could be consistently ranked according to the results of the 15-min observation periods. The ranks assigned to a bird based on behavior observed away from bait-sites were consistent with the data from the observation periods. Kruskal-Wallis and multiple comparisons tests indicated that the mean number of seeds acquired/bird/observation period was not significantly different between birds in flocks of three members or less. In the larger flocks (N = 4) the alpha (i.e., most dominant) males acquired a significantly greater number of seeds/observation period ($P < 0.05$) than the birds with the lowest social status.

Social dominance, within a sex, appeared to be a function of seniority on the flock territory. During the 1978–79 winter all of the alpha males and females were birds that had bred (as pairs) during the previous spring on areas within their flock's territory. The determination of dominance among

juveniles of the same sex was also governed by seniority on a flock territory. Three juvenile males that gained membership to flocks early in the fall were dominant over other juvenile males that joined the same flock later.

Fate of flock members during the breeding period.—In late February and March, male titmice began to give the characteristic *peto-peto* breeding vocalization and courtship feeding was observed. Courtship feeding was useful in determining the sex of individuals whose sex was previously unknown.

Alpha males and females became or proved to be paired together in 12 of the 14 flocks. These pairs were the first (N = 5) or only (N = 7) to breed within their respective flock territories. Two exceptions to this pattern were found: (1) the RB3:77–78 flock in which the alpha female disappeared and the alpha male paired with a subordinate female; and (2) the CC3:78–79 flock in which the alpha male disappeared and the beta male paired with the alpha female. These two pairs were also the first titmice to initiate breeding within their flock territories.

The fate of subordinate individuals during the breeding period (N = 9, both years pooled) was more variable. Three females and two males remained on their flock territories and were observed with mates. Two females, one juvenile and one of unknown age, emigrated off their flock territories and found mates. Two males were not seen with mates and were seen on and off their flocks' territories.

The titmice preferred fellow flock members as mates. All of the alpha males and females and four of the seven subordinate birds that became paired did so with members of their flocks of the previous winter.

During the spring the flock territories supported one or two breeding pairs (Fig. 3). The number of breeding pairs supported in each flock territory was the same during the two breeding seasons.

The alpha pairs established territories from 3–4 weeks earlier than the second breeding pairs on a flock territory (Table 3). Titmice that emigrated off their flock territories, and found mates, established territories 4–5 weeks after their flock's alpha pair.

Feeding associates.—The titmouse flocks in this study were essentially single-species flocks. We did not observe the titmice actively participating in the mixed-species flocks that were present on both study plots. The mixed-species flocks varied in composition but typically included the Black-capped Chickadee (*P. atricapillus*), Yellow-rumped Warbler (*Dendroica coronata*), Downy Woodpecker (*Picoides pubescens*), and Brown Creeper (*Certhia familiaris*). Titmice occasionally travelled with the mixed-species flocks when such flocks were present within their territories. Titmice did not leave their flock territories in association with the mixed flocks.

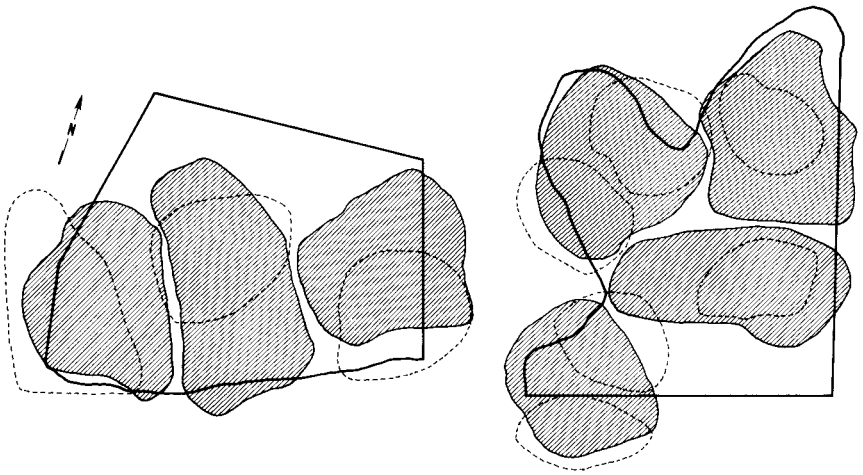

FIG. 3. Sample of spatial arrangement of winter flock territories and subsequent breeding territories of Tufted Titmice, RB plot; 1978–79. Winter flock territories are denoted by striped areas. Breeding territories are enclosed by dashed lines.

DISCUSSION

The participation of Tufted Titmice in winter flocks was clearly evident in our study. The aforementioned confusion concerning titmouse social behavior in winter likely arose from the following: (1) winter flock size is variable and may be as small as two birds, (2) the cohesiveness of flocks varies throughout the day, and (3) pairs of titmice within flocks comprised of three or more birds favor certain areas within their flock territories. Samson and Lewis (1979) found that titmouse flocks in Pennsylvania were comprised of up to eight birds but noted that no pairs traversed the entire flock range. Our study and that of Samson and Lewis (1979) suggest that, regardless of size, the pair is the basic social unit in Tufted Titmouse flocks (sensu Saitou 1978). Certain pairs accept other titmice on their winter range and other pairs remain alone throughout the winter.

Winter flocks of Tufted Titmice and those of other congeneric species appear to have several characteristics in common. A linearly peck-right social hierarchy with dominance governed by sex and seniority within the flock territory is typical of species in Paridae (Odum 1941, Hinde 1952, Dixon 1956). Virtually all studies of parid flocks in which social dominance patterns were delineated indicate that alpha males and females remain within a winter flock territory to breed. If present, subordinate birds usually disperse, but may remain within their flock territories if they become paired with a fellow flock member (Hartzler 1970, Glase 1973, Smith 1976).

TABLE 3
CHARACTERISTICS OF BREEDING TERRITORIES OF DOMINANT AND SUBORDINATE TUFTED TITMICE

Study plot and year	Position in social hierarchy	Breeding territories		
		Mean date of establishment[c]	Mean size (ha)	Mean linear distance from center of flock territory to center of breeding territory (m)
CC:78-79	Dominant pair[a]	13 April	3.6	23
	Subordinates[b]	29 April	3.8	675
CC:78–79	Dominant pair	4 April	3.4	18
	Subordinates	8 May	3.4	598
RB:77–78	Dominant pair	28 March	3.2	12
	Subordinates	25 April	3.3	428
RB:78–79	Dominant pair	24 March	2.9	18
	Subordinates	17 April	3.1	519

[a] Includes pairs consisting of one formerly subordinate individual (see text).
[b] Does not include males which remained unpaired.
[c] Calculated by converting dates to day-number of year, e.g., 2 Feb. = day # 33.

Samson and Lewis (1979) reported that 3–4 male titmice from one flock established territories within their flock's range. Presumably these birds included an alpha male and subordinates. We cannot account for the differences in the titmice's spring activity in our study and that of Samson and Lewis (1979).

Winter flocks of the various species in Paridae have been categorized into two groups by Saitou (1978). The first group is made up of species that form conspecific flocks, often of more than two individuals, and regularly participate in mixed-species flocks. Great Tits (*P. major*), Black-capped Chickadees, and Carolina Chickadees (*P. carolinensis*) are species belonging to this group. The second group consists of species such as Marsh Tits (*P. palustris*), Plain Titmice (*P. inornatus*), and Willow Tits (*P. montanus*). These species spend the winter in pairs, rarely form larger conspecific groups, and participate in mixed flocks when they are present within a pair's territory. Saitou (1978) tentatively classified Tufted Titmice as a species of the first category. Our data indicate that Tufted Titmice share characteristics of both groups but may be more appropriately assigned to the second group. Six of the 14 flocks in our study were comprised of a single pair whose participation in mixed-species flocks was limited.

In recent years there has been considerable study devoted to determining the advantages of flocking over solitary existence during the non-breeding period. Greater foraging efficiency and/or increased protection from predators are general factors that are most often suggested as advantages of flocking (Krebs et al. 1972, Morse 1977, Rubenstein et al. 1977). Other, more specific, analyses have considered flock-size, composition and movements in relation to rates of inter- and intra-specific aggression (Barash 1974, Caraco 1980) and weather (Grubb 1975).

All of the above advantages and considerations are likely relevant to titmouse flocks; however, there are certain aspects of the flocks that are also related to events in the breeding season. For example, titmouse dominance hierarchy may serve all flock members by reducing intra-specific aggression during a time of energetic stress (Smith 1976). Dominant birds clearly are afforded an additional advantage the following spring by being able to breed before subordinate conspecifics in habitats where nest-sites may be limited (Hardin and Evans 1977) and on areas with which they are familiar.

The asynchrony in initiation of breeding between dominant and subordinate birds was likely due to alpha males' intolerance of other titmice, especially males. This behavior typically resulted in the alpha males and females having sole ownership of the flock range after the groups broke up. Thus, subordinate birds were forced to seek undefended areas. We observed subordinate birds travelling over relatively long distances during this period (Table 3). Some subordinates eventually gained access to a part of their former flock's winter range. A female that is forced to search for a breeding territory and/or a mate may expend energy that might otherwise be allocated to reproduction. Other studies of parids have documented that birds breeding early have greater reproductive success than those that breed relatively late (Perrins 1979).

SUMMARY

Fourteen winter flocks of Tufted Titmice (*Parus bicolor*) were studied in central Missouri from 1977 to 1979. The flocks formed during late September and early October. Flock size ranged from 2–5 individuals ($\bar{x} = 2.9$). Males were more common than females among adults and juveniles.

Six of the flocks consisted of one adult male and one female. The flock structure was generally stable throughout the flocking period. Seven birds disappeared from the flocks during the two field seasons. The intra-flock dominance hierarchies were linearly peck-right. Males were dominant over females. Dominance within a sex appeared to be determined by seniority on the flock territory. Titmice typically travelled alone, in pairs, or in groups of three. Certain pairs preferred specific portions of their flock's range for winter activity. The flocks disbanded during late February and March. In 12 of 14 cases the dominant males and females of the flocks proved to be paired and established breeding territories within the winter flock ranges. Consistently, these pairs were the first or only titmice to breed on the

flock ranges. The asynchrony in the initiation of breeding between the dominant and subordinate birds may be an important aspect of the titmice's winter flock dominance hierarchy.

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