SITE-RELATED DOMINANCE AND SPACING AMONG WINTER FLOCKS OF BLACK-CAPPED CHICKADEES[1]

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Abstract. We studied spacing and social behavior of winter flocks of Black-capped Chickadees (*Parus atricapillus*) in food-supplemented and nonsupplemented (control) areas. Flocks of Black-capped Chickadees did not forage in exclusive areas, unlike most other populations of parids. In winters 1985–1986 and 1986–1987, each of 22 feeding stations in the food-supplemented area was visited by two to 10 flocks. Also, at least 50% (1985–1986) and 33% (1986–1987) of the control area was used by two to seven flocks over the winter. When flocks met, agonistic interactions between members of different flocks were less likely than between members of the same flock, suggesting that flocks were not defending areas. However, when agonistic interactions occurred between flocks, members of resident flocks dominated intruders. This "site-related dominance" may reflect the ability of flocks to space themselves when conditions favor use of exclusive areas.

Key words: Black-capped Chickadee; Parus atricapillus; *territoriality; flock; site-related dominance; spacing; feeding.*

INTRODUCTION

Most studies of agonistic behavior in populations of winter-flocking birds have focused on dominance relationships within flocks (reviewed by Schein 1975, Wilson 1975, and Gauthreaux 1978). Much less is known about the relationships between adjacent flocks, perhaps because of the infrequent encounters between groups, or the lack of recognition of individual groups within large, but temporary aggregations. Additionally, most of the information on interflock relationships comes from populations using supplemented food, which might have influenced spacing (Ekman 1979).

Winter flocks of titmice are generally described as "territorial" (reviewed by Smith and van Buskirk 1988), but studies often failed to assess different definitions of territoriality separately. Kaufmann (1983) identified three widely-used definitions of territoriality: (1) use of defended areas, (2) exclusive use of areas, and (3) site-related dominance. In this paper, we address the three definitions above. We show that, in northern food-supplemented and "control" (not food-supplemented) populations, flocks of Black-capped Chickadees (*Parus atricapillus*) did not

occupy exclusive or defended areas. We describe the relationship between home ranges of winter flocks and the dominance relationships between members of contiguous flocks in our food-supplemented and control areas.

STUDY AREA AND METHODS

This study was conducted at the Meanook Biological Station (54°37'N, 113°20'W), near Athabasca, Alberta, Canada, in the winters 1985–1986 and 1986–1987. The study area is a 500-ha mosaic of aspen (*Populus tremuloides*) woodland interspersed with small fields, and stands of willows (*Salix* spp.; see Desrochers et al. 1988 for more details). From late October to early April each year, half of the study area was provided with 4.5-1 feeders filled with sunflower seeds (feeder area), and the remainder was undisturbed (control area). Nine feeding stations were present in the feeder area in 1985–1986, and 14 in 1986–1987. Several birds could feed at the same time at each feeding station. Feeders were distributed at regular distances along paths. The movement of birds between the two areas was limited as they were separated by fields; however, flocks from woodland adjacent to the outer edge of the study area were drawn in by nearby feeders. Each winter, >95% of our population (ca. 350 chickadees) were captured in mist nets and individually marked with colored leg bands.

We defined "flocks" as groups of chickadees that invariably foraged together throughout winter. Each flock consisted of unrelated (nonsibling)

birds of both sexes (sex ratio approximately 1:1; Desrochers 1988). Mean flock size was 8.1 (range = 3–15, $n = 61$) and did not differ significantly between years (Desrochers et al. 1988) or feeder/control areas (t-test, df = 59, $P = 0.12$). Wintering population densities (about 75 individuals/km²) were also similar between years and areas (Desrochers et al. 1988).

FLOCK HOME RANGES

In winters 1985–1986 and 1986–1987, we identified each member of each group of chickadees encountered. The flock membership apparently stabilized in late October each year, and from November, we recorded the positions of flocks when we positively identified at least three of their known members.

We plotted locations of each flock at least once a week (four to five times a week during most of the winter) on detailed maps of the study area (scale 1:7,500) based on aerial photos. The accuracy of the locations was ±25 m. When we followed a flock (by foot), we generally recorded its location once every 5 min, for periods of 5 min to 3 hr. Such a short interval between observations probably resulted in autocorrelated sightings (Ford and Myers 1981, Swihart and Slade 1985), but we assume this is not critical here, since we neither used minimum convex polygons nor probabilistic home-range models to describe spatial relationships.

We observed 20 "control" flocks in 1985–1986, from October to March, and 22 control flocks in 1986–1987. We also recorded locations of 13 "feeder" flocks in 1985–1986 and 18 in 1986–1987 in an area where we provided supplemental food. We determined the location of home-range centers of each flock by computing the average x and y coordinates of all sightings of each flock (Hayne 1949). We used locations of actual sightings rather than home ranges to estimate spatial overlap between each flock's foraging area. We calculated home-range centers of feeder flocks only from data obtained before they started to use the supplemented food.

SITE-RELATED DOMINANCE

When two or more flocks were found together, we recorded the winner and the loser of all observed agonistic interactions between members of different flocks. Agonistic interactions were either displacements, chases, or unsuccessful attempts to displace a bird. Birds that initiated displacements and chases or whose presence at a feeder made other individuals wait for their departure were considered "winners" (see Dixon 1965, Smith 1984). When a sequence of several consecutive chases or displacements involving the same two birds occurred, only one interaction was recorded. Thus, we considered all the interactions of one particular encounter between flocks as independent.

We observed dominance interactions primarily in the feeder area, where several flocks often used the feeding stations at the same time. We also recorded all interactions between members of neighboring flocks of the undisturbed area, whenever two or more flocks were found together. In three cases, we induced grouping of two flocks in the control area by attracting a flock to a feeder, then carrying the feeder, followed by the flock, to the neighboring flock's range to attract the second flock. The location of all encounters between flocks was recorded on study area maps. Finally, we determined the dominance hierarchy within each flock by recording agonistic interactions between members of the flocks at and away from feeders (Desrochers 1988).

AGONISTIC DEFENSE OF SPACE BETWEEN FLOCKS

If flocks agonistically defend a communal area, then individuals should direct relatively more aggressive behavior towards members of the "intruding" flock(s) than towards the members of their own flock when two or more flocks encounter each other. We noted all the individuals that were displaced or chased by the most dominant bird of the flock closest to the center of its range (resident flock). This was done only in 1985–1986, with flocks on the control area, away from feeders. Observations at feeders were not included, because the frequency of interactions of all birds with the most dominant bird was presumably dependent on the frequency of use of the feeder. Use of feeders was highly variable between individuals.

This method generated frequencies of attacks on (1) "residents" and (2) "intruders" that could be compared to the null hypothesis that target birds were selected independently with respect to flock membership. We concentrated on the most dominant resident bird to standardize the focal bird's rank for all observations and because the most dominant flock member is the only
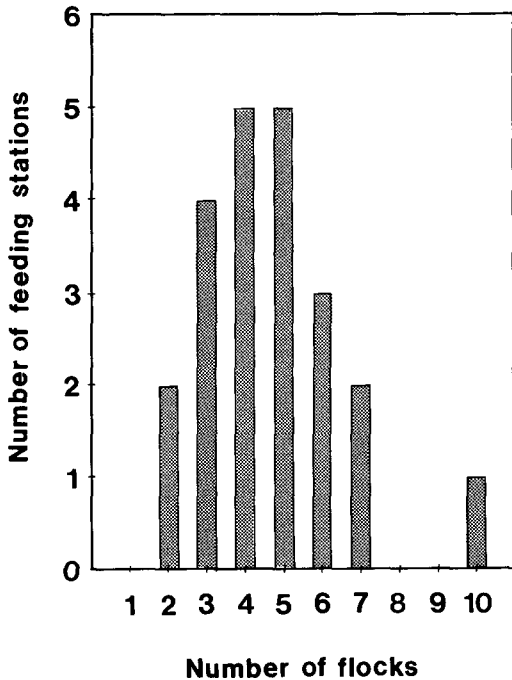
FIGURE 1. Numbers of flocks seen at feeding stations, throughout the winter. All feeding stations represented were used by birds for at least 1 week. Feeders were visited by observers at least 1 hr per week. Data pooled from 1985–1986 and 1986–1987 feeders.
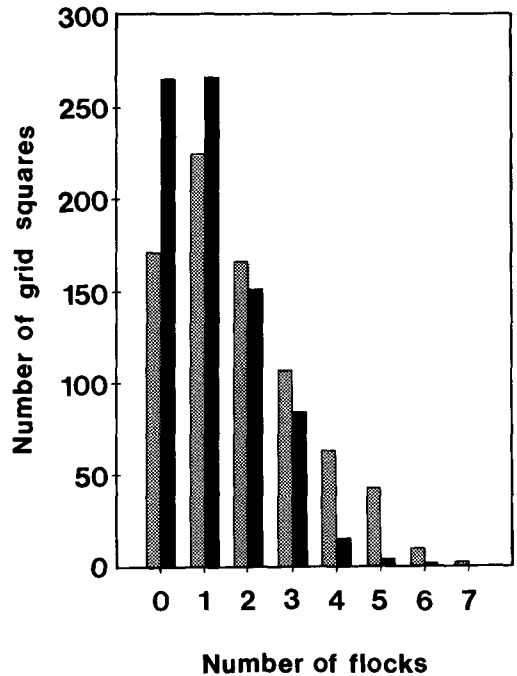

FIGURE 2. Cumulative number of flocks observed on 0.25-ha quadrats in the undisturbed area, in winters 1985–1986 (hatched bars) and 1986–1987 (solid bars). Only quadrats containing woodland were included.

individual that initiates all its interactions with other birds (and thus "chooses" all its targets), due to its highest rank. We used two-tailed statistical tests, and expected proportions of $P = 0.5$ were used as null hypotheses in binomial tests.

RESULTS

SPATIAL OVERLAP BETWEEN FLOCKS

Feeders were not exclusively used by one flock, but shared by all flocks that discovered them (Fig. 1). Similarly, overlap occurred in the control area; at least 50% (1985–1986) and 33% (1986–1987) of 0.25-ha quadrats (woodland only) were used by two or more flocks over the winter (Fig. 2). Spatial overlap between flocks' foraging areas was higher in 1985–1986 than in 1986–1987 (Kolmogorov-Smirnov two-sample test, two-tailed, $n = 1,584, P < 0.001$), suggesting that yearly variation in flock spacing occurred. Since free-roaming flocks usually occupied an area three to four times larger than a quadrat at any one time, one can rule out the possibility of undetected "core areas" within quadrats.

Estimates of overlap between winter home

ranges do not contain information on the dispersion pattern between flocks at any time: despite their overlapping ranges, flocks may avoid each other ("group space": Brown and Orians 1970). Mutual avoidance was probably unimportant in this population, as foraging groups of up to five different flocks were regularly observed. The maximum size of the large temporary groups observed reached 50 individuals in 1985–1986, and 31 individuals in 1986–1987.

SITE-RELATED DOMINANCE

In feeder and control areas the rank of a chickadee within its flock remained constant, regardless of the location of the flock (unpubl. data). However, in groups of two or more flocks at a feeding station, the outcome of agonistic interactions between birds of different flocks was dependent on location. In 29 of 30 instances where ≥ 10 interactions were observed, birds of the flock closest to the center of its home range (resident flock) won more interactions than members of the intruding flock (Sign test, $n = 30, P < 0.001$). Resident birds won 73% of the 1,467 interactions observed.
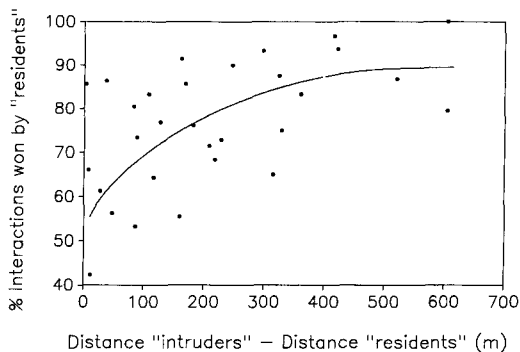
FIGURE 3. Percentage of agonistic interactions won by resident flock members in relation to the difference between the distance of intruders and residents from their respective home-range centers. Curve fitted by hand. Each point represents a percentage of wins generated from at least 10 interactions.

The percentage of wins by residents decreased as residents and intruders became nearly equidistant to their home-range centers (Fig. 3; Kendall's Tau = 0.37, n = 30, P = 0.002). However, if we set the Y-intercept to 50% (i.e., flocks equidistant to the center of their home ranges have similar dominance status when they interact), the relationship in Figure 3 does not appear linear. Figure 3 remains similar when percent wins are plotted against the *ratio* of flock distances instead of the *difference* between flock distances. Residents could win substantially more interactions than intruders even when the difference between the distance of intruders and residents from their home-range centers was less than 100 m. Thus, narrow zones of rapid dominance change were present between home-range centers. Site-related dominance applied to all flock members; the most dominant birds of the intruding flock were displaced by lowest ranking birds of the resident flock in 19 cases.

When flocks encountered each other away from feeders (in the control area), members of resident flocks also won most agonistic interactions against birds of intruding flocks (50 wins vs. 12 losses by birds of resident flocks in 1985–1986, binomial test: P < 0.0001; 61 wins vs. 10 losses in 1986–1987, P < 0.0001).

AGONISTIC DEFENSE OF SPACE
BETWEEN FLOCKS

Although birds of a resident flock were socially dominant to members of intruding flocks and were theoretically able to displace or chase intruders, they directed more agonistic interactions towards the members of their own flock than towards members of intruding flocks, away from feeders. In 1985–1986, when two or more flocks foraged together, "alpha" males initiated 51 interactions towards flock mates vs. 24 interactions towards intruders (binomial test: P < 0.001, controlled for flock size). No data are available for 1986–1987. Whether the high rate of intraflock aggression was due to the members of the same flock being closer to each other (and consequently more likely to interact) than members of different flocks is unknown, but it nevertheless appears that members of different flocks tolerated each other, at least away from feeders.

DISCUSSION

Pitelka (1959) and Schoener (1968) suggested that territoriality should be an ecological rather than a behavioral concept and that only individuals with nonoverlapping home ranges should be called territorial. Kaufmann (1983), however, maintained that agonistic defense of space was a necessary part of territoriality. Using either widely-used definition, chickadee flocks in this study were not territorial, either in feeder or control areas. Flocks were sharing natural and artificial resources, often in large aggregations of several flocks. Also, we found no evidence for higher frequency of agonistic behavior between members of different flocks (compared to within flocks) during flock encounters, despite the site-related dominance. Thus, flocks of chickadees showed a high degree of mutual "tolerance."

The higher interaction rate within flocks possibly reflects the greater importance of maintaining one bird's social status within its flock, since rank within a chickadee flock can determine breeding status (Smith 1976, 1984; Desrochers et al. 1988) and survivorship (Ekman and Askenmo 1984, Smith 1984, Desrochers et al. 1988). It is also possible that members of the same flock were closer to one another than to members of another flock; as nearby individuals are probably more likely to interact than remote individuals, one can argue that this caused the higher interaction rate within flocks. However, we found no evidence of such spatial separation of flocks when two or more flocks met. Instead, flocks seemed to "blend" spatially during encounters.

The broad spatial overlap between flock ranges in our study contrasts with the spacing described in most other North American populations of

parids. Authors of previous studies on Carolina Chickadees, *Parus carolinensis* (Dixon 1963), Mountain Chickadees, *P. gambeli* (Dixon 1965), Tufted Titmice, *P. bicolor* (Condee 1970), and Black-capped Chickadees (e.g., Hartzler 1970, Glase 1973, Smith 1984) found that flocks were using exclusive ranges. The situation is analogous to that in Scandinavia, where Willow Tit (*P. montanus*) and Crested Tit (*P. cristatus*) flocks used exclusive feeding areas (Ekman 1979, Ekman et al. 1981). However, a nonbreeding population of Black-capped Chickadees studied by Smith and van Buskirk (1988) had unstable flocks with ranges overlapping extensively. Great Tit (*P. major*) flocks in Japan (Saitou 1979) also had overlapping home ranges and they often united in large temporary groups of several flocks, similar to ours.

How can we explain the differences in spacing among flocks between populations of Black-capped Chickadees? Food abundance can differ greatly among populations and years, and shortage of food may induce flock spacing (Ekman 1979). We did not find enough variation of spacing between feeder and control areas to support this hypothesis, and Smith and van Buskirk (1988) found no correlation between winter food and territoriality in their review on several populations of wintering chickadees. However, the year with lower overlap between flock ranges (1986–1987) was also a year of lower winter survival (Desrochers et al. 1988), which suggests that the degree of spacing among chickadee flocks may respond to winter food availability.

The difference among studies is possibly an artifact of the method by which flocks and home ranges were defined, as suggested by Smith and van Buskirk (1988). Even if flocks and home ranges are defined similarly, sampling effort may yield different estimates of overlap, since the estimated size of each home range increases logarithmically as a function of the number of sightings (Odum and Kuenzler 1955). Since we used actual locations of sightings rather than home ranges, we had a conservative measure of space use (and consequently range overlap), and it is unlikely that we failed to detect exclusively used areas.

The distribution of food may also affect the "decision" of flock members to defend an area. If resources are distributed heterogeneously, use of exclusive areas may be advantageous to birds that use "high quality" resources (Davies and

Houston 1984). In this case, intrusion by other flocks could deplete these resources more than the "territorial" flock could obtain from other flock ranges. If so, the cost of defense could be offset by the resources gained. However, clumped resources of high quality can attract intruders (e.g., our feeder area drew in peripheral flocks), and the cost of excluding intruders may become higher than the value of the resource defended (Myers et al. 1979). When resources are uniformly distributed and not limited, the net "payoff" to flocks of not defending an area may be higher than the alternative tactic of defense.

Resources in the feeder area were more clumped than in the control area, and not every flock had a feeding station within its initial home range. Thus, one would expect flocks to defend food sources more in the feeder than in the control area. This was clearly not the case, and one possible explanation for this is that intruder pressure varied in parallel to the resource quality and patchiness. This is especially true for our wintering population, because of its high density. Also, concentrated sources of sunflower seeds from feeding stations were practically unlimited. This may have lowered competition for food among chickadee flocks, and in turn lowered the need for exclusive foraging areas.

Unfortunately, the effects of food abundance and intruder pressure are hard to separate, as these two factors are often positively correlated (Davies and Houston 1984, but see Myers et al. 1979 and Mares et al. 1982). The cost-benefit model is further complicated by the effect of temperature: the cost of defense may increase when temperature decreases, since titmice have to feed more and thus have less time for other activities (Perrins 1979). However, the value of resources to survival may also be higher at lower temperatures, making predictions about the relationship between weather and territorial behavior difficult to make.

Although our flocks were not using exclusive or defended areas, they exhibited site-related dominance, which is often viewed as territoriality (e.g., Willis 1968, Kaufmann 1983). Site-related dominance was described in qualitative accounts of chickadee behavior at feeders (Odum 1941, Dixon 1965, Glase 1973). Site-related dominance in our study was not a by-product of food supplementation, as it occurred both at and away from feeding stations. It was not an early manifestation of spring territory defense either,

since it was observed throughout the winter, occurring as early as October. Also, a large number of female and male flock members that did not stay to secure a breeding territory exhibited site-related dominance. Quantitative work on Great Tits (De Laet 1984) also showed that an adult male's dominance status at winter feeders was dependent on its location with respect to its winter home range.

The ecological significance of site-related dominance is not well understood, and it may be the expression of latent spacing behavior when conditions do not favor defense of exclusive areas. In our population, the proportion of wins by residents was in general substantially high, and only a few instances yielded percentages of wins close to 50% (Fig. 3). This suggests that dominance did not follow broad gradients (as flocks moved to and from their center of activity), but instead that there were relatively narrow "boundaries" between adjacent home-range centers in which dominance status of each neighbor changed rapidly. Such narrow interfaces between centers of adjacent home ranges could become true territory borders when conditions would favor use of exclusive, defended areas.

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LITERATURE CITED

BROWN, J. L., AND G. H. ORIANS. 1970. Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. 1:239–262.

CONDEE, R. W. 1970. The winter territories of Tufted Titmice. Wilson Bull. 82:177–183.

DAVIES, N. B., AND A. I. HOUSTON. 1984. Territory economics, p. 148–169. In J. R. Krebs and N. B. Davies [eds.], Behavioural ecology: an evolutionary approach. 2nd ed. Blackwell, Oxford.

DE LAET, J. 1984. Site-related dominance in the Great Tit Parus major major. Ornis Scand. 15:73–78.

DESROCHERS, A. 1988. Ecological correlates of social dominance in winter flocks of Black-capped Chickadees. M.Sc.thesis, Univ. of Alberta, Edmonton, Canada.

DESROCHERS, A., S. J. HANNON, AND K. E. NORDIN. 1988. Winter survival and territory acquisition in a northern population of Black-capped Chickadees. Auk 105:727–736.

DIXON, K. L. 1963. Some aspects of social organization in the Carolina Chickadee. Proc. XIII Int. Ornithol. Congr. (1962): 240–258.

DIXON, K. L. 1965. Dominance-subordination relationships in Mountain Chickadees. Condor 67: 291–299.

EKMAN, J. 1979. Coherence, composition and territories of winter social groups of the Willow Tit Parus montanus and the Crested Tit P. cristatus. Ornis Scand. 10:56–68.

EKMAN, J., AND C. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. Anim. Behav. 32:508–514.

EKMAN, J., G. CEDERHOLM, AND C. ASKENMO. 1981. Spacing and survival in winter groups of Willow Tit Parus montanus and Crested Tit P. cristatus— a removal study. J. Anim. Ecol. 50:1–9.

FORD, R. G., AND J. P. MYERS. 1981. An evaluation and comparison of techniques for estimating home range and territory size. Stud. Avian Biology 6: 461–465.

GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioural dominance. Perspect. Ethol. 3:17–54.

GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. Living Bird 12:235–267.

HARTZLER, J. E. 1970. Winter dominance relationship in Black-capped Chickadees. Wilson Bull. 82: 427–434.

HAYNE, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1–18.

KAUFMANN, J. H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. Camb. Philos. Soc. 58:1–20.

MARES, M. A., T. E. LACHER, M. R. WILLIG, N. A. BITAR, R. ADAMS, A. KLINGER, AND D. TAZIK. 1982. An experimental analysis of social spacing in Tamias striatus. Ecology 63:267–273.

MYERS, J. P., P. G. CONNORS, AND F. A. PITELKA. 1979. Territory size in wintering Sanderling: the effects of prey abundance and intruder density. Auk 96:551–561.

ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee—1. Auk 58:314–333.

ODUM, E. P., AND E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72:128–137.

PERRINS, C. M. 1979. British tits. Collins, London.

PITELKA, F. A. 1959. Numbers, breeding schedule and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61:233–264.

SAITOU, T. 1979. Ecological study of social organization in the Great Tit, Parus major L. III. Home range of the basic flocks and dominance relationship of the members in a basic flock. J. Yamashina Inst. Ornithol. 11:149–171.

SCHEIN, N. W. 1975. Social hierarchy and dominance. Academic Press, San Diego, CA.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.

SMITH, D. C., AND J. VAN BUSKIRK. 1988. Winter territoriality and flock cohesion in the Black-capped Chickadee *Parus atricapillus.* Anim. Behav. 36: 466–476.

SMITH, S. M. 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. Auk 93: 95–107.

SMITH, S. M. 1984. Flock switching in chickadees: why be a winter floater? Am. Nat. 123:81–98.

SWIHART, R. K., AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. J. Wildl. Manage. 49:1019–1025.

WILLIS, E. O. 1968. Studies of Lunulated and Salvin's antbirds. Condor 70:128–148.

WILSON, E. O. 1975. Sociobiology: the new synthesis. Belknap Press, Harvard Univ. Cambridge, MA.