

WINTER SURVIVAL AND TERRITORY ACQUISITION IN A NORTHERN POPULATION OF BLACK-CAPPED CHICKADEES

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ABSTRACT.—We assessed the effects of winter food supplementation on differential survival between sex, age and dominance classes, and the effects of feeding and territorial defense on breeding density in a northern population of Black-capped Chickadees (*Parus atricapillus*). Survival rates were higher in a food-supplemented area than in a control area, which suggests that food abundance limited winter survival. Survival was greater among males than lower-ranking females in 1 of 2 years, and greater in dominants than in subordinates, within sex and age classes. Survival of adults and first-year birds, however, did not differ significantly. In the 2 years of this study, a sharp decline of population size occurred at the onset of territoriality in spring. Birds that disappeared in spring were mainly subordinates of each sex. Breeding densities in control and feeder areas were similar in the two years. Eight of 14 territorial birds removed in 2 years were replaced, implying that a nonbreeding surplus was present in early spring. Received 22 January 1988, accepted 23 June 1988.

SINCE the early days of avian population ecology, there has been controversy over the importance of winter mortality or territoriality in limiting numbers of temperate-zone birds. This controversy is exemplified by studies of parids (e.g. Kluyver 1951, Krebs 1971, Perrins 1979, Jansson et al. 1981, Ekman 1984). Winter food limitation, especially in socially subordinate birds, can limit the size of breeding populations of parids in Scandinavia (Cederholm and Ekman 1976, Ekman et al. 1981, Jansson et al. 1981). Winter roost sites may also limit subsequent breeding densities (Dhondt et al. 1982). However, winter mortality (van Balen 1980, Klomp 1980) is only one of several possible factors limiting breeding tit densities in central Europe (Perrins 1979). Fall territoriality (Kluyver 1971), spring territoriality (Krebs 1971, 1977), and late summer mortality of fledglings (Perrins 1979) also influence the numbers of breeders. Nest-site availability may also limit densities of parids that do not excavate nests (Perrins 1979, Brawn and Balda 1988).

In North America, less is known about factors that limit breeding density of parids (but see

Brush and Stiles 1986 on the effect of summer food abundance). Mountain Chickadees (*P. gambeli*) in California appear to be limited by the number of nest sites (Dahlsten and Cooper 1979). However, breeding numbers of Black-capped Chickadees (*Parus atricapillus*) are usually limited by spring territorial behavior of socially dominant birds (Smith 1967), although no study has demonstrated that individuals are denied access to resources for breeding. Also, most studies of Black-capped Chickadees have been conducted on populations that use feeders, and the impact of supplementary food on survival, territory acquisition, and breeding density is poorly known.

We investigated factors that limit the numbers of breeding Black-capped Chickadees. We compare winter survival rates, territory acquisition rates, and breeding densities of chickadees under natural and food-supplemented conditions in central Alberta, Canada. We also considered factors (age, sex, and dominance status) that determine which individuals are recruited to the breeding population. Finally, we analyze a removal experiment that tested for the occurrence of a floating population in spring.

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STUDY AREA AND METHODS

This study was carried out at the Meanook Biological Station (54°37'N, 113°20'W), near Athabasca, Alberta, Canada, from March 1985 to August 1987. The area of 5.0 km² was a combination of public and pri-

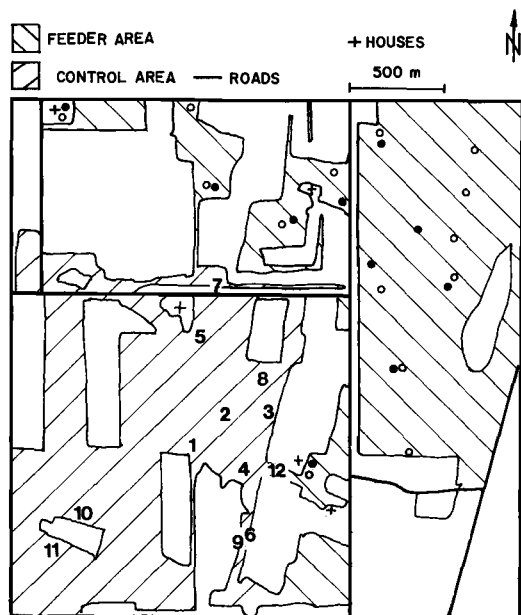


Fig. 1. The Meanook study area. Blank spaces are fields. Circles denote feeding stations (solid: 1985-1986; open: 1986-1987). Numbers refer to individuals removed in spring: 1-4 = females (1986), 5 = male (1986), 6-7 = pairs (1986), 8-12 = females (1987).

vate land. The habitat was a mosaic of poplar (*Populus tremuloides* and *P. balsamifera*) woodland interspersed with fields and stands of willows (*Salix* spp.).

A woodland area of 2.6 km² (fields excluded) was provided with feeders, filled weekly with sunflower seeds, from late October to early April each year, and the remaining woodland area (1.9 km²) lacked feeders (Fig. 1). Each feeding station had 2-4 feeders, and we provided at least 300 kg of seeds each winter. The feeder and undisturbed areas were in the same location in both years and were separated by grain fields. The few birds that visited both control and feeder areas were excluded from the analyses.

In both winters, about 95% of the locally wintering birds were marked with colored leg bands covered with strips of electrician's tape (1 cm long) of the corresponding color to enhance visibility of combinations. Birds were attracted near mist nets with feeders or a recording of chickadee vocalizations. The feeders used in the control area were removed immediately after netting. Most of the banding was conducted before the feeding experiment began each year. Three hundred and twenty marked birds were studied in winter 1985-1986, and 363 in winter 1986-1987. Additionally, 26 birds were captured and marked in early March 1985 for preliminary observations. Birds that were last seen on the day they were handled and birds observed on less than 3 separate days (250 individuals) were considered as transients or possibly

killed by handling and were not included in the analyses.

To determine sex, a discriminant analysis was performed on the combination of body mass, flattened wing length, and the length of the outer right rectrix (Desrochers 1988). Reference samples of 143 females and 171 males (known from their behavior in the breeding season) were used to compute the discriminant function. The function classified correctly 94% of the birds of a sample of 143 known individuals of both sexes other than the reference sample.

Banded individuals known to be more than 1 y old were classified as adults, and unbanded immigrants in summer and fall were considered to be yearlings. We tested this classification by recording the molt of late-summer birds. Yearlings do not replace their rectrices in late summer as do adults (Meigs et al. 1983). None of the unbanded late-summer immigrants observed in both years had a molting tail, unlike late-summer adults.

Flock membership and social status.—We observed flocks on 113 days (September-March) in the first year, and on 128 in the second. Observations were made throughout the day, for ca. 4 h/day. We did not usually search all of the study area on a given day, because of its large size. We observed flocks on 1,525 occasions, for 5-298 min (median 15 min), and until each banded bird was located at least twice. We estimated the number of unbanded flock members. Flock membership became stable in late October. Twenty control and 13 feeder flocks were observed in 1985-1986, and 22 control and 18 feeder flocks in 1986-1987.

Dominance hierarchies were determined in 12 control and 5 feeder flocks in 1985-1986, and in 13 control and 13 feeder flocks in 1986-1987. We used Kaufmann's (1983: 2) definition of dominance, "a relationship between two individuals in which one (the subordinate) defers to the other (the dominant) in contest situations." Four interaction types were considered: displacement of one bird by another, chase, unsuccessful supplanting attempt, and waiting by one bird until another leaves the feeder (Smith 1984). All agonistic interactions seen in flocks at and away from feeders were recorded.

To eliminate confounding effects of rank, sex, and age in the analysis of survival and territory acquisition, we designated as dominant each bird that ranked higher than more than half of its flock-mates of the same sex and age. Other flock members were classified as subordinates. Individuals exactly in the middle of the hierarchy of their sex/age group were termed undefined. Birds that were the only flock members of their category were also assigned an undefined dominance status. Our method of assessing dominance yielded about 30% of birds with undefined dominance status, but it provided a dominance measure less dependent on flock size than ranks.

Temporary feeders were provided to control flocks

to increase the number of interactions observed in the control area. Each of the control flocks had access to a temporary feeder for no more than 5–6 days over the winter. Birds in the control area hoarded seeds from temporary feeders, but they took no more than 5 kg of seeds each year, compared to about 300 kg taken by chickadees in the feeder area. Thus, we assume that our food had little effect on the survival of control birds relative to the effect on experimental birds.

All the interactions recorded for each flock were pooled in a dominance matrix and rearranged to generate dominance hierarchies (Brown 1975).

Survival and territory acquisition.—Black-capped Chickadees are site-tenacious in winter (Weise and Meyer 1979, Loery and Nichols 1985), and we found virtually no unbanded immigrants in areas where all the chickadees were banded in fall. All the chickadees that disappeared during the period of site-tenacity (1 November to 1 March; see below) were classified as dead. Birds that disappeared after this period were considered as either dead or having left the study area. From March to June, all pairs of chickadees remaining on the study area were counted and their positions mapped (61 daily censuses in 1986, 60 in 1987), and as many nests as possible were found. In 1985, we studied breeding pairs in a 1.6 km² portion of the control area.

We analysed the survival data (Table 1) with multidimensional contingency table analysis (MDCTA; Fienberg 1970, Norusis 1986). An advantage of using MDCTAs rather than two-way contingency tables is that it allows for the testing of three-way and higher-order interactions. As in ANOVA, several models can be created that include different combinations of main effects and interaction terms. We used log-likelihood ratios as goodness-of-fit statistics (Sokal and Rohlf 1981) for survival data. Log-likelihood ratios decrease (and fit improves) as the models become more complex. Our model selection method started with the most complex model (all main and interaction terms) and sequentially removed interaction terms that did not contribute significantly to the variation until the remaining model yielded a significant ($P < 0.05$) log-likelihood ratio (Benedetti and Brown 1978). The "best fit" model was the simplest one that allowed for the variation in survival rates among years, feeding conditions, sexes, ages and dominance. Fienberg (1970) and Addicott (1979) provide other examples of the application of MDCTA to ecological data.

We divided the original survival data into 3 nonexclusive subsets: 1) birds of known age, 2) birds of known sex, and 3) birds of known dominance status (Table 2). To avoid having more than 20% of cells with expected values < 5 (Sokal and Rohlf 1981), we pooled sexes and dominance status in the first subset, ages and dominance status in the second, and ages and sexes in the third subset. To facilitate the presentation of the analyses, we abbreviated particular

TABLE 1. Survival rates of Black-capped Chickadees at Meanook, 1985–1987.

	% Survivors (<i>n</i>)	
	Adults	Yearlings
Control 1985–1986	74 (19)	79 (108)
Control 1986–1987	64 (44)	48 (93)
Feeder 1985–1986	50 (2)	91 (89)
Feeder 1986–1987	69 (55)	62 (135)
	Males	Females
Control 1985–1986	79 (75)	82 (66)
Control 1986–1987	64 (70)	44 (64)
Feeder 1985–1986	88 (82)	92 (75)
Feeder 1986–1987	60 (97)	69 (94)
	Dominants	Subordinates
Control 1985–1986	91 (46)	82 (49)
Control 1986–1987	76 (38)	47 (36)
Feeder 1985–1986	96 (26)	89 (18)
Feeder 1986–1987	87 (38)	65 (43)

interaction terms by joining associated variables by a star (*). For example, the interaction between year and survival rate was denoted by (YEAR*SURVIVAL).

Removal experiments.—To determine if there was a nonbreeding surplus present in spring, we mist-netted 4 females and 1 pair (all territorial) from 19–26 April 1986. In addition, 1 male and 1 pair (also territorial) were accidentally caught and killed in stored fish traps at the research station in the first week of May 1986. Between 20 April and 3 May 1987, we removed 5 more females (Fig. 1).

To document the timing of the removals in relation to the breeding of chickadees, we estimated the time of flock "break up" (Odum 1941, Glase 1973) and the time the first egg was laid. Surviving birds were released at least 65 km away, less than 24 h after capture. Daily searches were made for replacement birds during the week following the experiment, and about twice a week in the following 4–5 weeks.

RESULTS

Flock membership and social status.—Flocks had a stable membership from late October to early March in winters 1985–1986 and 1986–1987. Unlike Smith's (1987) population, only 0.6% of 683 individuals in the Meanook area (2 years pooled) were known to switch from one flock to another regularly. Permanent changes of membership from one flock to another occurred twice. Mean flock size was 8.1 individuals in November 1985 (SE = 0.55, $n = 26$) and 8.1 in November 1986 (SE = 0.41, $n = 38$). In winter

TABLE 2. Analyses of the survival rates of chickadees with multidimensional contingency tables (MDCTAs). G^2 is the log-likelihood ratio. Models with $P > 0.05$ were considered to fit the data.

Subset of data	Best-fit model	G^2	df	P
Known age	(YEAR*AREA**AGE) (AREA*SURVIVAL) (YEAR*SURVIVAL)	7.15	5	0.210
Known sex	(AREA*SEX*SURVIVAL) (AREA*YEAR) (YEAR*SURVIVAL)	4.99	5	0.417
Known dominance status	(AREA*SURVIVAL) (YEAR*SURVIVAL) (DOMINANCE*SURVIVAL) (AREA*YEAR)	2.57	7	0.922

* Control or feeder area.

1985–1986, most flocks with members of known age class had only 1 adult pair, unlike winter 1986–1987, when flocks typically had 2 adult pairs. Flock age ratios were not well-known in the feeder area in 1985–1986 because of insufficient census data in summer/fall 1985. Sex ratio in all flocks studied was close to one.

In November and December, several chickadees from neighboring areas discovered the feeder area and settled there for the rest of the winter. These birds were not considered as part of the "feeder" population. Nearly all the unbanded immigrants used feeders on the perimeter of the study area and most likely came from flocks in adjacent areas.

All 24 flocks in which all possible pair-wise interactions were observed (i.e. any 2 individuals were involved in at least 1 interaction) showed a linear hierarchy. Two percent of 7,896

intraflock interactions recorded at feeders were in the opposite direction of that predicted by a perfectly linear hierarchy; only 0.2% of the 825 interactions observed in free-roaming flocks were reversals. All but 1 of the shifts in ranks observed throughout the winter coincided with the disappearance of 1 or more flock members (the rank of birds lower than the missing bird in the hierarchy automatically increased by 1). Males generally dominated females: females "won" only 109 of 3,114 male-female interactions at feeders and only 1 of the 327 male-female interactions away from feeders. Adults always dominated young of the same sex. Females ranked higher than males in only 21 of 462 male-female comparisons in dominance hierarchies. Thus, adult males were generally at the top of hierarchies, followed by yearling males, then adult females and, finally, yearling females.

In 1986 and 1987, the proportion of groups observed that were still in flocks decreased sharply between 20 February and 10 March (from 88–48% in 1986; from 77–25% in 1987; each percentage was based on at least 20 observations). We defined the date of onset of territoriality as the midpoint of the periods of decrease above (2 March each year).

Survival and territory acquisition.—The interaction between year and survival rate was present in the best-fit model for all three subsets of data (Table 2). Survival rates in 1985–1986 were consistently higher than in 1986–1987 (Table 1). Lower survival rates in 1986–1987 were apparently not due to colder weather, since winter 1986–1987 was milder than the previous winter (Table 3). Preliminary data taken at the end of the cold 1984–1985 winter indicated that at least

TABLE 3. Mean monthly temperatures (°C) and cold spells at the Athabasca meteorological station, 14 km from Meanook. Data from Alberta Environment.

	1984– 1985	1985– 1986	1986– 1987	1951– 1980
Month				
Oct.	1.4	3.3	6.1	4.6
Nov.	-11.1	-15.1	-9.7	-6.1
Dec.	-18.1	-8.5	-6.2	-13.8
Jan.	-10.3	-8.1	-7.6	-17.9
Feb.	-14.6	-12.9	-5.4	-11.9
Mar.	-1.8	-0.2	-5.9	-6.4
Apr.	4.2	3.1	6.5	3.4
Average	-7.2	-5.5	-3.2	-6.9
Days below -20.0°C	32	21	2	—
Longest spell (d) below -20.0°C	11	11	2	—

TABLE 4. Net population changes in control and food supplemented areas from November to May. $P > 0.45$ for all comparisons.

	Control population size, 1.86 km ² woodland	Feeder population size, 2.55 km ² woodland	χ^2
1985-1986			
1 November	143	163	
1 March (survivors)	114	144	
15 May (breeders)	64	78	
% change 1 Nov.-15 May	-55.2	-52.2	0.183
% change 1 Mar.-15 May	-43.9	-45.8	0.036
Density (pairs/km ²)	17.2	15.3	0.028 ^a
1986-1987			
1 November	137	192	
1 March (survivors)	73	124	
15 May (breeders)	52	82	
% change 1 Nov.-15 May	-62.0	-57.3	0.564
% change 1 Mar.-15 May	-28.8	-33.9	0.525
Density (pairs/km ²)	14.0	16.1	0.043 ^a

^a Compared to expected densities calculated by dividing the total number of pairs (feeder + control) by the total area (feeder + control) each year.

77% of 26 winter survivors remained to breed, compared to 54% in 1985-1986 and 66% in 1986-1987 ($\chi^2 = 6.98$, $df = 2$, $P = 0.03$). If the proportion of birds that cannot secure a territory increases as winter survival increases, then these percentages suggest that survival was lower in 1984-1985 than in the 2 years of this study. Also, only 14 pairs of chickadees nested on an area censused in summer 1985, compared to 25 on the same area in 1986 and 26 in 1987.

Survival was related to the area where birds spent the winter, as indicated by the association between feeding status ("AREA") and SURVIVAL in all models of Table 2. Birds that used feeders only occasionally were not included in the analyses that compared feeder and control areas. Although this suggests (Table 1) that food addition helped winter survival of chickadees, we cannot conclude this indisputably, because we did not replicate food treatments. Despite higher numbers of winter survivors in the feeder area, we found no difference between the subsequent density of breeding birds in control and food-supplemented woods (Table 4). Also, similar proportions of winter survivors acquired territories in the 2 areas (Table 4).

Adults and yearlings survived equally well, as the AGE factor was not associated with SURVIVAL in the interaction terms of the best-fit model with birds of known age (Table 2). A significant three-way interaction was found between SEX, AREA (feeder or control area), and

SURVIVAL (Table 2). This interaction was possibly the result of the particularly low female survival in the control area in 1986-1987 (Table 1).

Finally, the MDCTA revealed a significant interaction between dominance and survival rate (Table 2). Dominant birds (pooled sex/age classes) had a higher over-winter survival rate than subordinates in both years, with or without feeders (Table 1).

Among the survivors, dominant yearlings of each sex were far more likely than subordinates to acquire a breeding territory, in feeder and control areas, in both years (Table 5, Fig. 2). A MDCTA showed a significant interaction between dominance and territory acquisition in yearlings ($G^2 = 99$, $df = 1$, $P < 0.001$), further supporting the effect of dominance on territory acquisition. There were too few adults of defined dominance status to detect a difference in probabilities of territory acquisition. However, nearly all adults secured a territory (Table 5). In March-April, many banded winter survivors disappeared (125 in 1986 and 76 in 1987), leaving only breeders and a few unpaired birds.

We found no evidence of a spring immigrant acquiring a territory on the study area. During March-April each year, transient unbanded birds were observed on nearly every census day, but their numbers were difficult to estimate, as they were mobile and silent. There were also more than 20 instances of banded birds moving

TABLE 5. Probability of obtaining a territory for dominant and subordinate chickadees that survived the winter. (* = $P < 0.005$, ** = $P < 0.001$.)

	% obtaining territory (n)		χ^2
	Dominants	Subordinates	
All birds			
Control 1985-1986	88 (41)	15 (40)	40.1**
Control 1986-1987	93 (27)	46 (22)	11.0**
Feeder 1985-1986	100 (25)	12 (17)	30.6**
Feeder 1986-1987	91 (33)	50 (26)	10.3*
Yearlings only			
Control 1985-1986	85 (27)	13 (38)	30.5**
Control 1986-1987	100 (17)	20 (15)	18.5**
Feeder 1985-1986	100 (11)	6 (16)	19.6**
Feeder 1986-1987	88 (24)	35 (20)	10.8*
Adults only			
Control 1985-1986	100 (4)	100 (1)	—
Control 1986-1987	80 (10)	100 (7)	NS ^a
Feeder 1985-1986	?	?	? ^b
Feeder 1986-1987	100 (9)	100 (6)	—

^a G-test, with Yates' Correction: $G = 0.26$, $0.5 < P < 0.9$.

^b No data available.

to locations where they had never been seen before (all these birds failed to get a territory in the study area and disappeared). Some unbanded chickadees bred near the perimeter of the study area, but we do not know whether they were unbanded winter residents or spring immigrants (the proportion of unbanded chickadees increased rapidly beyond the perimeter of the study area). Some subordinates must have moved far from the study area. For example, a subordinate yearling female, last seen at Meanoon at 24 March 1987 was observed at a feeder 39 km south of Meanoon on 29 March 1987.

Removal experiment.—Females were removed about 50 days after onset of territoriality, in both years; but removals in 1987 were made closer to initiation of laying than in 1986. Median dates of laying first egg were 3 May in 1987 and 16 May in 1986 (Mann-Whitney U -test, $df = 24$, $P = 0.0003$).

In 1986, 3 females and 2 pairs that were removed were replaced by previously unsettled birds. The fastest replacement occurred 1 day after the removal; and the slowest, 16 days after the removal. Three of these 7 unsettled birds were banded unpaired yearlings that had remained on the study area in the spring. The others were unbanded birds of unknown origin and age. The remaining widowed birds (1 fe-

male and 1 male) were on adjacent territories and formed a new pair, leaving 1 vacant area. In 1987, the outcome differed: only 1 of the 5 females removed was replaced. One widowed male disappeared after singing for several days; another paired with the female of an adjacent pair (leaving the original mate unpaired), but did not breed. Two others stayed on their territories as solitaires. One of these 2 birds was seen once with an unbanded bird, but did not breed. Overall, 8 of 14 birds removed were replaced in 2 years.

DISCUSSION

Winter survival, weather, and food.—Winter temperatures do not generally influence survival of parids in Britain, but survival may decline (Perrins 1979) in severe winters (especially in continental Europe). The winter of 1984-1985 was colder than average, and we suggest that survival may have been low compared to the following 2 winters which were not particularly cold. Nevertheless, winter survival was significantly lower in 1986-1987 than in 1985-1986, and factors other than temperature per se must have been responsible for the differences in survival rates between the two mild winters.

Chickadees in our food-supplemented area had higher survival. Fewer chickadees may have starved in the feeder area, or they may have reduced their foraging time and increased the time spent scanning for and avoiding predators (Jansson et al. 1981, Ekman 1987). Northern Shrikes (*Lanius excubitor*) were common and Northern Hawk-Owls (*Surnia ulula*) were seen occasionally. Both were observed stalking chickadees. Evidence of shrike predation (plucked or impaled remains) of 5 chickadees was found near the forest edge. However, we could not adequately assess the importance of predation on over-winter survival.

Contrary to our results, all winter feeding experiments in Europe, except one on Great Tits (Krebs 1971), produced larger breeding populations in food-supplemented areas (van Balen 1980, and references therein; Jansson et al. 1981). These support Lack's (1964) "winter food limitation" hypothesis. The effect of food on breeding density would be more important when low survival in winter eliminates the local surplus of nonterritorial survivors. Such low survival has never been documented in Black-capped Chickadees (e.g. Odum 1941; Glase 1973; Smith

1967, 1984), and we found a local surplus of nonterritorial birds in both feeder and control areas. In spring 1985 (after a cold winter; Table 3), however, there may not have been a surplus as most birds that survived were later observed breeding.

Differential winter survival among individuals.—Smith (1984) also found no relationship between age and survival in a food-supplemented population. Presumably the experience of adults per se did not confer greater foraging efficiency. If it did, however, it was either not essential to survival or it was offset by some advantage held by yearlings. Foraging ability was not important in determining survival of Scandinavian parids: survival of young was similar to that of adults, when the latter were removed from flocks (Ekman et al. 1981). These results, however, may have been caused by the lower densities of tits after removals (but see Ekman and Askenmo 1984).

If survival rate is a function of only social rank, then survival should decline with decreasing rank. This correlation occurred in a natural population of Willow Tits (*P. montanus*; Ekman and Askenmo 1984), and in other avian species (e.g. Fretwell 1969, Kikkawa 1981, Arcese and Smith 1985). At Meanook, as in other studies of Black-capped Chickadees (e.g. Hamerstrom 1942; Hartzler 1970; Glase 1973; Smith 1976, 1984), males dominated females, and adults dominated young of their sex. If dominance per se influences survival, males should, on average, have higher survival rates than females. We did not find a simple relationship between gender and survival, as male and female rates of survival were similar in 3 of 4 comparisons (Table 1). Relative survival of the sexes was dependent, however, on feeding conditions. Survival rates were higher in areas with supplemental food, and it is not surprising that the difference between survival rates of males and females was lower in the feeder area. This is because superabundant resources reduce competition and presumably the difference between "payoffs" (benefits/costs) to unequal competitors (Wittenberger 1981).

Alternatively, differences in survival of the sexes may be related to sexual size dimorphism (Hamilton 1961, Calder 1974, Wiley 1974). Lehikoinen (1986) found that larger Great Tits survived better than smaller ones in winter. As body size was related to dominance (Lehikoinen 1986), no inference could be made on the

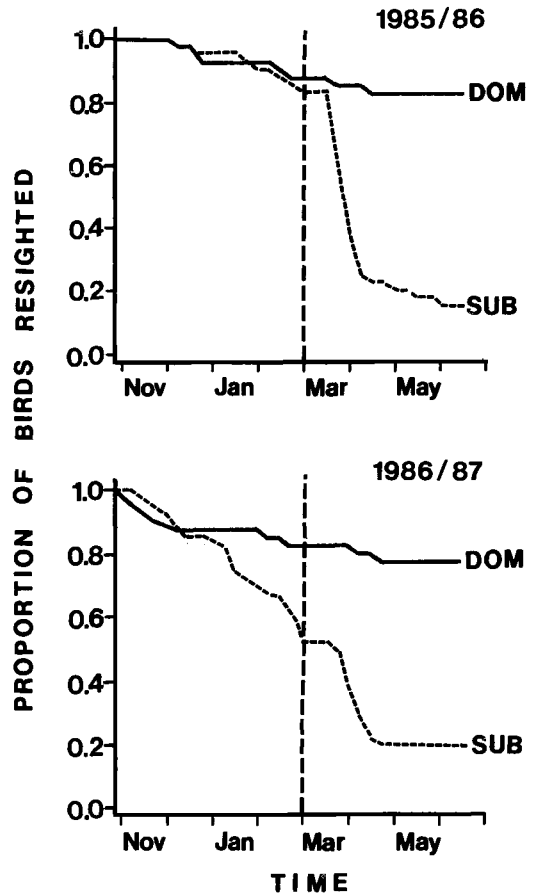


Fig. 2. Proportion of dominant (DOM) and subordinate (SUB) yearling Black-capped Chickadees that survived or stayed in the study area (feeder and control pooled). Vertical lines indicate onset of territoriality. Numbers of birds on 1 November were: 72 dominants and 68 subordinates (1985-1986); 79 dominants and 95 subordinates (1986-1987).

effect of body size alone. Smith (1984) found no relationship between sex and survival in Black-capped Chickadees. As in this study, she found that intrasexual dominance status influenced survival rate (dominant chickadees survived better than subordinates of their sex).

A high reproductive effort of females in summer could decrease their survival in winter. If females invest more than males, they may enter the winter in poorer condition. Yearling males and females which did not breed the previous year had survival rates similar to adults. This indicates that sexual differences in reproductive cost did not affect the relative winter survival of either sex.

We believe that high social rank increased the probability of winter survival in this population. Little is known as to how dominants achieve higher survival than subordinates in winter flocking birds, but exclusion of subordinates from better foraging sites or areas less visited by predators (Ekman and Askenmo 1984, Desrochers in press) and kleptoparasitism by dominants (Rohwer and Ewald 1981) are potentially important factors.

Territory acquisition.—If over-winter survival is high enough to produce more potential breeders than the available habitat can contain, then birds must compete for a territory and some will become floaters. This requirement is true for several bird species (e.g. Wittenberger 1981, Hannon 1983), and anecdotal accounts suggest that it applies to Black-capped Chickadees (Glase 1973; Smith 1967, 1984). As in Glase's and Smith's studies of chickadees, the number of birds at Meanook at the end of winters 1985–1986 and 1986–1987 was substantially greater than the number of subsequent breeders.

Even though nearly all adults became territorial, only dominant yearlings had a high probability of settling in the study area. If most of the surplus winter survivors looked for breeding opportunities later in spring, then all the territorial birds that were removed should have been replaced. This was nearly true in 1986, as only 1 territory remained unused after removals. Krebs (1971) found in Great Tits that replacement birds previously had territories in nearby marginal areas in which breeding success was lower than in optimal habitat. Vacated marginal areas (Krebs 1971) remained unoccupied after desertion by replacement birds. Thus, replacement of removed Great Tits did not demonstrate the existence of a nonbreeding surplus, but it showed the exclusion of some individuals from the best breeding habitat. Later, Krebs (1977) established the presence of a true nonbreeding surplus of Great Tits.

Replacement chickadees were unlikely to have come from nearby marginal areas in Meanook in 1986, because 3 of the replacement birds were banded and nonterritorial before removals. In addition, there was no marginal area comparable to that of Krebs' (1971) study. Clumps of willows were present in the area, but did not contain nest boxes (Krebs 1977) and shrubs were too small to allow excavation of nests. Thus, a nonbreeding surplus was apparently present in 1986.

Surplus Black-capped Chickadees may remain in the area for only a few weeks. The surplus was small or nonexistent about 1 week before laying in 1987, as only 1 of 5 removed females was replaced. Differences in replacement rates between 1986 and 1987 may have been because the breeding season was more advanced at the time of removals in 1987 than in 1986, and surplus birds may have left or died by May 1987. Also, there were fewer subordinate birds of each sex at the onset of territoriality in 1987 (Fig. 2). Lastly, the lower survival rate of females in 1986–1987 may have led to a small or nonexistent surplus of females by the time of breeding.

The gradual decrease of the nonbreeding surplus in spring might have been due to migration, mortality, or simply secretive behavior. Secretive behavior is unlikely. No adults other than the known breeders were observed in late summer flocks, when all chickadees were easily observed. Secretive birds would probably have replaced birds removed early in spring.

Subordinates in winter may have been visitors from more northern populations and returned to their breeding grounds in spring. There is, however, little evidence for cyclic large-scale movements between breeding and wintering grounds in North American parids. Other studies (Odum 1941; Smith 1967, 1984; Glase 1973) failed to demonstrate the arrival of breeding immigrants in spring (but see Odum 1942 for regional movements); moreover, chickadees are winter residents as far north as Fairbanks, Alaska (Kessel 1976) near the edge of their range. Finally, we searched a 25-ha isolated stand of willows near the study area in March to April 1986 and counted only 2–3 chickadees on each of 6 visits. We conclude that willow stands were not used as a buffer area for a large nonbreeding surplus.

We have demonstrated a spring floating population in North American parids. Spring territoriality by dominant Black-capped Chickadees can limit densities of breeders in some years. Nonbreeding chickadees seemed to be gradually eliminated before the laying period. Birds moving to new areas would presumably face costs such as unfamiliarity with new resources and increased energy expenditure (Greenwood and Harvey 1982). Because dead passerines are rarely found in the wild, such costs can lead to high mortality but are hard to document.

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LITERATURE CITED

- ADDICOTT, J. F. 1979. A multispecies aphid-ant association: density dependence and species-specific effects. *Can. J. Zool.* 57: 558-569.
- ARCESE, P., & J. N. M. SMITH. 1985. Phenotypic correlates and ecological consequences of dominance in Song Sparrows. *J. Anim. Ecol.* 54: 817-830.
- BENEDETTI, J. K., & M. B. BROWN. 1978. Strategies for the selection of log-linear models. *Biometrics* 34: 680-686.
- BRAWN, J. D., & R. P. BALDA. 1988. Population biology of cavity nesters in northern Arizona: do nest sites limit breeding densities? *Condor* 90: 61-71.
- BROWN, J. L. 1975. *The evolution of behavior*. New York, W. W. Norton Inc.
- BRUSH, T., & E. W. STILES. 1986. Using food abundance to predict habitat use by birds. Pp. 57-65 in *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates* (J. Verner, M. L. Morrison, and C. J. Ralph, Eds.). Madison, Univ. Wisconsin Press.
- CALDER, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86-144 in *Avian Energetics* (R. A. Paynter Jr., Ed.). Nuttall Ornithol. Club, Publ. 15.
- CEDERHOLM, G., & J. EKMAN. 1976. A removal experiment of Crested Tit *Parus cristatus* and Willow Tit *P. montanus* in the breeding season. *Ornis Scandinavica* 7: 207-213.
- DAHLSTEN, D. C., & W. A. COOPER. 1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and the impact on selected forest insects. Pp. 217-260 in *The role of insectivorous birds in forest ecosystems* (J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, Eds.). New York, Academic Press.
- DESROCHERS, A. 1988. Ecological correlates of social dominance in winter flocks of Black-capped Chickadees. M.Sc. thesis, Edmonton, Univ. Alberta.
- . In press. Sex, dominance and microhabitat use in wintering Black-capped Chickadees: a field experiment. *Ecology*.
- DHONDT, A. A., J. SCHILLEMANS, & J. DELAET. 1982. Blue Tit territories in populations at different density levels. *Ardea* 70: 185-188.
- EKMAN, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). *J. Anim. Ecol.* 53: 119-134.
- . 1987. Exposure and time use in Willow Tit flocks: the cost of subordination. *Anim. Behav.* 35: 445-452.
- , & C. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. *Anim. Behav.* 32: 508-514.
- , G. CEDERHOLM, & 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.
- FIENBERG, S. E. 1970. The analysis of multidimensional contingency tables. *Ecology* 51: 419-433.
- FRETWELL, S. D. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* 40: 1-25.
- GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. *Living Bird* 12: 235-267.
- GREENWOOD, P. J., & P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13: 1-21.
- HAMERSTROM, F. 1942. Dominance in winter flocks of chickadees. *Wilson Bull.* 54: 32-42.
- HAMILTON, T. H. 1961. The adaptive significances of intra-specific trends of variation in wing length and body size among bird species. *Evolution* 15: 180-195.
- HANNON, S. J. 1983. Spacing and breeding density of Willow Ptarmigan in response to an experimental alteration of sex ratio. *J. Anim. Ecol.* 52: 807-820.
- HARTZLER, J. E. 1970. Winter dominance relationship in Black-capped Chickadees. *Wilson Bull.* 82: 427-434.
- JANSSON, C., J. EKMAN, & A. VON BROMSSEN. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* 37: 313-322.
- KAUFMANN, J. H. 1983. On the definitions and functions of dominance and territoriality. *Biol. Rev.* 58: 1-20.
- KESSEL, B. 1976. Winter activity patterns of Black-capped Chickadees in interior Alaska. *Wilson Bull.* 88: 36-61.
- KIKKAWA, J. 1981. Winter survival in relation to dominance classes among Silvereyes *Zosterops lateralis chlorocephala*, of Heron Island, Great Barrier Reef. *Ibis* 122: 437-446.
- KLOMP, H. 1980. Fluctuations and stability in Great Tit populations. *Ardea* 68: 205-224.

- KLUYVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea* 9: 1-135.
- . 1971. Regulation of numbers in populations of Great Tits (*Parus m. major*). Pp. 507-523 in *Dynamics of populations, Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970)* (P. J. den Bower and G. R. Gradwell, Eds.). Wageningen, Pudoc.
- KREBS, J. R. 1971. Territory and breeding densities in the Great Tit. *Ecology* 52: 2-22.
- . 1977. Song and territory in the Great Tit *Parus major*. Pp. 47-62 in *Evolutionary ecology* (B. Stonehouse and C. Perrins, Eds.). London, MacMillan.
- LACK, D. 1964. A long-term study of the Great Tit. *J. Anim. Ecol.* 33: 159-173.
- LEHIKONEN, E. 1986. Dependence of winter survival on size in the Great Tit *Parus major*. *Ornis Fenn.* 63: 10-16.
- LOERY, G., & J. D. NICHOLS. 1985. Dynamics of a Black-capped Chickadee population, 1958-1983. *Ecology* 66: 1195-1203.
- MEIGS, J. B., D. C. SMITH, & J. VAN BUSKIRK. 1983. Age determination of Black-capped Chickadees. *J. Field Ornithol.* 54: 283-286.
- NORUSIS, M. J. 1986. *SPSS/PC+ advanced statistics*. Chicago, SPSS Inc.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee: 1. *Auk* 58: 314-333.
- . 1942. Annual cycle of the Black-capped Chickadee: 2. *Auk* 59: 499-531.
- PERRINS, C. M. 1979. *British tits*. London, Collins.
- ROHWER, S., & P. W. EWALD. 1981. The cost of dominance and advantage of subordination in a badge signaling system. *Evolution* 35: 441-454.
- SMITH, S. M. 1967. Seasonal changes in the survival of the Black-capped Chickadee. *Condor* 69: 344-359.
- . 1976. Ecological aspects of dominance hierarchies in Black-capped Chickadees. *Auk* 93: 95-107.
- . 1984. Flock switching in chickadees: why be a winter floater? *Am. Nat.* 123: 81-98.
- . 1987. Responses of floaters to removal experiments on wintering chickadees. *Behav. Ecol. Sociobiol.* 20: 363-367.
- SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*, 2nd ed. San Francisco, Freeman.
- VAN BALEN, J. H. 1980. Population fluctuations of the Great Tit and feeding conditions in winter. *Ardea* 68: 143-164.
- WEISE, C. M., & J. R. MEYER. 1979. Juvenile dispersal and development of site-fidelity in the Black-capped Chickadee. *Auk* 96: 40-55.
- WILEY, R. H. 1974. Evolution of social organization and life-history patterns among grouse (Aves: Tetraonidae). *Quart. Rev. Biol.* 49: 207-227.
- WITTENBERGER, J. F. 1981. *Animal social behavior*. California, Wadsworth Inc.