

MATE PROTECTION AND WINTER PAIR-BONDS IN BLACK-CAPPED CHICKADEES¹

DAVID LEMMON

Department of Biological Sciences, University at Albany, SUNY, Albany, NY 12222,
e-mail: dl0296@cnsibm.albany.edu

MATTHEW L. WITHIAM

Children's Hospital of Buffalo, Department of Gynecology and Obstetrics, 219 Bryant St., Buffalo, NY 14210

CHRISTOPHER P. L. BARKAN

Research & Test Department, Environmental and Hazardous Materials Division, Association of American
Railroads, 50 F Street NW, Washington, D.C. 20001-1564

Abstract. Black-capped Chickadees (*Parus atricapillus*) that bred together in the spring had significantly higher winter association indices than birds that did not breed together, indicating winter pairing. Most members of winter flocks were paired, and pair members had the same within-sex dominance rank in nine out of ten cases. These results confirm the findings of other studies of wintering chickadees. We report the first quantified example of mate protection in a North American parid. From observations of chickadees visiting feeders in winter, we identified three benefits for females paired to alpha males that are consistent with the hypothesis of mate protection: (1) these females were subject to less intense aggression from their mate, compared with that between other dominants and subordinates. When accompanied by their mate, these females experienced (2) less frequent aggression and (3) maintained a higher feeding rate than other subordinates in the presence of dominant flock members. Chickadees commonly form a "pair-hierarchy" within a flock. We suggest that mate protection has a role in the formation of pair-hierarchies, and that mate protection is the main cause of the overlap in survival rates between the sexes. These results, and this view, suggest that a wintering female's pair bond status may have a greater effect on her fitness than her dominance rank.

Key words: Black-capped Chickadee, dominance rank, mate protection, *Parus atricapillus*, winter association indices, winter pair-bonds.

INTRODUCTION

Pair bonding in birds has been described primarily in the context of the breeding season (Emlen and Oring 1977, Wittenberger 1979, Wittenberger and Tilson 1980). Until recently, less attention has been paid to pair bonds (i.e., close associations) during the nonbreeding season. Winter pair-bonding has been demonstrated in Black-capped Chickadees (*Parus atricapillus*) (Ficken et al. 1981, Smith 1984, 1990), and Smith (1984) has shown that members of the highest-ranked chickadee pair of a flock survive the winter better and are more likely to obtain a breeding territory than members of lower-ranked pairs (also see Desrochers et al. 1988). However, the immediate costs and benefits of the winter pair-bond to each sex, and the nature of the influence of dominance rank, remain to be examined.

Work on a European parid, the Willow Tit (*Parus montanus*), has identified some immediate benefits of winter pair-bonds to females. In Willow Tit flocks, males usually are dominant to females (Hogstad 1987b), and winter survival is closely related to an individual's dominance rank within its sex (Koivula and Orell 1988, Ekman 1990). Nevertheless, female Willow Tits paired to dominant males survive the winter better than some subordinate males that rank above them (Ekman 1984, Hogstad 1989, Ekman 1990). This probably comes about through mate protection. Dominant males appear to protect their mates from aggressive encounters and exposure to predators by excluding other flock members from preferred foraging areas (Ekman and Eskenmo 1984, Hogstad 1988, Ekman 1990, Koivula et al. 1994). Protected females show lower vigilance rates (Ekman 1990, Hogstad 1992) and higher feeding rates (Hogstad 1992) than other subordinates. Dominant males also may directly protect their mates from predators

¹ Received 4 January 1996. Accepted 20 November 1996.

by alarm calling. When presented with a model predator, a dominant male Willow Tit was more likely to give an alarm call if its mate was nearby (Hogstad 1995).

Mate protection has not been demonstrated in North American parids. Smith (1991) cites an unpublished study by J. A. Leak (1986) which describes circumstantial evidence of mate protection (different levels of male aggression toward old and young females), but other causes could not be ruled out. In the present study, we examine the behavior of pair bonded Black-capped Chickadees in winter and evaluate evidence of mate protection.

Wintering chickadees form flocks of up to twelve unrelated individuals, but more commonly six to ten (Smith 1991). Within a flock there is a linear dominance hierarchy in which males are nearly always dominant to females (Glase 1973, Smith 1976), and winter survival is closely linked to dominance rank within a sex (Smith 1984, 1994, Desrochers et al. 1988). Yet, like Willow Tits, females paired to dominant males survive the winter better than some subordinate males (Smith 1984). If female survival is linked to mate protection, then mate protection might be expected to occur in Black-capped Chickadees.

Dominance interactions can be potentially costly in terms of energy and injury, and can determine access to preferred foraging sites. Thus, the frequency, intensity and effectiveness of dominance interactions are likely to influence the relative survival rate of flock members, probably largely through their effects on foraging time (Ekman 1990). For example, the level of aggression experienced by a flock member affects its feeding rate (Hogstad 1992). If mate protection operates in chickadees, we predict that: (1) an alpha male's level of aggression toward his mate would be less than that between other dominants and subordinates, (2) a female accompanied by her alpha mate would be subject to fewer aggressive interactions, and (3) she would maintain a higher feeding rate than other subordinates in the presence of dominant flock members. Predictions (2) and (3) are similar to those of Hogstad (1992).

METHODS

STUDY AREA

The study was conducted at Byron Wood, a 90-ha mixed forest located in Guilderland, Al-

bany County, New York. We captured chickadees during the fall and winter and marked each bird with a unique combination of colored leg bands to allow the identification of individuals. Wingchord length and details of skull ossification were taken at the time of banding. We attached coded flagging tape to trees at regular intervals throughout the study area to serve as landmarks. The study area was surveyed and a scale map constructed, enabling us to plot sightings of chickadees with 10 m accuracy.

We made observations of social dominance interactions and feeding behavior at feeders containing small amounts of sunflower seed fragments. This was the only time supplemental food was provided. Food was available only for a short period on any given day and was never available when association data were collected. Providing food in this way probably had little effect on the chickadees' long-term use of space or association patterns. Additionally, landowners near Byron Wood agreed not to set up feeders for the duration of the study.

FLOCK COMPOSITION

Chickadees were considered members of a flock if they had high association indices (see below) and similar home-range centers (Withiam and Barkan, unpubl. data). We also use the term group for a collection of chickadees, and this is not used synonymously with flock. A group was a temporary assemblage of chickadees, which could comprise all or some members of one flock, or members from several flocks.

ASSOCIATION INDICES

Chickadees found within 20 m of one another were considered associates. We calculated an association index (coincidence index of Dice 1945) for all combinations of birds within each of six flocks (ranging in size from three to eight individuals) using the formula:

$$\text{Association index} = 2H/(A + B),$$

where: H = the number of sightings in which individuals a and b were considered associates, A = the total number of sightings of bird a, and B = the total number of sightings of bird b. An association index of 1.0 indicates that birds a and b were always seen as associates, and an index of 0.0 indicates that birds a and b were never seen as associates.

To minimize any site-dependent bias in esti-

mating association indices, we allocated equal search effort to each hectare of the study area. In the winter of 1983/1984, each hectare was systematically searched five times for a total of 100 (± 15) min. In the winter of 1984/1985 each hectare was systematically searched five to eight times for a total of 110 (± 5) min. All searches were made between January and March, with similar search efforts in each month. When chickadees were sighted, we recorded their location and associations. To assure statistical independence of sightings, we never followed a chickadee group after an encounter. The same group of chickadees rarely was encountered more than once in a particular search. For those that were, we considered them independent sightings only if they were separated by more than 10 min. Over 98% of all sightings were separated by one hour or more.

BREEDING PAIRS

We established the identity of breeding pairs, between April 15–June 30, in several ways. The most important of these was the response of pairs to a tape recording of the chickadee's "fee-bee" song, played systematically throughout the study area. To be classified as a breeding pair, the same two birds had to respond to the recording on at least five different days during the breeding season. The bird that sang when a pair arrived at the tape player was assumed to be male (Ficken et al. 1978, Weise 1979). Pair identity was further confirmed from independent sightings of the male presenting food to the female (Orr and Verbeek 1981). Pairs responded to recordings at a particular site on the study area in a manner consistent with the defense of territories, and incidental sightings of pairs always occurred in the same areas in which they originally responded to the recordings. The sex of individuals was established from breeding pair information and winter dominance rank. Age was determined from skull ossification patterns in the fall.

SOCIAL DOMINANCE

A chickadee's dominance rank within its flock was determined by recording the winners and losers of aggressive interactions at a feeder and entering the outcomes into dominance matrices using the method of Brown (1975). The dominance hierarchy of a *Parus* flock does not change at feeders (Smith 1976, Hogstad 1987b).

During the winters of 1983/1984 and 1984/1985, the collection of dominance data continued until each dyad in a flock showed a statistically significant dominance relationship using a binomial test. During the winter of 1985/1986, a complete record of dominance relationships and home range use patterns was not collected. However, we did obtain significant dominance relationships for all birds used in the estimates of feeding rate (see below).

Four types of aggressive interaction were used to determine dominance relationships: (1) chase; the winner chased the loser away from the feeder with overt aggressive behavior (e.g., calling, wing displays), (2) supplant; the winner displaced the loser from the feeder with overt aggressive behavior, (3) avoid; the winner displaced the loser without overt aggressive behavior, and (4) wait; the winner occupied the feeder while the loser waited nearby (< 3 m); the loser gained access to the feeder only after the winner left. These criteria are similar to those used in other studies of chickadee dominance relationships (e.g., Dixon 1965, Glase 1973). In our analyses, these four dominance criteria were separated into two categories, active (1 and 2) and passive (3 and 4). Active interactions often entailed the aggressor approaching within 1 m of the loser and sometimes resulted in physical contact. We therefore assumed that active dominance interactions were more costly energetically and more likely to result in injury than passive interactions.

FEEDING RATE

Individuals were observed from nine flocks, ranging in size from five to eight members. We estimated the feeding rate of individuals in groups of one to three from film records of their behavior at a specialized feeder. The feeder was a small elevated cup fitted with a cardboard collar to narrow the opening, and contained small fragments of sunflower seeds of a standardized size. The cup was secured to a pole at a height of about 1.4 m and positioned within the home range of each flock in areas with similar amounts of cover. This placement of the feeder controlled for the effects of feeder height (Lendrem 1983) and distance to cover (Caraco et al. 1980) on the time an individual might spend scanning for predators. By observing only small groups, the importance of a central or peripheral position in a flock on predator-scanning behavior

also was minimized (Hamilton 1971, Jennings and Evans 1980).

We characterized the social context for an individual's visit to the feeder in terms of group size (the number of birds within 10 m of the feeder), and the presence or absence of more dominant birds in the group (see below). We filmed feeder visits with a Bell and Howell Super 8 camera. We attempted to film a bird on the feeder for at least 20 sec, but no more than 30 sec, to minimize effects of satiation. For the same reason, birds were not filmed once they had accumulated more than 60 sec of feeder-time during a flock's visit to the feeder. Filming was ended early if a bird was displaced (most common occurrence), group size changed (including a change because another species joined the flock), or an alarm call was given. Repeat filming of a flock was separated by at least two hours. We did not limit filming with respect to time of day or temperature. Feeder visits were filmed at a distance of 20–30 m, without a blind, but in a position partially obscured by vegetation. A bird visiting the feeder could either peck for food (have its head below the rim of the cup), or it could scan (have its head above the rim of the cup). When taking food, its vision was completely obscured by the cardboard collar and walls of the cup. Hence, pecking and scanning were alternating and mutually exclusive behaviors and were easily observable on film during a frame-by-frame analysis.

Using an identical feeder in a laboratory setting, we found a linear relationship between peck rate and food consumption; that is, no correlation was found between peck duration (the time an individual had its head below the rim of the cup) and the mass of food taken ($r_s = -0.143$, $P > 0.05$, $n = 50$). Thus, feeding rate was estimated as the mean of the inverse of the sum of a peck and subsequent scan duration, or pecks sec^{-1} . Feeding rates were log transformed to achieve normal distributions; therefore, geometric means are reported. We compared feeding rates within each group size using independent-sample two-tailed t -tests.

RESULTS

ASSOCIATION INDICES

We obtained association indices for all combinations of two birds within a winter flock. There were four association categories: (a) male-fe-

male mates (birds that bred together the following spring), (b) male-female nonmates (birds that did not breed together the following spring), (c) male-male, and (d) female-female. The mean association index for each of the four association categories is shown in Figure 1. We tested for significantly different means using Duncan's multiple range test for unequal sample sizes (Milton and Tsokos 1983) with arcsine transformed data. Males and females that bred together had a significantly higher mean association index the previous winter than all other association categories ($P < 0.01$ for all comparisons). The mean association indices of the other three categories did not differ significantly from one another ($P > 0.05$ for all comparisons). These data indicate the existence of winter pair-bonds in Black-capped Chickadees.

Chickadee pair bonding appeared to take place mostly in the fall, during the onset of flock formation. Some first-year birds were pair bonded in winter, and some adults were paired with birds other than those with whom they had bred the previous summer. However, pair bonds also could form in midwinter. In two instances, birds that were from different flocks in early winter were later found in the same flock with association indices typical of pair bonded birds. Both pairs bred the following spring. These patterns of pairing are consistent with those generally found in chickadees (Smith 1991).

BREEDING STATUS

Over the course of the study, 20 of the 27 birds for which winter association indices were obtained bred the following summer. In all cases, the members of a breeding pair had been members of the same flock the preceding winter. In nine out of the ten breeding pairs, the male and female had the same within-sex dominance rank; that is, alpha males bred with alpha females, beta males bred with beta females, and so on. This is commonly the case (Smith 1991).

INTENSITY OF DOMINANCE INTERACTIONS

We found a clear dominance-subordination relationship for all dyads in the dominance matrix for each flock. In all flocks, individuals could be ranked in a linear hierarchy within which all males were dominant to all females. This is the usual pattern (Glase 1973), but exceptions can occur (Smith 1991).

The mean proportion of active dominance in-

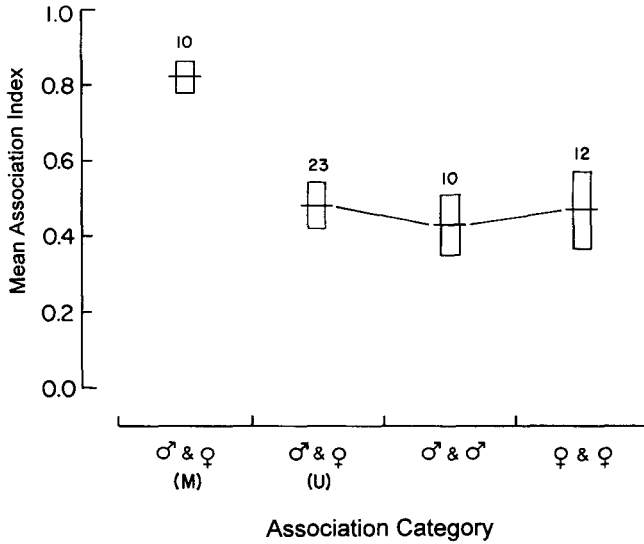


FIGURE 1. Mean association indices (± 2 SE) for wintering Black-capped Chickadees in each association category. Male-female associations are separated into birds that were mated (M) or unmated (U) the following spring. Bars are standard errors, line through bar is mean, and numbers above bars are sample sizes. Means connected by lines do not differ significantly ($P > 0.05$, Duncan's multiple range test).

teractions for each association category is shown in Figure 2. We compared means using Duncan's multiple range test for unequal sample sizes with arcsine transformed data. The mean proportion of active dominance interactions between pair bonded birds was significantly lower than that

for all other association categories ($P < 0.05$ for all comparisons). The means of the remaining three association categories did not differ significantly from one another ($P > 0.05$ for all comparisons). These results support prediction 1: an alpha male's level of aggression toward his

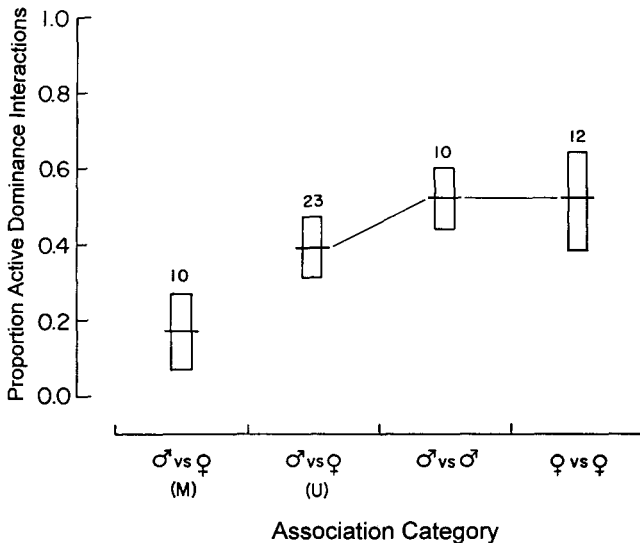


FIGURE 2. Mean proportion of active dominance interactions (± 2 SE) between wintering chickadees in each association category. (M) and (U) are the same as in Figure 1. Numbers above bars are sample sizes. Means connected by lines do not differ significantly ($P > 0.05$, Duncan's multiple range test).

TABLE 1. Distribution of time spent at a feeder in two social contexts by two classes of chickadee: females paired to alphas, and subordinates.

	Time at feeder (sec)				Mean ^a
	1-5	6-10	11-15	16-20	
Solitary					
Paired females	2	1	2	16	15.6
Subordinates	0	2	4	23	16.9
					$P > 0.7$
Social					
Paired females	1	2	1	26	17.4
Subordinates	17	12	5	17	10.1
					$P < 0.001$

^a Mann-Whitney *U*-test was used to test for differences between means.

mate is less than that between other dominants and subordinates.

FREQUENCY OF DOMINANCE INTERACTIONS

Birds usually fed at a feeder until they were displaced by a dominant. Therefore, we estimated the frequency of dominance interactions experienced by individuals from the amount of time they spent at a feeder, using film records of feeder visits. Two categories of individual were filmed: (1) females paired to alphas (the most dominant male of each flock) and (2) subordinates, both in groups of one to three and in specific social contexts. A female paired to alpha could feed solitarily (group size one), with her mate (group size two), or with her mate and another bird dominant to herself, but subordinate to alpha (group size three). Thus, a paired female was always with her mate when feeding socially. A subordinate was any bird subordinate to alpha (except alpha's mate), and, when feeding socially, always in the presence of at least one dominant.

Distributions of the time spent at a feeder by females paired to alphas, and by subordinates, were obtained by grouping visit times into the following intervals (in seconds): 1-5, 6-10, 11-15, 16-20 (Table 1; because filming was ended soon after 20 sec, feeding events longer than 20 sec were included in the last interval). The mean time spent on the feeder was then estimated using the midpoint of each interval. Pair-bonded females and subordinates did not differ in the amount of time spent on the feeder when feeding solitarily (Mann-Whitney *U*-test, $P > 0.7$, Table 1). However, when feeding socially, females paired to alphas spent significantly more time on

the feeder than subordinates (Mann-Whitney *U*-test, $P < 0.001$, Table 1), indicating that paired females were less frequently displaced than subordinates. This result is highly conservative because paired females commonly stayed on the feeder for several minutes, even in a group of three (i.e., when a dominant, apart from her mate, was present). This contrasts with subordinates feeding socially, which rarely stayed for more than 30 sec. These results support prediction 2: a female accompanied by her alpha mate experiences fewer dominance interactions than other subordinates in the presence of dominant flock members.

FEEDING RATE

The mean feeding rates for females paired to alphas and for subordinates in groups of one to three are shown in Figure 3. The social context for each class of individual is the same as that described in the preceding section.

When feeding solitarily, the mean feeding rate of females paired to alphas did not differ significantly ($P > 0.05$) from that of subordinates. But when feeding socially, paired females had a significantly higher feeding rate than subordinates in groups of both two and three ($P < 0.001$ for both group sizes). Paired females had a 15%

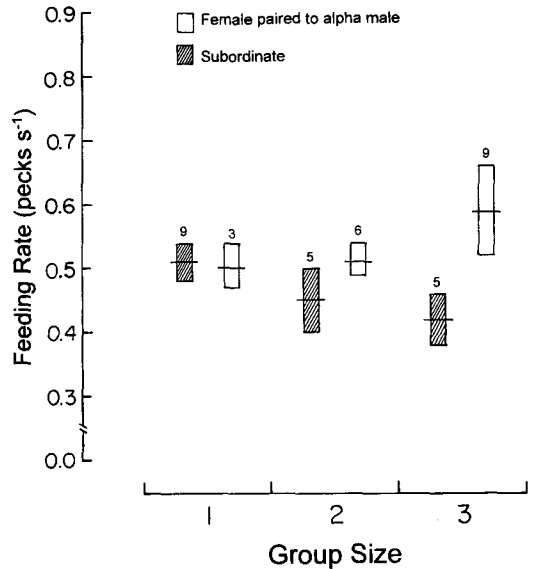


FIGURE 3. Geometric mean feeding rate (pecks sec⁻¹) ± 95% C.L. for two classes of chickadee in groups of one to three: females paired to alphas, and subordinates. Numbers above bars are sample sizes.

higher feeding rate than subordinates in a group of two and a 43% higher feeding rate in a group of three. These results support prediction 3: a female accompanied by her alpha mate maintains a higher feeding rate than other subordinates in the presence of dominant flock members.

Recall that feeding rate (pecks sec^{-1}) is the mean of the inverse of the sum of a peck and subsequent scan duration. Mean peck duration for females paired to alphas and for subordinates did not vary significantly within each group-size, whereas mean scanning duration was significantly shorter for paired females in groups of two and three (unpubl. data). Therefore, the differences in feeding rate when dominants were present (groups of two and three) was due to paired females spending less time scanning than subordinates. That is, paired females had a higher feeding rate because they had a shorter interval between pecks. These differences in feeding rate can be attributed to dominance effects, and not group-size effects, because comparisons were made within a group-size. The higher feeding rate of paired females cannot be explained by their holding a higher dominance rank than the subordinates; on the contrary, 78% of the subordinate feeding rate data were for males, which rank above females.

DISCUSSION

We have confirmed Ficken et al. (1981) and Smith's (1984, 1990) findings that Black-capped Chickadees are commonly pair bonded in winter, and that members of a pair are often matched in dominance rank (Smith 1991). Pairs that bred together were found together in winter over 80% of the time, compared with 40% to 50% for the other association categories. We identified three immediate benefits of the pair bond for females accompanied by their alpha mate: compared with other subordinates in the presence of dominants, these females experienced (1) less intense aggression from a dominant—their mate, (2) less frequent aggression, and (3) a higher feeding rate as a result of less time spent scanning for aggressors. These results represent the first quantified example of mate protection in a North American parid. Wintering female Willow Tits paired to alpha males derive the same benefits we documented for chickadees (Ekman 1990, Hogstad 1992). The Willow Tit studies in-

clude data from birds foraging naturally and visiting feeders.

The benefits to females demonstrated in our study cannot be explained by atypical dominance relationships; as noted, all males were dominant to all females. Neither can our results be explained by males and females being less aggressive toward one another generally, regardless of the pair bond. The proportion of active dominance interactions between nonpaired males and females was significantly higher than the proportion between paired birds (Fig. 2). Although we do not have an estimate of feeding rate for females that were not pair bonded, these females did experience a higher proportion of active dominance interactions than paired females (unpubl. data). Because the level of aggression a chickadee experiences is a good indicator of its feeding rate (Fig. 3), unpaired females probably had a lower feeding rate than females accompanied by their mates, especially those accompanied by alpha males.

The finding that a female accompanied by her alpha mate receives less aggression than other subordinates in a group is not solely a result of reduced aggression by her mate. On several occasions, we witnessed the supplanter of a female paired to alpha being immediately chased by alpha (cf. Ekman 1990). The data on feeding rate (Fig. 3) suggest that such protection forms the larger part of the pair bond benefit. Consider the feeding rate of a female paired to alpha in a group of three. If reduced aggression by alpha was the sole benefit, these females would be expected at best to maintain a feeding rate comparable to a subordinate in a group of two. That is, the effect of the presence of the two dominants on a paired female's feeding rate in a group of three could be discounted by one dominant (her mate). But these females have an elevated feeding rate compared with a subordinate in a group of two—and the difference can be attributed to the presence of alpha. This comparison is not confounded by a positive effect of group-size on the feeding rate of subordinates, because subordinate feeding rate drops across groups of one to three (Fig. 3).

The benefits of mate protection for females appear to operate in the short-term through an influence on survival. From patterns of induced feather growth (indicating nutritional condition) among flock members, Hogstad (1992) demonstrated that mate protection is probably directly

responsible for an enhanced nutritional condition of female Willow Tits paired to alphas. Mate protection appears to influence directly the amount of food available to these females through alpha excluding subordinates from preferred foraging sites (Ekman and Askenmo 1984, Hogstad 1988, Ekman 1990) and foraging close to his mate (Hogstad 1992). Under these circumstances, paired females reduce their vigilance for potential aggressors and thereby increase the time available for foraging (Ekman 1990, Hogstad 1992). There also is some release from vigilance for predators at preferred sites (Ekman 1987). Because winter survival in parids can be directly linked to food availability (Jansson et al. 1981, Desrochers et al. 1988) and its effect on exposure to predators (Jansson et al. 1981), Hogstad's (1992) work provides a strong link between mate protection and the survival of paired females.

For males, benefits of mate protection are probably delayed, while costs (from dominant behavior) are incurred immediately. Maintaining alpha status is costly metabolically (Røskaft et al. 1986, Hogstad 1987a), and there are potential injury costs associated with dominance interactions and predator-alarm behavior. In contrast to females, the benefits of mate protection for males seem to be deferred until the following breeding season. Female parids generally survive the winter less well than their mates (e.g., Ekman 1990), although in Black-capped Chickadees this appears not to be so until after their first breeding attempt (Smith 1994). For male Willow Tits, the loss of a mate could result in the loss of a breeding season (potential mates are scarce due to male-biased sex ratios in the spring [Ekman 1990]). Male chickadees do not face the same problem of replacing a mate (Smith 1991), but finding a replacement or a mate in poor condition could delay the start of breeding (S. Smith, pers. comm.). In Willow Tits, the timing of the start of breeding, and thus the timing of dispersal of young, is important in determining dominance rank (and thereby survival) of young in their first winter (Hogstad 1987b, 1990). Early-arriving young in winter flocks were dominant to those arriving later. The same situation seems to be true for other parids (see Smith 1991), including chickadees (Glase 1973), and especially when there is an opportunity for a young bird to pair with a widowed adult (Smith 1991). It has been noted previously

(Hogstad 1988, Ekman 1990, Hogstad 1992), that by improving the survival chances and overwinter condition of his mate, the male improves his chances of having a mate in the spring, breeding early and producing surviving young.

Mate protection benefits also should accrue to pairs of a lower rank than alpha. Females paired to beta males in the present study appeared to experience less aggression than expected (unpubl. data) and this should translate into a higher feeding rate. Beta male Willow Tits appear to adopt the same predator-warning behavior as alphas in regard to their mates (Hogstad 1995). Because members of chickadee pairs usually match in rank (alpha with alpha, beta with beta, etc.), Smith (1991) suggested that the structure of a chickadee flock might be seen more usefully as one of a hierarchy of pairs rather than one of individuals. Hogstad (1987b) and Ekman (1990) viewed Willow Tit flocks as comprising subunits of pairs matching in rank. Mate protection may have a role in this pattern of pairing. Several factors (e.g., age, size) affect a female's dominance rank (Smith 1991), but the effect of her mate's rank and associated protection behavior may supersede other factors that ordinarily determine her rank. There are examples of young female chickadees being dominant to older females when the young birds are paired with alpha males (e.g., Glase 1973, Ficken et al. 1990). In Willow Tits, Hogstad (1987b) showed that the rank of juvenile females correlated with that of their mate, regardless of the body size of the females. Moreover, Hogstad found that the rank of a juvenile female could be lowered by the removal of her mate. Through its influence on female rank, male mate protection may thus influence the pairing pattern. The effect of mate protection on rank usually would be limited to just the female hierarchy because male and female ranks do not overlap as a rule. Exceptions to this ranking (when a female is dominant to a male) often involve age differences, but not always (Smith 1991), and in either situation mate protection could still play a role.

Mate protection appears to exert its largest influence on female survival, and we suggest that it is the main cause of the pattern of overlap in survival between the sexes. Unlike dominance rank, male and female survival rates usually overlap to an extent in both chickadees and Willow Tits (Ekman 1984, Smith 1984, 1994, Hogs-

tad 1989, Ekman 1990). In chickadees, members of the dominant pair survive the winter better than members of lower-ranked pairs (Smith 1984). Ekman (1990) found a similar survival ranking in Willow Tits. Mate protection probably explains this overlap in male and female survival: benefits gained by paired females (elevated feeding rate, reduced predation risk) translate into survival rates above those expected from their dominance ranks alone. Due to the influence of mate protection on female rank and survival, the pattern of survival between the sexes more closely matches that predicted by a flock structure of pairs than one of individuals.

Chickadees commonly pair for life (Smith 1991), and it seems likely that mate protection fosters such long-term pair bonding. For species that show mate protection, this behavior probably contributes to the enhanced reproductive success found of pairs that breed together season after season (see Rowley 1983).

The phenomenon of mate protection might be a general one among species that remain in pairs in dominance-structured groups during the nonbreeding season. Benefits of mate protection have now been documented in passerines, but similar results exist for another group. In winter flocks of waterfowl, females accompanied by their mates have a greater success in dominance interactions (Scott 1980, Afton and Saylor 1982, Paulus 1983) and higher feeding rates (Scott 1980, Afton and Saylor 1982) than females that are not paired. It may prove common to find that a female's pair-bond status in a flock during the nonbreeding season has a greater effect on her fitness than her dominance rank.

ACKNOWLEDGMENTS

K. P. Able, N. K. Bhagabati, J. L. Brown, T. Caraco, W. G. Ellison, S-H. Li, B. Shao, S. Smith, and two anonymous reviewers provided helpful discussion and/or comments. We are grateful to K. Beal, B. Shao, and J. Chen for statistical advice. K. P. Able, J. L. Brown, and T. Caraco kindly lent equipment. We thank R. and M. Thorstenson, G. Fleweling, K. and J. Glastetter, and especially R. and G. Byron for their friendly cooperation and generous use of their land. We are grateful to E. L. Barkan for her tolerance of early mornings and snowy boots. M. L. Withiam thanks E. M. Spiegel for help and support during the study. This research was supported by NSF grants BNS-8418714 to T. Caraco, BNS-8410123 to J. L. Brown, and BSR-8313495 to C. P. L. Barkan. D. Lemmon and C. P. L. Barkan thank the American Ornithologists' Union's Van Tyne Fund and the American Museum of Natural History's Frank M. Chapman Memorial Fund for support.

LITERATURE CITED

- AFTON, A. D., AND R. D. SAYLER. 1982. Social courtship and pair bonding of Common Goldeneyes, *Bucephala clangula*, wintering in Minnesota. *Can. Field-Nat.* 96:295-300.
- BROWN, J. L. 1975. The evolution of behavior. Norton, New York.
- CARACO, T., S. MARTINDALE, AND H. R. PULLIAM. 1980. Avian time budgets and distance to cover. *Auk* 97:872-875.
- 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.
- DICE, L. R. 1945. Measures of the amount of ecological association among species. *Ecology* 26:297-302.
- DIXON, K. L. 1965. Dominance-subordination relationships in Mountain Chickadees. *Condor* 67:291-299.
- EKMAN, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate zone Willow Tit *Parus montanus*. *J. Anim. Ecol.* 53:119-134.
- EKMAN, J. 1987. Exposure and time use in Willow Tit flocks: the cost of subordination. *Anim. Behav.* 35:445-452.
- EKMAN, J. 1990. Alliances in winter flocks of Willow Tits: effects of rank on survival and reproductive success in male-female associations. *Behav. Ecol. Sociobiol.* 26:239-245.
- EKMAN, J., AND C. ASKENMO. 1984. Social rank and habitat use in Willow Tit groups. *Anim. Behav.* 32:508-514.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215-233.
- FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. *Auk* 95:34-48.
- FICKEN, M. S., C. M. WEISE, AND J. W. POPP. 1990. Dominance rank and resource access in winter flocks of Black-capped Chickadees. *Wilson. Bull.* 102:623-633.
- FICKEN, M. S., S. R. WITKIN, AND C. M. WEISE. 1981. Associations among members of a Black-capped Chickadee flock. *Behav. Ecol. Sociobiol.* 8:245-249.
- GLASE, J. C. 1973. Ecology of social organization in the Black-capped Chickadee. *Living Bird* 12:235-267.
- HAMILTON, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.* 31:295-311.
- HOGSTAD, O. 1987a. It is expensive to be dominant. *Auk* 104:333-336.
- HOGSTAD, O. 1987b. Social rank in winter flocks of Willow Tits (*Parus montanus*). *Ibis* 129:1-9.
- HOGSTAD, O. 1988. Rank-related resource access in winter flocks of Willow Tit *Parus montanus*. *Ornis Scand.* 19:169-174.
- HOGSTAD, O. 1989. Subordination in mixed-age bird flocks—a removal study. *Ibis* 131:128-134.
- HOGSTAD, O. 1990. Natal dispersal and settlement of

- juvenile Willow Tits *Parus montanus* in winter flocks. *Fauna norv. Ser. C, Cinclus* 13:49–55.
- HOGSTAD, O. 1992. Mate protection in wintering Willow Tits *Parus montanus*. *Anim. Behav.* 43:323–328.
- HOGSTAD, O. 1995. Alarm calling by Willow Tits, *Parus montanus*, as mate investment. *Anim. Behav.* 49:221–225.
- JANSSON, C. J., J. EKMAN, AND A. VON BRÖMSEN. 1981. Winter mortality and food supply in tits *Parus* spp. *Oikos* 37:313–322.
- JENNINGS, T., AND S. M. EVANS. 1980. Influence of the position in the flock and flock size on vigilance in starlings *Sturnus vulgaris*. *Anim. Behav.* 28:634–635.
- KOIVULA, K., K. LAHTI, S. RYTKÖNEN, AND M. ORELL. 1994. Do subordinates expose themselves to predation? Field experiments on feeding site selection by Willow Tits. *J. Avian Biol.* 25:178–183.
- KOIVULA, K., AND M. ORELL. 1988. Social rank and winter survival in the Willow Tit *Parus montanus*. *Ornis Fennica* 65:114–120.
- LENDREM, D. W. 1983. Predation risk and vigilance in the Blue Tit *Parus caeruleus*. *Behav. Ecol. Sociobiol.* 14:9–13.
- MILTON, J. S., AND J. V. TSOKOS. 1983. Statistical methods in the biological and health sciences. McGraw Hill, New York.
- ORR, G. D., AND A. M. VERBEEK. 1981. Female demands: some fitness implications in chickadee flocks. *Can. J. Zool.* 62:2550–2552.
- PAULUS, L. 1983. Dominance relations, resource use, and pairing chronology of Gadwalls in winter. *Auk* 100:947–952.
- RØSKAFT, E., M. JÄRVI, M. BAKKEN, C. BECH, AND R. E. REINERTSEN. 1986. The relationship between social status and resting metabolic rate in Great Tits (*Parus major*) and Pied Flycatchers (*Ficedula hypoleuca*). *Anim. Behav.* 34:838–842.
- ROWLEY, I. 1983. Re-mating in birds, p. 331–360. In P. Bateson [ed.], *Mate choice*. Cambridge Univ. Press, Cambridge.
- SCOTT, D. K. 1980. Functional aspects of the pair-bond in winter Bewick's Swans (*Cygnus columbianus bewickii*). *Behav. Ecol. Sociobiol.* 7:323–327.
- 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 floater? *Am. Nat.* 123:81–98.
- SMITH, S. M. 1990. Winter replacement rates of high-ranked chickadees vary with floater density, p. 453–460. In J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery [eds.], *Population of passerine birds, an integrated approach*. Springer-Verlag, Heidelberg.
- SMITH, S. M. 1991. *The Black-capped Chickadee*. Comstock Publishing, Ithaca, NY.
- SMITH, S. M. 1994. Social influences on the dynamics of a northeastern Black-capped Chickadee population. *Ecology* 75:2043–2051.
- WEISE, C. M. 1979. Sex identification in Black-capped Chickadees. *Milwaukee Fld. Sta. Bull.* 12:16–19.
- WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals, p. 271–349. In P. Marler and J. Vandenbergh [eds.], *Handbook of behavioral neurobiology*. Plenum Press, New York.
- WITTENBERGER, J. F., AND R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. *Annu. Rev. Ecol. Syst.* 11:197–232.