

Social rank influences conspicuous behaviour of black-capped chickadees, *Parus atricapillus*

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Abstract. This study on black-capped chickadees, *Parus atricapillus*, assesses whether social rank influences the behaviour of chickadees in predator situations. Chickadee flocks were restricted to an area of an outdoor aviary containing no vegetative cover to ensure that all flock members were equally exposed to potential danger. Each flock was presented with two different predator stimuli and one control stimulus. All flocks formed stable, linear hierarchies and there appeared to be dominance-related risk-taking. After hearing hawk vocalizations, the chickadees uttered 'seeet' alarm calls and all birds became immobile (froze), but subordinate and middle-ranked birds (subdominants) typically were the first to break the freeze. No differences were found for the 'seeet' alarm call. When exposed to a hawk mount, all birds gave repeated 'chick-a-dee' calls but subdominants consistently gave the call sooner than their dominant flockmate. These results could not be attributed to a bird's sex. It is suggested that greater risk-taking by subdominants could be one mechanism causing higher rates of winter mortality among low-ranking birds in free-ranging chickadee flocks.

Although individuals may reduce their risk of being preyed upon by forming groups (Edmunds 1974; Bertram 1978; Barnard 1983), all group members may not benefit equally. In some species, an individual's risk of predation is related to social rank. Winter mortality in black-capped chickadee, *Parus atricapillus* (Glase 1973) and willow tit, *Parus montanus* (Ekman & Askenmo 1984) flocks is higher for subordinates than dominants, and there is evidence that subordinate birds are preyed upon more often than dominants (Ekman et al. 1981). Predation rates could be influenced by at least two factors, including an individual's location within the group (Hamilton 1971; Powell 1974; Lazarus 1978; Jennings & Evans 1980) and how conspicuously it behaves in the presence of a predator (Sherman 1977).

Subordinate chickadees and willow tits may be relegated to more exposed areas within the flock (Glase 1973; Ekman 1987) and therefore are expected to scan more than dominants (Ekman 1987) because scanning levels increase as exposure (Caraco 1979) and predation risk (Lendrem 1983) increase. Ekman (1987) found that subordinates

in free-ranging willow tit flocks spent more time scanning than dominants. However, no association between scanning levels and social rank was found in a different willow tit population (Hogstad 1988) or in captive blue tit, *P. caeruleus*, flocks (Hegner 1985).

Conflicting results have also been found regarding whether subordinates behave more conspicuously in the presence of a predator. Several studies have demonstrated that individuals in flocks of great tits, *P. major* (De Laet 1985), blue tits (Hegner 1985) and willow tits (Hogstad 1988) will become immobile (i.e. freeze) once a predator has been detected and that the subordinate group member is the first to return to a feeder once the predator has moved out of sight. In contrast, among captive willow tits (Alatalo & Helle 1990), dominant individuals have been found to utter alarm calls more often than subordinates.

Winter flocks of black-capped chickadees may freeze and give high frequency alarm calls ('seeet', Marler 1955; or 'high zee', Ficken et al. 1978) when a predator has been detected (Ficken & Witkin 1977). Chickadees also give 'seeet' calls when the predator is out of sight (Ficken & Witkin 1977). Giving the 'seeet' call and being the first to break the freeze are conspicuous behaviour

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patterns that may involve risk (Hegner 1985; Alatalo & Helle 1990), especially if performed when the predator has moved out of sight but, in fact, has not departed (Hegner 1985). No study has examined the sequence of resumed movement in groups of chickadees.

Winter flocks of chickadees may also respond to a predator by moving about rapidly and giving repeated chick-a-dee calls. This call is loud and easy to locate (see Latimer 1977) and attracts conspecifics and heterospecifics to the vicinity of the predator (see Pettifor 1990). Chick-a-dee calling in this context is typically followed by the alarm calling of other species. Individuals that initiate chick-a-dee calling may be more conspicuous to a predator than individuals that are initially silent and only join in chick-a-dee calling later.

Attempts to explain why subordinate group members are preyed upon more often than dominants have focused on the spatial relationships of individuals within the group (Glase 1973; Ekman 1986, 1987). In this study, we present mock predators to flocks of black-capped chickadees in order to examine whether there is any relationship between social rank and conspicuous behaviour in an environment that controls for differences in location within the flock.

METHODS

In winter, black-capped chickadees form non-kin flocks that defend an area on which they forage and roost (Glase 1973). Flock sizes vary from a mean of 2.9 (Smith & Van Buskirk 1988) to 11.2 individuals (Smith 1984). Flocks form linear, stable hierarchies in which males are typically dominant to females, and, within each sex class, adults are dominant to juveniles (Glase 1973).

Subjects and Housing

Experiments were conducted on eight captive flocks, each composed of three black-capped chickadees, at Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34'N, 76°19'W) between October and December 1989. To decrease the possibility that captive flock members were familiar, related, or mates, each flock member was caught (using live

traps) from a different feeder location ranging from 4 to 16 km from the field station.

Birds were sexed using flattened wing length, rectrix length and body weight (following Glase 1973; Desrochers 1988), aged using rectrices (following Meigs et al. 1983), and banded with an aluminium Canadian Wildlife Service band and three colour bands in unique combinations. A 2-cm strip of coloured electrician's tape was fastened to all leg bands and non-toxic paint was dotted in two places on the bird's breast. Each flock member was randomly assigned, without replacement, to one of four possible colours of tape and paint (yellow, blue, red, green).

To create each flock, three birds were released into one of three large (5 × 3 × 2.5 m) outdoor aviaries simultaneously to avoid the potentially confounding effect of prior residency. Birds were given snow, grit and sunflower seeds *ad libitum* (except when conducting hierarchy observations, see below), and nine mealworms per day. We used three-member flocks because it was the maximum number of individuals we could observe simultaneously (see below). Linear hierarchies with stable social relationships have been found in chickadee flocks consisting of two to three individuals (Brown 1975).

Aviaries were separated from each other by more than 300 m. They were constructed of a wooden roof, frame, and 2 × 1 m door overlaid with 6.3 mm hardware-cloth. The interior of the aviary was layered with black fibreglass screening to protect the birds from injury and exposure to wind. Each aviary was divided into two compartments by a door which opened and closed manually. One compartment was one-third the size of the aviary and contained cedar trees and nest-boxes that birds used for cover and roosting. The other compartment was used to conduct experiments and contained a wooden feeder platform (12 × 12 cm) which was nailed onto a stand (1 m high), four bare tree branches (averaging 1 m in height) that served as perches, one hanging perch (33 cm in length), and a stand (2 m high) situated about 1.75 m from the feeder that we used to mount the hawk model. We controlled for an individual's location within the group by keeping the experimental area free of cover, ensuring that all perches and stands were situated only along the perimeter of the experimental area, and by varying the location of perches and the hawk stand (the feeder was stationary) before each trial.

Experimental Procedure

We used three types of experimental stimuli: (1) hawk playback; (2) control playback; and (3) hawk mount. Eight flocks experienced all three stimulus types with the exception of one flock for which the hawk mount trial was interrupted. Each flock was exposed to a different stimulus type every day for 3 consecutive days beginning on the fifth day of captivity. We attempted to balance the order of stimulus presentation among flocks so that all possible orders ($N=6$) were used at least once.

Trials were conducted between 0730 and 0930 hours. Before each trial, we restricted each flock to the experimental compartment of the aviary for 15–60 min. We permitted access to the roosting compartment after each trial was complete. We continuously recorded observations from a blind located 2 m from the aviary using a Sony Walkman (WM-D6C) and lapel microphone.

We measured the following patterns of behaviour: 'seeting', chick-a-dee calling, movement, and scanning. Birds were considered to have uttered a chick-a-dee call if they gave any one, or a combination of the four note types (A, B, C and D) that comprise this call (Ficken et al. 1978). We assessed movement by calculating the number of times each individual moved from one perch to another or moved two body lengths along the same perch. We measured scanning only during active foraging (when an individual took a seed). The individual's behaviour was noted every 2 s (timed by a digital metronome) and classified as scanning if the bill was at or above the horizontal line parallel with its eye, as feeding if the bill was below the horizontal, or as shifting if the bird was in the process of changing its position within the aviary (Lendrem 1983; Hogstad 1988; Ekman 1987). We then calculated the amount of time an individual spent scanning by dividing the number of scanning events by the total number of 2-s observations.

Hawk playback

To assess responses to a predator that was obviously in the area but not in view, we exposed each chickadee flock to one of three possible red-shouldered hawk, *Buteo lineatus*, playbacks. Each playback contained the vocalizations of a different individual and we attempted to balance

the assignment of playbacks among flocks. We placed an Aiwa SC-A8 broadcast speaker in one of four randomly assigned positions on the aviary roof and subsequently restricted birds to the experimental area. Prior to observations, the observer sat behind the blind for 5 min and then began the trial.

We monitored the behaviour of flock members before, during and after the stimulus presentation. Before the stimulus presentation, we observed each flock member sequentially for two separate, 3-min intervals and measured 'seeting', chick-a-dee calling, movement and scanning, as well as aggressive interactions (including chases and displacements). The sequence of observation within the flock was assigned at random.

We then presented the red-shouldered hawk playback (broadcast at 90 ± 4 dB, from 1 m) for 12–14 s. All chickadees were observed simultaneously once the playback began until the sequence of resumed movement (i.e. breaking the freeze) occurred. A bird was considered to have resumed movement once it moved at least two body lengths within a 5-s period. During the stimulus period, we also measured all 'seeting' and chick-a-dee calling by individuals. The 'during' period ended once all birds had resumed movement.

In the 'after' period, we followed the same procedure described for the 'before' period except that we observed each flock member for six separate, 1-min intervals. We decreased the focal-time interval to avoid the possibility that the first bird sampled would behave differently from the last because birds may return to baseline rates of behaviour only as time passes.

Control playback

The control playback consisted of a recorded series of purple finch, *Capodacus purpureus*, vocalizations. Five separate recordings were used each from a different individual, otherwise, the methodology was the same as for the hawk playback trials.

Hawk mount

To assess responses to a predator perched in full view, we presented chickadees with a taxidermic model of a sharp-shinned hawk, *Accipiter striatus*, mounted in a perched position. The observer

covered the hawk mount with a paper bag, took it into the aviary, and placed it on a stand. Two pieces of twine were attached to the bag and run along the aviary ceiling to the observer's blind so that the mount could be uncovered from the blind. Birds were then placed in the experimental area. Prior to observations, the observer sat behind the blind for 5 min and then began the trial.

We monitored the behaviour of flock members before, during and after the stimulus presentation. The 'before' period followed the same procedure described above.

During the stimulus presentation, we uncovered the mount and sampled the birds simultaneously to determine the sequence in which they gave the chick-a-dee call. Once all group members had uttered the chick-a-dee call, we observed the behaviour of each flock member for three separate, 40-s intervals with the order of observation randomly assigned. We recorded all 'seeeting', chick-a-dee calling, and movement of focal birds. Because birds were never observed to eat seed in the 'during' period, scanning could not be recorded. We observed the birds for a total of 6 min at which time we re-covered the mount and continued observations for the 'after' period as described previously.

Determining Hierarchies

The social hierarchy was determined after a flock had experienced all treatments (day 8 of captivity) to decrease the possibility that the observer was aware of the social rank of birds while conducting experiments. Food was removed at 1500 hours on days preceding hierarchy observations. Each flock was observed for two, 30-min periods every day at 0800 and 1100 hours, for a total of 5 days. We calculated wins and losses by observing aggressive interactions at the feeder. A winner was any individual that chased or successfully displaced another flock member (Smith 1984). We tallied the number of encounters each bird won or lost and arranged each score in a hierarchy matrix so that each bird's rank reflected the number of individuals it dominated (Brown 1975). To assess whether hierarchies were fluid before this time, we compared these data with those collected during the experimental period. We did not expect social relationships to be fluid because free-ranging chickadee flocks form stable

hierarchies (Glase 1973), and captive black-capped chickadee flocks consisting of five members had been found to form dominance relationships within 1 week (Nowicki 1989). We also recorded the number of seeds taken by birds and calculated individual feeding rates to determine whether the amounts of food obtained differed among birds of different rank (see Discussion). Once all observations for a flock were complete, we removed the coloured electrician's tape from the birds' leg bands and released the birds in the area in which they were caught originally.

RESULTS

Responses to Experiments

Birds typically froze at the onset of the hawk playback. Rates of 'seeeting' varied significantly over the course of observations only in the hawk playback experiment (Table I), with birds 'seeeting' at a higher rate during hawk playbacks than either before (Tukey-type post hoc, in Zar 1984, $P < 0.05$) or after ($P < 0.05$) presentation. Birds 'seeeted' in all eight trials, but only one (in six trials) or two (in two trials) individuals in each flock uttered 'seeets'.

Birds were clearly more alarmed after hearing the hawk than the control vocalizations. They 'seeeted' at a higher rate (Wilcoxon matched-pairs signed-ranks, $t=3$, $N=8$, one-tailed $P=0.018$) and seven of eight flocks took longer to resume movement after the hawk than after the control playback (Binomial, one-tailed $P=0.035$). There was a non-significant tendency for birds to take more time to resume movement during the hawk presentation ($\bar{X} \pm SE = 1.8 \pm 0.8$ min, $N=8$) compared with the control (1.2 ± 0.8 min) trials (Wilcoxon matched-pairs signed-ranks, $t=8$, $N=8$, one-tailed $P=0.08$).

Rates of movement varied significantly in the hawk mount experiment (repeated measures ANOVA, $F_{2,12}=7.68$, $P=0.007$), with birds moving at a greater rate when exposed to the mount ($\bar{X} \pm SE = 25.7 \pm 2.7$) than either 'before' (17.1 ± 2.5) or 'after' (16.4 ± 2.3) presentation (Fisher's paired least-significant difference, $P < 0.05$ for 'before' versus 'during' and 'after' versus 'during'). Chick-a-dee calling rates varied significantly over the course of observations in the hawk mount experiment only (Table I). When

Table I. Statistical analyses of alarm calling rates ($\bar{X} \pm \text{SE}$ per min) using Friedman two-way ANOVA

Call type	Treatment	N	Time relative to stimulus presentation			χ_r^2
			Before	During	After	
'Seeet'	Hawk playback	8	0.03 \pm 0.02	0.43 \pm 0.13	0.03 \pm 0.02	12.06**
	Control playback	8	0.04 \pm 0.02	0.06 \pm 0.04	0.02 \pm 0.01	1.31
	Hawk mount	7	0.04 \pm 0.02	0.11 \pm 0.05	0.06 \pm 0.01	0.29
Chick-a-dee	Hawk playback	8	0.23 \pm 0.08	0.31 \pm 0.26	0.23 \pm 0.07	0.81
	Control playback	8	0.15 \pm 0.05	0.48 \pm 0.31	0.24 \pm 0.12	0.19
	Hawk mount	7	0.10 \pm 0.04	3.93 \pm 0.67	0.30 \pm 0.21	10.50**

Mean rates are the mean of the means of each flock.

** $P \leq 0.005$.

exposed to the mount, all flock members uttered chick-a-dee calls and the rate of calling was significantly higher than when the mount was absent (Table I; Tukey-type post hoc, $P < 0.05$ for 'before' versus 'during' and 'after' versus 'during'). This high rate of calling by aviary birds was effective in attracting free-ranging conspecifics and heterospecifics to the immediate vicinity of the mount where they would accompany the captive birds in calling rapidly, and, on occasion, would perch on the wire mesh of the aviary wall.

Hierarchies

Hierarchies of all captive flocks were linear. In no cases did a reversal occur (Table II). Hierarchies were also stable throughout the experimental period. Individuals in seven out of eight flocks behaved aggressively in the experimental period, and these data show that the winners of the first altercations observed were also the winners of all subsequent altercations (Table II). Social rank was not significantly associated with age ($G = 0.74$, $df = 2$, $P = 0.696$, William's correction), or sex ($G = 5.51$, $df = 2$, $P = 0.064$, William's correction), although dominant birds tended to be male (in five or seven cases; the sex of one dominant bird could not be determined) compared with subordinates, which were more often female (in seven of eight cases) (Fisher's exact, $P = 0.07$). There was no interaction between social rank, age and sex ($G = 8.54$, $df = 6$, $P = 0.394$, William's correction), and social rank was not associated with the colour of tape and paint birds were assigned ($G = 4.61$, $df = 6$, $P = 0.595$, William's correction). Because we found a tendency for the social rank to be sex-related, we examined

whether these two variables influenced the behaviour of chickadees in predator situations.

Effects of Social Rank and Sex

For each individual, we pooled the scanning data collected in the 'before' period of the experimental trials across all three experiments. We used these baseline scanning levels so that we could assess whether birds perceived themselves as equally exposed or vulnerable to danger. Scanning data were available for seven flocks. A two-way ANOVA showed no significant effects of social rank ($F_{2,7} = 0.40$, $P = 0.684$), sex ($F_{1,7} = 0.18$, $P = 0.684$), and no interaction ($F_{2,7} = 0.14$, $P = 0.875$).

During hawk playbacks, birds were equally likely to 'seeet' regardless of their social rank ($G = 0.31$, $df = 2$, $P = 0.854$, William's correction), or sex (Fisher's exact, $P > 0.05$). However, social rank was significantly associated with the mean length of time it took birds to resume movement (Friedman two-way ANOVA, $\chi_r^2 = 6.44$, $P = 0.04$, $N = 8$). Subordinate and middle-ranking birds took a mean (\pm SE) of 0.9 ± 0.3 and 1.0 ± 0.3 min, respectively, while dominant birds took 3.3 ± 1.9 min. Post-hoc tests showed significant differences between subordinate and dominant birds only (Tukey-type, $P < 0.05$), but 75% of all subordinate birds were observed to break the freeze first, while 63% of all middle-ranking birds broke the freeze second, and 75% of all dominants broke the freeze last. There was no association between sex and the latency to resume movement (U -test, $U = 9$, $n_1 = 6$, $n_2 = 7$, $P = 0.102$).

A two-way ANOVA examining the mean length of time it took birds to chick-a-dee call in

Table II. Dominance hierarchies of captive chickadee flocks

Flock	Sex	Age	ID	Experimental trials			Hierarchy trials		
				Loser			Loser		
1	M	A	Y	—	6	6	—	8	13
	M	J	B	—	—	3	—	—	22
	M	J	R	—	—	—	—	—	—
2	F	A	B	—	2	3	—	19	5
	F	A	R	—	—	2	—	—	2
	F	A	G	—	—	—	—	—	—
3	F	?	R	—	—	—	—	17	13
	F	A	B	—	—	—	—	—	3
	F	A	G	—	—	—	—	—	—
4	?	A	G	—	2	1	—	1	7
	M	A	B	—	—	1	—	—	8
	F	J	R	—	—	—	—	—	—
5	M	J	R	—	14	23	—	18	18
	F	J	B	—	—	4	—	—	5
	F	A	Y	—	—	—	—	—	—
6	M	J	B	—	1	1	—	2	2
	F	J	G	—	—	2	—	—	8
	F	J	R	—	—	—	—	—	—
7	M	A	G	—	3	10	—	11	2
	M	J	R	—	—	1	—	—	13
	F	?	B	—	—	—	—	—	—
8	M	A	G	—	1	6	—	10	14
	M	A	R	—	—	3	—	—	10
	F	J	Y	—	—	—	—	—	—

Sex: M: males; F: females; ?: undetermined. Age: A: adult; J: juvenile; ?: undetermined. ID: Y: yellow; B: blue; R: red; G: green tape and paint.

response to the mount showed a significant effect of rank ($F_{2,8}=6.77$, $P=0.019$) (Fig. 1), but no effect of sex ($F_{1,8}=2.95$, $P=0.124$), and no interaction ($F_{2,8}=0.97$, $P=0.419$). Dominant birds took significantly more time to call than either subordinate or middle-ranking birds (Fisher's paired least-significant difference, $P<0.05$). No differences between subordinate and middle-ranking birds were found ($P>0.05$).

DISCUSSION

How chickadees in three-member flocks behaved in the presence of the predator stimuli was associated with social rank. After hearing the hawk playback, subordinate and middle-ranking birds typically broke the freeze before their dominant flockmate. All birds were equally likely to

'seeet'. Subordinate and middle-ranking birds also were found to chick-a-dee call before the dominant flockmate when exposed to the hawk mount. The sex of a bird did not appear to influence whether it behaved conspicuously. Although most subordinate birds were female, half of the middle-ranking birds were male and they too behaved conspicuously. Furthermore, three of our captive flocks consisted of same-sex individuals and the patterns found here were consistent with our overall results.

'Seeeting' is a behaviour that is probably risky to the caller if it is done when the predator is close enough to hear the call (Shalter 1978; Alatalo & Helle 1990). Individuals are more likely to 'seeet' when a predator is distant rather than nearby (Klump & Curio 1983; Alatalo & Helle 1990) which may reduce the chances of being detected, but 'seeets' are also given once the predator is no

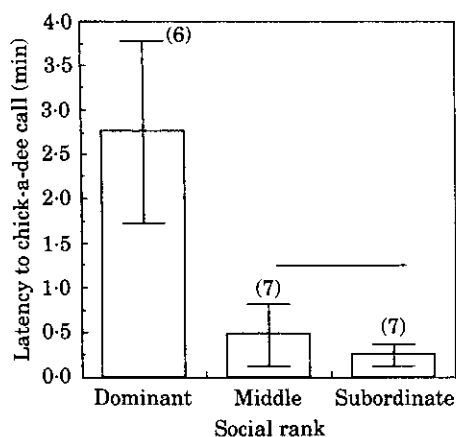


Figure 1. The mean (\pm SE) latency to chick-a-dee call in response to the hawk mount by birds of different social rank. The horizontal line connects values not significantly different ($P > 0.05$) as determined by Fisher's paired least-significant difference tests. Values in parentheses denote sample sizes.

longer visible (Ficken & Witkin 1977; Alatalo & Helle 1990). In these cases, an individual that 'seeets' could be exposing itself to the predator if it has not moved away from the flock but has moved to a new location within hearing range. Similarly, birds tend to break the freeze posture once the predator is out of sight (De Laet 1985; Hegner 1985; Hogstad 1988), again risking exposure if the predator, in fact, has not departed (Hegner 1985). Individuals that are silent do not risk detection and those that break the freeze only after others can be assured that the predator is no longer in the area (De Laet 1985).

Unlike 'seeets', chick-a-dee calls are loud, given repeatedly, and are easy to locate (Latimer 1977). The 'trill' alarm call given by individuals in Belding's ground squirrel, *Spermophilus beldingi*, colonies, also have these characteristics, and Sherman (1977) found that callers were more conspicuous than non-callers because callers were stalked or chased more often by predators. Similarly, chickadees that are the first to utter a chick-a-dee call may be more conspicuous to a predator and therefore may incur most of the predation risk compared with those that are initially silent.

In our study, all flock members were equally likely to 'seeet' and so presumably they shared the risk of being detected. In contrast, Alatalo & Helle (1990) found that dominant captive willow tits

were slightly more prone to call than subordinates. However, in their study, the rank of each individual was based on its sex and age rather than its interactions with other group members, and each bird was tested individually rather than in a social context. Because the 'seeet' is a high-frequency, low-intensity whistle (Ficken et al. 1978) that predators may find difficult to hear at a distance of 40 m (Klump et al. 1986), the lack of association between social rank and 'seeeting' in our study could have arisen if callers were misidentified. However, this possibility is unlikely because the observer was only 2 m from the aviary, the experimental area was free of vegetation (thus, minimizing the chance for the sound to scatter), and flock members were usually perched 1–2 m apart.

It is not clear from this study why subdominants would risk predation by breaking the freeze first. The sooner an individual breaks the freeze, the sooner it can resume foraging (Hegner 1985). In this case, subdominants may risk predation to attain food if they are hungrier than others (e.g. see De Laet 1985; Hegner 1985). However, Waite (1989) found no evidence that subordinate tufted titmice, *Parus bicolor*, which were the first to resume movement, were hungrier than dominants, and, in our study, there was no difference in the mean rate at which birds of different rank acquired seeds ($F_{2,10} = 0.65$, $P = 0.543$). It seems that subdominants may be more willing to risk predation regardless of their hunger levels. Also, our chickadees often did not resume foraging immediately after breaking the freeze (personal observation; also see Waite 1989), so subdominants do not necessarily receive a foraging advantage by breaking the freeze posture first.

It is also not clear why subdominants would chick-a-dee call first. All captive group members scanned at similar levels and were therefore equally likely to see the mount first so there was probably no relation between the sequence of calling and the sequence in which individuals perceived the mount. In some group-living species, individuals will alarm call presumably to warn nearby relatives of potential danger (Sherman 1977). However, free-ranging black-capped chickadee flocks are not composed of kin members (Glase 1973) and it is unlikely that individuals in our captive flocks were related. None the less, subdominants consistently gave the chick-a-dee call sooner than dominants suggesting

that dominant birds may reduce their risk of predation by waiting for others to chick-a-dee call first. In general, it appears that subdominants are less averse to taking predation risks than dominants, but the underlying mechanisms need exploring.

To explain why subdominant, free-ranging chickadee and willow tits experience higher predation rates than dominant flockmates, many suggest that subdominants may occupy an area within the flock that provides less cover than areas occupied by dominants (Glase 1973; Ekman 1986, 1987; Desrochers 1988) thus exposing subdominants more to potential danger (Ekman 1987). Our study has shown that subdominants behave more conspicuously than dominants in predator situations. Consequently, greater risk-taking by subdominants also may be a reason they experience higher rates of predation although few have considered this possibility.

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