OIKOS 50: 225–230. Copenhagen 1987

Protective cover and the use of space by finches: is closer better?

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Lima, S. L., Wiebe, K. L. and Dill, L. M. 1987. Protective cover and the use of space by finches: is closer better? – Oikos 50: 225–230.

The use of space by small birds is strongly influenced by dense vegetation which serves as protection from attacking predators. Current evidence suggests that birds dependent upon such cover for safety will venture away from it only if their energy intake rate is significantly enhanced in doing so. We found, however, that three species of finches (Emberizidae) regularly fed well away from cover without a corresponding increase in energy intake rate. Observations and experimental results strongly suggest that the birds perceived cover as both safety and a source of attacks. For instance, birds fed farther away from cover containing visual obstructions that might conceal predators lying in ambush. Their use of space appeared to reflect a trade-off between the perceived risk of feeding too close to cover vs that of feeding too far away. This trade-off was also influenced by a bird's social environment; subordinate species fed farther from cover than dominant ones in an apparent effort to avoid direct aggression.

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Introduction

The use of space by many small birds is strongly influenced by dense vegetation that may provide safety from attacking predators (cf. Pulliam and Mills 1977). Some birds show a marked reluctance to leave such cover. For example, Schneider (1984) and Pulliam and Dodd (unpubl.) found that foraging white-throated sparrows (*Zonotrichia albicollis*) may be reluctant to venture as little as 20 cm from protective cover. Grubb and Greenwald (1982) and Lima (1987a) similarly found that house sparrows were reluctant to feed away from cover. Many birds, however, face a dilemma in that higher energy intake rates may be achieved only when feeding farther from cover, due to food depletion near cover, the aggressive control of food close to cover by dominant individuals (Schneider 1984, Ekman 1987, Pulliam and Dodd, unpubl.), and/or the thermal advantages afforded by cover (Grubb and Greenwald 1982). Overall, the available evidence suggests that the use of space around cover reflects cost-benefit decisions made by individuals attempting to maximize their fitness.

The perception of predation risk by feeding birds appears to play a major role in their use of space. Thus, in the present study, we examined the perception of risk as it relates to cover via a simple question: do birds feed as close as possible to cover if foraging conditions do not vary with distance to cover? In this situation, given the common assumption that distance to cover determines the probability of escaping an attack (see Lima 1987b), and the fact that birds quickly rush to cover upon detecting an attack (Morse 1973, Pulliam and Mills 1977), we would expect birds to feed as close as possible to cover. However, we found that dark-eyed juncos (*Junco hyemalis*), song sparrows (*Melospiza melodia*) and rufous-sided towhees (*Pipilo erythrophthalmus*) rarely fed as close as possible, though they clearly perceived cover as potentially safe. The birds' reluctance to feed near cover strongly suggested a sensitivity to potential attacks from within cover itself. Their overall use of space appeared to reflect a trade-off between the risk of feeding too far or too close to cover. In addition, we found a strong role for interspecific dominance relationships in the use of space (cf. Schneider 1984, Pulliam and Dodd, unpubl.).

Accepted 29 April 1987

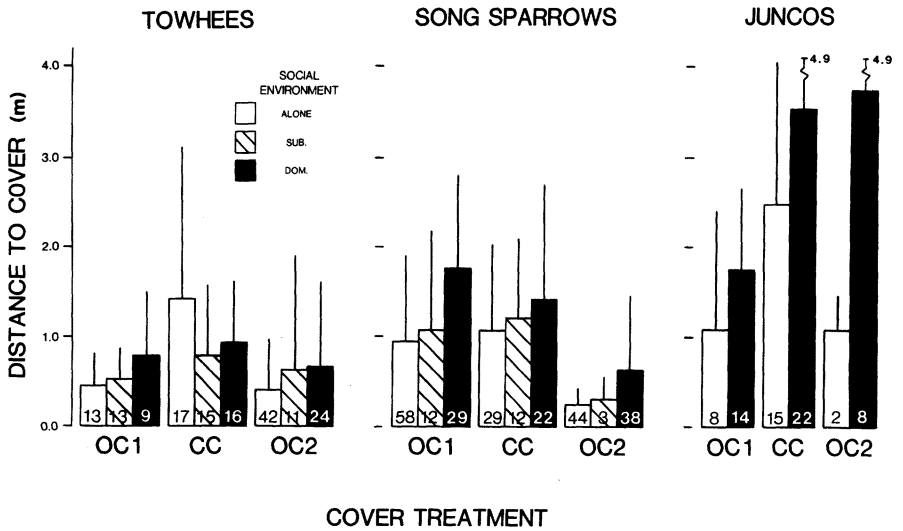

Fig. 1. The distance to cover chosen by the towhees, song sparrows and juncos. Data are broken-down according to cover treatment and social environment; the SUB social environment is not applicable to juncos (see methods). Bars and numbers represent means and sample sizes, respectively; vertical lines are standard deviations.

Methods

Study site and birds

This study was conducted from May to July 1986 at a site on Burnaby Mountain, British Columbia, near the campus of Simon Fraser University. The study site itself was a large, open area bordered by a forest composed mainly of red alder (*Alnus rubra*) and western red cedar (*Thuja plicata*). Parallel and adjacent to the forest edge was placed a 7 × 2 × 1.5 m high pile of dead, dense brush which served as protective cover.

A 5 × 5 m area immediately adjacent to the front edge of cover was kept abundantly supplied with millet seeds, the food items used throughout the study. To facilitate observations (see below), lengths of string were placed at 1 m intervals parallel to the edge of cover up to 5 m from cover. Note also that there was little live vegetation growing in this area, and what did grow was kept cropped close to the ground (<1 cm).

Birds feeding at the study site were not individually marked, but judging from simultaneous sightings of individuals, there were at least four, six and nine juncos, song sparrows and towhees, respectively, participating throughout the study. Approximately seven brown-headed cowbirds (*Molothrus ater*) also fed at the study site, but they often engaged in breeding activities (courtship) and were excluded from the analysis. The presence of cowbirds was important, however, in that they were dominant over all other species studied (see below).

Procedures and observations

The main portion of the study was divided into four sequential segments, referred to as cover treatments, each consisting of 10 sessions (one session per day, see below). During the first and third cover treatments, cover was left "open" (easy to see into); these are referred to as the OC1 and OC2 treatments. Cover was "closed" during the second treatment by enclosing the sides of cover with boughs of western red cedar (a coniferous tree), thus making it difficult to see into cover; this is referred to as the CC treatment. During the fourth segment (referred to as the I/O treatment), cover was again open, but food was placed both in and away from cover. To summarize, the order of treatments was OC1, CC, OC2, I/O.

Each day during the study, except during heavy rain, a session lasting 1.5 h was begun about 1 h after sunrise. When a bird arrived at the study site, its social environment was recorded (see below) and its position from cover was recorded to the nearest 0.1 m (relative to the strings mentioned above). The position of the bird was then recorded every 10 s until it left the site. Any aggressive acts that occurred were also recorded. During the I/O treatment, any birds feeding in cover were recorded as such. All observations were made from within a blind situated at the forest edge 20 m from cover.

A series of consecutive distance to cover measurements for a given individual defined a feeding bout. Each bout was characterized by its average distance to cover, and these values served as the basic data in the analysis below. Only bouts of 3 time intervals (30 s) or longer were included in the analysis. Note that the distribution of these data proved to be skewed away from cover such that the mean and variance were positively correlated. Thus, all values were log-transformed before performing t-tests and two-way ANOVAS (see Sokal and Rohlf 1981).

As mentioned earlier, a bird's social environment was recorded when it arrived at the site. The social environment was defined according to the potential for aggression directed at the bird in question. Interspecific aggression greatly predominated over intraspecific aggression, perhaps reflecting the heterospecific nature of most foraging groups and the likelihood that conspecifics in a group included mated pairs. In any case, the social environment was thus defined according to the ob-

Tab. 1. Results from two-way ANOVAs of data summarized in Fig. 1. S and C denote, respectively, the social environment (alone, subordinate present, dominant present) and the condition of cover (OC1, CC, OC2).

Source	SS	df	MS	F	P
a. rufous-sided towhee					
S	3.1	2	1.5	2.0	0.14
C	14.4	2	7.2	9.4	<0.001
S × C	2.0	4	0.5	0.7	NS
ERROR	116.5	151	0.8		
b. song sparrow					
S	6.8	2	3.4	5.9	0.003
C	26.6	2	13.3	22.8	<0.001
S × C	1.1	4	0.3	0.5	NS
ERROR	138.8	238	0.6		
c. dark-eyed junco					
S	7.5	1	7.5	12.8	<0.001
C	5.4	2	2.7	4.6	0.013
S × C	0.7	2	0.3	0.6	NS
ERROR	36.9	63	0.6		

vious interspecific dominance hierarchy at the study site: cowbirds > towhees > song sparrows > juncos. A bird was recorded as feeding in a "subordinate" environment (denoted by SUB) if it was the most dominant species present; a bird was feeding in a "dominant" environment (denoted by DOM) if there was a more dominant species present. A solitary bird was in the "alone" environment. The social environment for a bird entering what would be a monospecific group was undefined, and the data for the few such cases were excluded from the analysis.

Results and discussion

Fig. 1 shows the average distance to cover chosen by feeding towhees, song sparrows, and juncos during the first three cover treatments of the study. Individuals of all species tended to feed farther from closed than open cover. This effect is significant in all species (Tab. 1 a–c), although significance for the song sparrows follows largely from a marked decrease in the distance to cover after the CC treatment. The social environment had a significant effect only in song sparrows and juncos (Tab. 1); both fed farther from cover when dominants were present (Fig. 1).

The birds' tendency to feed farther from closed than open cover suggests that the choice of a feeding site is sensitive to aspects of cover which influence the risk of predation. For instance, closed cover may obscure a bird's view of its surroundings such that it moves farther from cover to compensate. Alternatively, "cover" may actually conceal predators lying in ambush. The behaviour underlying the trends in Fig. 1 suggests the latter effect may hold.

During the first treatment (OC1), it appeared that birds passing through cover before feeding generally fed closer than those starting away from cover. Thus, during the CC and OC2 treatments, we recorded this aspect

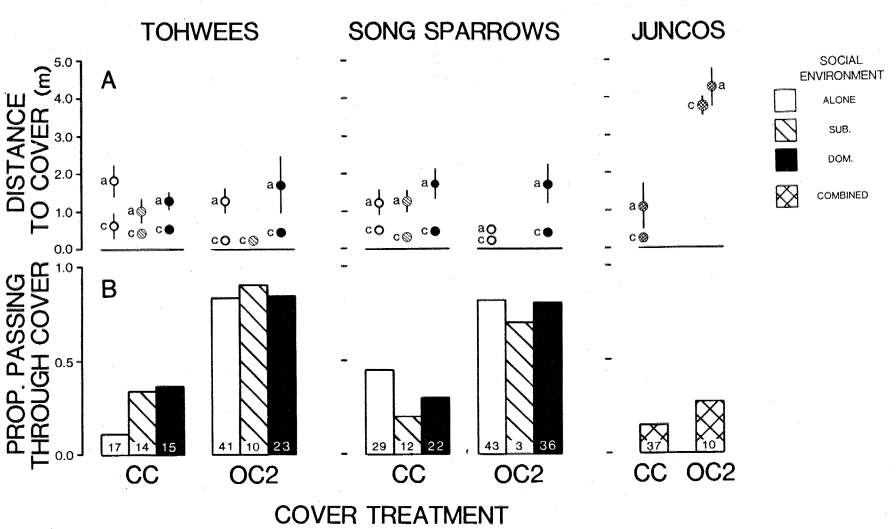

Fig. 2. (A) Average distance to cover (+,−SE) chosen by towhees, song sparrows and juncos given that a bird passed through cover before feeding (c) or started its bout away from cover (a). Data are broken-down further according to cover treatment and social environment. Some categories lack entries due to small sample sizes (n=1) resulting from the c/a breakdown of the data. Small sample sizes also necessitated the pooling of data across social environments for the juncos. There is a significant difference between relevant means (where two exist; t-tests, P <0.05) in all cases except for the juncos in OC2.
(B) Proportion of bouts passing through cover. The data are broken-down as in (A); numbers represent sample sizes. All differences (for relevant social environments) are significantly different (G-tests, P <0.05) except for that between the CC and OC2 treatments for song sparrows in a subordinate environment.

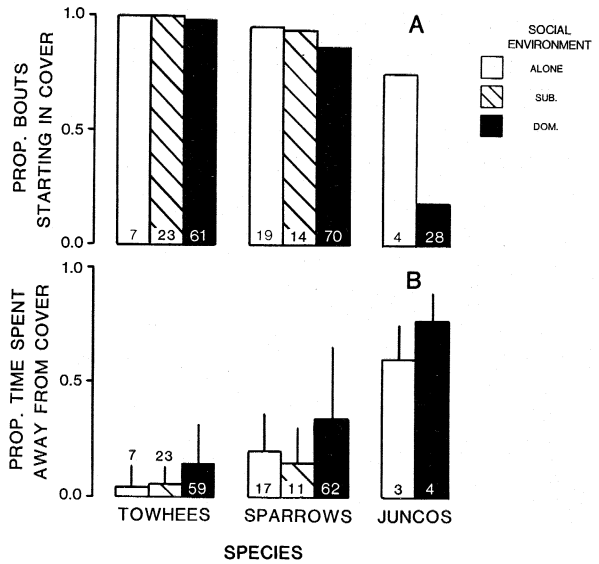

Fig. 3. (A) Proportion of bouts starting in cover for the I/O treatment. Numbers represent sample sizes. Data are broken down according to social environment; the SUB environment is not applicable to juncos.
(B) Average (SD) proportion of each bout spent away from cover during the I/O treatment. All else as in (A).

of behaviour along with those described earlier. For these two treatments, Fig. 2A shows the average distance to cover chosen by each species depending upon whether a bird passed through cover before feeding. For each species, regardless of the social environment, there is a strong tendency to feed closer to cover after passing through it. This trend did not differ greatly between the two treatments, but the proportion of bouts passing through cover differed considerably. As seen in Fig. 2B, the tendency to pass through cover before feeding was significantly greater with open cover (OC2) than with closed cover (CC), regardless of the social environment.

The behaviour in Fig. 2B suggests that the apparent avoidance of cover reflects a perception of a risk of attack from within cover itself, rather than an attempt to overcome any visual obstructions posed by cover. If the latter was a major factor in the choice of a feeding site, then all bouts would take place farther from cover in the CC treatment in order to get an unobstructed view, regardless of where they started. If the birds were concerned with attack from concealed predators in cover, then those birds passing through cover before feeding would have information about such potential predators and thus feed closer. Those not passing through cover, lacking such information, would feed farther from cover. Since the decision to gain this information would strongly depend upon the risk involved, it is not surprising that fewer bouts would start in closed than open cover.

We thus envision a situation where only a bird with perfect, cost-free information about predators in cover and, perhaps, a perfect view of its surroundings, would feed as close as possible to cover. In the real world, a bird should avoid feeding very close to cover, and modify its choice of a feeding site according to its assessment of the risk of feeding near cover. Accordingly, what would be expected if food was available both away and *inside* cover? There is still the risk of predation in the initial approach to cover, but once in cover, a bird can feed in relatively great safety. We therefore expect that birds would prefer to feed in cover if possible, even though they tend to avoid cover otherwise. This expectation was examined during the I/O treatment.

The proportion of bouts starting in cover during the I/O treatment is shown in Fig. 3A. The towhees started virtually every bout in cover, representing a significant increase (G-tests, $P < 0.05$) over the corresponding proportions for both treatments and all social environments in Fig. 2B. Similarly, song sparrows started the great majority of their bouts in cover; their tendency to start in cover was greater in the I/O than in the CC or OC2 treatments (compare Figs 3A and 2B), but the increase relative to the OC2 treatment was significant (G-test, $P < 0.05$) only for sparrows feeding alone. Finally, juncos feeding alone tended to start in cover. When dominant individuals were present, however, juncos showed only a small tendency to start bouts in cover (Fig. 3A). Statistical comparisons of junco behaviour between this treatment and those in Fig. 2B are hampered by small sample sizes and the necessity to pool data in Fig. 2B, but the trends are clear.

In the I/O treatment, starting a bout in cover was equivalent to starting by feeding in cover. Birds starting in cover, however, did not necessarily stay in cover. Fig. 3B shows the average proportion of each bout spent away from cover given bouts that started in cover. The towhees spent little time away from cover when feeding alone or with subordinates. However, they averaged 14% of their time away from cover in the presence of dominant individuals, representing a significant increase over the other social environments (t-tests, $P < 0.05$; arc-sine square-root transformed data for this and following t-tests). The song sparrows showed similar behaviour; time spent away from cover was significantly greater (t-tests, $P < 0.05$) in the presence of dominants than when feeding alone or with subordinates (the latter two did not differ significantly). In addition, the song sparrows' overall tendency to spend more time away from cover than towhees was significant for all social environments (t-tests, $P < 0.05$). Contrasting with the towhees and song sparrows was the juncos' tendency to spend over 50% of their time away from cover. Despite the small sample sizes in the junco data (Fig. 3B), they spent significantly more time away from cover than did the towhees or song sparrows for all relevant pairwise comparisons.

Overall, when given the choice of feeding in or away from cover, the birds chose to feed in cover. This supports our view that cover is indeed perceived as safety.

Tab. 2. The proportion of bouts, in the presence of dominants, during which aggression was directed towards the species in question. Sample sizes are in parentheses.

Species	Treatment			
	OC1	CC	OC2	I/O
towhees	0.0 (9)	0.0 (16)	0.0 (24)	0.13 (61)
song sparrows	0.10 (29)	0.13 (22)	0.08 (38)	0.33 (70)
juncos	0.36 (14)	0.14 (21)	0.0 (8)	0.0 (28)

However, some feeding was done away from cover; indeed juncos spent most of their time feeding away from cover. Why would a bird choose to feed away from cover? The answer appears to lie in interspecific aggression.

Tab. 2 shows the proportion of bouts during which each of the species studied experienced direct aggression from more dominant species (mainly short chases or supplantations). The towhees did not suffer much aggression during the first three cover treatments, but direct aggression did occur during the I/O treatment. Song sparrows experienced direct aggression during all treatments, with significantly more during the I/O treatment than during the other three (G-tests, $P < 0.05$). Juncos experienced considerable aggression during the first two treatments, but none at all during the last two. Note that aggression during I/O treatment occurred only in cover; summing over all three species, no aggressive acts occurred during the 34 bouts with no time spent in cover, whereas aggression occurred during 31 of 124 bouts that started in cover.

The obvious importance of aggression is that it may force subordinate species away from cover. The towhees' tendency to feed away from cover when dominants were present (in the I/O treatment, Fig. 3B) probably reflected the avoidance of aggression. Similarly, the behaviour of song sparrows in the I/O environment probably reflected an avoidance of aggression from towhees and cowbirds, both of whom often attempted to control access to the food in cover. The song sparrows' behaviour in the presence of dominants during the first three treatments (Fig. 1) may also represent a similar avoidance, since aggression occurred when the sparrows fed closer to cover (Tab. 3).

Tab. 3. Average (SD, n) distance to cover (in metres) for those bouts, in the presence of dominants, during which aggression did (A) or did not (NA) occur.+

Species		Treatment		
		OC1	CC	OC2
song sparrows	A	1.6 (0.5,3)	0.9 (0.6,6) *	0.2 (0.1,3) *
	NA	1.8 (1.0,26)	1.5 (1.5,16)	0.7 (0.8,35)
juncos	A	1.6 (1.2,5)	2.5 (0.7,3) *	
	NA	1.9 (0.7,9)	3.7 (1.4,19)	

+ The towhees experienced no aggression during these treatments (Tab. 2); juncos experienced no direct aggression during the OC2 treatment (Tab. 2).
* t-test, $P < 0.05$; data were log-transformed prior to test.

Contrary to the pattern in towhees and song sparrows, juncos experienced a decline in aggression during this study (Tab. 2). This did not indicate that juncos somehow became more "fierce". The lack of aggression during the last two treatments reflects the fact that juncos, in the presence of dominant individuals, fed very far from cover during the OC2 treatment, and spent much time away from cover during the I/O treatment (if they fed in cover at all). This appeared to be an effective strategy in avoiding aggression, since, as with the song sparrows, juncos experienced more aggression when feeding closer to cover (Tab. 3), and aggression occurred only in cover during the I/O treatment. It is not clear, however, why their avoidance of dominants would increase with time.

We have argued that a prime determinant of a finch's use of space was the potential of attack from cover itself, but we did not actually observe any attacks at the study site. Potential ambush predators were present in the area, such as Cooper's hawks (*Accipiter cooperii*), which did make a few sudden appearances and low flights over the study site; these appearances greatly reduced feeding at the site for the remainder of an experimental session. In addition, raccoons (*Procyon lotor*), an opportunistic predator, would occasionally appear in cover and nearby vegetation, and this greatly disturbed any feeding birds. Given the lack of actual attacks, however, we attempted to further test our view concerning the avoidance of cover by experimentally increasing the probability of attack from cover by having a mounted cat unpredictably "pounce" out of (closed) cover toward feeding birds, with the expectation that they would feed farther from cover. We found, however, that the birds quickly stopped feeding at the study site, and that they showed a great reluctance to return until the closed cover was removed. While these observations provide some support for our view, they also demonstrate that there are usually several options in responding to an increase in the risk of predation; in this case, the birds simply chose to feed elsewhere.

Conclusions

Small birds that feed in and around brushy vegetation do indeed take advantage of the protection it affords from predators, as evidenced by their propensity to rush to cover when startled or attacked (Morse 1973, Pulliam and Mills 1977, Schneider 1984, pers. obs.). It is clear from the present study, however, that birds may not feed as close to cover as possible. They also do not feed as far from cover as possible. The overall results

strongly suggest that a bird's use of space depends upon its perception of the risks associated with feeding too far or too close to cover. In other words, behaviour reflects a trade-off between the need to escape attacks occurring away from cover versus those from within.

This is not the first suggestion that the behaviour of feeding animals is sensitive to cover that may harbour predators. Underwood (1982) found that African ungulates were more vigilant when near cover that might conceal lions. Caldwell (1986) found that various heron species (Ardeidae) would avoid feeding near vegetation that might conceal attacking hawks (*Buteo* spp.). Similarly, Carey (1985) found that yellow-bellied marmots (*Marmota flaviventris*) avoided areas of high vegetation that might obscure predators. The behaviour described in these studies is not surprising given that such cover is essential to the success of ambush predators (Curio 1976). However, cover did not afford safety from predators for any of these animals; it was strictly a source of risk. "Protective cover" may indeed be a double-edged sword for those animals which depend upon it for safety.

Our results are in marked contrast to those of Schneider (1984) and Pulliam and Dodd (unpubl.) where white-throated sparrows would venture away from cover only if food was significantly depleted near cover, or if dominants forced them to do so. It is important to emphasize that food depletion was not a factor in the present study; the birds would walk over abundant, easily accessible food closer to cover in choosing a feeding site farther away. This difference in observed behaviour may reflect differences in study sites regarding cover (the cover for the white-throated sparrows would be considered open), potential predators, or the thermal environment (Grubb and Greenwald 1982). Site-specific social environments may also help explain these behavioural differences (cf. Davis 1973). The differences may also reflect differing selective pressures over evolutionary time (cf. Pulliam and Mills 1977, Ekman 1986). Future work may shed light on these possibilities, and in doing so provide greater insight into the organization of avian communities.

Acknowledgements – T. Caraco, R. Cartar, J. Ekman and R. C. Ydenberg made several helpful comments on the manuscript. This work was supported in part by a NATO Postdoctoral Fellowship to S.L.L., and NSERC Canada grant A6869 to L.M.D., and a Challenge 86 grant to K.L.W.

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