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EXPOSURE TO PREDATORS AND ACCESS TO FOOD IN WINTERING WHITE-THROATED SPARROWS ZONOTRICHIA ALBICOLLIS

by

WALTER H. PIPER[1][2]

(Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, 27599-3280, U.S.A.)

(With 5 Figures)
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Introduction

The ability of a wintering passerine to dominate conspecifics appears to influence its likelihood of avoiding predation and starvation, the two main threats to survival in winter. Among juncos (*Junco* spp.) and tits (*Parus* spp.), for example, subordinate individuals in flocks obtain less or poorer quality food because of the interference of dominants (BAKER *et al.*, 1981; EKMAN & ASKENMO, 1984). Other studies indicate that, as a means of offsetting their disadvantage in foraging flocks, subordinate birds feed in situations where predation risk is high but dominants are absent (SCHNEIDER, 1984; HEGNER, 1985; DELAET, 1985; WAITE & GRUBB, 1987; HOGSTAD, 1988).

Though the effects of dominance status on the risks of predation and starvation seem clear, most studies that have reported such effects have ignored other factors (including correlates of dominance like sex and age) that might also affect predation and starvation. Thus, it is possible that factors other than dominance affect survival in wintering passerines.

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[2]) Present address: Department of Biological Sciences, Purdue University, West Lafayette, IN, 47907, U.S.A.

In this study, I examined the risks of predation and starvation in a wintering population of white-throated sparrows (*Zonotrichia albicollis*) by means of two indices: (1) individuals' distances from cover while feeding (a presumed index of predation risk), and (2) time spent feeding (a presumed index of starvation risk). Multivariate analyses were then used to determine the relationships between these two indices and eleven behavioural, morphological and situational variables (including dominance). I also analysed the influence of environmental factors and dominant heterospecifics on the use of feeding stations by white-throated sparrows.

Methods

Study area and measurements.

This study, carried out between October 1984 and May 1985, was part of an investigation of the behaviour of white-throated sparrows during the winters of 1982-1983 through 1986-1987 at Mason Farm Biological Reserve in Chapel Hill, North Carolina.

R. H. WILEY and I captured sparrows 2-3 times weekly in 17 six-celled treadle traps spaced 25 m apart along a linear hedgerow flanked by fields (PIPER & WILEY, 1989a). Most individuals were captured repeatedly (mean number of captures = 12.3 ± 8.7 SD, N = 98 individuals). Newly-trapped sparrows were examined to determine age (by extent of skull pneumatization, see Mellenkamp, 1969), length of wing chord (nearest 0.5 mm), brightness of crown stripes and morph (see PIPER & WILEY, 1989a, b, for detailed descriptions of these measurements). In addition, we sexed 81 of the 98 birds in the study (83%) by laparotomy. The remaining 17 birds were considered to be males if their wing chords measured 70 mm or greater and females otherwise, a criterion with over 90% accuracy (PIPER & WILEY, 1990a). Overall, an estimated 98% of all sparrows were correctly sexed.

Observation sites.

All behavioural observations took place at three observation sites located roughly 75 m apart along the trapline. Each site consisted of a small plywood blind (approximately 0.8 × 0.8 × 1.5 m) and a set of six feeding platforms, each a concrete block (20 × 20 × 40 cm) set on end, upon which I placed 20 ml of a mixture of millet and sunflower seed. The blocks were arranged in two parallel rows of three each such that two blocks were at the edge of a hedgerow of multiflora rose and 0.7 m apart, two more were 0.7 m farther from the hedgerow 0.7 m apart, and the last were 1.4 m from the hedgerow 0.7 m apart. The blinds were placed 2.7, 2.1 and 1.7 m from the two blocks farthest from cover at sites 1, 2 and 3, respectively.

Scan samples.

I conducted scan samples (ALTMANN, 1974) between 1 February and 18 March 1985 at all three sites to estimate absolute and relative distances to cover, time spent feeding and flock size (see below) for each sparrow. Because individuals constantly moved between blocks and bushes and from block to block while feeding, it was impossible to record the identities of all birds on all six blocks at once. For this reason, I tossed a coin before each scanning session to determine which row of three blocks at a site I would observe. I then recorded at 30-second intervals the identities and distances to cover (*i.e.* whether adjacent to, 0.7 m away from or 1.4 m away from cover) of all white-throated sparrows and other species that fed on the selected row of blocks. Only one session was conducted at a site each day. Sessions usually lasted for 50 minutes (100 scans) but were terminated at any point if no bird had appeared on any block for 5 minutes or if the food on any block was finished. The temperature and percentage of cloud cover were recorded before and after each session. I obtained 1086 scans at site 1, 995 at site 2, and 544 at site 3.

Absolute distance to cover.

Absolute distance to cover, a bird's mean distance to cover based on all scans in which it appeared, was used as an index of its safety from predators while feeding. To eliminate any effect of location on the behaviour of individuals (see PIPER & WILEY, 1989a), I computed absolute distance to cover using only the scans at the single site where an individual was seen most often (37 of 98 birds were seen at more than one site). Furthermore, this index was not computed for birds seen in fewer than 5 scans or observed only during a single foraging bout (mean number of scans per bird in the analysis of absolute distance to cover = 24 ± 27 SD, N = 98).

Relative distance to cover.

Relative distance to cover, also computed from scan samples, estimated the distance to cover at which a bird fed relative to other individuals (see SCHNEIDER, 1984; HOGSTAD, 1988). Each scan in which two birds fed simultaneously at different distances from cover was viewed as a "distance interaction" between the two birds. If Bird A fed closer to cover than Bird B, Bird A was considered to rank above Bird B in priority to cover in this interaction. However, when two birds' positions remained the same in consecutive scans, only the first scan was considered an interaction.

Distance relationships were stable. In 123 of 145 (85%) dyads with two interactions, the relationship was the same in both interactions. I therefore considered one scan sufficient to determine a distance relationship and counted one bird as having "distance priority" over another if it fed closer to cover in 75% or more of the distance interactions between the two birds.

Relative distance to cover was the proportion of birds over which a bird had distance priority at the site where it had the largest number of distance interactions and was computed only for individuals that had distance interactions with five or more marked birds. The logit transformation (SNEDECOR & COCHRAN, 1967) was used to normalize the index. A mean of 12 (± 6.3 SD, N = 80) distance dyads was recorded per individual.

Time spent feeding.

An individual's time spent feeding, the total number of scans in which it appeared, was used to estimate its access to food. Again, I excluded all scans except those from the single site where each individual was observed most often.

Possible correlates of distance to cover and time spent feeding.

In addition to the basic measurements described above, four other potential correlates of distance to cover and time spent feeding were determined. First, mean flock size was computed for each white-throated sparrow using scan samples. Mean flock size was the mean number of birds, regardless of species, present on all three blocks in all scans that contained a given bird. Second, a bird's location within its winter range was indicated by the distance between its mean trapping point (PIPER & WILEY, 1989a) and the site where it was observed most often. Third, number of years of residence was determined for each bird based on captures in 1984-1985 and two previous winters. A bird trapped or observed over a 60-day or greater interval in a given year was considered a resident in that year. Fourth, dominance interactions recorded among colour-banded birds from 11 December 1984 through 26 March 1985 were used to estimate birds' abilities to dominate conspecifics. A bird that successfully supplanted an opponent in 75% or more of the interactions within a dyad was considered the dominant bird (see PIPER & WILEY, 1989a). I used dominance proportion, the total number of opponents a bird dominated divided by the total number of opponents with which it interacted at the site where it was observed most often, to estimate dominance. Dominance proportion was normalized with the logit transformation.

Statistical analyses.

The predictor (independent) variables examined as potential correlates of absolute and relative distances to cover comprised dominance proportion, flock size, length of residence in the study area, site where the bird was observed, distance between the bird's mean trapping point and the site where it was observed, number of opponents in dominance interactions (an index of the amount of time that a bird spent at an observation site throughout the winter), age, sex, morph, length of wing chord, and brightness of crown stripes in basic (winter) plumage.

The analysis of time spent feeding included the same predictor variables as the analyses of distances to cover with two exceptions: absolute distance to cover was added as a predictor variable, and number of opponents in dominance interactions, another measure of time spent feeding, was omitted.

Initially, stepwise multiple regressions (Systat Inc., Evanston, Ill.) were used to test all potential predictor variables of absolute and relative distances to cover and time spent feeding. The procedure eliminated all variables not significant at the 0.15 level. I then added all interaction terms between selected variables and used backwards elimination (DRAPER & SMITH, 1966) to produce the final models.

To reduce the likelihood that correlations would be statistically significant simply because of the large number of variables examined, I reduced the usual significance level by a factor of 11 (the number of variables tested; see the Bonferroni technique in KEPPEL, 1982). Thus, an α level of 0.005 was used in the analyses of absolute and relative distances to cover and time spent feeding.

Additional analyses.

Preliminary observations indicated that the number of birds present during a session was affected both by the site where scans took place and by weather conditions. I analyzed this background variability by calculating the mean number of birds per scan (regardless of species or distance to cover) during each session. I carried out an analysis of covariance on the number of birds present during a session (the criterion variable) using three environmental variables as predictors: mean cloud cover, mean temperature and observation site. As above, backwards elimination was used to produce the final model with a significance level of 0.02 (adjusted for three variables).

The foraging behaviour of white-throated sparrows also appeared to be affected by interactions with dominant heterospecifics, which were present in 1028 of 2625 total scans (39%). I therefore calculated the number of scans in which each white-throated sparrow shared a feeding block with a dominant species and used this tendency as a criterion variable in another analysis of covariance. The analysis was carried out as described above; the predictor variables examined were time spent feeding itself and all of the predictor variables in the analysis of time spent feeding (see above). The α level used was 0.004.

TABLE 1. Partial correlation coefficients from analyses of absolute and relative distance to cover

Criterion variable	N	Significant predictor variables			
		Flock size	Age	Sex	Dominance proportion
Absolute distance to cover	98	0.33**	-0.31*	0.28*	el
Relative distance to cover	80	el	el	-0.37*	0.49**

* = $p < 0.005$; ** = $p < 0.0005$; el = variable was eliminated by stepwise regression. Sample sizes indicate numbers of birds.

Results

Absolute distance to cover.

In order of decreasing statistical significance, the variables correlated with absolute distance to cover were flock size, age and sex ($R^2 = 0.28$, N = 98; see Table 1). Individuals feeding in small flocks (Fig. 1), older birds (Fig. 2) and females (Fig. 3) tended to feed close to cover. No interaction between variables was significant. Variables not correlated with absolute distance to cover were dominance proportion (but see below), morph, brightness of crown, length of wing chord, observation site, distance between mean trapping point and observation site, number of years resident and number of opponents in dominance interactions.

While dominance proportion was not selected by the stepwise procedure as a correlate of absolute distance to cover, it explained almost as much of the variance as did age when substituted for age in the final model (overall R^2 with dominance substituted for age = 0.27). Moreover, when one controls for the effect of age by looking at the correlation between dominance and absolute distance to cover within age-classes, one finds a consistent tendency for dominant birds to feed closer to cover among first- ($r = -0.15$, N = 30), second- ($r = -0.18$, N = 30) and third-winter birds ($r = -0.27$, N = 31), though small sample sizes made each correlation nonsignificant. Apparently both dominance and age should be considered correlates of absolute distance to cover.

Relative distance to cover.

Relative distance to cover had only two correlates. Dominant birds fed closer to cover than subordinates (Fig. 4), and females fed closer to cover than males ($R^2 = 0.26$, N = 80; Table 1).

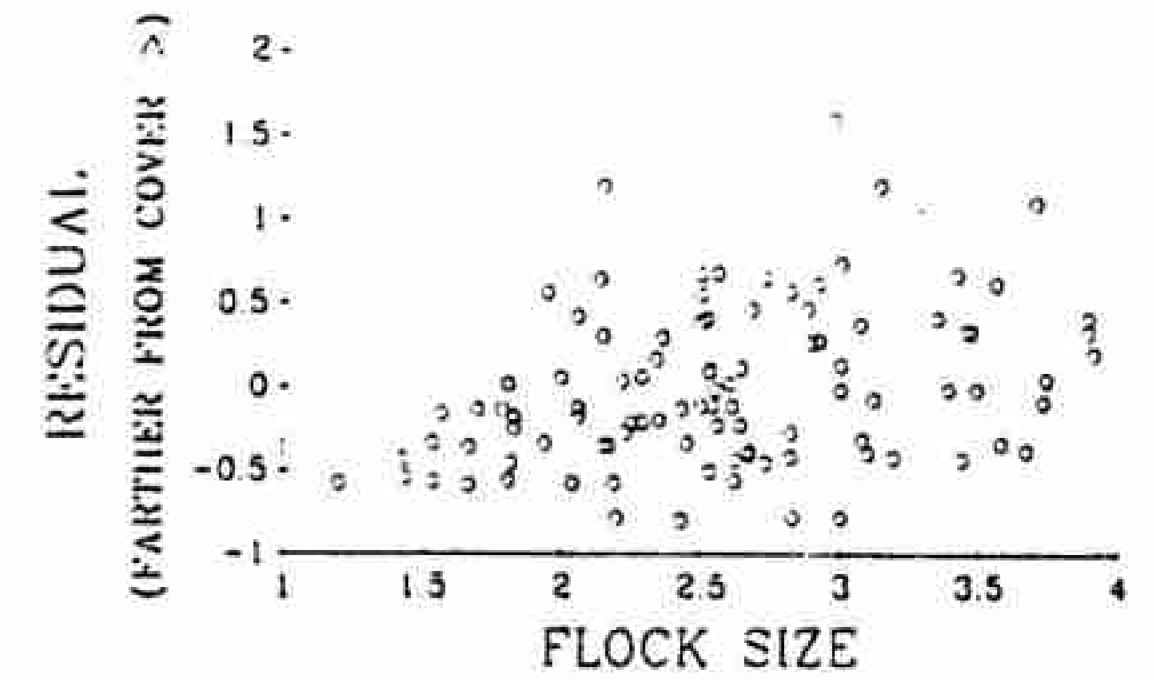

Fig. 1. Relation between flock size and residual from model of absolute distance to cover that included only age, sex and dominance proportion as predictors. The figure indicates that, with other variables controlled, individuals that fed in large flocks fed close to cover.

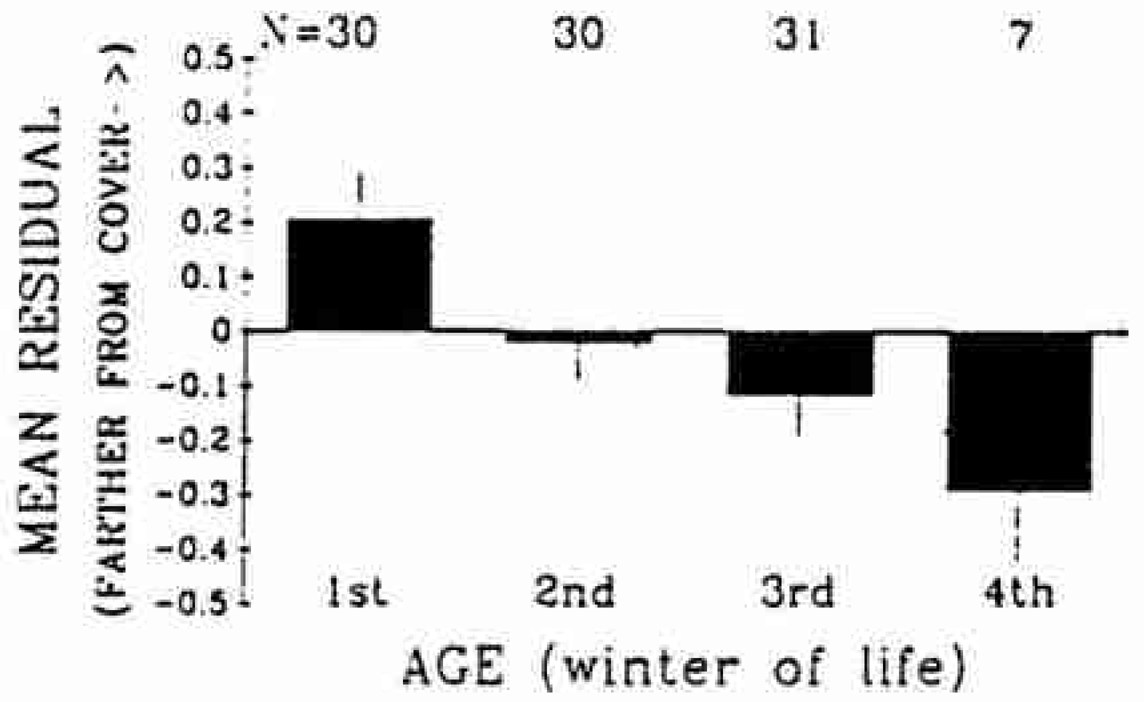

Fig. 2. Means and standard errors of residuals from model of absolute distance to cover that included only flock size, sex and dominance proportion as predictors. Residuals are grouped by age-class. The figure indicates that, with other variables controlled, older birds fed close to cover.

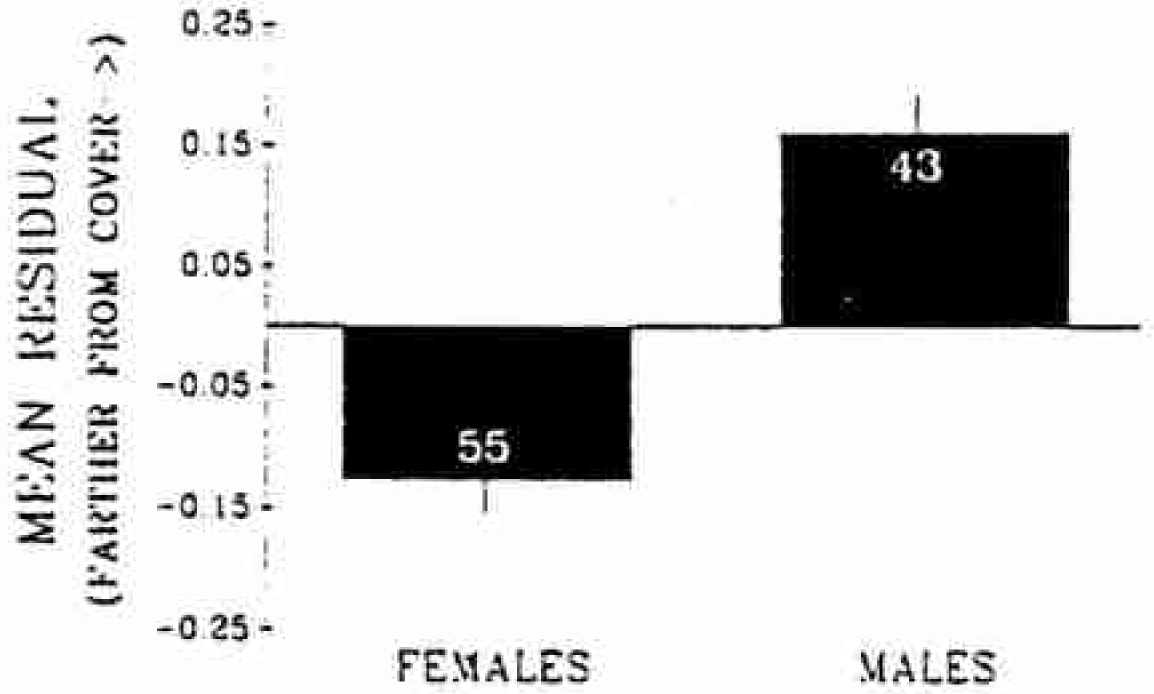

Fig. 3. Means and standard errors of residuals from model of absolute distance to cover that included only flock size, age and dominance proportion as predictors. Residuals are grouped by sex. The figure shows that, with other variables controlled, females fed closer to cover than males.

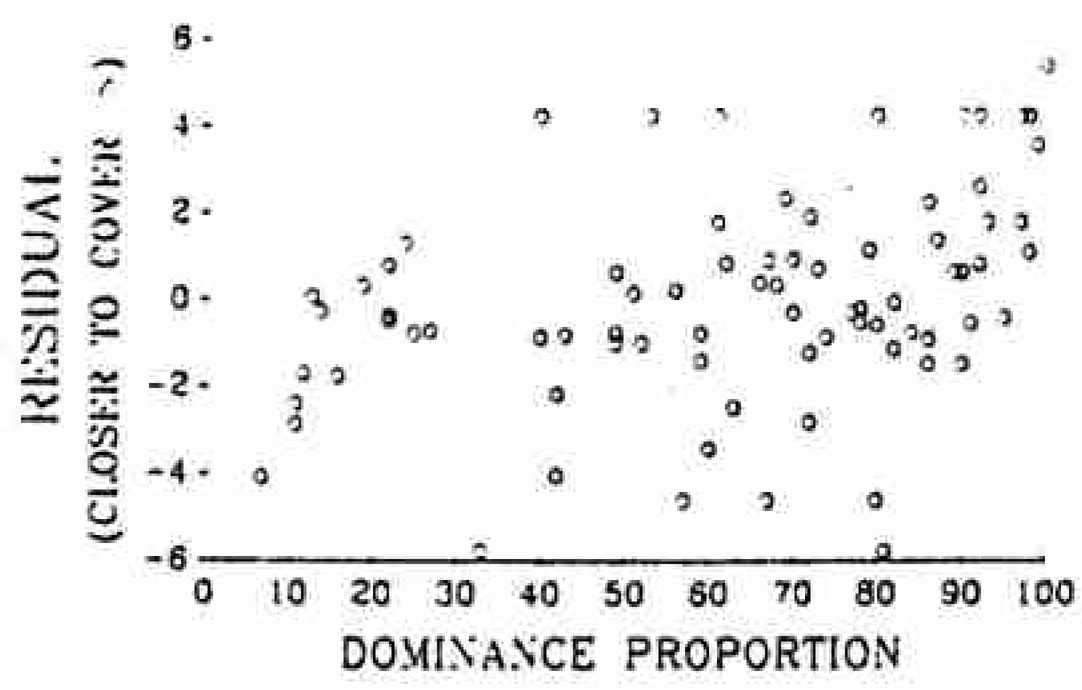

Fig. 4. Relation between dominance proportion and residual from model of relative distance to cover that included only sex as a predictor. The figure indicates that, with the effect of sex controlled, dominant birds fed relatively close to cover.

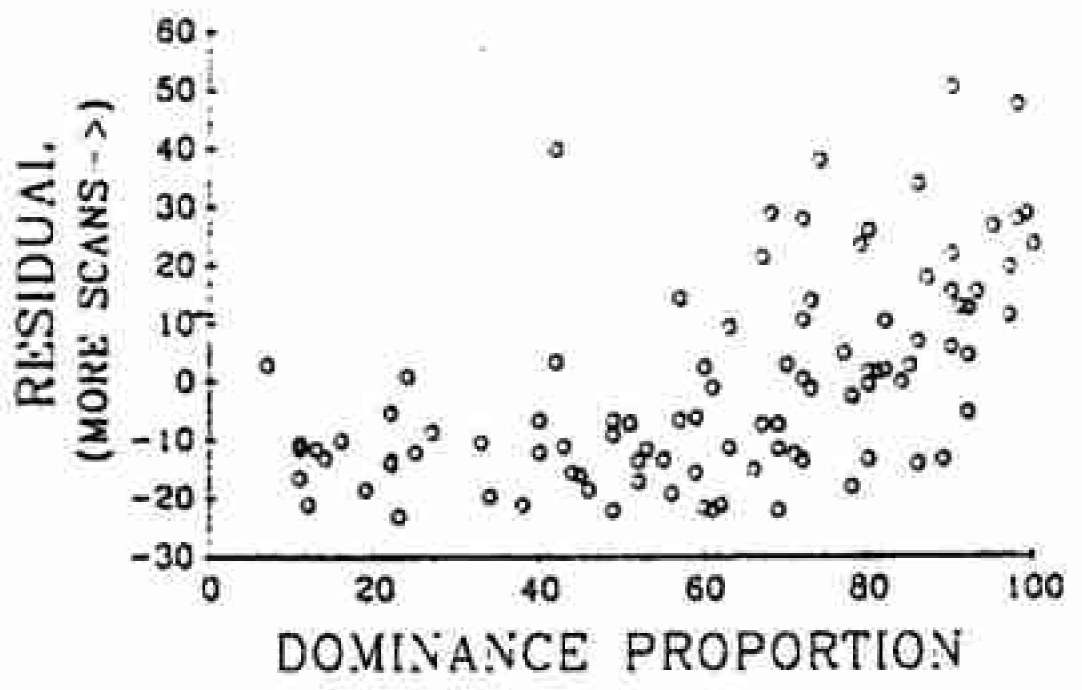

Fig. 5. Relation between dominance proportion and residual from model of time spent feeding (number of scans) that included only observation site as a predictor. The figure indicates that, with the effect of observation site controlled, dominant birds spent more time feeding.

Time spent feeding.

Dominance proportion and observation site were correlated with time spent feeding ($R^2 = 0.39$, $N = 98$; Fig. 5). Dominant birds ($F_{1,94} = 56$, $p \ll 0.001$) and those at sites where more scans were recorded ($F_{2,94} = 8$, $p < 0.001$) tended to spend more time on the blocks. Observation site was a concomitant (nuisance) variable whose inclusion in the model reduced overall variance in time spent feeding.

Influence of weather and dominance heterospecifics on feeding.

The number of birds at feeding stations fluctuated greatly from one day to the next but was largest when cloud cover was heavy ($F_{1,22} = 12$, $p < 0.005$) and temperatures were cold ($F_{1,22} = 7.1$, $p < 0.02$) and depended also upon the observation site where scans were recorded ($F_{2,22} = 10$, $p < 0.005$).

The number of scans in which a white-throated sparrow fed with dominant heterospecifics was correlated with the length of its wing chord ($r = -0.18$, $p < 0.004$) and three concomitant variables: overall time spent feeding ($r = 0.63$, $p < 0.004$), flock size ($r = 0.31$, $p < 0.004$) and absolute distance to cover ($r = -0.28$, $p < 0.004$). this result ($R^2 = 0.53$, $N = 140$) indicates that small white-throated sparrows tended to share blocks with dominant heterospecifics. Such block sharing usually occurred at the block nearest cover (245 of 310 instances, 79%).

Discussion

Distance to cover and risk of predation.

Though distance to cover has been used widely as an indication of predation risk in wintering passerines (Schneider, 1984; Lima, 1987; Lima *et al.*, 1987; Hogstad, 1988), its adequacy depends upon four conditions. First, predators must be a threat to a bird's survival during a winter. Sharp-shinned hawks (*Accipiter striatus*), which subsist on small birds, are common at Mason Farm throughout the winter, and colleagues and I have observed their attacks on flocks and kills that probably resulted from such attacks. Second, birds must commonly feed at various distances from cover under natural circumstances. Observations in the study area have shown that white-throated sparrows frequently venture several metres from cover in flocks to feed in fields and along roadsides. Third, cover must serve as a source of protection from predators. Lima *et al.* (1987) suggest that being close to cover does not always make a bird safe from predators, because cover can serve as a hiding place for mammalian predators lying in ambush. Though potential mammalian predators (foxes, bobcats and weasels) occur in the study area, they were rarely seen during daylight hours and were never seen to threaten the sparrows. More importantly, white-throated sparrows tended to feed at the block nearest cover when alone (458 of 516 total scans, 89%). Fourth, birds must be able to escape predators more easily when close to cover. It is certainly true that birds close to cover in a flock can reach it before those farther away, providing they can detect a predator at the same time, but sparrows feeding near bushes might have difficulty detecting the approaches of avian predators. Since white-throated sparrows, like many flocking birds, emit alarm calls upon detection of avian predators (see

MARLER, 1955), all individuals feeding together probably learn of an attack at about the same time. Therefore, distance to cover and not the ability to spot predators probably determines the amount of time that a bird takes to reach cover.

Although it seems apparent that the threat of predation increases as a sparrow moves farther from cover, the exact nature of the relationship between distance to cover and risk of predation is unclear. Predation risk might increase in a linear fashion as a bird moves farther from cover (as assumed here), but the relationship is likely to be more complex.

Comparison of absolute and relative distances to cover.

Absolute and relative distances to cover are highly correlated ($r = 0.77$, $N = 80$, $p < 0.001$), but the uses of the two indices reflect two distinct views of predators' attacks on foraging sparrows. In using absolute distance to cover as an index of predation risk, one assumes that a sparrow's risk of being killed by a predator depends on the amount of time that it spends far from cover and that the relative positions of its flockmates are not important. On the other hand, by using relative distance to cover as an index of predation risk (*e.g.* SCHNEIDER, 1984; HOGSTAD, 1988), one assumes that a predator is most likely to attack sparrows on the outer edges of flocks (*i.e.* farther from cover than their flockmates), so a bird's position relative to others in a foraging flock (not its absolute distance to cover per se) determines its safety from predators. The accuracy with which each index measures predation risk depends upon the ways in which predators attack flocks.

Correlates of absolute and relative distances to cover.

Flock size.

The strong relationship between flock size and absolute distance to cover (see Fig. 1) revealed that sparrows feeding with many other birds tended to feed far from cover. This relationship is not surprising; the severe competition for blocks near cover in large flocks made it necessary for many birds to feed far from cover if they were to feed at all. However, the implications of this result are important. Since large flocks of birds are able to spot predators more rapidly than small flocks (PULLIAM, 1973; POWELL, 1974; SIEGFRIED & UNDERHILL, 1975; LAZARUS, 1979), individuals in large groups are less at risk feeding far from cover, where densities of seeds might be higher (see SCHNEIDER, 1984). If density of food is higher far from cover, one might expect sparrows to form large flocks and feed far from cover when scarcity of food or cold temperatures make it necessary for them to feed rapidly. Indeed, at cold temperatures yellow-eyed and dark-eyed juncos (*Junco phaeonotus* and *J. hyemalis*) feed in large flocks in areas of abundant food (KETTERSON, 1978; CARACO, 1979), a behaviour that apparently allows the former species to increase its feeding rate (CARACO, 1979). The large number of white-throated sparrows at feeding stations during cold and cloudly conditions (see below) suggests that this species too might form large feeding aggregations as a means of increasing feeding rates when metabolic demands are greatest.

Age.

Age was correlated with absolute but not relative distance to cover. The partial correlation between age and distance to cover suggests that age itself (in addition to dominance) affected absolute distance to cover.

Why older birds, regardless of dominance status, feed closer to cover than young birds is not clear. However, white-throated sparrows that are second- or third-year residents in a wintering area, and hence are older, tend to store more subcutaneous fat than first-winter birds. Perhaps selection has resulted in young birds being less cautious in feeding in order to offset this disparity.

Sex.

Sex was correlated with both absolute and relative distances to cover. In a number of other wintering passerines, males and females differ in foraging behaviour (*e.g.* GLASE, 1973; MCELLIN, 1979; WAITE, 1987), but these differences seem to result from sex-related dominance rather than sex itself. That cannot be the case here, because males, which tend to outrank females in white-throated sparrows (PIPER & WILEY, 1989a), and might therefore be expected to feed more safely (see SCHNEIDER, 1984), actually feed farther from cover. This pattern exists both when the other three correlates are controlled (see Fig. 3) and when only sex is considered (mean of absolute distance to cover for females = 1.06 m $\pm$ 0.34 SD, N = 55; for males = 1.25 m $\pm$ 0.41 SD, N = 43; $p < 0.05$, two-tailed t-test).

An additional report of male house sparrows (*Passer domesticus*) feeding in more dangerous situations than females (BREITWISCH & HUDAK, 1989) suggests that male passerines might generally run higher risks of predation, but the reason for this behavioural pattern is unclear. It is possible that males are less selective about where they feed because, being larger, they have somewhat greater energy needs than females. If so, it is puzzling that sex and not size was the predominant factor affecting distance to cover. If sex is the best genetic predictor of size, though, natural selection might have acted on sex rather than size in making large birds bolder in feeding. On the basis of this pattern in feeding behaviour, one might predict that males should be killed more often by avian predators.

The smaller size of female white-throated sparrows probably made it easier for them to feed near cover, since small individuals are more successful than large individuals at sharing blocks with dominant heterospecifics.

Dominance.

Dominance proportion was strongly correlated with relative distance to cover and was also correlated with absolute distance to cover.

Taken together, the two analyses indicate that dominant birds successfully use their status to feed near cover but that dominance is not the only determinant of distance to cover. Indeed, my data revealed that dominants fed closer to cover than their subordinates in only 570 of 849 (67%) total dyads. By comparison, SCHNEIDER (1984), who reported a strong relationship between dominance and distance to cover, found dominants fed closer than their subordinates in 24 of 31 dyads (77%), a result not significantly different from mine ($G = 0.75$, G-test of independence).

The inability of dominant white-throated sparrows to monopolize safe feeding sites appeared to result in part from the presence of several other seed-eating species that fed with white-throated sparrows (both at feeding stations and in nature) and were always dominant to them: cardinals (*Cardinalis cardinalis*), rufous-sided towhees (*Pipilo erythrophthalmus*), fox sparrows (*Passerella iliaca*), and song sparrows (*Melospiza melodia*). Individuals of these dominant species continually supplanted white-throated sparrows (both dominants and subordinates) at feeding blocks near cover, so possession of blocks, particularly those nearest cover, was constantly changing. The constant state of flux at feeding blocks reduced the ability of dominant white-throated sparrows to exclude subordinates from blocks nearest cover. The apparent tendency of dominant heterospecifics to tolerate small (but not large) white-throated sparrows feeding alongside them (see Results) further reduced the success with which dominant white-throated sparrows could monopolize feeding blocks near cover, because dominant birds tend to be large.

Time spent feeding.

The strong correlation between time spent feeding and dominance (Fig. 5) showed that dominant white-throated sparrows spent more time feeding at observation sites than subordinates when distance from cover was disregarded. Providing dominants and subordinates fed at equal rates while on the blocks, dominant birds consumed more food at observation sites. Although I did not measure feeding rates of the sparrows during scans in 1984-1985, an examination of feeding rates computed from scan samples in 1983-1984 showed no correlation between dominance and feeding rate ($r = -0.15$, $N = 99$, NS).

The tendency of dominant birds to spend large amounts of time at feeding locations seems unlikely to be a meaningless artifact that resulted from the presentation of highly-concentrated food. Observations of white-throated sparrows feeding on natural food in the study site from January through March 1986 indicated that individuals often encountered patches of food where they would remain feeding for 30 s or more, just as they did at feeding blocks. The higher fat levels of dominant white-throated sparrows in the study area (PIPER & WILEY, 1990b) are a further indication that they enjoy advantages over subordinates in foraging.

The effect of environmental factors on feeding safety.

White-throated sparrows fed at feeding stations in large numbers on cloudy and cold days, a finding that has been reported in other wintering passerines (KETTERSON, 1978; CARACO, 1979) and apparently results from birds' greater need for food to meet metabolic requirements during cold periods with snowfall (KETTERSON, 1978). The large daily fluctuations in the use of feeding stations and the lack of a correlation between this use and calendar date (adjusted $r = 0$, $N = 17$, $p > 0.4$) suggests that it was environmental rather than seasonal factors (*e.g.* hormone-induced changes in tolerance of conspecifics brought on by the approach of spring) that determined the number of sparrows visiting feeding sites.

Since the number of birds feeding at observation sites was also strongly correlated with overall distance to cover, the mean distance to cover for the population fluctuated greatly from day to day according to weather conditions, ranging between 0.80 and 1.37 m (mean = 1.12 ± 0.16 SD, N = 27). Considering the influence of weather conditions on overall distance to cover, the distance to cover at which a given bird feeds on a given day can be viewed as having two components: one resulting from a bird's individual characteristics (sex, age and dominating ability), the other from the circumstances under which it feeds (flock size, temperature and cloud cover).

Dominance and feeding in white-throated sparrows.

Dominance is by definition the ability of an animal to gain priority over others in access to a resource, and thus it seems reasonable that dominants might gain access to resources in safe areas, leaving subordinates to feed in more dangerous ones (GLASE, 1973; CARACO *et al.*, 1980; SCHNEIDER, 1984; LIMA *et al.*, 1987; HOGSTAD, 1988). My results indicate that, while dominance is related to distance to cover, it is only one of a complex array of factors that determines the distance from cover at which a white-throated sparrow feeds. In view of this complexity, it seems that more detailed analyses than have been done previously might be necessary to clarify the degree to which distance to cover is associated with dominance in other species.

Dominance affects time spent feeding much more strongly than it does distance from cover (compare Figs 4 and 5). This suggests that dominant birds benefit more from increased access to food than from reduced exposure to predators.

Summary

I studied a free-living population of white-throated sparrows (*Zonotrichia albicollis*) to determine which, among eleven behavioural, morphological and situational variables, were correlated with the distance from cover at which individuals fed (a presumed index of predation risk) and the amount of time they spent feeding at three observation sites. Time spent feeding was correlated only with dominance, an indication that dominant birds obtained greater access to high quality food. In contrast, an assortment of factors affected distance to cover. Individuals tended to feed far from cover if they were: (1) in large flocks, (2) males, (3) young and (4) subordinate. Distance to cover for the population as a whole increased during cold and cloudy conditions. The failure of dominance alone to determine a bird's distance to cover probably resulted in part from the confusion caused by dominant heterospecifics (*e.g.* cardinals, *Cardinalis cardinalis*) and from their apparent tendency to tolerate mainly small white-throated sparrows (which tended to be subordinate) feeding with them. Overall, this study indicates that while dominance clearly allows easy access to food, it is only one of several factors affecting exposure to predators.

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