

BOTH HIGH- AND LOW-RANKING WHITE-THROATED SPARROWS FIND NOVEL LOCATIONS OF FOOD

R. HAVEN WILEY

Department of Biology, University of North Carolina,
Chapel Hill, North Carolina 27599-3280, USA

ABSTRACT.—I examined the hypothesis that low-ranking White-throated Sparrows (*Zonotrichia albicollis*) during winter are more likely than high-ranking birds to find novel sources of food near a known feeding site. If so, high- and low-ranking birds might use different tactics during foraging, each with compensating advantages and disadvantages (Rohwer and Ewald 1981). I presented small, partially hidden concentrations of seed at random locations within 2 m of regularly supplied feeding sites, used by individually marked birds with known dominance relationships. Individuals that found the novel sources of food included approximately equal numbers of birds in all four quartiles of the distribution of dominance proportions. Once the novel food was found, disproportionate numbers of high-ranking birds tended to feed there. They gained access to the food in most cases by supplanting subordinates, whereas the low-ranking birds waited until they could approach the food without interactions. In addition, high-ranking birds usually left the food of their own accord, whereas low-ranking birds were usually supplanted by dominants. I suggest that high-ranking birds found new sources of food as often as low-ranking birds and also appropriated sources of food once found by others. I found no evidence that advantages in finding food compensated birds with low rank for disadvantages in competing for food once found. Received 3 October 1989, accepted 4 July 1990.

DOMINANCE relationships can affect survival of wintering birds in a number of ways. In the first place, high-ranking birds often supplant subordinates from food (Czikeli 1983). In addition, high-ranking birds in some situations obtain more food (Krebs et al. 1972, Baker et al. 1981, Ens and Goss-Custard 1984, Theimer 1987), have lower disappearance rates (Fretwell 1969, Piper and Wiley 1990), preempt feeding sites that are less exposed to predators (Schneider 1984, Piper 1990), and accumulate larger stores of fat (Weidenmann and Rabenold 1987, Piper and Wiley 1990).

In contrast, Rohwer and Ewald (1981) suggested that high and low rank in dominance might have balancing advantages and disadvantages, so that birds of all ranks have the same expectation of survival. For instance, their observations suggested that, although high-ranking Harris' Sparrows (*Zonotrichia querula*) had the advantage of appropriating food found by subordinates, they also interacted more frequently with each other than did low-ranking birds among themselves. Rohwer and Ewald (1981) proposed that, with food neither too sparse nor too clumped, the time required for interactions by high-ranking birds might re-

duce their feeding rates to levels about equal to those of low-ranking birds. In addition, high-ranking individuals' advantages in appropriating food once found might be balanced by low-ranking birds' advantages in finding food. If high-ranking individuals focused on competing for access to known concentrations of food, novel sources in the vicinity of a known feeding site should be found most often by low-ranking individuals. It has even been proposed that House Sparrows (*Passer domesticus*) feeding in flocks are of two distinct types, those finding food ("producers") and those approaching others already feeding ("scroungers") (Barnard and Sibly 1981).

White-throated Sparrows (*Zonotrichia albicollis*) wintering in North Carolina have stable dominance relationships that depend in part on the birds' locations, sex, age, and dominance achieved in their first winters (Piper and Wiley 1989a). Although they do not form cohesive flocks with stable membership, they often congregate when feeding on natural as well as artificial sources of food. I attempted to determine whether or not high- and low-ranking individuals differ in their chances of finding new locations of food in the vicinity of an established

source of food. I also asked if, once found, these new locations of food were appropriated by high-ranking birds.

METHODS

Subjects.—This study was conducted during January and February 1985 in the Mason Farm Biological Reserve near Chapel Hill, North Carolina. I used an individually marked population of White-throated Sparrows followed from 1982–1988. Basic procedures for marking and examining these birds have been described previously (Piper and Wiley 1989a, b). The primary study area was a line of 17 trapping stations 25 m apart along a hedgerow. Each winter, approximately 300 White-throated Sparrows, all marked individually, were resident in this area. In collaboration with Walter Piper, I determined the age of each bird by the pneumatization of its skull when first captured and its sex by laparotomy.

At four locations 75–100 m apart along the trapline, Piper and I observed dominance interactions of feeding birds from blinds (Piper and Wiley 1989a). A bird was considered dominant over an opponent if it supplanted (opponent moved away as the former approached with approximately normal locomotion), attacked (the opponent avoided a vigorous approach, occasionally resulting in contact), or won a face-to-face fight in 75% or more of its interactions with the opponent. As an index of a bird's dominance at any one location, we used a bird's dominance proportion: the proportion of opponents dominated divided by the total number of opponents with which it interacted (Piper and Wiley 1989a).

As dominance is a social relationship between two individuals, I have restricted my use of the terms "dominant" and "subordinate" to statements about such relationships. The terms "high-ranking" and "low-ranking" refer to individuals that rank high or low in overall dominance proportion. Rankings by dominance proportion accorded well with a nearly linear hierarchy among the birds that used any one site regularly (Piper and Wiley 1989a), although there always were some pairs of birds never observed to interact and some involved in nontransitive relationships.

Observations of food finding.—I observed birds at new sources of food at three of the four locations used for observations of dominance. Each site included a small wooden blind (0.9 × 0.9 × 1.2 m) located 2–2.5 m from an array of 6 cement blocks placed on end in a 2 × 3 array, with two blocks 0.7 m apart at the edge of a thick bush, two more 0.7 m from the bush, and two 1.4 m from the bush. During observations of dominance, on three or four mornings a week, I placed small amounts of millet on top of each block on no more than three occasions about one hour apart. Thus this array of blocks was a regular, but not continuous, source of concentrated food.

For each trial, I placed about 2 cc of millet on the ground at one of four distances (0.5, 1.0, 1.5, or 2.0 m) to one side of the feeding blocks and at one of four distances (0, 0.35, 0.7, or 1.4 m) from the edge of the bushes at one of the regular observation sites. There were thus 16 possible locations on each side of the feeding blocks (4 distances from the blocks multiplied by 4 distances from cover), a total of 32 possible locations at each observation site. The location for each trial was determined by coin tosses, with the restriction that successive trials at any one observation site alternated between locations to the left and right of the cement blocks. I never conducted trials on two days in succession at any one site and rotated the hours of the morning during which I used each of the three sites. Trials began between 0800 and 1100 standard time. At the start of each trial, I also placed food on the cement blocks as usual. Observations began as soon as birds began to feed on the blocks (usually as soon as I had entered the blind) and continued for 50 min. Altogether I conducted 53 trials in 1985 between 21 January and 26 March, 15–20 trials at each of the three sites (sites 2, 6, and 10).

The ground around the cement blocks had short grass and leaves 2–5 cm deep, so that the small amount of food was partially concealed from a sparrow on the ground more than 5–15 cm away. To discourage the birds from using my actions as a cue to the location of the new source of food, I routinely visited all positions on both sides of the cement blocks and at each position reached down in the same motion used to deposit the small amount of food. Preliminary trials showed that these precautions ensured that the new sources of food were not located immediately.

During observations, I recorded the identity of the first bird to feed at the new source of food and the latency to first feeding. After the food was found, I recorded the identity of each bird that fed at the food during the hour of observation, how it initiated feeding (by attacking or supplanting a feeding bird or by initiating feeding when no other bird occupied the food), and how it terminated feeding (by being attacked or supplanted by a conspecific, by leaving of its own accord, or for miscellaneous other reasons, such as being supplanted by another species). There were a few occasions on which I could not identify a bird visiting the food, because the vegetation blocked my view of its bands. These occasions included long as well as short stays at the food. These few unidentified visitors appeared representative of the entire sample.

Statistical analysis.—To determine if low-ranking birds were more likely than high-ranking birds to find novel sources of food, I divided the birds regularly visiting each established feeding site into quartiles according to their dominance proportions. Regular visitors were those with 10 or more known dominance relationships ($n = 104$ at Site 2, 87 at Site 6, and 81 at Site 10). Among regular visitors, both

low- and high-ranking birds were present continuously near established feeding sites. The null hypothesis for this study was that birds in all four quartiles of dominance proportion should have equal chance of finding a novel source of food. I used goodness-of-fit tests to compare the observed distributions of finders among quartiles of dominance proportion with an even distribution.

RESULTS

Before these experiments were conducted, the birds had become relatively tame at the feeding sites. Birds congregated in the bushes near the cement blocks when I approached, and they began to feed on the blocks as soon as I entered the blind. The blocks closest to cover were often occupied continuously. Blocks farther from the bushes also attracted many feeding birds (for an analysis of the use of these regular feeding sites, see Piper 1990).

At any one time a few birds fed on the ground around the blocks. Within 50 cm or so there were scattered seeds dropped from the blocks. Some birds searched the short grass farther from the blocks as well, only occasionally finding an item of food. Normally, the density of birds decreased away from the blocks with food. These more peripheral searchers found the novel sources of food.

In 35 of the trials, an individually identified White-throated Sparrow found the food at the new location. In the remaining 18 trials, either another species found the food first ($n = 8$), the food was not found during observations ($n = 6$), or the individual White-throated Sparrow finding the food was unbanded ($n = 2$) or unidentified ($n = 2$). In the 39 trials in which a White-throated Sparrow found the food, the mean latency increased with the distance of the novel location from the regularly used blocks, although variation around the means was high (Fig. 1). In several preliminary trials with novel locations for food at distances of 3–6 m, none was ever found within one hour. Once discovered, the novel sources of food normally continued to attract birds for at least 30 min, well after nearly all the food had been eaten. Indeed, a few birds briefly visited these sites even during observations the following day.

The 35 occasions on which White-throated Sparrows found the food involved 32 different individuals. No individual found the novel locations more than twice; the three that found

food twice included both high- and low-ranking birds. These results implied that there were no pronounced differences among individual birds in the chances of finding the novel locations of food. Consequently, I treated the 35 cases as independent trials.

The finders included birds in all quartiles of the distribution of dominance at each site (Fig. 2). The overall distribution of finders among quartiles of dominance did not differ significantly from equal probabilities (Kolmogorov-Smirnov test, $D = 0.08$, $n = 35$, $P > 0.2$). In 13 cases the finder had been supplanted from the food on the regularly supplied blocks earlier in the trial.

Even the highest-ranking birds were represented among the finders. Among birds with dominance proportions >0.9 at each site ($n = 5, 5$, and 6 at the three sites, respectively), one found the new source of food in one trial. Because the combined top quartiles of dominance proportions at the three sites included a total of 68 birds, 1 finder in 16 for the birds with dominance proportions >0.9 is only 1 less than expected on the null hypothesis that the most dominant birds did not differ from others in the top quartile in the chances of finding a new source of food.

Novel locations for food at a distance from cover were found just as often by birds in the top quartiles of dominance proportions as were those close to cover. Of 18 trials at distances of 0.7 m or more from cover, 10 (56%) were found by birds in the upper two quartiles of dominance proportions, whereas 10 of 17 trials (59%) at distances of 0.35 m or less from cover were found by such high-ranking birds. Of 6 trials at the distance farthest from cover (1.4 m), 5 were found by birds in the upper two quartiles. These results provide no indication that distance from cover, within the limits tested, affected the chances that a novel location for food was found by high- or low-ranking birds. There was also no effect of distance from cover on the latency to finding novel locations of food (5.5 ± 6.2 min at 0–0.7 m from cover, 5.5 ± 5.7 min at 0.7–1.4 m).

Although Site 2 differed from sites 6 and 10 in having a majority of finders from the lowest two quartiles of the dominance distribution, the heterogeneity among sites is not statistically significant (analysis of the 3×2 contingency table for sites \times quartiles of dominance proportions for finders, with quartiles 1–2 and

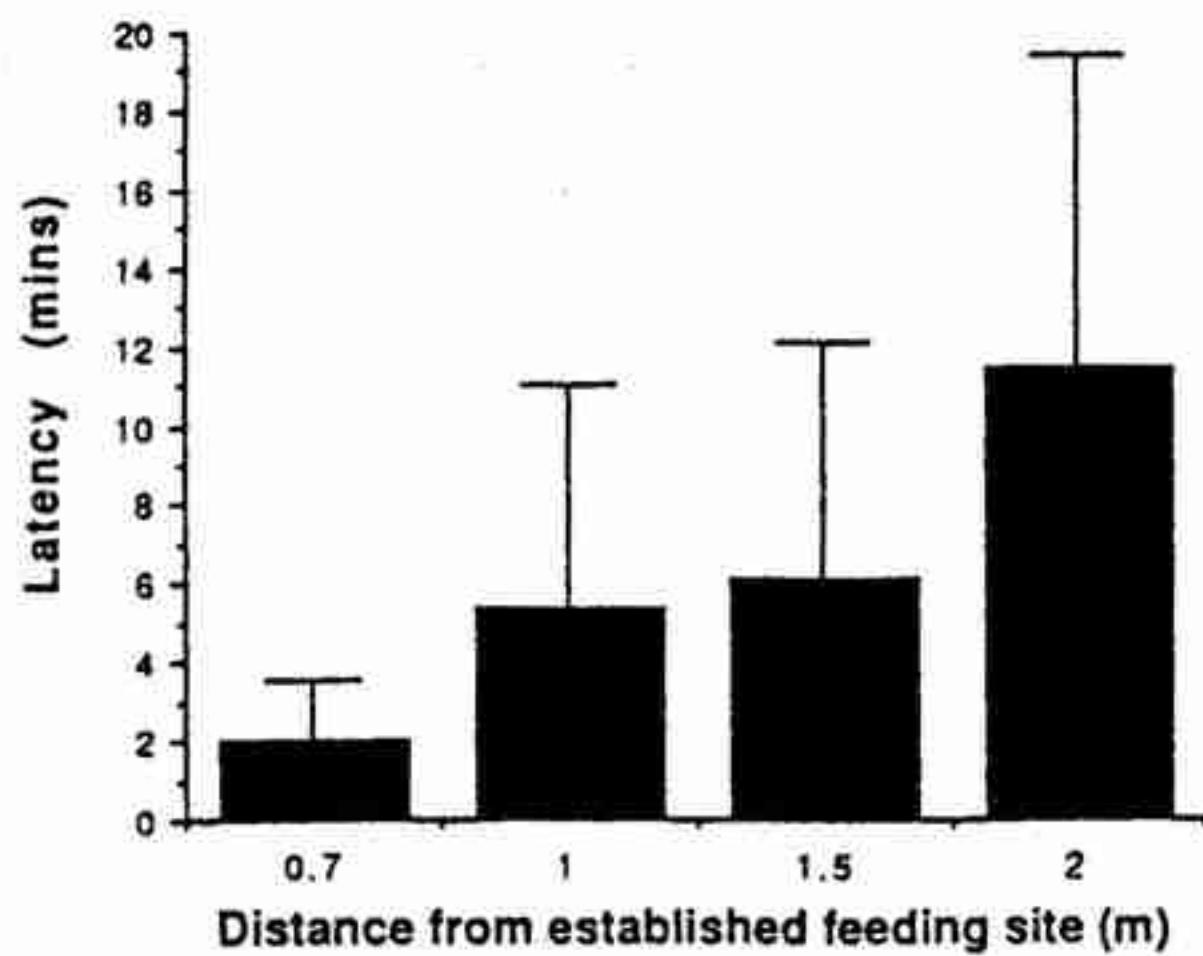


Fig. 1. Mean latencies for White-throated Sparrows to find the novel locations of food at different distances of food from the regularly supplied blocks. Vertical lines represent SD.

quartiles 3-4 lumped to reduce sparse cells [$\chi^2 = 4.12$, corrected for continuity, $df = 2$, $n = 35$, $P > 0.05$]).

Once found, the new location attracted high-ranking birds disproportionately. The novel locations attracted 5.6 ± 3.32 individual White-throated Sparrows, and birds from the most dominant quartile predominated at each observation site (Fig. 3). The distribution of visitors among quartiles of dominance proportion differed significantly from equal probabilities (Kolmogorov-Smirnov test, $D = 0.16$, $n = 259$, $P < 0.01$).

On 113 occasions, I observed individuals as they began to feed after the novel source of food had been discovered. Birds in the lowest quar-

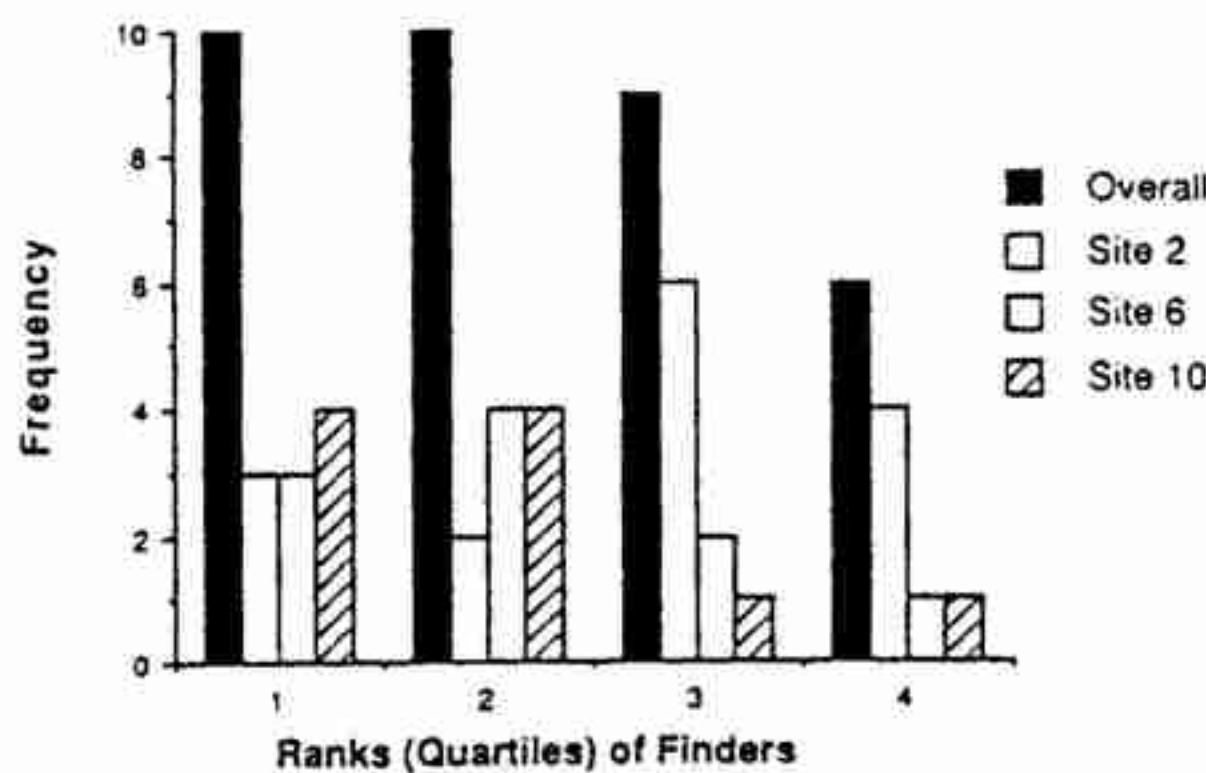


Fig. 2. The ranks (quartiles of the distribution of dominance proportions) of White-throated Sparrows that found the novel locations of food at three observation sites (2, 6, and 10). Quartiles 1-4 include birds with the highest through the lowest dominance proportions, respectively.

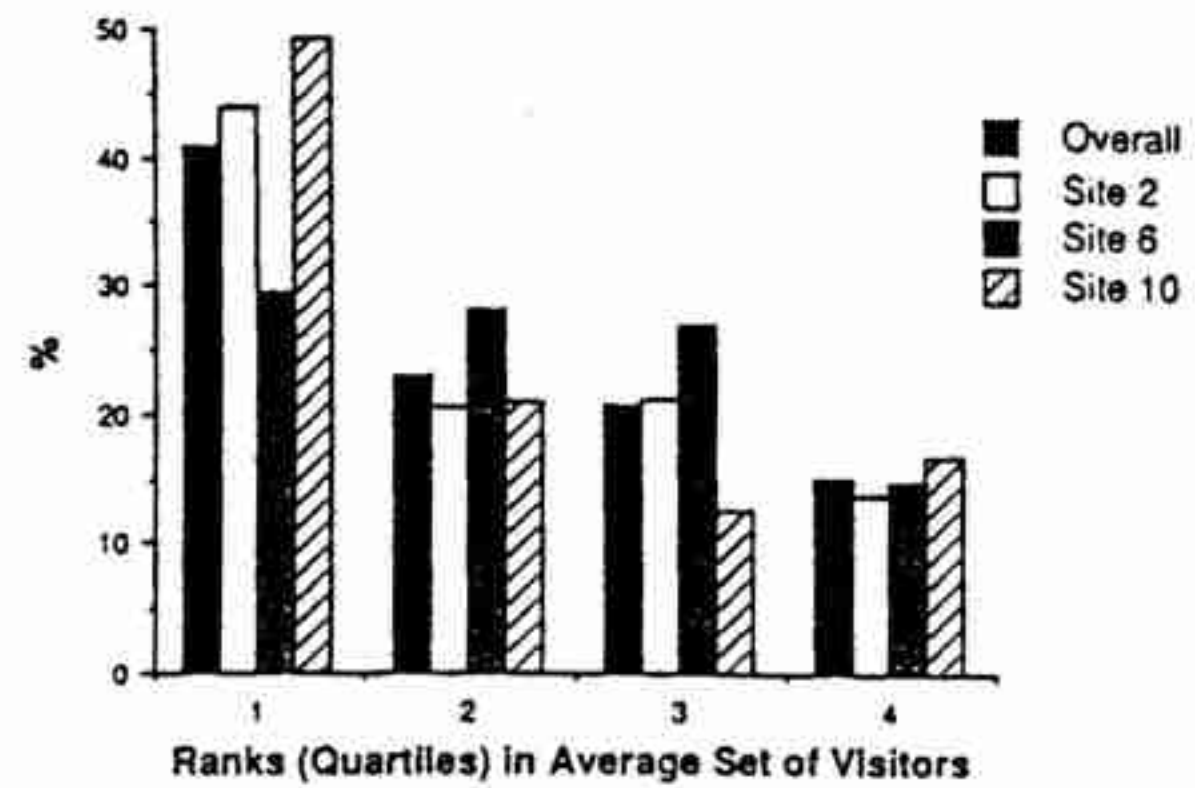


Fig. 3. The ranks (quartiles of the distribution of dominance proportions) of individually marked White-throated Sparrows that visited the novel locations of food after they had been found at three observation sites (2, 6, and 10).

tile of dominance initiated feeding when the food source was not occupied by another bird in 90% of cases. Birds in the highest quartile of dominance supplanted or attacked birds at the food more often than they initiated feeding at the food when unoccupied (Fig. 4; $\chi^2 = 7.1$, quartiles 1-2 and quartiles 3-4 lumped to reduce sparse cells, $df = 2$, $n = 112$, $P = 0.03$). Birds of intermediate rank had correspondingly intermediate behavior in gaining access to the food.

Once feeding at the novel source of food, a bird might leave of its own accord, be supplanted or attacked by another White-throated Sparrow, or be supplanted by another species. Birds in the lowest two quartiles of dominance were

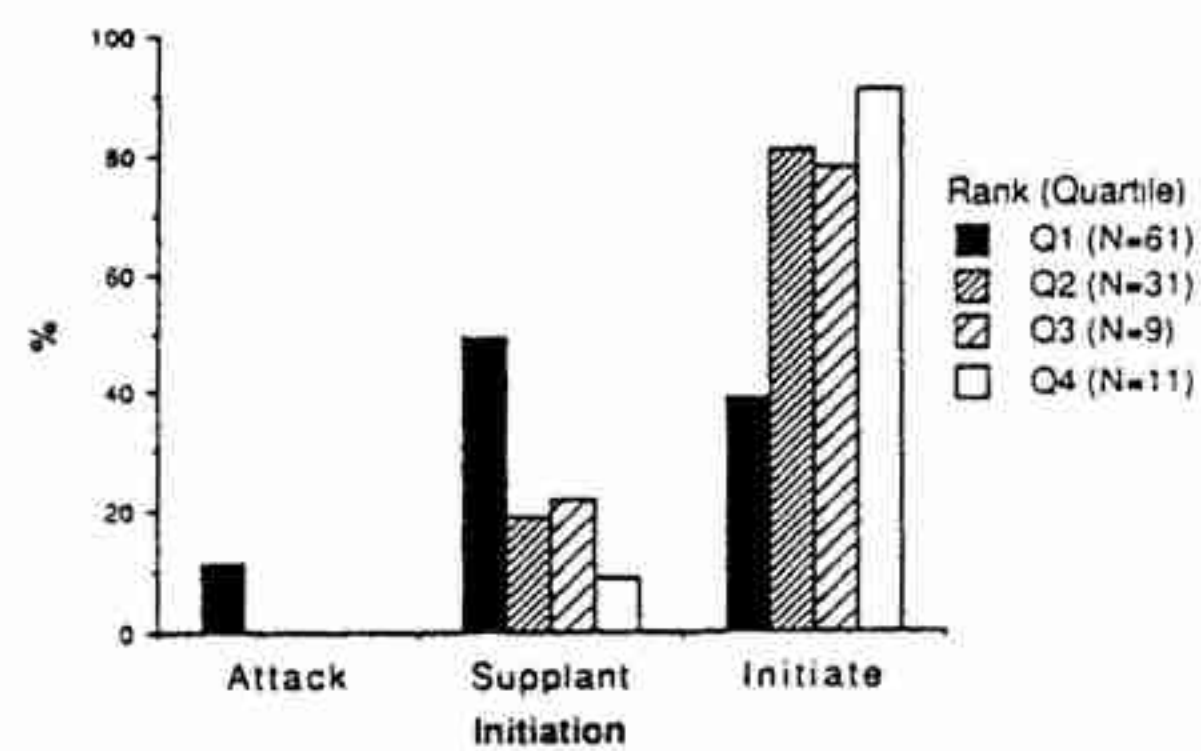


Fig. 4. Distributions of types of behavior used by marked White-throated Sparrows of different ranks (quartiles of the distribution of dominance proportions) to obtain access to novel locations of food. Types of behavior: newcomer attacked a conspecific feeding at the novel location (attack); newcomer supplanted a conspecific feeding at this location (supplant); newcomer started feeding when no other bird occupied this location (initiate).

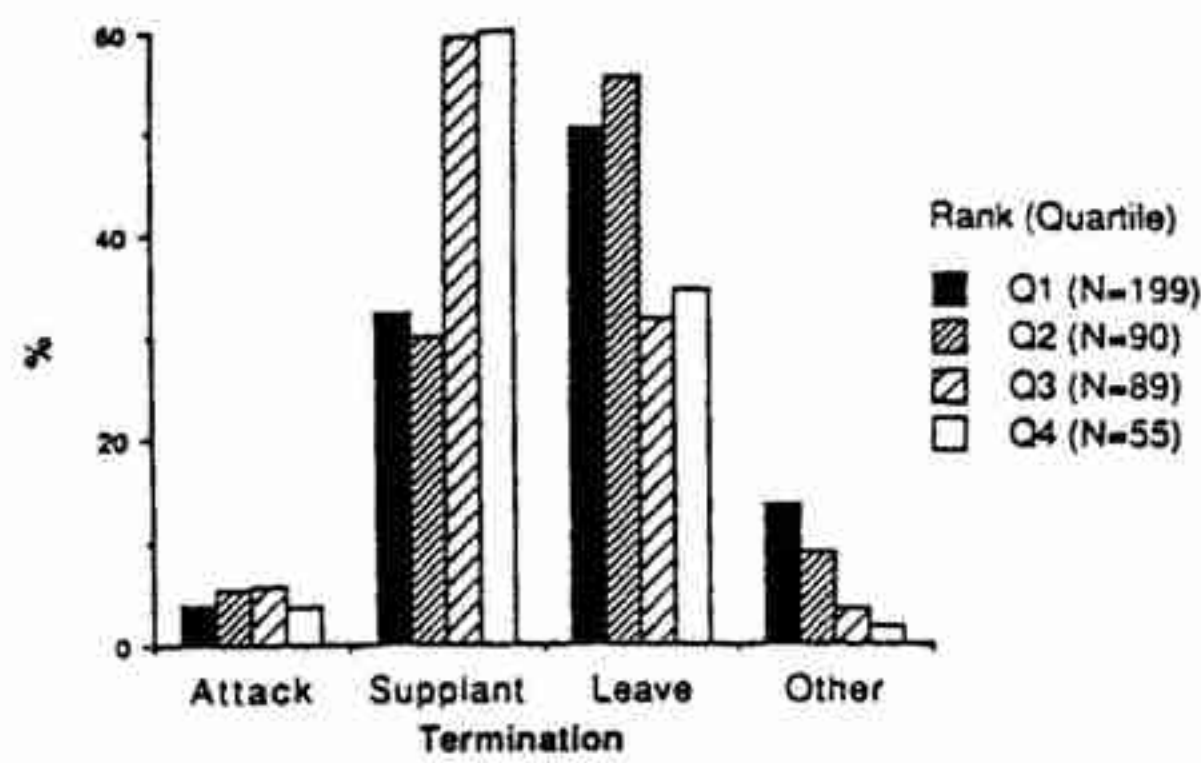


Fig. 5. Distributions of types of behavior involved in leaving the novel locations of food for marked White-throated Sparrows of different ranks (quartiles of the distribution of dominance proportions). Types of behavior: feeding bird attacked by a conspecific (attack); feeding bird supplanted by a conspecific (supplant); feeding bird left the food without interaction (leave); feeding bird supplanted by another species (other).

usually supplanted, whereas birds in the highest two quartiles of dominance were more likely to leave of their own accord. (Fig. 5; $\chi^2 = 38.6$, $df = 9$, $n = 433$, $P < 0.01$).

On several occasions a low-ranking bird that had discovered one of the novel sources of food behaved as if it were trying to conceal the discovery from nearby dominants. The bird hopped back and forth, never stopping to feed continuously, and took one or two seeds each time it passed the food. It seemed possible that this tactic prolonged the time before a dominant appropriated the food. More often, low-ranking birds began frenetic feeding immediately on discovering one of the novel food sources, as if to eat as much as possible before a dominant bird arrived. It is not clear which of these two tactics by low-ranking birds resulted in greater food intake before the inevitable supplantation by a dominant.

Once a new source of food was located, birds often arranged themselves in more or less concentric zones according to their dominance. The highest-ranking bird present preempted the food, several somewhat lower-ranking birds would hop back and forth, often looking for food, in a zone 10–30 cm away, and still lower-ranking birds searched in a zone 30–60 cm away. If a bird left this arrangement, another from farther away took its place. Such clear spatial distributions based on dominance were noted in only a minority of the trials, however.

DISCUSSION

Finding food and appropriating food once found.— I found that birds in all quartiles of the dominance distribution located novel sources of food with nearly equal probability. Even individuals among the highest in dominance at each site appeared to find food with equal probability. Thus high- and low-ranking birds did not differ markedly in finding new locations of food. Once food was discovered, the high-ranking birds preempted it.

New locations of food farther from cover were no more likely to be found by low-ranking birds than those closer to cover. If low-ranking birds spent more time far from cover, they should have found more of the novel sites for food there. Although subordinate White-throated Sparrows are forced to feed farther from cover under conditions of strong competition for sites close to cover (Schneider 1984, Piper 1990), the amounts of time birds spend at different distances from cover depend on a variety of factors, including age, sex, dominance, and tolerance by other species (Piper 1990). While searching in places away from known locations of food, birds in this study had few direct interactions with conspecifics. Perhaps for this reason, dominance had little influence on the distances that foraging individuals moved from cover.

I determined only the frequencies, not the efficiencies, with which birds of different rank found novel sources of food. Measures of efficiency would require focal-individual sampling of searching birds in a more controlled environment. Nevertheless, I did not notice any marked differences in the probability that birds of different rank found the novel food for a given amount of search time. Nor did I notice any differences in their behavior while they searched.

The spatial arrangement of food in this study attempted to simulate a situation that birds might face in nature, in which individuals attracted to a regularly used patch of food could also search in the vicinity for a new patch of similar food. If high-ranking birds spent more time competing for food at the known site, then the numbers of high-ranking birds searching for new sources of food nearby would be reduced.

As each regular feeding site consisted of only six small locations for feeding (on the six cement blocks), not all high-ranking birds present

could feed at once. Indeed no White-throated Sparrow had unrestricted access to food at the regularly stocked sites. In addition to supplantations by conspecifics, they all were supplanted by larger species (mostly Northern Cardinals, *Cardinalis cardinalis*, and Rufous-sided Towhees, *Pipilo erythrophthalmus*) and even the slightly smaller Song Sparrows (*Melospiza melodia*). Interspecific interactions occurred frequently, even though White-throated Sparrows greatly outnumbered other species using the regular feeding sites and nearly always had available to them one or more of the six cement blocks at each site. As a consequence of the frequent intra- and interspecific interactions, even high-ranking White-throated Sparrows were often unable to feed at the regular sites. The question was whether high-ranking birds, once supplanted, remained near the known feeding sites to compete for chances to feed there or searched nearby for new sources of food. My analysis suggests that any individual, when excluded from a known feeding site, searched for food in new locations.

A different temporal and spatial distribution of food might have changed the foraging tactics of high-ranking birds. Rohwer and Ewald (1981) predicted that large, exposed concentrations of food would be easily monopolized by high-ranking birds, which would then not use subordinates to find food for them. Conversely, food dispersed as single seeds, quickly consumed by the finder, would not offer possibilities for high-ranking birds to appropriate food from subordinates. Only in the intermediate situation, with small, concealed concentrations of food, could high-ranking individuals exploit subordinates as food finders. Their observations suggested that low-ranking Harris' Sparrows were more likely than high-ranking birds to find dispersed seeds located near concentrations. High-ranking birds, on the other hand, supplanted feeding subordinates to obtain access to clumps of food once found.

Thus according to Rohwer and Ewald (1981), high-ranking birds adjust their behavior to current circumstances: they compete for concentrations of food, supplant subordinates, or search on their own depending on their best chances of obtaining food. This proposal is consistent with my results. In this case, when high-ranking birds were excluded from feeding at known concentrations of food, they searched for new sources of food. Once a new source was found,

high-ranking birds supplanted low-ranking ones in order to feed there.

Barnard and Sibly (1981) went further and proposed that small flocks of House Sparrows included two discrete types of individuals, "producers" that found dispersed, concealed food and "scroungers" that obtained food by "interacting" with producers. In their study of three groups of six captive birds, food was presented in a clumped spatial distribution. The commonest form of "interaction" did not involve supplantation or aggression but area-copying instead, "responding to some cue from another forager (not necessarily a successful find) by moving across to search in the immediate area around the forager" (Barnard and Sibly 1981: 546). It is not clear, in view of this definition of "scrounging" by area-copying, whether or not the "producers" actually located new sources of food more often than the "scroungers," nor is it clear that "scroungers" supplanted feeding "producers."

In my experiments, by contrast, there was no evidence for differentiation of individuals into those that searched for new sources of food and those that watched for subordinates to supplant. Instead, all birds that were excluded from a known source of food searched, all seemed to have approximately equal chances of finding food, and all supplanted subordinates from food whenever possible. Indeed, the behavior of White-throated Sparrows suggests that individuals often combined searching with intermittently looking for a feeding subordinate that could be displaced. In direct competition for a known source of food, on the other hand, dominants clearly had an advantage.

If birds of all ranks are equally likely to find food when excluded from a known source, low-ranking birds would be expected to find new sources of food disproportionately only when most high-ranking birds could feed at known sources. In Rohwer and Ewald's (1981) tests at intermediate concentrations of food, these conditions evidently were met. In my tests, most high-ranking birds were excluded from known sources of food at any one time, so they—like low-ranking birds—searched for new sources. After a new concentration of food had been found, only subordinate birds continued searching, while dominants fed.

As a consequence, there was no evidence that high rank involved balancing advantages and disadvantages in foraging. Instead, high-rank-

ing birds had the best of both options. High-ranking birds exploited feeding subordinates that had discovered new sources of food and still located food much like low-ranking birds. They thus would have advantages in exploiting patchy food and do no worse than low-ranking birds on dispersed resources.

Possible other compensating advantages of low rank.—The question remains whether or not low-ranking birds in groups obtain any other advantages that could compensate, in whole or in part, for their reduced ability to compete for access to food. There are several possibilities: (1) individuals in groups might have greater chances of finding food, some of which could be obtained even by low-ranking birds (Thompson et al. 1974, Baker et al. 1981); (2) association with a group might reduce an individual's chances of predation (Powell 1974); and (3) low-ranking individuals might have less frequent interactions and thus avoid some risk, loss of time, or expenditure of energy (Rohwer and Ewald 1981, Rubenstein 1981).

The first two might well apply to White-throated Sparrows, although there is currently no direct evidence. However, because high-ranking birds would presumably receive the same, or even greater, benefits from associating with groups, these first two effects cannot completely compensate low-ranking birds for their disadvantage in competing with high-ranking birds for food.

Lower interaction rates among low-ranking birds as compared with high-ranking birds are also unlikely to compensate completely for their disadvantages in access to food. Note that the high interaction rates among dominant individuals reported by Rohwer and Ewald (1981) presumably resulted from aggregation of dominants at preferred locations for food. High-ranking birds might find it advantageous to visit productive feeding sites, even though they were supplanted on occasion by more dominant individuals. In contrast, low-ranking birds might not find it advantageous to visit such sites because they would be so frequently supplanted. If so, interactions among high-ranking birds at a preferred feeding site would occur more frequently than either those between high- and low-ranking birds or those among low-ranking birds.

Nevertheless, game theory applied to asymmetrical contests for resources predicts that the higher interaction rates of dominant individ-

uals at preferred feeding sites should not reduce intake of food to levels matching those of subordinates (Sutherland and Parker 1985). In studies of birds and other animals both in captivity and in the field, dominant individuals have obtained more food than subordinates, especially under conditions with higher rates of aggression or clumped distributions of food (Ens and Goss-Custard 1984, Monaghan 1980, Rubenstein 1981, Theimer 1987, Schwabl et al. 1988). On the whole, competition among dominant individuals usually does not result in lower food intake by dominants than by subordinates. On the other hand, in captive groups of the fish *Elassoma evergladei*, dominants did not always grow faster than subordinates, perhaps because their greater activity balanced their greater food intake, so that energy balance did not differ appreciably between high- and low-ranking individuals (Rubenstein 1981).

The behavior and ecology of White-throated Sparrows during winter make it unlikely that high- and low-ranking birds have either equal access to food or equal energy balance (Piper 1990, Piper and Wiley 1990). Instead, the higher a bird's rank the greater advantages it can realize, the lower its rank the more it must make the best of a bad situation.

ACKNOWLEDGMENTS

This study could not have been undertaken without Walter Piper's collaboration in marking and determining the dominance relationships of White-throated Sparrows at Mason Farm. For helpful comments on the manuscript, I thank N. B. Davies, B. Watts, and W. Piper. This report is a contribution from the Behavioral Research Station in the Mason Farm Biological Reserve, North Carolina Botanical Garden.

LITERATURE CITED

- BAKER, M. C., C. S. BELCHER, L. C. DEUTSCH, G. L. SHERMAN, & D. B. THOMPSON. 1981. Foraging success in junco flocks and the effects of social hierarchy. *Anim. Behav.* 29: 137-142.
- BARNARD, C. J., & R. M. SIBLY. 1981. Producers and scroungers: a general model and its application to captive flocks of House Sparrows. *Anim. Behav.* 29: 543-550.
- CZIKELI, H. 1983. Agonistic interactions within a winter flock of Slate-colored Juncos (*Junco hyemalis*). Evidence for the dominants' strategy. *Z. Tierpsychol.* 61: 61-66.
- ENS, B., & J. D. GOSS-CUSTARD. 1984. Interference among oystercatchers *Haematopus ostralegus* feed-

- ing on mussels *Mytilus edulis* on the Exe estuary. *J. Anim. Ecol.* 53: 217-231.
- FRETWELL, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird-Banding* 40: 1-25.
- KREBS, J. R., M. H. MACROBERTS, & J. M. CULLEN. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis* 114: 507-530.
- MONAGHAN, P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). *Anim. Behav.* 28: 521-527.
- PIPER, W. H. 1990. Exposure to predators and access to food in wintering White-throated Sparrows *Zonotrichia albicollis*. *Behaviour* 112: 284-298.
- , & R. H. WILEY. 1989a. Correlates of dominance in wintering White-throated Sparrows: age, sex and location. *Anim. Behav.* 37: 298-310.
- , & ———. 1989b. Distinguishing morphs of the White-throated Sparrow in basic plumage. *J. Field Ornithol.* 60: 73-83.
- , & ———. 1990. The relationship between social dominance, subcutaneous fat and annual survival in wintering White-throated Sparrows (*Zonotrichia albicollis*). *Behav. Ecol. Sociobiol.* 26: 201-208.
- POWELL, G. V. N. 1974. Experimental analysis of the social value of flocking in starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* 22: 501-505.
- ROHWER, S., & P. W. EWALD. 1981. The cost of dominance and advantage of subordination in a badge-signalling system. *Evolution* 35: 441-454.
- RUBENSTEIN, D. I. 1981. Population density, resource patterning, and territoriality in the Everglades pygmy sunfish. *Anim. Behav.* 29: 155-172.
- SCHNEIDER, K. J. 1984. Dominance, predation, and optimal foraging in the White-throated Sparrow. *Ecology* 65: 1820-1827.
- SCHWABL, H., M. RAMENOVSKY, I. SCHWABL-BEZINGER, D. S. FARNER, & J. C. WINGFIELD. 1988. Social status, circulating levels of hormones, and competition for food in winter flocks of the White-throated Sparrow. *Behaviour* 107: 107-121.
- SUTHERLAND, W. J., & G. A. PARKER. 1985. Distribution of unequal competitors. Pp. 255-273 in *Behavioural ecology* (R. Sibly and R. H. Smith, Eds.). Oxford, Blackwell Sci. Publ.
- THEIMER, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate Dark-eyed Juncos, *Junco hyemalis*. *Anim. Behav.* 35: 1883-1890.
- THOMPSON, W. A., I. VERTINSKY, & J. KREBS. 1974. The survival value of flocking in birds: a simulation model. *J. Anim. Ecol.* 43: 785-820.
- WEIDENMANN, R. N., & K. N. RABENOLD. 1987. The effects of social dominance between two subspecies of Dark-eyed Juncos, *Junco hyemalis*. *Anim. Behav.* 35: 856-864.