

FOOD PATCHES AND THE SPACING OF INDIVIDUAL FORAGERS

SCOTT M. PEARSON

Department of Zoology, University of Georgia, Athens, Georgia 30602 USA

ABSTRACT.—I compared spacing of Field Sparrow (*Spizella pusilla*) and White-throated Sparrow (*Zonotrichia albicollis*) groups feeding on three different-sized food patches with random spacing generated by a computer simulation. I used mean nearest-neighbor distance to measure spacing in groups of 2–4 birds. Both species fed farther apart than random on the smallest patch. Field Sparrows fed closer than randomly positioned birds on the largest patch and similar to random on the medium-sized patch. White-throated Sparrows, with larger individual distances, spaced themselves farther apart on the medium patch, and closer than or similar to random on the large patch. Both species preferred to feed close to cover, provided by a brush pile. Maintenance of individual distances tended to increase nearest-neighbor distance, relative to random spacing, on small patches. The birds' affinity for cover tended to concentrate individuals near a brush pile on large patches. Sparrows faced a trade-off of feeding close to cover or maintaining individual distances that reduce the probability of social aggression. Received 29 May 1990, accepted 25 October 1990.

EMLÉN (1952: 162) proposed that "two opposing forces, a positive force of mutual attraction and a negative force of mutual repulsion," interact to regulate the spacing of individuals in bird flocks. The attractive or cohesive force functions to hold flocks together in time and space. The negative force maintains space between individuals, which prevents crowding (Emlén 1952).

For an individual bird, interbird distance at any given time lies between *individual distance*, the minimum distance that an individual will tolerate an approach by another animal without conflict (Conder 1949), and *social distance*, the "maximum distance that a group-living animal will tolerate before moving toward others" (Craig 1981: 34). Individual distance and social distance are not likely to be finite boundaries. Instead they represent points along a spatial gradient where either the attractive or the repulsive force begins to influence an individual's positioning. Actual spacing may be a balance between these two forces (Emlén 1952, Balph 1977, Grzybowski 1983), depending on the spatial scale of this gradient and the environment (Prescott 1987).

Although the cohesive nature of bird flocks is obvious, repulsion between individuals is not readily observed except under conditions of limited space. Some birds are excluded from patches of food that are too small to accommodate all flock members (Barnard 1980, Pearson 1989). Excluded individuals are frequently subordi-

nate in social status (Fretwell 1969, Martin 1970, Balph 1977, Morse 1978, Ketterson 1979, Barnard 1980). Agonistic encounters are more prevalent on smaller food patches where foraging group members are forced to feed closer together (Balph 1977, Feare and Inglis 1979, Elgar 1987, Pearson 1989). Confinement may increase the probability that birds violate others' individual distances. Individual distances are defended by outright aggression (Marler 1956) or by more subtle threat postures (Balph 1977). Repulsion may serve to limit group size and composition under conditions of limited space (Pearson 1989).

Field Sparrows (*Spizella pusilla*) and White-throated Sparrows (*Zonotrichia albicollis*) are common winter residents in the southeastern United States. Wintering Field Sparrows may be seen in open, grassland habitats relatively far from shrubs and trees that provide refuge from predators. White-throated Sparrows are usually observed near dense woody vegetation (Bent 1968, pers. obs.). In addition to their affinities for cover, these species also differ in their flocking characteristics. White-throated Sparrows have larger individual distances and higher rates of aggression than Field Sparrows (Pearson 1989). Therefore, these species should differ in spacing within their flocks.

Several authors have used nearest-neighbor distance to measure spacing within bird flocks and to measure individual distance (Caraco and Bayhnam 1982, Elgar 1987, Prescott 1987, Pear-

son 1989). In this study, I used this technique to compare the spacing within Field Sparrow and White-throated Sparrow groups to groups of randomly positioned birds generated by a computer simulation. I could thus investigate interactions between individual distance and foraging-patch size. By comparing the real sparrows to these random patterns, I determined whether (1) observed spacing within sparrow flocks differed from random, (2) spacing changed when food-patch size changed, and (3) positions of birds on the patch were influenced by protective cover provided by a brush pile.

METHODS

I studied spacing within foraging groups in captive flocks of Field and White-throated sparrows near Athens, Georgia, during the winter of 1987. Five birds of each species were captured to form two monospecific flocks. The feeding behavior of each flock was studied separately as they fed at an artificial food patch in an outdoor aviary. This patch was created with millet (*Panicum* sp.) seed spread in the center of a 120 × 120 cm board on the ground. I used 3 patch sizes: 30 × 30 cm (small), 60 × 60 cm (medium), and 120 × 120 cm (large). The same amount of seed (10 g) was used to create each patch. This amount of seed was high enough that sparrow feeding rates did not vary over the different seed densities on the different board sizes (H. R. Pulliam unpubl. data). During the experiment, patches were not depleted to the point that feeding rates declined. A brush pile, approximately 120 cm in diameter and 70 cm high, was next to the board.

Each patch size was available to each flock for 30 min per day for 6 days. Though all 5 birds were in the aviary during the experiment, the number of birds actually foraging on the food patch varied. *Group size* was defined as the number that participated in the foraging group at any one time. Activities of the birds on the feeding board were recorded by a video camera in the aviary. Further information regarding this experiment is given in Pearson (1989).

Distance to the nearest neighbor for each group member was measured from the video image with a sonic digitizer. The coordinates obtained from the digitizer measured the position of the birds along two orthogonal axes. One axis ran parallel to the side of the patch near the brush pile, and the other axis ran perpendicular to the brush pile. These measurements were taken once for every 5 s that the board was occupied. These groups were dynamic; group size as well as the positions of flock members often changed several times between measurements. For each 5-s interval, nearest-neighbor distances of group mem-

bers were averaged for each group. I combined these mean distances for each combination of group size (2–4 birds) and patch size over the 6-day experiment to estimate the distribution of interbird distances for each species.

A computer model simulated the spacing of imaginary birds placed randomly on a food patch. The same three patch sizes listed above were used. In groups of 2, 3, or 4 birds, the model randomly located each group member on the patch with adjacent birds at least 1 cm apart. Then, the model measured the nearest-neighbor distance for each group member. Nearest-neighbor distances for all group members were averaged as done with the aviary experiments. This procedure was performed 1,000 times for each group-size/patch-size combination.

I used mean nearest-neighbor distance as a measure of spacing within a given foraging group. To compare the observed and simulated patterns of spacing, I examined the distribution (mean and variance) of the mean nearest-neighbor distances within each patch-size/group-size combination.

To further quantify the sparrows' use of space on the food patches, I used the digitized coordinates to examine the birds' position on the patch relative to the brush pile. Positions on the different patch sizes were normalized by dividing the patch into six zones along each of the two axes described. One axis ran parallel to the brush pile. An axis orthogonal to the first ran perpendicular to the brush pile. These rectangular zones were arranged from left to right on the axis parallel to the brush pile and progressively farther away from the brush pile on the axis perpendicular to the brush pile (Fig. 7). I quantified zone use by counting the number of times a bird occupied each zone (Figs. 4–6).

I used a Chi-square contingency table to compare the observed use of zone of the food patch to the expectation of uniform use of all zones. Data from zones with <5 bird positions were combined with data from the next zone closer to the brush pile to meet the assumptions of the test. The analysis for each axis was performed separately.

RESULTS

The frequency distributions of the simulated interbird distances were only slightly different from normal (Fig. 1). They were skewed to the right ($0.13 \leq g_1 \leq 0.41$, Sokal and Rohlf 1981), and those with group size of 2 were significantly platykurtic ($-0.80 \leq g_2 \leq -0.75$, Sokal and Rohlf 1981). The observed data were not significantly different from normal (Kolmogorov-Smirnov test, all $P > 0.05$).

Spacing within groups on medium and large patches was more consistent in the real spar-

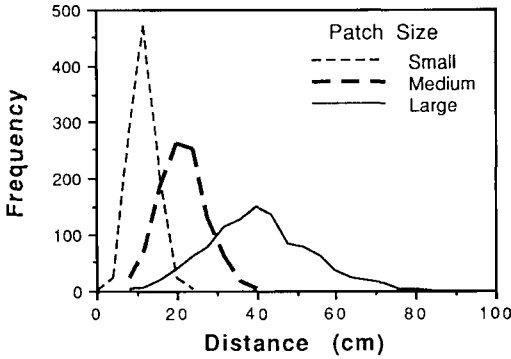


Fig. 1. Frequency distribution of mean nearest-neighbor distances obtained from computer simulation. Four birds were positioned randomly on 3 sizes of feeding patches. Number of observations per 1,000 is plotted. See Methods.

rows (*F*-test, ratio of variances, all $P < 0.05$, Table 1). That is, real sparrow groups had variances in mean nearest-neighbor distance lower than those of the simulated groups. Groups of 4 White-throated Sparrows feeding on large patches were the only exception (no difference, $P > 0.10$). On small patches, differences in variance between the real and simulated groups were mixed (Table 1).

In Field Sparrows using the large patch, the lowest percentiles are close to those of the simulations (Fig. 2), but the higher percentiles deviate progressively farther from the simulations (deviating away from the isopleth with slope of < 1). Though the lower tails of both distributions were similar, the Field Sparrow distri-

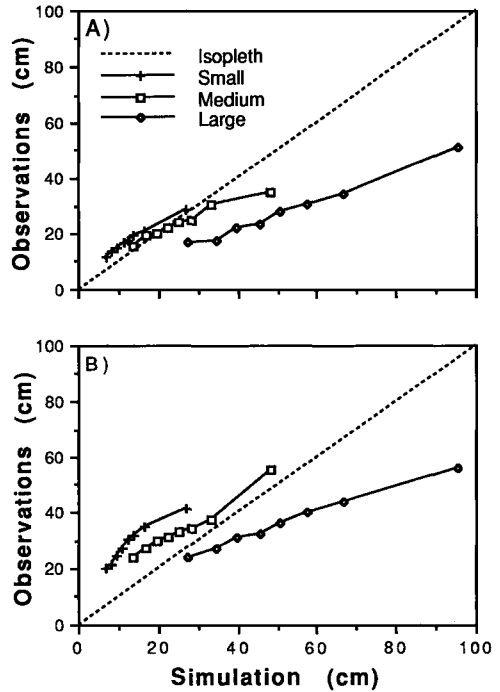


Fig. 2. Percentiles of observed versus simulated mean nearest-neighbor distances from groups of 3 birds for Field Sparrows (A) and White-throated Sparrows (B) feeding on 3 patch sizes. Percentiles plotted are 0.125, 0.25, 0.375, 0.5, 0.625, 0.75, 0.875, and 1.0. Dotted line is an isopleth. Percentiles on the isopleth are identical in both observed and simulated. Displacement of lines above or below isopleth indicate differences in location of distribution (mean). Slope of lines indicates ratio of variances (or spread) of the two distributions, i.e. slope of < 1 means spread of simulation greater than spread of observed.

TABLE 1. Overall mean (\pm SD) nearest-neighbor distance (cm) of observed and simulated sparrow groups. The number of 5-s intervals (*n*) observed is in parentheses; $n = 1,000$ for all simulations; * = variance greater than simulation ($P < 0.05$); § = variance less than simulation ($P < 0.05$).

Patch size	Group size		
	2	3	4
Field Sparrows			
Small	19.9 \pm 5.8§ (35)	16.9 \pm 4.4 (34)	13.0 \pm 2.9§ (19)
Medium	29.8 \pm 10.6§ (38)	22.8 \pm 5.3§ (29)	19.7 \pm 2.3§ (24)
Large	28.9 \pm 11.0§ (46)	25.8 \pm 8.8§ (33)	23.8 \pm 7.4§ (25)
White-throated Sparrows			
Small	30.1 \pm 5.6§ (104)	27.6 \pm 6.5* (43)	21.9 \pm 5.5* (12)
Medium	39.1 \pm 10.3§ (188)	31.2 \pm 6.2§ (79)	29.1 \pm 3.6§ (30)
Large	52.8 \pm 20.8§ (147)	34.5 \pm 8.4§ (37)	39.5 \pm 13.3 (27)
Simulation			
Small	15.7 \pm 7.7	11.4 \pm 4.2	9.8 \pm 2.1
Medium	32.0 \pm 15.2	23.1 \pm 8.4	19.4 \pm 5.8
Large	63.7 \pm 30.5	46.7 \pm 16.8	38.3 \pm 12.3

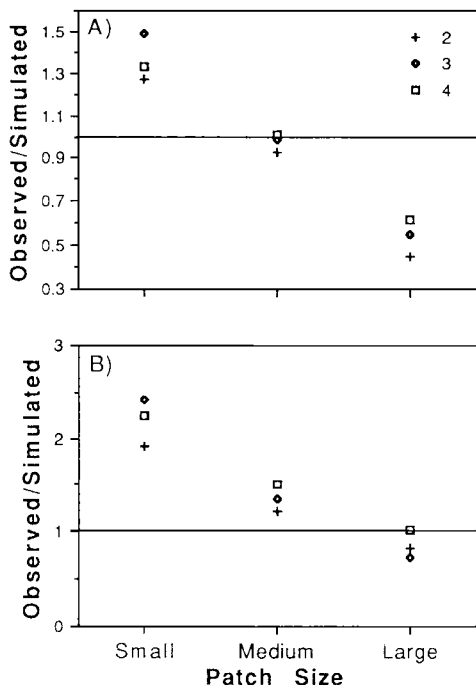


Fig. 3. Ratio of observed to random means of mean nearest-neighbor distances for Field Sparrows (A) and White-throated Sparrows (B). Three group sizes are shown.

bution had less spread (smaller variance, see Table 1). That is, Field Sparrows had near the random number of closely spaced groups, but fewer widely spaced groups than expected. A similar effect was observed in groups of 2 and 3 White-throated Sparrows feeding on the large board (Fig. 2, Table 1).

The observed mean nearest-neighbor distances in Field Sparrows feeding on the medium patch were not distributed differently from the simulation for all group sizes (two-sample Kolmogorov-Smirnov test, $P > 0.10$; Figs. 2 and 3). The observed groups were different from random groups on the large and small patches for all group sizes ($P < 0.01$). Field Sparrows fed farther apart than expected on the small patch and more closely than expected on the large patch (Figs. 2 and 3; Wilcoxon rank sum test, all $P < 0.05$).

Distributions of distances for White-throated Sparrows were different from random (two-sample Kolmogorov-Smirnov test, $P < 0.01$) except for 4 birds feeding on the large patch ($P > 0.10$; Fig. 3). This species spaced themselves

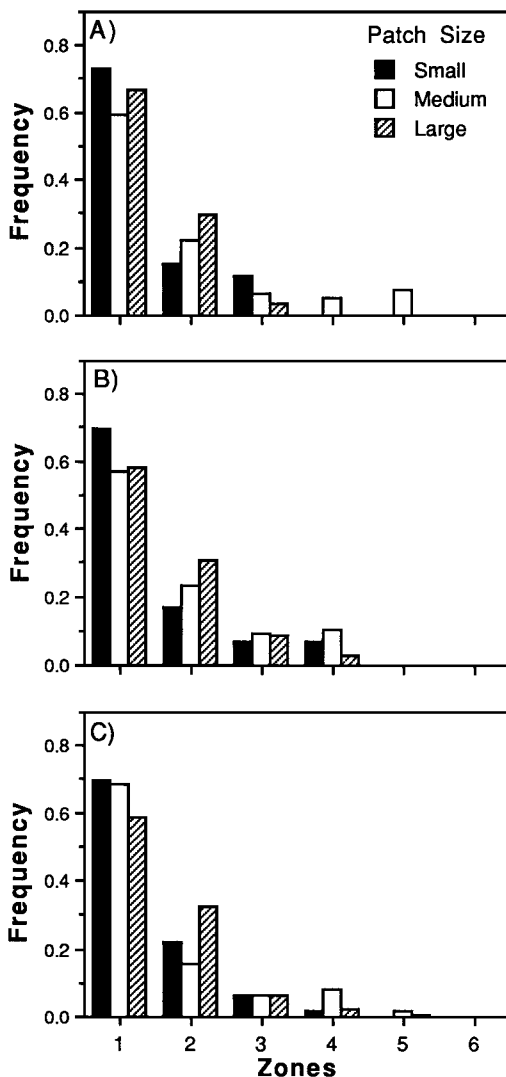


Fig. 4. Frequency of Field Sparrow positions on an axis perpendicular to the brush pile. Food patches were divided into 6 equal zones. Zone 1 is closest to brush pile. See Figure 7. Groups of 2 (A), 3 (B), and 4 (C) birds are shown. Three patch sizes are shown.

farther apart than expected on the small and medium patches. However, they fed closer than expected on the large patch in groups of two's and three's (Wilcoxon rank sum test, all $P < 0.01$; Fig. 3).

Both species used portions of the patch near the brush pile most heavily (Figs. 4 and 5). Use of these zones for all combinations of group-size/patch-size in both species was significantly different from expected ($P < 0.01$, $df = 2-5$).

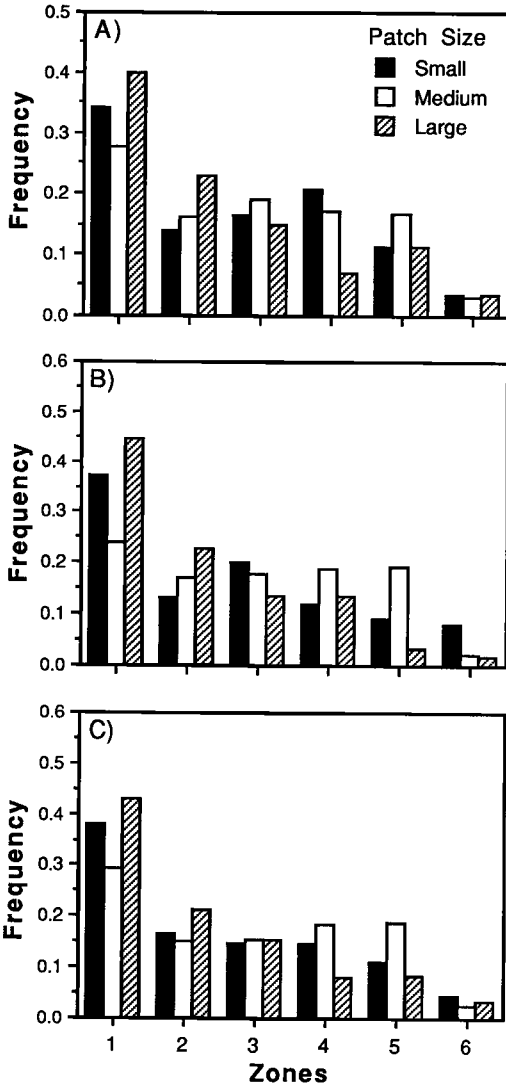


Fig. 5. Frequency of White-throated Sparrow positions on an axis perpendicular to the brush pile. See Figure 4.

Field Sparrows showed this preference most strongly, rarely using the one third of the patch farthest away from the brush pile (cf. Figs. 4 and 5, zones 5 and 6). White-throated Sparrows also preferred to be near the brush pile, but their use of the outer zones was more equitable (Fig. 5). In contrast, there was no consistent pattern of use in either Field Sparrows or White-throated Sparrows (Fig. 6) on the axis parallel to the brush pile, although they may have preferred the middle of the patch on the largest patch size.

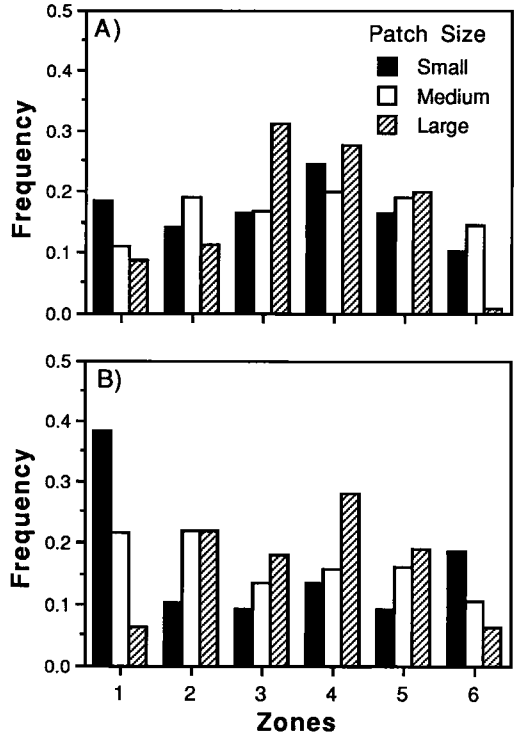


Fig. 6. Frequency of Field Sparrow (A) and White-throated Sparrow (B) positions on an axis parallel to the brush pile. Zone 1 is the left-most zone. Groups of 3 birds are shown feeding on 3 patch sizes.

DISCUSSION

Compared with the random groups, sparrows tended to be more aggregated on larger patches. On smaller patches, the real birds were spaced farther apart than the random ones. I interpret these patterns to be the result of two conflicting forces: the repulsive action of individual distance and affinity for the protective cover of the brush pile.

Individual distance and social distance vary between species (e.g. Morse 1978) and probably between individuals. Though cohesive forces may not be detectable on the sizes of food patch I used, this experiment allows comparison of individual distance in these two species. Field Sparrows have shorter individual distances and tend to feed closer, in tighter flocks, than White-throated Sparrows (Fig. 7, Pearson 1989). Their spacing is less affected by changes in patch size at this scale and may be related to their lack of aggression in flocks (Pearson 1989). Field Spar-

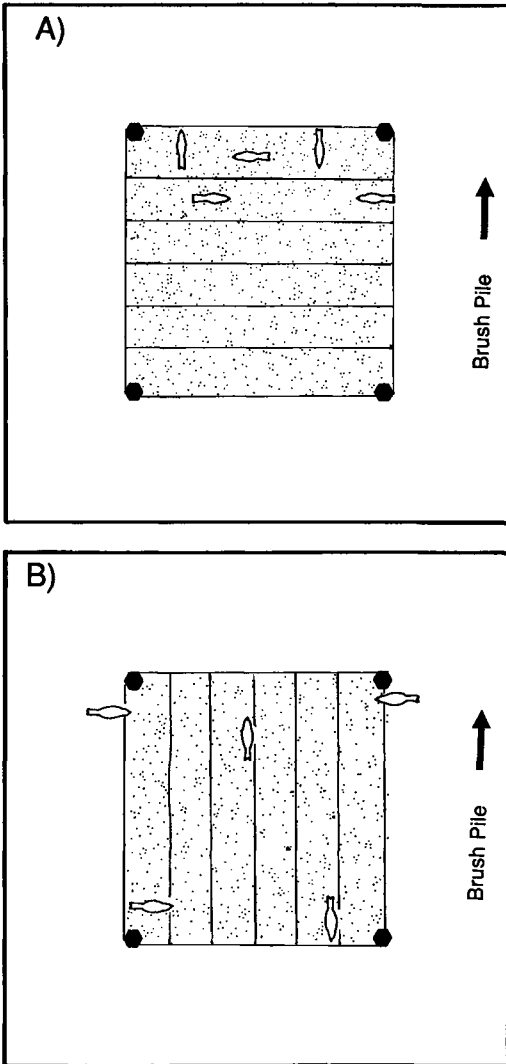


Fig. 7. Typical arrangement of Field Sparrows (A) and White-throated Sparrows (B) feeding on a medium-sized food patch. Field Sparrows were able to crowd close to brush pile (located on side of patch near top of figure); however, White-throated Sparrows used entire patch to avoid violating individual distances. Each patch was divided into 6 zones that were positioned along an axis oriented either perpendicular (A) to or parallel (B) to the brush pile.

rows spaced themselves randomly on the medium patch (Figs. 2 and 3). However, spacing similar to random occurred on the large patch in White-throated Sparrows, which have larger individual distances. The large patch had four

times the area and twice the maximum interbird distance as the medium-sized patch.

An alternative to the idea of conflicting forces acting on these flocks is that sparrows space themselves according to a simple rule of maintaining a constant distance between individual birds. This constant distance may be different for two sparrow species. This explanation is inadequate for this data because nearest-neighbor distance changes relative to patch size (Table 1; Pearson 1989).

Spacing within observed groups was more consistent than within simulated groups on the medium and large patches (Table 1). Both species had fewer widely spaced groups than the simulation, though the numbers of closely spaced groups were similar to random (Fig. 2). These patterns suggest that, as patch size increases relative to individual distance, spacing within sparrow groups may be constrained more by social distance or affinity to cover than by the repulsive force of individual distance. Whereas individual distance imposed a limit on the minimum interbird distance, affinity for the brush pile limited the maximum interbird distance.

Both sparrow species fed close to the brush pile, underutilizing portions of the patch farther from cover. The maximum nearest-neighbor distances, where 2 birds were positioned in opposite corners, seldom occurred, especially on the large patches. Sparrows fed as close to cover as possible without violating the individual distances of birds already positioned near the brush pile. In contrast, simulated groups used the whole patch with equal probability. This difference in behavior between the real sparrows and the simulated birds explains why the sparrows were more closely spaced and why variances in mean nearest-neighbor distances were smaller on the larger patches. Unfortunately, any effect of Emlen's attractive force within flocks could not be separated from these birds' affinity for cover.

These results imply that Field Sparrows were more attracted to cover than White-throated Sparrows. In fact, the natural history of these species suggests the opposite. From observations of habitat use, White-throated Sparrows are more cover dependent. They are seldom seen far from cover (Schneider 1984), whereas Field Sparrows frequently use habitats dominated by grasses and forbs with little woody vegetation

(Bent 1968, pers. obs.). The short individual distances of Field Sparrows allowed them to congregate near cover without social conflict.

Sparrows were facing a trade-off in their spacing. With limited space at a food patch, there was a conflict between feeding close to cover and maintaining individual distances. Moreover, the severity of the trade-off differed between species. Field Sparrows with small individual distances could more easily crowd into the space close to the brush pile. White-throated Sparrows with larger individual distances were forced to feed farther from cover to maintain individual distance (cf. Figs. 4 and 5; Fig. 7).

Schneider (1984) found that dominant White-throated Sparrows occupied foraging sites close to cover, which forced subordinates to feed at more exposed patches. A nonlinear dominance hierarchy and lack of appropriate data did not permit such an analysis with this experiment. Maintaining individual distance reduces the probability of outright aggression and the associated loss of foraging time and energy. However, the constraints of patch size and geometry may force some flock members to accept foraging positions farther from refuge cover.

Spacing within these sparrow flocks was influenced by two conflicting forces. The repulsion of individual distance maintained space between individual birds, whereas attraction to cover tended to concentrate individuals close to the brush pile and, therefore, closer together. The relative importance of these two forces depended on the size of food patch and number of birds on patch. On the limited space of small patches and in large groups, sparrows disperse to maintain individual distance. However, on larger patches and in smaller groups, birds were able to position themselves close to cover without violating individual distances, often leaving portions of the patch far from cover unused. The observed spacing of individuals within any given flock was a trade-off between maintaining individual distance and remaining close to cover.

ACKNOWLEDGMENTS

Ideas and suggestions for this analysis were gleaned from conversations from B. J. Danielson, J. B. Dunning Jr., H. R. Pulliam, and B. D. Watts. R. J. Craig, D. Duffy, and J. Liu made useful comments on earlier drafts. P. King-Smith prepared Figure 7. This research

was supported by a grant from Stoddard-Sutton-Burleigh Fund at the University of Georgia and in part by National Science Foundation Grants BSR 8415770 to H. R. Pulliam and BSR 8817950 to H. R. Pulliam and J. B. Dunning Jr.

LITERATURE CITED

- BALPH, M. H. 1977. Winter social behaviour of Dark-eyed Juncos: communication, social organization, and ecological implications. *Anim. Behav.* 25: 859-884.
- BARNARD, C. J. 1980. Equilibrium flocks size and factors affecting arrival and departure in feeding House Sparrows. *Anim. Behav.* 28: 503-511.
- BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies, U.S. Natl. Mus. Bull. 237.
- CARACO, T., & M. C. BAYHNAM. 1982. Some geometric aspects of House Sparrow flocks. *Anim. Behav.* 30: 990-996.
- CONDER, P. 1949. Individual distance. *Ibis* 91: 649-655.
- CRAIG, J. V. 1981. Domestic animal behavior: causes and implications for animal care and management. Englewood Cliffs, New Jersey, Prentice-Hall, Inc.
- ELGAR, M. A. 1987. Food intake and resource availability: flocking decisions in House Sparrows. *Anim. Behav.* 35: 1168-1176.
- EMLEN, J. T. Jr. 1952. Flocking behavior in birds. *Auk* 69: 160-170.
- FEARE, C. J., & I. R. INGLIS. 1979. The effects of reduction of feeding space on the behavior of captive starlings *Sturnus vulgaris*. *Ornis Scandinavica* 10: 42-47.
- FRETWELL, S. 1969. Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*). *Bird Banding* 40: 1-25.
- GRZYBOWSKI, J. A. 1983. Patterns of space use in grassland bird communities during winter. *Wilson Bull.* 95: 591-602.
- KETTERSON, E. D. 1979. Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. *Wilson Bull.* 91: 371-383.
- MARLER, P. 1956. Studies of fighting in chaffinches (3), proximity as a cause of aggression. *Br. J. Anim. Behav.* 4: 23-30.
- MARTIN, S. G. 1970. The agonistic behavior of Varied Thrushes (*Ixoreus naevius*) on winter assemblages. *Condor* 72: 452-459.
- MORSE, D. H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during winter. *Ibis* 120: 298-312.
- PEARSON, S. M. 1989. Food patches and foraging group size in granivorous birds. *Anim. Behav.* 38: 665-674.

PRESCOTT, D. R. C. 1987. The effects of habitat density and the spatial distribution of food on the social behaviour of captive wintering American Tree Sparrows. *Can. J. Zool.* 65: 522-526.

SCHNEIDER, K. J. 1984. Dominance, predation, and

optimal foraging in White-throated Sparrow flocks. *Ecology* 65: 1820-1827.

SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*. New York, W. H. Freeman and Company.

100 Years Ago in The Auk



From "The Labrador Duck:—a revised list of the extant specimens in North America, with some historical notes" by William Dutcher (1891, *Auk* 8: 201):

"THE OBJECT of this revised list is to bring before the ornithologists of North America the great desirability of search among the private collections of mounted birds, scattered throughout this country, for specimens of this species of Duck, which in all probability is now nearly, if not altogether extinct. A further object is to record the exact history of the extant specimens so far as it can be gathered at this late day. There are but few naturalists or sportsmen now living who have had any experience with the Labrador Duck in life, and these are one by one passing away. Of the life history of this interesting species but little is known, for when it was common there were but few, if any, observers in the field, and the science of ornithology had not advanced to its present high plane. As long ago as when Audubon was in Labrador (see his 'Birds of America') it was so rare that he did not meet with it and the great Wilson said of it: 'This is rather a scarce species on our coast.' [American Ornithology. Vol. III, 1829, p. 369.] Giraud, in his 'Birds of Long Island' says: 'With us it is rather rare.'

"It is true that at a later date than the above, say during the period from 1840 to 1860, there were apparently more of these Ducks seen than earlier.

"This, however, I think, may be easily explained as follows: during the later period there were a far greater number of scientific collectors, and there was a market demand for game and waterfowl which gave employment to professional gunners who shot and sent to market great numbers of birds. During the open season one can see hanging in our markets hundreds and sometimes thousands of Ducks of the commoner varieties; this has been the case for many years, perhaps to a lesser degree formerly because the demand was not then so great. . . [The paper then lists the location and condition of mounted specimens].

Vol. 8 (2) also included a fold-out map of the "Distribution of the Ivory-billed Woodpecker." The article was by Edwin M. Hasbrouck, "The present status of the Ivory-billed Woodpecker [Campephilus principalis]" (1891, Auk 8: 174-186).—Ed.