

SPACING AND ORIENTATION AMONG FEEDING GOLDEN-CROWNED SPARROWS

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For many years I have fed wild birds by sprinkling grain over a large area of the asphalt driveway at my home in Orinda, Contra Costa County, California. The most frequent visitor is the Golden-crowned Sparrow (*Zonotrichia atricapilla*), but many other species feed also. While watching the interactions between the different species and among the Golden-crowned Sparrows themselves, I realized that this situation would permit easy but precise measurement and analysis of the distances between feeding individuals. Numerous previous studies had focused on behavioral interactions and establishment of dominance hierarchies among birds competing at a restricted source of food and had analyzed the importance of such factors as body size, plumage, and sex in these interactions. Perhaps new insights into flock dynamics could be gained by using a more dispersed food supply? Perhaps winter flocks of Golden-crowned Sparrows, accustomed to grazing at the margins of large uniform expanses of short grass such as lawns, would be found to be organized differently than flocks of other species that in the wild depend upon a limited number of concentrated sources of food?

METHODS

To analyze the spacing of Golden-crowned Sparrows while feeding, I painted stripes on the tails of many of them so that individuals would be recognizable in photographs taken from the roof of the garage looking downward. The tail of each bird was marked with either three or four stripes of two colors. The colors used were orange, blue, and green—colors not likely to be used by these sparrows for signaling. So that the distribution of grain would not influence spacing of the birds, I constructed a tray 2.44×1.83 m and 3 cm deep, filled it with cracked corn, and set it on 5-cm blocks on the driveway. In addition, the tray was divided into a grid of 20.3 cm^2 compartments, and coordinates were painted on the margins so that the tray became essentially a large piece of graph paper. To reduce the birds' tendency to perch on the edges, I stretched a taut string around the periphery about 4 cm above the edge. To overcome an initial reluctance of the birds to stand in the corn, I covered the tray with 2.5×2.5 cm mesh welded wire. Birds came to the tray only to eat.

After each photograph the birds were deliberately frightened away. They usually returned within a few minutes and then would be photographed again. The spacing and orientation of birds in any one photograph was, therefore, independent of the spacing and orientation in the preceding photographs. I operated the

camera from a window in the house. Different species could be recognized from this window, but individual birds could not be distinguished. Consequently, no bias based on individual recognition could be introduced. I made a conscious effort, however, to secure photographs containing only a few birds as well as photos containing many birds. The following data were recorded by examining the 35-mm color transparencies by transmitted light under a dissecting microscope: identification number of each marked bird; its coordinates on the feeding tray (as well as coordinates of all other birds); orientation on the tray; and condition of the plumage on the crown. The coordinates recorded were those of the head of the bird at a point between the eyes; error was probably less than 3 cm except for occasional gross misreadings or misrecordings. The distance between each bird and every other bird in the photograph was then computed with a programmable desk calculator. Orientation refers to the direction toward which the tail of the bird pointed; it was recorded in 12 sectors of a circle as on the face of a clock. Conspicuousness of crown was recorded on a scale of from 1 (dull) to 4 (conspicuous yellow with black stripes). When a bird was captured for marking, its crown was scored subjectively and recorded as a whole number. This number was refined by using the photographs in which the crowns of individuals were visible. Since most birds were captured at the end of the study, as well as at the beginning, I weighted the system to arrive at a single crown number for each marked individual: first capture weighted $\frac{1}{4}$, average of all photos $\frac{1}{4}$, and final capture $\frac{1}{2}$. No crown molt was detected during the study. Sex was determined by laparotomy. All gonads were quiescent.

Thirty-four Golden-crowned Sparrows were painted. The greatest number of birds in any one photo was 27. Judging from the ratio of marked to unmarked birds in the photos, the total population was about 40 birds. None of the marked individuals appeared at another feeding station 300 m away, so the population was not being drawn from a large area.

Photographs were taken between 10 February and 1 March 1978. About 350 photos were used in the following analyses. Of the more than 2,000 birds in the photos, 85% were Golden-crowned Sparrows.

RESULTS AND DISCUSSION

SITE TENACITY

After a few photographic sessions I noticed that a Fox Sparrow (*Passerella iliaca*) returned repeatedly to the same part of the feeding tray. I soon realized that many of the Golden-crowned Sparrows were doing the same thing. Figure 1 displays the recorded locations of each of 24 of the 34 marked birds. Not one of the 34 visited the tray in a random manner, and some of them were remarkably site-specific. Even if a photograph contained only one or a few birds, those individuals tended to be close

to their usual site, so they were not being forced into a particular place by pressure from other birds; they *preferred* the site where they were usually found.

I do not know how the birds achieved their partitioning of the tray. Even when the tray was first presented to the birds, they did not squabble much or engage in obvious disputes. In fact, only occasionally did I see disputes between Golden-crowned Sparrows; they usually amounted only to one bird's landing among a feeding flock, and running directly at another bird, who invariably flew off. I believe that division of the space must have been accomplished much earlier on the driveway, or at some other feeding area, and that it was simply transferred onto the tray.

In most photographs, more birds occupied the left half of the tray than the right, and review of the records for all birds (Fig. 1 plus 10 additional birds) confirms this impression. Since the tray was uniform, I believe that the left end was more popular because most of the birds approached from bushes about 6 m to the left of the tray and less frequently from bushes that were 4 m to the right.

To determine whether birds were returning to a location on the tray (tray-tenacity) and not to some spot influenced by the location of bushes, house, or other features (terrain-tenacity), I moved the tray 39 cm and rotated it 30°, then compared the birds' sites with the center of distribution of their previous records. This was done for the 14 most site-tenacious individuals. The centers of their previous distributions were chosen by inspection of scatter diagrams such as those in Figure 1. Nine of the 14 birds were more tray-tenacious (i.e., most of their returns were closer to the tray-tenacity center than to the terrain-tenacity center). Lumping the returns of all 14 birds, 37 of 65 returns were closer to the tray-tenacity center. Thirty-nine of the 65 returns fell in the half-circle that contained the terrain-tenacity center. I conclude from this, and from study of the individual records, that some of the birds tended to return to the same place on the tray even after it was moved and rotated, and that when the birds returned to the rotated tray they tended to return to a position that lay in the direction of their former feeding site. They must have been using both the tray itself and features of the surroundings for orientation.

The lower right frame in Figure 1 shows locations of two or more unmarked Song Sparrows (*Melospiza melodia*). They showed

a strong preference for the lower left corner. Also shown is the record of a marked Fox Sparrow. An unmarked Fox Sparrow fed on the tray occasionally, but a third Fox Sparrow, which was marked, appeared frequently in the photographs but was always searching for spilled grain on the surrounding driveway, never on the tray itself. The Fox Sparrow represented in Figure 1 was highly site-specific. The records indicated by arrows were from photographs in which its usual feeding site was occupied by an unmarked Fox Sparrow. Such displacement was easily documented for Fox Sparrows because they were much less tolerant of conspecifics than they were of Golden-crowned Sparrows (see below). The marked individual obviously had been displaced, but it returned to its usual site in subsequent photos. This Fox Sparrow was recorded more often than any of the Golden-crowned Sparrows and undoubtedly spent more time on the tray than any of the latter species.

Scatter diagrams for each of the birds, such as those in Figure 1, were examined and subjectively sorted into five categories ranging from highly site-tenacious to dispersed. The ratio of sexes in the different groups was then compared. Males tended to be more site-tenacious than females, but the trend was not statistically significant (by chi-square). Similarly, the conspicuousness of the crown was compared with degree of site tenacity. Records of individuals with contrasty crowns tended to be tightly clustered, but neither the coefficient of correlation nor a *t*-test of lumped data departed significantly from random expectation.

NEAREST-NEIGHBOR DISTANCES

Golden-crowned Sparrows. The mean distance from the head of one sparrow to the head of its nearest neighbor ranged from 165 cm in one photo with two birds to a mean of 16 cm in a photo containing 22 birds. The relationship between number of birds on the tray and mean distance to nearest neighbor is shown in Figure 2. This graph gives insight into the sociality of this species. Their flocking nature is revealed by the fact that they never spread themselves as far apart as possible; in fact, in most photos the mean distance to the nearest neighbor was only about half of what it could have been if the same number of birds had positioned themselves on the tray as far apart as possible. In photos containing from 2 through 13 birds, the mean distance to nearest neighbor did not differ appreciably

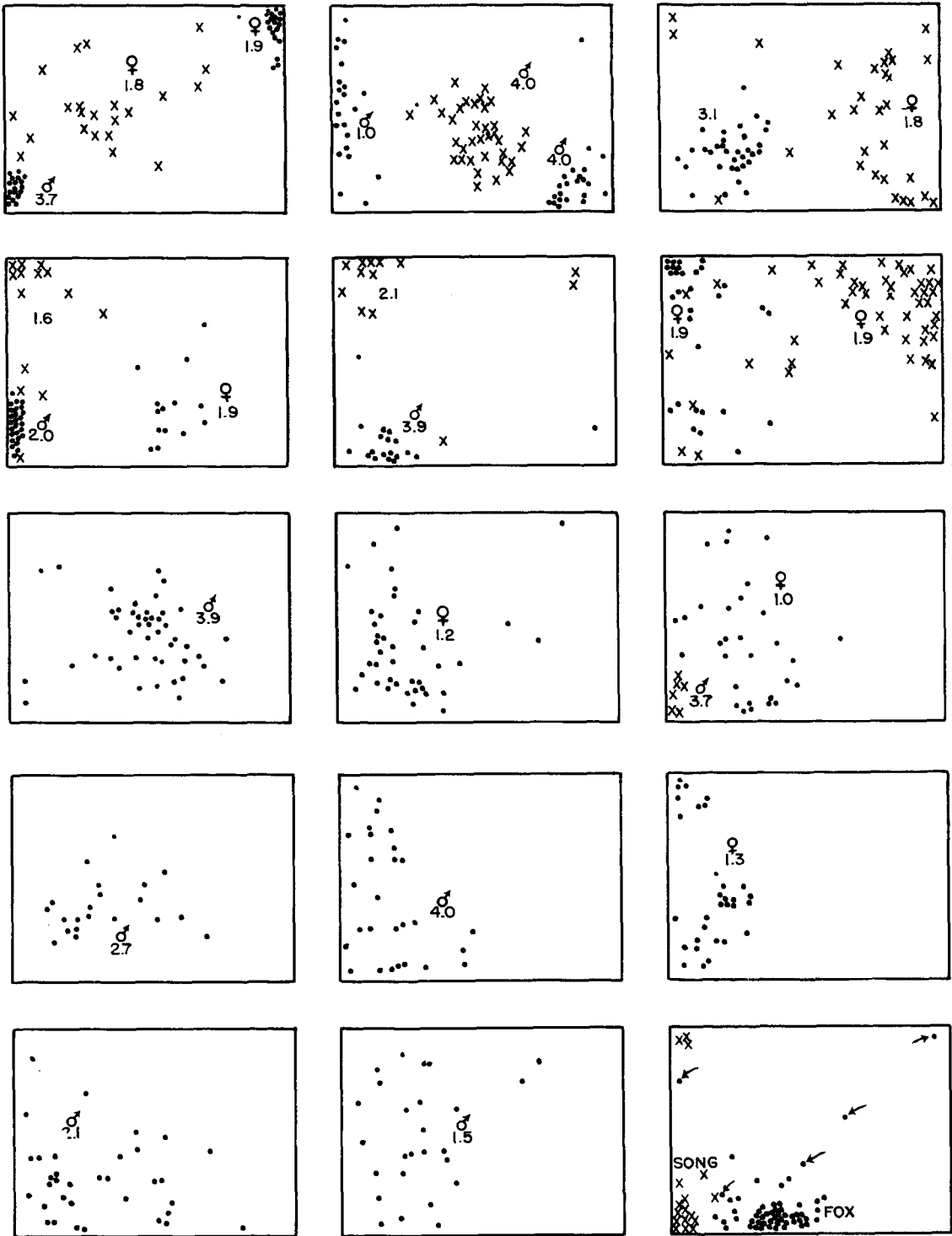


FIGURE 1. Feeding locations of 24 of the 34 marked Golden-crowned Sparrows. Some of the frames contain records of as many as three different individuals. The numerals refer to the conspicuousness of the crown, ranging from 1.0 (dull) to 4.0 (contrasty). The lower right frame displays the records of two or more unmarked Song Sparrows and one marked Fox Sparrow. The arrows in this frame indicate records obtained when another Fox Sparrow was feeding near the place usually occupied by the marked bird.

from computer-generated random distances for birds at similar densities (“Random Spacing” in Fig. 2). When the number of birds was greater than 13, the mean distance

to nearest neighbor was almost always greater than it would have been had the birds been randomly dispersed. This change from random spacing to overdispersed spac-

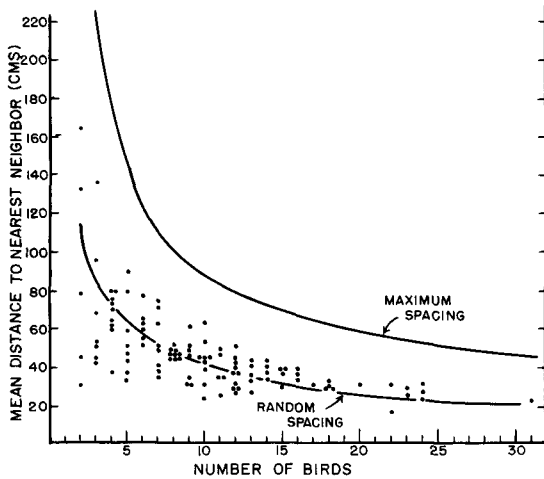


FIGURE 2. The relationship between the number of birds on the entire feeding tray and the mean distance to nearest neighbor between Golden-crowned Sparrows. Each dot represents one photograph. No photos containing thrashers or towhees are included. The "Maximum Spacing" curve shows what the nearest-neighbor distance would have been if each bird had stayed as far as possible from its neighbors. The "Random Spacing" curve could not be generated conventionally, as in Clark and Evans (1954), because of border effects; it was computer-generated with random coordinates using 2,300 tests with 2 birds down to 400 tests with 30 birds.

ing at a density of 13 birds on the tray resulted from an interplay of the size of the tray and sociality of the sparrows. For example, if the tray had been one hectare in size, comparison of the nearest-neighbor measurements of a flock with those expected for random spacing would have proven a single flock to have been highly clustered, but at densities greater than 13 birds on the 4.46 m² tray (2.9 birds/m²), the minimum distance tolerated by the birds made itself apparent, so that the mean distance to nearest neighbor became greater than random. This effect became more obvious when the birds were compressed onto a smaller feeding area.

Figure 3 shows what happened when the area of the tray was reduced by covering part of it with blankets, leaving a smaller rectangular or square area of corn exposed. In an attempt to record maximum crowding of birds, each photo (represented by a circle in the figure) was taken at a moment when density was high. The smallest distance to nearest neighbor averaged 9 cm in a photo of 0.16 m² occupied by 10 birds. This must have been near the maximum tolerable crowding limit. I believe that at densities greater than this the sparrows would separate themselves in time rather than reduce

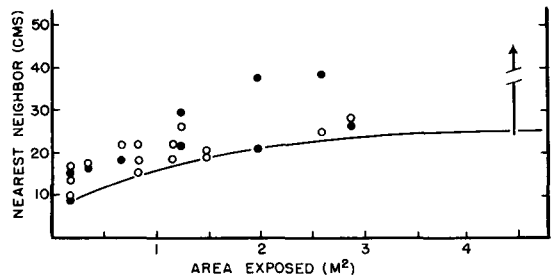


FIGURE 3. Nearest-neighbor distance between Golden-crowned Sparrows crowded onto a portion of the feeding tray. The plotted curve represents the minimal distance acceptable to the birds at the observed densities. At the right, the curve was drawn through the lower end of the range of nearest-neighbor distances in photos of the entire tray. Each circle represents one photograph; solid circles are from photos containing thrashers or towhees, whose presence may have influenced the spacing of sparrows.

distance among themselves. The flatness at the right end of the curve indicates that the feeding tray was large enough to provide ample space for the entire population; enlarging the tray would not have increased the spacing of the birds appreciably.

Figure 4 is a frequency distribution of 1,493 nearest-neighbor distances on the unrestricted tray. The modal distance was 22 cm, which probably represents the preferred spacing when plenty of space is available. Under these uncrowded conditions the least distance between birds (head-to-head) was 6 cm. The most obvious response to reducing the feeding area (Fig. 4—open bars) was a denser packing of birds (up to 62 birds/m²), reflected in a reduced mean distance to nearest neighbor (with a mode of 16 cm) and, of course, absence of the longer distances that could be attained only on the full-sized tray. Reducing the feeding area reduced the minimum inter-bird distance only slightly (to 4 cm).

Nearest-neighbor distances from photos of the entire tray area were analyzed for sex differences. Mean distance to nearest neighbor of 14 males was 39 cm and for 12 females was 42 cm, a non-significant difference (*t*-test). Mean distance to nearest neighbor was unrelated to conspicuousness of crown. Birds with contrasty crowns tended to be more widely spaced, but the coefficient of correlation was only +0.24 (*n* = 31, n.s.).

The relationship between distance to nearest neighbor and body size was tested in two ways. The coefficient of correlation between nearest-neighbor distance and wing chord was -0.04 (*n* = 30, n.s.). The range of wing sizes was 74–85.5 mm. In or-

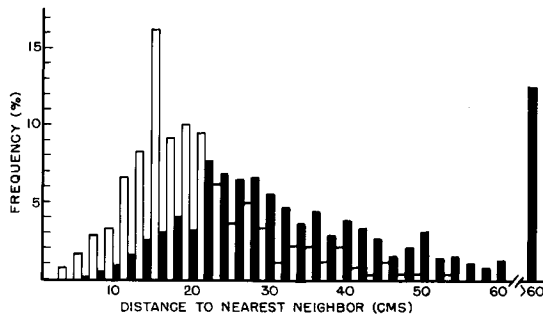


FIGURE 4. Comparison of 1,493 nearest-neighbor distances between Golden-crowned Sparrows on the entire tray (solid bars) and on the tray when the area was reduced to between 2.8 and 0.16 m² (open bars).

der to exaggerate size differences, I placed a circular mirror (13 cm diameter) vertically on the feeding tray. One face of the mirror was flat and the other concave. To a distance of about 50 cm, the image seen in the concave side appeared to be greatly enlarged. Beyond this distance the image became distorted or inverted. I compared the bird-to-mirror distance in a series of photographs, using only those birds within 50 cm of the mirror and directly in front of it. I could detect no difference in their response to the reflections in the opposite sides of the mirror. From this I conclude that either they were totally ignoring the mirror's images or the apparent size of the neighbor does not influence spacing.

Although nearest-neighbor distances were not noticeably influenced by sex, size, or crown marking, analysis of variance showed that each bird tended to be a distinct distance from its nearest neighbor ($F = 7.33$, $df = 30, 771$; $P < 0.01$). The range varied from a mean of 75 cm for a crown-1.9 female to 25 cm for a crown-2.0 male. It seems probable that spacing was achieved not by an interaction based on the physical characteristics of the neighbors but by position on the tray. If a bird wanted more isolation it chose either a less densely populated region of the tray or a time when density was low.

Other species. The photographs were examined to determine if Golden-crowned Sparrows tended to avoid any of the other species that fed on the tray at the same time. Since nearest-neighbor distances varied with density of birds on the tray, I compared the distance from an individual of the other species to the closest Golden-crowned Sparrow with the mean nearest-neighbor distance between Golden-crowned Sparrows in the same photo. Only photos of the entire tray were used in this analysis.

In 17 of 19 photos containing Golden-crowned Sparrows and one or more California Thrashers (*Toxostoma redivivum*), the interspecific distance was greater than the mean nearest-neighbor distance between Golden-crowned Sparrows. The average interspecific distance was, in fact, 47 cm greater (significant by Wilcoxon signed rank test). Brown Towhees (*Pipilo fuscus*) were a significant 24 cm farther away (farther away in 33 of 47 photos). These results indicate that when either of these species was present, it denied Golden-crowned Sparrows use of an appreciable part of the tray. For this reason, I did not use photos containing thrashers or towhees when computing density-dependent measurements (e.g., Fig. 2) or I identified them by different symbols (e.g., Fig. 3).

The distance between Golden-crowned Sparrows and Fox Sparrows, Mourning Doves (*Zenaidura macroura*), and California Quail (*Lophortyx californicus*) did not differ significantly from the *Zonotrichia-Zonotrichia* distance. However, the average distance from Song Sparrows to the nearest Golden-crowned Sparrow was 25 cm less than the mean nearest-neighbor distance between Golden-crowned Sparrows in the same photos. I noticed that the smaller Song Sparrows did not hesitate to "sneak" in close to feeding Golden-crowned Sparrows. However, Song Sparrows may not have been seeking any advantage by doing so. They always visited the lower left region of the tray (Fig. 1), which was heavily used by Golden-crowned Sparrows. Consequently, any bird visiting the lower left corner was likely to be recorded close to a Golden-crowned Sparrow.

In the 16 photos containing two Fox Sparrows, the mean distance between them was 100 cm, with a range from 38 to 208 cm. Comparison of these distances with the solid bars in Figure 4 demonstrates that Fox Sparrows were much less tolerant of nearby conspecifics than were Golden-crowned Sparrows. In fact, Fox Sparrows permitted much closer approach by Golden-crowned Sparrows and were accepted by them as though they were conspecifics (see below).

In 10 photos containing two or more Brown Towhees, the mean distance between these birds was 130 cm, with a range from 62 to 194 cm. This demonstrates greater intolerance within Brown Towhees than within Golden-crowned Sparrows (compare with Fig. 4). The distance between towhees was considerably greater than that between *Zonotrichias* but, as shown above, the to-

whee-*Zonotrichia* distance was much greater than that between *Zonotrichias*.

Distance-to-conspecific averaged 60 cm in six photos containing two or more California Quail, and 40 cm in seven photos containing two or more Mourning Doves. These distances were not clearly different from those between *Zonotrichias* in photos with comparable densities of birds.

Heterosexual pairs. The sex composition of 315 pairs of nearest neighbors was tallied to determine whether male-female pairs of Golden-crowned Sparrows might be associating closely in winter flocks. Heterosexual pairs were considerably less frequent than expected on a random basis, pairs of males were slightly more frequent than expected, and pairs of females considerably more frequent than expected. A chi-square test indicated that the observed departure from expectation for random pairing was significant at the 10% level but not at the 5% level. I conclude that the sparrows were not pairing heterosexually.

ORIENTATION

Using 1,060 observations on the direction in which the tails of the sparrows were pointing, and analyzing them by the Rayleigh Test (Batschelet 1965), I found that the birds were not orienting at random (upper left circle in Fig. 5). The mean direction was 63° to the left of "vertical," which is the upper edge of the feeding tray as displayed in Figure 1. This means that the head of the average bird was toward the lower right.

Of 31 individual sparrows tested, 17 were found to have departed significantly ($P < 0.05$) from random orientation. The records of four of these individuals are shown in Figure 5. Comparing the mean direction of orientation of each individual with its feeding position on the tray showed a tendency for the bird to be pointing into the tray. It was as though the bird had simply maintained its arrival trajectory with its tail pointing in the direction from which it had come. There were numerous exceptions, however. No bi-directional patterns were detected by inspection of the individual records.

The single Fox Sparrow, for which there were enough records, showed strong orientation (Fig. 5).

After the tray had been rotated 30° counter-clockwise, I expected that the mean direction of orientation (with respect to the "top" of the tray) would remain at 63° to the left if the birds were maintaining the same orientation with respect to the tray, or to

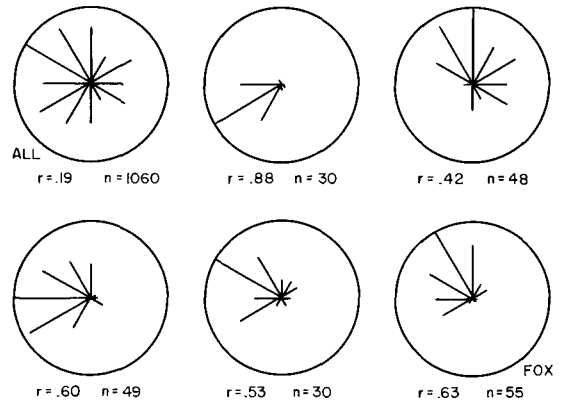


FIGURE 5. Orientation of the tails of all Golden-crowned Sparrows combined (upper left), a Fox Sparrow (lower right), and four individual Golden-crowned Sparrows; n refers to the size of the sample, and r is the length of the mean vector corrected for the 30° grouping of the data (see Batschelet 1965). All six of these displays depart significantly from random ($P < 0.001$).

become 33° if the birds retained an orientation dependent upon surrounding features. The orientation of 192 birds after rotation was significantly clustered ($P < 0.001$ by the Rayleigh test), and the mean was 85° to the left, not significantly different from the original 63°. Since the change in the mean direction after rotation was in the opposite direction from that expected if the birds were maintaining the same orientation with respect to the surroundings (terrain-tenacity), their orientation was clearly influenced by the tray more than the terrain.

To examine these findings further, I analyzed data for 17 individuals that provided significantly clustered orientation records before rotation of the tray, and additional records after rotation. The direction of each after-rotation bearing was compared with the before-rotation mean of that individual. After removing all deviations greater than 90°, 23 deviations were clockwise and 23 were counter-clockwise. I conclude that the position of the tray had a greater influence on the orientation of the Golden-crowned Sparrows than did surrounding features.

Nine post-rotation records of the marked Fox Sparrow also demonstrated a tendency to adhere to the original tray-orientation rather than maintaining the original terrain-orientation.

The orientation of 78 pairs of nearest neighbors that were not more than 20 cm apart was compared and tested by chi-square. Members of these pairs strongly tended to be heading in the same direction and the departure from a random relation-

ship was statistically highly significant. More pairs than expected were pointing in the same direction, more were within 30° of each other, and more were within 60° of each other, whereas many fewer than expected were pointing in opposite directions. The same highly significant results were obtained using 440 nearest-neighbor pairs that were as much as 40 cm apart.

CONCLUSIONS

Wintering flocks of Golden-crowned Sparrows have an exclusive home range (Mewaldt 1964), and birds within a single flock achieve, in some manner, an orderly partitioning of the space within the flock (this study). The subdivision is so effective that I seldom saw disputes between two birds. Each bird tended to take up its accustomed position at the feeding site, even when no potential rivals were present. Even when the feeding area was restricted so that the birds were forced closer together than their preferred inter-bird distance, fighting was not evoked; the birds merely entered and left the feeding area more frequently. Such a system based on site-specificity of individuals would seem to be appropriate in this species, which grazes on lawns and other diffuse food sources, unlike species that are committed to more patchily distributed, defensible food. The latter species develop dominance hierarchies that are established by intra-specific aggression. Plumage variability plays an important role in establishing and maintaining these hierarchies (Marler 1956, Dilger 1960, Rohwer 1975, 1977, Balph et al. 1979, Ketterson 1979, Parsons and Baptista, unpubl. data). A dominance hierarchy serves to reduce energy-expensive fighting within the flock. Indeed, Rohwer (1977) found that flocks of Harris Sparrows (*Zonotrichia querula*), known to have strong dominance hierarchies, could function with very few disputes over status. In view of this, absence of fighting among Golden-crowned Sparrows is not proof that a dominance hierarchy does not exist. Perhaps Golden-crowned Sparrows, at a single-point source of food, would reveal a distinct hierarchy. This is not certain, because features such as size, sex, and plumage, which are used by other species in establishing and maintaining hierarchies, were not used by these sparrows in regulating distances among themselves. The variable plumage of Golden-crowned Sparrows, however, suggests that they may belong with those species in which flocks are organized in hierarchies through plumage-signaling,

rather than with the plumage-monomorphic species that divide resources territorially (Rowher 1975).

I believe that in addition to the site-specificity measured at the dispersed food source used in this study, there may have been also an undetected component of dominance hierarchy. Similarly, there may be an undetected component of site-specificity in the species known to be hierarchical. Attempts should be made to reveal it.

SUMMARY

A winter flock of color-marked Golden-crowned Sparrows was photographed repeatedly while feeding on a gridded 2.44 × 1.83 m feeding tray. Each bird tended to return to the same place on the tray, even when no other birds were nearby. Song Sparrows and a Fox Sparrow showed strong site-tenacity also.

Mean distance to nearest neighbor was random up to 13 birds on the tray; at higher densities the distance was greater than random (birds over-dispersed). Nearest-neighbor distance was unrelated to sex, conspicuousness of crown markings, or size of wing. Nevertheless, each individual maintained a specific inter-bird distance. There was no tendency for the nearest neighbor to be of the opposite sex.

Golden-crowned Sparrows avoided California Thrashers and Brown Towhees, maintained the same spacing between conspecifics as between themselves and Fox Sparrows, Mourning Doves, and California Quail, but allowed closer spacing with Song Sparrows. Fox Sparrows permitted closer approach by Golden-crowned Sparrows than by other Fox Sparrows.

Each bird within the flock tended to point in a particular direction, and the flock itself was not oriented at random. Nearest neighbors tended to point in the same direction.

Site-specificity within a flock may reduce intra-flock aggression.

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RECENT PUBLICATIONS

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Status and Distribution of Alaska Birds.—Brina Kessel and Daniel D. Gibson. 1978. *Studies in Avian Biology* No. 1, Cooper Ornithological Society. 100 p. Paper cover. \$8.00. Available: see back cover. This publication inaugurates a new series, the successor to *Pacific Coast Avifauna*. Despite its title, it does not attempt to cover all the birds of Alaska. Rather, it treats those species—slightly more than half the total number—whose status and distribution differ substantially from those described by Gabrielson and Lincoln in *Birds of Alaska* (1959). This means that both publications must be used together for a complete picture of the avifauna but it has allowed the present work to be smaller than otherwise. With the aid of abbreviations and symbols, the accounts for the selected species report status and distribution, citing significant records, both published and unpublished. References are listed. Although not easy to use, this checklist will be indispensable for anyone studying birds of Alaska.

Birds of Southwestern Oklahoma.—Jack D. Tyler. 1979. *Contributions from the Stovall Museum* No. 2, University of Oklahoma, Norman. 66 p. Paper cover.

\$2.25. A checklist of the birds of the Wichita Mountains and vicinity. Given for each species are its status, dates of occurrence, and records. Map and list of references.

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