

homing abilities; most birds returned relatively rapidly after being displaced more than 800 km from their nests. Furthermore, storm-petrels can navigate over unfamiliar territory at speeds twice those reported by Griffin (1940). The distance to Stephenville precludes direct sensory contact with familiar landmarks near Kent Island and, presumably, is outside the day-to-day experience of the experimental birds. This experiment indicates true navigation abilities (Able 1980). Explanations of individual variation in homing speeds await experimental studies in which we know both the characteristics (age, sex, stage of reproduction, physical condition, etc.) of individual birds, and their homing routes (e.g. Able et al. 1984).

E. Goldstein, W. Johnson, J. Pierson, and two anonymous reviewers provided helpful comments on an earlier version of the manuscript. We would like to acknowledge the field assistance of J. Suito, R. Suito, and F. Atwood. M. Tate and R. Fleiger (Air Canada) provided transportation. T. Grant performed the crucial role of releasing the birds at Stephenville. This research was supported by Bowdoin College and a grant from the Sloan Foundation, Smith College, to E. C. Pierson, who was responsible for the fieldwork. This study represents contribution No. 59 from the Bowdoin Scientific Station.

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Received 1 February 1988, accepted 1 September 1988.

Sex Differences in Risk-taking Behavior in Foraging Flocks of House Sparrows

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Birds that forage in flocks often lend themselves to analysis of costs and benefits associated with grouping behavior and how cost-benefit trade-offs may shift with changes in group size (Pulliam and Millikan 1982, Pulliam and Caraco 1984). Granivorous species have frequently been selected for these studies because of the limited variety of food items taken, and House Sparrows (*Passer domesticus*) have been a particularly popular species for study (Barnard 1980a, b, c; Barnard and Sibly 1981; Elgar and Catterall 1981,

1982; Caraco and Bayham 1982; Elcavage and Caraco 1983; Studd et al. 1983; Elgar et al. 1984, 1986; Elgar 1986; Lima 1987).

However, there has been surprisingly little study of possible sex differences in behavior for any flocking species. The single exception appears to be Caraco and Bayham's (1982) treatment of House Sparrow foraging flocks. Although the only difference they showed was that males occurred in flocks in greater proportion than in the local population, Caraco and Bayham indicated that there were other apparent behavioral differences not rigorously investigated in their study. Primary among these was the suggestion that females were more hesitant to forage where there were frequent disturbances.

Following the lead of Caraco and Bayham (1982), we studied two aspects of risk-taking behavior in for-

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aging flocks of House Sparrows. First, we sought to determine if members of one sex differentially initiate foraging flocks (Caraco and Bayham 1982). Second, we asked whether males or females were more likely to remain on a seed patch when a flock was disturbed and all other flock members retreated to cover (Barnard 1980b, c). We assume these types of behavior place an individual at a greater risk of predation than either joining an already feeding flock, or flying into cover with all other flock members at a disturbance.

We worked on the main campus of the Indiana University of Pennsylvania in western Pennsylvania. The habitat is sparsely wooded suburban lawn. In September 1987, we baited sparrows daily onto the one-story (5.6 m high) flat roof of Weyandt Hall. Before dawn we placed ca. 200 g of white millet seed in a subcircular patch ca. 1.5 m in diameter. The part of the roof we worked on was near one corner and had a 0.45-m-tall metal wall (0.25 m wide) around the edge on these two sides. The center of the seed patch was located 3 m from the wall in one direction and 3.5 m from the wall in the second. A third direction had a planetarium dome 9.3 m in diameter projecting ca. 3 m through the roof, rising 6.5 m from the patch. In the fourth direction was an additional two-story part of the building, with its base 15.5 m from the seed patch. Within 1 m of the building at the corner with the seed patch was an Eastern Hemlock (*Tsuga canadensis*) projecting 1.25 m above the wall. A ca. 15-m-tall Red Oak (*Quercus rubra*) stood with closest branches ca. 6 m away from the building off the adjacent side. Sparrows retreated to both of these trees in alarm flights, although predominantly into the hemlock, the closer of the two.

From mid-October to early December 1987, we continued to bait sparrows with the same quantity of millet seed placed daily before dawn. The seed was completely depleted during each day. On 20 mornings between 0800 and 1100 EST, we used binoculars to observe sparrows from a room ca. 17 m away from the seed patch. We worked only on days with no precipitation. On several mornings, we swept fresh snow off the roof in the area of the patch before placing seed. Temperature on most mornings was 5°–15°C.

Occasionally, other granivorous species, such as Chipping Sparrows (*Spizella passerina*) and White-crowned Sparrows (*Zonotrichia leucophrys*), foraged on the patch. We did not record data on House Sparrow behavior when any other species was present at the seed patch.

Total observation time was 27.25 h; most sample periods were 1 h long. During 26 sample periods (two on several mornings), we recorded whether a male or female was the first individual to fly to the patch. Typically, birds landed on the wall and then flew down to the seed patch after a short delay of a few seconds to nearly a minute. Similar behavior was described in Barnard (1980b), Caraco and Bayham (1982),

TABLE 1. Sex ratios (% males) in House Sparrow feeding flocks of different sizes.

Flock size	Sex ratio ^a	Sex composition ^b	<i>n</i>
3	58.9	0.58	30
4	55.0	0.08	25
5	49.0	3.86	29
6–15	48.0	—	63

^a Test for heterogeneity for four different flock sizes, $G = 4.75$, $df = 3$, $P > 0.05$.

^b G-statistics for goodness-of-fit tests, compared to binomial distributions, all P 's > 0.05 .

and Elgar et al. (1984). Thus, numbers on the wall usually increased from one to several birds before one flew to the patch. We recorded how many birds of each sex were on the wall when the first individual flew to the patch, and we noted this first forager's sex.

Sometimes, entire flocks flew from the roof to cover when disturbed by loud (human-caused) noises, alarm calls by Blue Jays (*Cyanocitta cristata*) or other sparrows, or large birds flying overhead (Summers-Smith 1963). In other cases with similar disturbances, one or a few sparrows remained on the roof at the patch, crouching and continuing to feed. In cases where only one individual remained, we recorded its sex and noted how many sparrows of each sex had been foraging at the patch when the disturbance occurred. We collected these data during 18 sample periods (17.1 h).

Overall, flock sizes were rather small. Mean flock size (\pm SD) was 6.6 ± 3.56 birds ($n = 179$ flocks). The distribution of flock sizes was strongly skewed, biased toward small flocks. We defined a flock as three or more sparrows that fed simultaneously at the seed patch. Fighting among sparrows was very infrequent, as previously shown in such small feeding flocks (Barnard 1980a, Caraco and Bayham 1982).

Sparrows roosted in a loose colony in gratings covering ventilation shafts on the side of the building facing the red oak. We counted 6–7 pairs and several additional birds in that group. These birds were frequent foragers at the seed patch, but others also foraged here. We recorded as many as 27 sparrows on the seed patch simultaneously ($\bar{x} \pm$ SE of maximum flock sizes from 18 sample periods = 16.9 ± 5.55 birds). The presence of these additional birds meant that, unlike Caraco and Bayham (1982), we could not calculate a sex ratio in the very local population of sparrows available for foraging on the patch.

In order to calculate the probability of a male or female engaging in a particular aspect of behavior, we required sex ratios. Ideally, we wanted to calculate the sex ratio for each flock. However, because many flocks consisted of only several birds, individual flock sex ratios for these small groups were not useful for comparison. We chose the next best option and pooled

all flocks of a particular size. We then calculated an overall sex ratio (% males) for flocks of that size.

The pooling procedure reflects the assumption that whether a sparrow joined a feeding flock was independent of the sex composition of the already formed flock. To verify this assumption we used the method of Caraco and Bayham (1982). We compared the observed sex composition of different sized flocks with those expected from the binomial distribution, using the sex ratio calculated from each flock size. We did this for flock sizes for which we had large samples (3-5). The null hypothesis was not rejected in any of these cases (Table 1). Then, we compared the sex ratios in these flocks with that for flocks with six or more sparrows and found no difference ($G = 4.75$, $df = 3$, $P > 0.05$; Table 1). The overall sex ratio for all feeding flocks of known composition was 50.1% males ($n = 147$ flocks).

The sex ratio in the assemblage of birds perched on the wall prior to foraging was 53.3% ($n = 468$ flocks). Of first foragers, 53.9% were males. There was no association between the sex of a sparrow and the probability of initiating a feeding flock as first forager ($G = 0.06$, $P > 0.05$).

We recorded the nature of dispersal from 325 foraging flocks, including some of unknown sex composition. Of these flocks, 287 (88.3%) dispersed due to disturbances (see above) rather than to gradual dispersal of members. Disturbance is thus a very common occurrence, and sparrow foraging behavior is undoubtedly shaped in part by risks of predation.

In cases where foraging flocks were disturbed and only one bird remained, we compared flock sizes for a male vs. a female remaining and found these to be similar (Kolmogorov-Smirnov 2-sample test, $D_{max} = 0.308$, $P > 0.05$, $n_m = 48$ flocks, $n_f = 19$ flocks). In flocks where one male stayed, the sex ratio was 56.9%. In flocks where one female stayed, the sex ratio was 47.4%. These sex ratios were similar ($G = 2.68$, $P > 0.05$).

We compared flock sizes in which one bird stayed (pooled between the sexes) vs. those in which all birds dispersed and found these to be similar (Kolmogorov-Smirnov 2-sample test, $D_{max} = 0.120$, $P > 0.05$, $n_s = 67$ flocks, $n_d = 112$ flocks). However, the sex ratio in flocks where one bird stayed (54.7%) was greater than that in flocks where all dispersed (46.4%) ($G = 6.07$, $P < 0.02$). Of 67 cases where one bird stayed, 48 were males (71.6%). Males stayed more frequently than expected from the sex ratio prior to disturbance ($G = 7.04$, $P < 0.01$).

We found no difference between the sexes in the tendency to initiate a feeding flock. Sparrows appeared hesitant to be the first to fly to the exposed seed patch. Our impression was that solitary females tended to perch longer on the wall, giving chirrup calls (Elgar 1986) longer, than did solitary males, waiting for other sparrows to arrive. Once other sparrows arrived, the solitary bird of either sex very rapidly

flew to the seed patch, immediately followed by the other sparrows. Therefore, our scoring of the sex of first forager did not reveal any difference in hesitancy. Sometimes, solitary birds gave chirrup calls to no avail, and they eventually flew to the seed patch as solitary foragers. We predict that if one measured the latency to flying to the patch as a solitary forager, females would display a longer latency than males.

We did not find as high a percentage of males in feeding flocks as Caraco and Bayham reported (1982). The overall sex ratio did not differ from 50% for any flock size. The most parsimonious explanation is that the local-population sex ratio was unity, and there was no differential tendency for either sex to join flocks. Nonetheless, it is unclear why this sex ratio differed from that found by Caraco and Bayham.

We found that it was more likely for a male than female to remain at the seed patch as a solitary forager when a disturbance caused all other sparrows to fly to cover. Barnard (1980c) found that sparrows staying behind in such circumstances were individuals that had lower pecking rates than the mean rate for the flock before the disturbance. Furthermore, pecking rates by these birds increased as they foraged alone immediately after departure by the rest of the flock in an alarm flight. They also hopped around the seed patch, pecking in different areas.

Barnard believed these observations indicated that birds remaining after a disturbance had been excluded by other flock members from the richest areas of patches and thereby benefited from remaining on the patch, even if they increased their risk of predation by doing so. Our observations have shown that male sparrows remain at a seed patch more often than females after a disturbance and thus potentially are more vulnerable to predators. We suspect that subordinate birds tend to be those that remained after a disturbance (Barnard 1980c), but why males were disproportionately represented was unclear.

There is little information on the details of dominance relationships in flocks of wild House Sparrows. Watson (1970) found no linear dominance hierarchies in small groups of captive sparrows, although each group contained an alpha male, and females appeared generally subordinate to males. Subordinate birds, including females, sometimes successfully repelled attacks by alpha males, and there appeared to be site-related dominance. It is perhaps significant to our own observations that females in Watson's study were frequently able to withstand male aggression by simply moving away a short distance. In contrast, inter-male aggression invariably caused one male to leave the immediate area.

It is unfortunate that we do not know how many individuals were represented by our records nor the age structure of these flocks. Although we were unable to band sparrows, future work would clearly benefit from study of a banded population.

We conclude that there are sex differences in risk-

taking behavior in flocks of House Sparrows under some foraging circumstances. Investigators of foraging behavior by flocking birds need to take into account the possibility of such differences in future studies.

Tom Caraco offered useful information at the planning stage of this study. We thank Tom Caraco, Tony Nastase, Sandy Newell, Fred Wasserman, and Julia Zaias for comments and suggestions on a previous version of this paper. Janet Hinshaw and the Josselyn Van Tyne Memorial Library provided references. Support for this project was provided by the Department of Biology, Indiana University of Pennsylvania.

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Received 17 June 1988, accepted 12 September 1988.