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Social Strategy and Cover in Savannah Sparrows

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In social vertebrates, group formation results from the collective response of individuals to environmental and social conditions. An individual's decision to join or leave a foraging group depends on the relative costs and benefits of group membership. Benefits to flock members include more effective predator detection (Powell 1974, Kenward 1978, Dekker 1980, Lindström 1989), an increase in foraging rate through reduced vigilance (e.g. Pulliam 1973, Caraco 1979, Barnard 1980), reduced probability of predation (Powell 1974, Dekker 1980, Lindström 1989), and an

enhanced capacity to locate high-quality patches (Krebs et al. 1972). Costs to flock members include division of available food resources between flock members (Pulliam and Millikan 1982), a reduction in foraging rate due to increased social interference or aggression (e.g. Goss-Custard 1976, Caraco 1979, Barnard 1980, Caraco et al. 1980, Elgar 1987), and an increased probability of detection by predators (Vine 1973, Taylor 1979).

Both the costs and benefits of flock membership may increase with group size. Thus, changes in group size may be a dynamic response to the shape of specific cost/benefit functions (Pulliam 1976, Pulliam and Caraco 1984, Elgar 1987). Cost/benefit functions may change with environmental conditions. In heterogeneous or dynamic environments, flock size may

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change over relatively fine spatial and temporal scales. Organisms may shift from a solitary existence to sharing a large group depending on environmental conditions.

In southeastern North America, Savannah Sparrows (*Passerculus sandwichensis*) spend the winter in large, early successional fields that contain a mosaic of open patches interspersed with patches of dense weeds. Savannah Sparrows are more vulnerable to predation by diurnal raptors when using open versus weedy patches (Watts 1990). In addition, temporal variation in predation risk (as mediated by weather conditions) influences the distribution of birds among patch types (Watts 1991). Consistent differences in predation risk among habitats should affect flock size, if flock size is driven by predation risk. Here, I evaluate this prediction by comparing flocking behavior for Savannah Sparrows occupying open versus weedy patches.

Field work was conducted on sites located approximately 15 km east of Athens, Georgia. All sites were agricultural fields that had been fallow for two to three years and contained dense, homogeneous stands of horseweed (*Erigeron canadensis*). Horseweed often dominates eastern plant communities in the first two years after cultivation (Crafton and Wells 1934, Keever 1950, Odum 1960), and it provides a major vegetative cover for sparrows wintering in fallow fields.

Four experimental plots containing uniform horseweed cover and measuring 180 × 120 m (2.16 ha) were chosen in mid-December of 1988 (all plots were embedded in larger horseweed fields ranging in size from 27 to 60 ha). Horseweed was manipulated on two plots (open treatment) by mowing stalks to a height of 15 cm with a small tractor. The remaining two plots (weedy treatment) were left as unmowed controls. Grid lines were marked off at 15-m intervals along the length and width of each plot.

I censused birds using a modification of the line transect method (Emlen 1974), which allowed for a more complete conservation of spatial information. I walked a zig-zag pattern down each of eight 180-m rows of grid cells and passed within 5 m of all points on the grid surface. The position of all birds detected, as well as my position at the time of detection, was plotted on a grid map to within 2 m. Censuses were done in 4-day time blocks where all grids were censused within each time period. Each grid was censused 15 times during the study period. Two censuses were conducted per day, five days per week. Censuses of grids were conducted between 9 January and 14 March 1989. All censuses were completed within 4 h of sunrise. See Watts (1990) for a more complete description of methods, including grid layout, analysis of detection distances, and estimation of expected errors.

Bird flocks were delineated according to the criteria of Grzybowski (1983). Birds were considered to be members of the same flock if they responded similarly

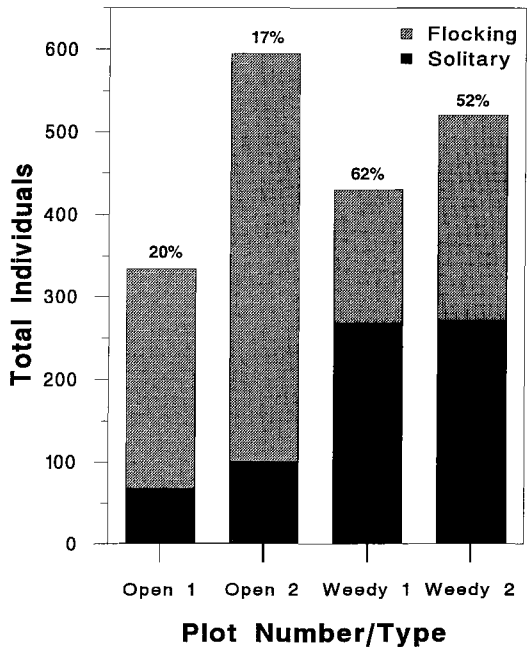


FIG. 1. Distribution of flocking vs. solitary Savannah Sparrows in experimental (open) and control (weedy) plots. Values above bars indicate percentage of individuals that were solitary.

to disturbance by the observer, or were observed foraging or resting together as a unit distinct from other individuals. The percent of solitary individuals was calculated from flock-size data. This variable presumably represents the proportion of individuals acting independently of other individuals.

A total of 1,724 observations of Savannah Sparrows was made on the census grids over the two-month study period (many of the observations were clearly of the same individuals). Density estimates ($\bar{x} \pm SE$) were 12.4 ± 2.53 birds/ha ($n = 30$) and 13.5 ± 8.29 birds/ha ($n = 30$) for weedy and open plots, respectively. The proportion of birds determined to be solitary was not significantly different between replicate plots ($\chi^2 < 3.0$, $df = 1$, $P_s > 0.05$, and $\chi^2 < 5.0$, $df = 1$, $P_s > 0.05$, for open and weedy patches, respectively; see Fig. 1). For this reason, replicate data were pooled to compare flocking tendency between treatment types. Savannah Sparrows were more than twice as likely to be solitary on weedy plots than on open plots ($\chi^2 > 100$, $df = 1$, $P < 0.0001$; Fig. 1). In order to compare flocking patterns between treatments, a frequency distribution of flock sizes was compiled for each cover type (Fig. 2). The distribution of flock sizes was skewed to small flocks for both cover treatments. However, large flocks were relatively more common in open plots than in weedy plots ($\chi^2 > 40$, $df = 7$, $P_s < 0.05$). In all, 50% of the individuals associated

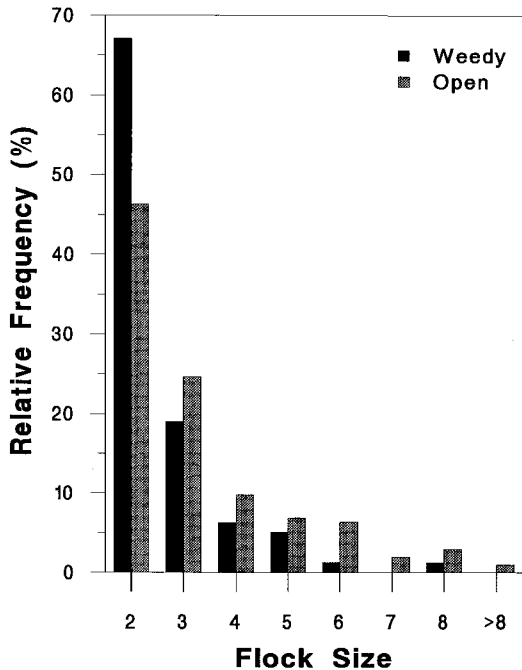


FIG. 2. Frequency distribution of flock sizes by treatment type. Data from replicate plots were pooled for analysis and presentation.

with flocks in open plots were in flocks larger than three, compared with only 25% in weedy plots.

Pulliam and Mills (1977) suggested that birds that feed in open areas should place a premium on predator detection, selecting for individuals that find refuge in flocks. Conversely, birds inhabiting areas of dense, uniform vegetation should gain greater refuge by remaining single and using weedy vegetation to provide a "visual refuge" (Pulliam and Mills 1977). Different species may specialize on one or the other strategy. Savannah Sparrows, however, appear to adjust their social strategy to match the conditions of the habitats they occupy. Sparrows observed in open patches were less likely to be solitary and more likely to form large flocks compared with those in weedy patches. This apparent shift in flocking strategy by Savannah Sparrows is consistent with strategies of other species that use one or the other habitat exclusively (Pulliam and Mills 1977, Grzybowski 1983). Savannah Sparrows appear to have enough behavioral plasticity to "bridge the gap" between these two extreme strategies (social vs. cryptic evasion). Observed flexibility may follow from their wide distribution and broad habitat requirements. Grzybowski (1983) showed that Savannah Sparrows used a wide range of conditions and varied considerably from site to site in the proportion of individuals that were solitary. He suggested that Savannah Sparrows appear

to have evolved a behavioral compromise between the potential costs and benefits of gregariousness.

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Begging as competition for food in Yellow-headed Blackbirds

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Theoretical models suggest that chicks compete with one another for food by begging (MacNair and Parker 1979, Harper 1986, Parker et al. 1989, Price 1994, Price et al. 1996). Several comparative studies support this idea by illustrating a positive correlation between brood size and begging level interspecifically (e.g. Cotingidae; Harper 1986), and between brood size and the ratio of begs to feeds intraspecifically (e.g. Cattle Egrets, *Bubulcus ibis* [Fujioka 1985]; Budgerigars, *Melopsittacus undulatus* [Stamps et al. 1989]), although Henderson (1975) found no brood size effect in Glaucous-winged Gulls (*Larus glaucescens*). No one has demonstrated changes in begging in response to experimental changes in brood size.

Experimental evidence that chicks change their begging behavior in relation to sibling competition comes from Smith and Montgomerie's (1991) study of begging in American Robins (*Turdus migratorius*). Smith and Montgomerie deprived individual nestlings of food and then returned them to their brood mates. Deprived chicks begged relatively more and were fed more than their "control" nest mates, which had remained in the nest during the deprivation period. The control chicks also altered their begging level, apparently in response to the changed begging

of their hungry nest mate. Smith and Montgomerie (1991) did not monitor parental provisioning to control chicks during the deprivation period, however, and the response of these controls may have been confounded by changes in hunger level. Similarly, Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) chicks tended to increase begging following the temporary food deprivation of a nest mate (Price and Ydenberg 1995), but again, the behavioral change might have followed changes in hunger level. Young Zebra Finches (*Taeniopygia guttata*) increased begging upon hearing played-back begging calls (Muller and Smith 1978), but Yellow-headed Blackbirds did not, likely because they were well fed and satiated (Price 1994).

In this paper, I return to the first approach and experimentally investigate the effect of brood size on begging to extend the comparative studies and to complement the begging manipulation studies. I assess the effect of increased competition on sibling behavior. I do not compare the behavior of individual nestlings of differing need and abilities, nor do I examine the relationship between begging and provisioning (other than as a potential confound), which forms the focus of many studies of nestling begging (e.g. Litovich and Power 1992).

Yellow-headed Blackbirds lay two to five eggs that hatch asynchronously within one to three days; brood reduction is common (Willson 1966, Richter 1984).

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