

Cover Use and Predator-related Mortality in Song and Savannah Sparrows

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Winter sparrow assemblages represent ideal systems for the investigation of mechanisms that act to structure terrestrial communities. Early investigations of these assemblages centered on the availability of food as a primary structuring mechanism (Fretwell 1972, Pulliam and Enders 1971, Pulliam 1975). Groups of sympatric sparrows that differed in their abilities to exploit seeds of varying sizes were thought to partition available seeds by size. These investigations led to the construction of idealized intake-maximization models that, along with the distribution of available seeds, were used to predict species' abundances and their patterns of coexistence (Pulliam 1975, 1985, 1986). Although this single criterion approach has met with some success in explaining the abundance of species (Dunning and Brown 1982), many distributional patterns remained inconsistent with theoretical predictions. For example, the experimental manipulation of seed abundance and size distribution had no observable effect on abundance or diversity of sparrows in the desert Southwest in the United States (Pulliam and Dunning 1987). This supports the suggestion that, on a local scale, the effect of food on sparrow community structure may be most profound during years when seed supply is low (Pulliam 1985, 1986). Other investigators have shown that the distribution of some species and species assemblages was strongly affected by the distribution of vegetation used as cover (e.g. Pulliam and Mills 1977, Grubb and Greenwald 1982, Schneider 1984). These observations suggest that the risk of mortality by avian predators may contribute to the spatial structure of winter sparrow communities.

The predicted relationship between mortality risk and sparrow community structure is simple. It is assumed that the risk of predation is nonrandom across a given landscape because of the patchiness of vegetation used as cover, and that prey species segregate spatially according to their specific abilities to utilize areas of varying risk. Unfortunately, unlike seed use and availability, predation risk is very difficult to quantify. This is so because observations of predatory acts are difficult to obtain due to their unpredictability in time. For this reason, researchers have utilized surrogate variables that are thought to change with predation risk. For example, patterns in foraging rate (e.g. Grubb and Greenwald 1982, Pulliam and Dodd MS, Schneider 1984), vigilance rate (e.g. Barnard 1980, Caraco et al. 1980), and flock size (e.g. Caraco 1979, 1980; Elgar 1986; Pulliam 1973) have been used to suggest patterns in predation risk. Although these variables are one step removed from predation risk, they are assumed to be related to the perception of risk by prey and so have been used as indicators.

However, no data that document a reduction in sparrow mortality as a function of cover use have been presented. I studied Savannah (*Passerculus sandwichensis*) and Song (*Melospiza melodia*) sparrows, to address the common assumption that cover influences the risk of predator-related mortality in some species. Data that indicate interspecific differences in both habitat use and mortality risk are also presented.

The fieldwork was done on three sites located 15 km east of Athens, Georgia. All sites were agricultural fields, fallow for 2–3 yr, and containing dense, homogeneous stands of horseweed (*Erigeron canadensis*). Horseweed is a common, early successional plant that often dominates the plant community in the first 2 years postcultivation (Crafton and Wells 1934, Keever 1950, Odum 1960). Odum (1960) showed that horseweed may produce >70% of the plant biomass in the first year after abandonment. Horseweed is one of only four species capable of dominating the plant community in the early phases of oldfield succession (Keever 1950). Because the plant grows in dense, uniform stands and has woody stalks that remain upright throughout the winter, it often provides the major vegetative structure for sparrows that winter in fallow fields. The uniformity of these stands makes them ideal for the experimental investigation of the effects of screening cover on sparrow habitat use in winter.

In mid-December 1988, I chose six experimental plots that contained uniform horseweed cover and measured 180 × 120 m (2.16 ha). All plots were within larger fields and had a minimum horseweed buffer of 15 m on all sides. On two of the plots all horseweed stems were mowed to a height of approximately 15 cm with a 2-m brushhog mounted on a small tractor. On two other plots, two 30-m wide strips were mowed lengthwise such that they alternated with two 30-m wide unmowed strips. The last two plots were left unmowed. Mowing began on 28 December 1988 and was completed on 9 January 1989. The very small, wind-dispersed seeds produced by this species are dropped in early autumn. Thus stalk removal in winter did not confound food availability. All study plots were marked off at 15-m intervals with white surveyor's flags. This produced a rectangular grid of 96 cells, each 225 m². Two refuge stations were established at one end of each grid. Each refuge station comprised 10–15 saplings (2–3 m tall) sharpened and driven into the ground to simulate an isolated tree island. The base of this 2-m-wide structure was filled with dense brush and vines. These stations were placed 30 m from each side of the grid, and 45 m from one end. This resulted in a split-plot design where half of the grid had no refuge cover and the other half had two refuge stations placed 60 m apart and at

its midpoint. All natural, woody vegetation on or near the grids was then removed.

I conducted censuses of experimental grids between 9 January and 14 March, 1989. Censuses were done in time blocks where all grids were censused in each block, and the census order within blocks was randomly determined. Each study grid was censused 15 times during the study period. Two censuses were conducted per day, 5 days per week. All censuses were completed within 4 h of sunrise.

I used 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. This allowed for the accurate determination of bird locations and detection distances. Mean (\pm SE) detection distance for unmowed areas was 13.0 ± 0.46 m ($n = 877$), and for mowed areas it was 21.5 ± 0.66 m ($n = 847$) (data from stripped plots were not included). Five meters was found to be well below the lower 99.9% confidence limit for the detection distances in both cover and open areas. I believe that virtually 100% of all birds present on the grids were detected.

An inherent problem with the use of adjacent census transects to estimate bird densities and distributions is the overestimation of bird numbers. This potential bias is due to the possibility of recounting birds that flush away from an observer but do not move entirely off the census area. Of all birds detected on experimental grids, 70% either moved beyond grid boundaries or moved to brush stations. Of the 30% remaining, 56.3% were detected on the ground and were not flushed to new locations. Only 13.1% of the birds detected flushed to new locations within the grid boundaries. By chance we would expect 50% of these birds to flush to areas already censused, leaving a predicted error of more than 6.5%. In an attempt to reduce this error further, I charted the movement of all birds from the time of detection as accurately as possible within the grid boundaries. Birds detected at the settlement location of a previously counted bird were not recounted. This produced a conservative estimate of bird densities. In addition to mapping bird locations and movements, all bird behaviors and observer activities during the census period were described on audio tape. Each census took 1–1.5 h to complete.

In addition to regular censuses, each grid was systematically searched twice for "sparrow kills." A *sparrow kill* refers to a distinct pile of feathers left by Northern Harriers (*Circus cyaneus*) (Bildstein 1978). After capture, harriers pluck sparrows on the ground before consuming them (pers. obs.). I searched all grids by walking 5 parallel transects through each grid cell—a process that took 5–6 h per grid. Feathers

from kills were collected and coded for later identification, and their position plotted on a grid map. Grids were searched between 25 and 30 January, and again between 7 and 14 March. Kills were identified to species by retriex shape and length, and Savannah Sparrows were aged by retriex shape (Pyle et al. 1987).

Savannah and Song sparrows dominated the sparrow community on the experimental grids. Of the 2,802 sparrow observations made over the 2-month period, Savannah and Song sparrows accounted for 97.6%. Other species seen included Vesper Sparrow (*Poocetes gramineus*; 1.4%), Grasshopper Sparrow (*Ammodramus savannarum*; 0.8%), Field Sparrow (*Spizella pusilla*; 0.1%), and Le Conte's Sparrow (*A. leconteii*; 0.1%). Because no kills of the latter 4 species were found, they were excluded from the following discussion.

Vegetation removal had a significant, but opposite, effect on the occurrence of Savannah and Song sparrows (Table 1). Over all censuses, Savannah Sparrows were observed more often on mowed grids than expected by chance ($\chi^2 = 10.46$, $P < 0.005$). In contrast, >85% of the Song Sparrows observed were located on unmowed grids ($\chi^2 = 222.48$, $P \ll 0.001$).

The addition of brush stations also affected the distribution of both sparrow species, though to different degrees. Whereas 88.1% of all Song Sparrows ($\chi^2 = 219.4$, $P \ll 0.001$) were on the "brush addition" half of grids, only 57.2% of Savannah Sparrows ($\chi^2 = 48.2$, $P < 0.001$) were there. A comparison of sparrow distribution patterns within and between experimental grids indicates that Song Sparrows depend on both weedy and woody cover more so than do Savannah Sparrows.

Bird locations from census observations were used to produce expected distributions of sparrow kills to test for the effects of cover on sparrow mortality. Both Song and Savannah sparrow kills were found in open areas more frequently than would be expected based on census observations. Song Sparrow kills were located in mowed areas significantly more often than would be expected by chance ($\chi^2 = 111.49$, $P \ll 0.001$), and there was a complete reversal in the direction of the habitat distribution. Whereas 88.4% of all Song Sparrows observed were in unmowed areas, 82.6% of kills found were located in mowed areas. This same open habitat bias in kill frequency was observed for Savannah Sparrows ($\chi^2 = 7.88$, $P < 0.005$), although the effect was not of the same magnitude. Of the 7 Savannah Sparrows that could be aged by retriex shape, 4 were hatching-year birds, and 3 were after-hatching-year birds.

A comparison between Song and Savannah sparrows over all grids indicated that Song Sparrows were significantly more prone to predation than were Savannah Sparrows ($\chi^2 = 90.73$, $P \ll 0.001$). Of 2,733 observations made of both species, Song Sparrows accounted for only 13.8%, but they represented 71.8% of all kills found. The data (Table 1) suggests that

Song Sparrows that used open areas were more than 60 times more likely to be taken by predators than were Savannah Sparrows that used the same habitat.

The distribution of sparrow remains after consumption is thought to represent accurately the location of kills made by harriers. Though harriers are known to carry prey, especially when moving to perches or feeding young, this distance is relatively short when prey is consumed on the ground, as is the case here (Bildstein 1978). Very few observations of prey-movement behavior exist for this species. The few quantified observations of harriers seen moving prey between open and weedy areas have not indicated any directional movement (Bildstein pers. comm.). Many harriers were regularly observed hunting in and around study areas, and none were ever seen carrying prey. Although no effort was made to quantify cotton rat (*Sigmodon hispidus*) remains left by harriers, these were at least as common as bird kills on the study plots. The distribution of cotton rat remains was clearly biased in favor of areas with cover. This observation supports the assumption of no directional movement of prey to mowed locations from the surrounding unmowed areas.

Visibility in areas with screening cover changes as a function of stem density, stem width, and the observer height relative to the average stem height (Janes 1985). All of these variables together determine the searchable area for visually oriented raptors at a given location. At any given height above ground, the available search area will be greater in open areas versus areas with cover. To achieve an equivalent search area in fields with cover, raptors must move vertically to increase their height above the vegetation. Although vertical movement increases the search area and the probability of detecting prey, it also increases the distance between predator and prey. This increased distance acts to increase the time needed to complete an attack. After detection, sparrows that use standing vegetation as cover escape advancing predators by moving out of sight. Because the search area is smaller in areas with cover (for a given height), the period of vulnerability for fleeing prey is shorter.

I suggest that prey that use screening cover are less vulnerable to predation. This is true because to obtain the same probability of prey detection, raptors that hunt in cover must accept a higher ratio of attack time to prey-vulnerability time. The difference between habitats in this ratio indicates that when hunting in cover, raptors have a reduced chance of success after prey is detected. When hunting highly mobile prey such as small birds and mammals, this ratio may be so high that the probability of capture is unreasonable at even moderate heights above the vegetation. In this way, highly mobile prey constrain the vertical location of raptors to just above the vegetation, which indirectly reduces the probability of being detected visually.

The effect of screening cover on raptor hunting

TABLE 1. The number of Song and Savannah sparrows observed during censuses, and the number of kills collected.

	Total	Birds/ha	Kills (n)
Savannah Sparrow			
Unmowed	1,099	11.31	0
Mowed	1,256	12.92	9
Song Sparrow			
Unmowed	334	3.44	4
Mowed	44	0.45	19

success, hunting method, and site use is well documented. For example, Sparrowe (1972) showed experimentally that both capture success and the number of capture attempts by American Kestrels (*Falco sparverius*) declined as prey-exposure time was reduced and cover density increased. He suggested that kestrels could differentiate between good and bad capture opportunities, and that some minimum prey exposure was necessary to initiate an attack. Toland (1987) showed, in the same species, that hunting success declined with increasing vegetation height from 83% in relatively open areas to 41% in cover areas. A difference in hunting method was also observed. Whereas hover hunting (an energetically costly method) was used most frequently in cover areas, perch hunting (method requiring the least effort and most visibility) was the dominant method used in open areas.

The reduced capture success and the need for more costly hunting methods in areas with cover have likely contributed to the observed preference for open foraging sites by many raptors. Several studies of habitat use in diurnal raptors have indicated that vegetative cover is of greater importance than prey density in the selection of hunting sites. For example, Swainson's Hawks (*Buteo swainsoni*) shifted their foraging activities to croplands only after crops had been harvested, even though prey biomass was greatly reduced at harvest time (Bechard 1982). Wakeley (1978) suggested that vegetative cover was the most important factor in hunting-site selection by Ferruginous Hawks (*B. regalis*). This species hunted in pastureland and in fields with bare ground significantly more often than in dense vegetation, even though prey biomass was higher in vegetated sites. Rough-legged Hawks (*B. lagopus*) and Red-tailed Hawks (*B. jamaicensis*) showed a similar pattern in utilizing shortgrass fields more often than straw and oldfields even though prey densities were higher in the latter. These studies indicate that vegetative cover in some way affects prey availability and so indirectly prey vulnerability.

The pattern of hunting success and site selection by raptors relative to cover supports the hypothesis that when both Song and Savannah sparrows used

areas with screening cover, they experienced reduced mortality due to predation. These findings are consistent with studies that used surrogate variables as indicators of risk and that documented related costs of using areas away from cover. The additional finding that Song Sparrows were more vulnerable to predation overall suggests a simple mechanism for the spatial structuring of sparrow communities. Sparrows that use habitats in some imagined landscape would be expected to adapt to the level of predation risk associated with the habitat. Because the ability of raptors to detect and extract prey seems greater in open versus cover areas, one might expect morphological and behavioral traits that are correlated with their use of these habitats. Species found in habitats with cover would be expected to exercise cover-dependent evasion tactics, while those in open fields might use cover-independent escape tactics. Evidence for functionally different escape tactics associated with cover have been presented (Pulliam and Mills 1977). Morphological adaptations to open or cover habitats may preclude the efficient use of alternate habitats. It is, of course, also possible that this relationship is asymmetrical. For example, cover-adapted species may be ill-equipped to use open habitats, where open-adapted species may experience no mechanical difficulty in exploiting cover areas, or vice versa. However, possible morphological and behavioral differences between sparrow species assemblages that use habitats of varying risk have not been addressed.

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