

TERRITORY PREFERENCE OF VESPER SPARROWS IN CROPLAND

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The Vesper Sparrow (*Pooecetes gramineus*) is an abundant species breeding in much of the cultivated land that extends across the plains and prairies of North America (Stewart and Kantrud 1972, Mikol et al. 1979, Dinsmore 1981, Henderson 1981). In central Iowa, Vesper Sparrows commonly establish territories along fencerows between fields of corn and soybeans. This sparrow sings primarily from fencerows and forages along their edges, but places its nest on the ground in the crop field. Despite the species' abundance in cropland, in some areas its productivity in this habitat may be below that needed to offset adult mortality (Rodenhouse and Best 1983). The question might then be asked, is the Vesper Sparrow preadapted to make an inappropriate choice in selecting agricultural cropland for breeding?

Vesper Sparrows are found in a variety of habitats other than corn and soybean fields (Rodenhouse 1981) but are associated with similar habitat characteristics in each. Typically, the species breeds in sparsely vegetated areas (Sutton 1960, Berger 1968, Wiens 1969, Whitmore 1979) and xeric sites (Grinnell and Miller 1944). Breeding Vesper Sparrows occur in very low densities, if at all, in areas with dense vegetation (Dambach 1948, Graber and Graber 1963). Preceding human settlement, the open xeric or disturbed sites used by Vesper Sparrows were maintained by fire (e.g., jack-pine [*Pinus banksiana*] stands in Michigan [L. H. Walkinshaw, unpubl.]), erosion of loose soils by wind (e.g., sand dunes [Olson 1958]), or overgrazing by bison (*Bison bison*) (Owens and Myers 1973). In the Midwest, Vesper Sparrows now breed primarily in areas disturbed annually by cultivation.

The objectives of this study were to (1) identify habitat characteristics preferred by Vesper Sparrows that establish territories in cropland; (2) determine the relationship between territory preference and nesting success; and (3) evaluate the adaptiveness of breeding on agricultural land.

METHODS

Study sites.—The study was conducted in Story County, Iowa, in 1979 and 1980. Study sites were selected in upland areas that contained a fencerow at least 300 m long between a corn and a soybean field. Eight sites were used in 1979; 13 additional sites were added in 1980. Study sites included the portion of the crop field on both sides of the fencerow that was used by Vesper Sparrows. Vegetative cover of fencerow study sites ranged from those dominated by grasses with negligible shrub (woody growth 1–3 m tall) cover, to fencerows

with high shrub coverage and low grass coverage. Trees (>3 m tall) occurred rarely on fencerows. Fencerows with greater shrub coverage were wider (Spearman's rank correlation, $r_s = 0.53$, $N = 31$, $P < 0.01$) and had higher plant species richness ($r_s = 0.73$, $P < 0.01$). Corn and soybeans were rotated annually on all fields studied.

Field methods.—Vegetation was measured every 20 m along fencerows on a representative sample (14) of the study sites. Sample plots were 0.5 m wide, with a variable length that corresponded to the fencerow width (distance between tilled fields). Canopy coverage of all plant species and growth forms (grasses, forbs, shrubs, and trees) within sample plots was estimated visually.

The location and height of all shrub groups along each fencerow were recorded. Shrub groups included one or more shrubs or saplings that formed a contiguous canopy. On fencerows planted with multiflora rose (*Rosa multiflora*), saplings or shrubs extending above the continuous rose hedge were designated shrub groups. The amount of crop residue was measured before planting by using the "bead-string" method (Sloneker and Moldenhauer 1977). At least three sites were sampled in each field at 80-m intervals along the fencerow. Each sample began 15 m from the fencerow and extended outward into the field, at a 45° angle to the crop rows.

Territories were located by walking along fencerows and observing singing males. Males singing from mid-field (usually about 200 m from a fencerow) as well as along fencerows could be detected easily. Attempts to delimit territories by using the repeated flushing technique (Wiens 1969) were only partly successful; territories were well-defined near fencerows but not in the crop fields. As many males and females as possible (26 and 11, respectively) were mist-netted and marked with colored leg bands and a U.S. Fish and Wildlife Service band in 1980. We visited each study site in the spring of 1981 to determine if any banded birds had returned, but did not search neighboring areas.

Agriculturally nonproductive areas on and surrounding each territory were mapped, and their coverages were estimated. "Nonproductive areas," other than fencerows, included grassy waterways (uncultivated watercourses covered by a grass sod), washes (cultivated watercourses where erosion severely stunted crop and weed growth), and weedy areas (low wet areas where crop growth was stunted by flooding or rank weed growth).

Territories on which nests were not found during routine visits were systematically searched for nests. Territories usually were visited every 4 days, and active nests were checked at least every other day.

Analysis methods.—The following territory characteristics were used as variables in evaluating territory preference and nesting success: number of shrub groups (within the fencerow), fencerow coverage, number of washes, crop residue before planting, and coverage of nonproductive areas (other than fencerows). These variables were selected because they represent the major structural and vegetational features within Vesper Sparrow territories. Because our data did not meet the assumptions of normality and homogeneity of variance required for parametric statistics, we tested for statistical significance by using a nonparametric procedure (Kruskal-Wallis one-way ANOVA, Nie et al. 1975). Statistical significance was set at $P \leq 0.05$.

RESULTS AND DISCUSSION

General breeding ecology.—Male Vesper Sparrows arrived unpaired and established territories during the first 3 weeks of April; most arrived before spring field operations for crop production had begun. Females began arriving within a week of the first males. Territories were situated along fencerows and usually extended no more than 80 m into the crop

field on both sides of the fencerow. (Rodenhouse and Best [1983] describe territory characteristics in detail.) Breeding densities were greater along fencerows with more shrubs.

Early in the breeding season, males sang primarily from the fencerows (using shrubs, fenceposts, and fence wire for song perches), whereas late in the season, they sang most frequently from perches in crop fields. Early nests were built in a clump of crop residue and were concentrated in fields with the most crop residue (i.e., corn residue). Once spring tillage began and initial nests were destroyed, nest placement shifted from one side of the fencerow to the other, away from the side most recently tilled. After the crop was approximately 10 cm tall, nests were placed at the base of the growing plants. Late in the season when the crop canopy closed, washes in soybean fields were used heavily as nest-sites. Nesting success on cropland was low (13% overall [Rodenhouse and Best 1983]), particularly early in the breeding season. Nest losses resulted primarily from agricultural field operations and predation.

Territory preference.—To identify territory characteristics preferred by Vesper Sparrows, we looked for significant relationships between variables measured on each territory and two indirect measures of territory preference: arrival date of males and pairing success. Territories occupied first were considered most preferred, and territories of paired males were considered more preferred than those of unpaired males. Males that arrived late were more likely to remain unmated. Sixteen of 17 males that arrived during the first week and 19 of 20 in the second week acquired mates, whereas only three of five males that arrived during the third week paired successfully.

Males arrived earlier on areas where fencerows had a greater number of shrub groups (Table 1). Although not statistically significant ($P = 0.1$), crop residue on fields tended to be greater and the areal coverage of fencerows less on territories occupied early. Pairing success was related significantly to the number of shrub groups and the amount of crop residue within territories and almost significantly ($P = 0.06$) to the coverage of nonproductive areas (other than fencerows) (Table 1).

Elevated perches, potentially used for singing, are associated with Vesper Sparrow territories in many uncultivated habitats: shrubs and fenceposts in pastured areas (Wiens 1969) and western rangelands (Mikol et al. 1979); woodlands bordering old fields (Sutton 1960, Berger 1968) or reclaimed surface mines (Wray et al. 1982); and shrubs in sagebrush-grassland (Feist 1968, McGee 1976, Mikol et al. 1979), pinyon-juniper (O'Meara et al. 1981), or young jack-pine communities (L. H. Walkinshaw, unpubl.). Although the species nests in open, sparsely vegetated areas, elevated song perches seemingly are a territory requisite. We found

TABLE 1
RELATIONSHIPS BETWEEN HABITAT CHARACTERISTICS OF VESPER SPARROW TERRITORIES (\bar{x} AND RANGE) AND EITHER DATE OF ARRIVAL OF MALES OR PAIRING STATUS

Habitat characteristics	Date of arrival ^a			Pairing status				χ^2	P
	Week 1 (17) ^b	Week 2 (20)	Week 3 (5)	χ^2	P	Paired (38)	Not paired (4)		
Shrub groups (N)	5.2 (0-16)	3.1 (0-11)	1.2 (0-6)	8.17	0.02	4.1 (0-16)	0 (0)	8.16	<0.01
Washes (N)	0.6 (0-2)	0.8 (0-2)	0.6 (0-2)	0.46	0.79	0.7 (0-2)	0.3 (0-1)	1.32	0.25
Crop residue ^d (kg/ha)	2730 (560-5040)	2440 (560-6050)	1320 (560-2470)	4.57	0.10	2570 (560-6050)	1040 (560-2470)	4.53	0.03
Fencerow coverage (m ²)	330 (120-610)	410 (230-790)	410 (350-520)	4.39	0.11	380 (120-790)	360 (200-520)	<0.01	0.95
Nonproduc- tive areas ^c (m ²)	970 (0-3000)	1510 (0-5820)	1730 (0-4260)	1.48	0.48	1410 (0-5820)	400 (0-1030)	3.48	0.06

^a The week during which the first males arrived was designated Week 1.
^b Number of territories established during each week of arrival.
^c χ^2 determined using Kruskal-Wallis one-way ANOVA.
^d Amount on field with the most crop residue; on 40 of 42 territories the crop residue was corn.
^e Includes grassy waterways, washes, and weedy areas.

that elevated perches (i.e., fencerow shrubs) enhanced territory preference (Table 1) and evidently affected territory location; 50 of the 51 territories located were associated with a fencerow.

Territory selection by Vesper Sparrows on corn and soybean fields may be related to the abundance and availability of foods fed to nestlings. Adults feed on both plant and animal materials (Evans 1964), and weed seeds (likely an abundant food resource along fencerows) constitute a large portion of their diet throughout the breeding season in both cultivated (Rodenhouse and Best, unpubl.) and uncultivated (Evans 1964) habitats. Nestlings, however, are fed almost exclusively animal foods, primarily insects (Evans 1964; Rodenhouse and Best, unpubl.), and insects are scarce in crop fields early in the breeding season (Price 1976).

Insects associated with cropland are most abundant in nonproductive areas (e.g., fencerows) (Dambach 1948, Wunz 1952) that serve as sources from which many insects colonize crop fields (Price 1976). Additionally, insects are more numerous on fields with more crop residue (Dambach 1948, Edwards and Lofty 1969). Vesper Sparrows concentrated their foraging activity near nonproductive areas, particularly early in the breeding season (85% of all foraging observations recorded before 31 May were ≤ 10 m from a nonproductive area; Rodenhouse and Best, unpubl.). Therefore, to maximize abundance of insect foods on their territories, one would expect Vesper Sparrows to select areas with the most crop residue and the greatest number or coverage of nonproductive areas. We found significant or nearly significant, positive relationships between the two measures of territory preference and the amount of crop residue, coverage of nonproductive areas, and coverage of fencerows (Table 1). That preferred territories contained fencerows with a greater number of shrub groups (and plant species richness; see Methods) also may represent a response by Vesper Sparrows to food availability. Fencerows with high structural diversity and species richness support more abundant and diverse insect communities (Dambach 1948, Wunz 1952). Because various insect species reach peak densities at different times (Dambach 1948, Pimentel 1961, Mayse and Price 1978, Maher 1979), nestling foods may be most consistently available where insect communities are diverse.

The significant relationship between quantity of crop residue on a territory and pairing success also suggests that Vesper Sparrows may assess availability of nest-sites during territory selection. Early in the season, nests were always placed in a clump of crop residue, and the amount of crop residue may affect concealment of the nest and (or) of birds as they approach the nest.

Although we did not evaluate directly the relative advantages of selecting a territory containing only one crop type vs two (see Methods),

two observations suggest that Vesper Sparrows may have benefitted from including both corn and soybean fields within their territories. First, field operations on opposite sides of the fencerow were asynchronous, and each field was tilled approximately every 2 weeks through late June (Rodenhouse and Best 1983). Although nesting sparrows were disturbed regularly and nests often were destroyed, only part of the territory was tilled at one time, leaving the birds a refuge within their territories. Nesting success probably was not increased by including both corn and soybean fields, but the likelihood of territory desertion may have been decreased. Secondly, weedy areas under the corn canopy received heavy use as foraging sites in late June and early July (overall, adults foraged for food for their young most frequently in soybean fields [61% of a total of 1991 foraging observations], but during 27 June–10 July, corn fields were used more heavily [56% of 403 foraging observations]; Rodenhouse and Best, unpubl.). Corn fields were too densely vegetated by late June to be suitable for nesting, but soybean fields were not. Consequently, adjacent corn and soybean fields provided suitable nesting sites and preferred foraging sites in close proximity during a period of the breeding season when the probability of successful nesting was highest.

Site fidelity.—Of 26 male and 11 female Vesper Sparrows banded in 1980, six (four males and two females) returned in 1981, all to the same fencerows they had used in 1980; two males occupied the same territories. All returning birds nested successfully (fledged at least one young) in 1980. Our data, and that of others (George [1952] and F. C. Evans [unpubl.] reported a return rate of about 50%), demonstrate site fidelity in this species.

Before pioneer settlement in the Midwest, the open xeric or disturbed sites used by breeding Vesper Sparrows usually occurred as patches within expanses of a given habitat. Such patches were maintained by fire, erosion of loose soils by wind, or overgrazing by bison. Although a particular site may have been suitable Vesper Sparrow breeding habitat for only a few years because of vegetation development, advantages gained from site fidelity evidently were great enough to favor its evolution. Site fidelity may have aided breeding birds in finding and defending a territory, and returning to a familiar site may have enabled birds to better exploit nesting and food resources (Best 1977).

The advantages of returning to a site on corn and soybean fields, however, are not readily apparent. Breeding habitat is abundant, and radical changes frequently occur on territories between breeding seasons—fencerows or fencerow shrubs may be removed and residue amounts may vary greatly depending on the crop grown, tillage practices, and weather. Thus, the location of suitable foraging and nesting sites and song perches may

TABLE 2
HABITAT CHARACTERISTICS (\bar{x} AND RANGE) POTENTIALLY RELATED TO NESTING SUCCESS
ON VESPER SPARROW TERRITORIES

Habitat characteristics	Number of successful nests			χ^2^b	P
	0 (8) ^a	1 (16)	2 (11)		
Shrub groups (N)	6.3 (1-16)	3.6 (0-11)	3.3 (0-10)	4.29	0.11
Washes (N)	0.3 (0-1)	0.7 (0-2)	1.1 (0-2)	5.19	0.08
Crop residue ^c (kg/ha)	1760 (560-2910)	3070 (560-6050)	2390 (560-4480)	5.70	0.06
Fencerow coverage (m ²)	420 (310-730)	360 (120-620)	380 (190-790)	1.45	0.48
Nonproductive areas ^d (m ²)	1420 (0-3040)	1310 (0-5820)	1650 (100-4260)	0.99	0.61

^a Number of territories sampled.

^b χ^2 determined using Kruskal-Wallis one-way ANOVA.

^c Amount on field with the most crop residue; on 33 of 35 territories the crop residue was corn.

^d Includes grassy waterways, washes, and weedy areas.

be unpredictable from one year to the next; i.e., the old territory may be "unfamiliar." In fact, site fidelity on corn and soybean fields may result in some returning birds occupying suboptimal territories in preference to more favorable areas. These factors may, in part, explain our low rate of return in comparison to those of F. C. Evans (unpubl.) and George (1952).

Territory characteristics related to nesting success.—No territory characteristics were significantly related to nesting success, although the number of washes and amount of crop residue were nearly so ($P = 0.08$ and 0.06 , respectively; Table 2). A nest was considered successful if it fledged at least one young.

Six of eight (75%) territories without a successful nest did not contain a wash, and territories with two successful nests ($N = 11$) had a mean of 1.1 washes. During the last month of the breeding season, washes in soybean fields were open areas in otherwise densely vegetated crop fields and were used heavily as nesting sites. As expected, the number of successful nests was closely related to the duration of territory occupancy ($r_s = 0.48$, $N = 35$, $P < 0.01$). Territories with at least one successful nest were occupied longer (by about 2 weeks) than those without a successful nest.

Because most Vesper Sparrow production occurred late in the breeding season, it would have been adaptive for Vesper Sparrows to select territories with washes in soybean fields (sites suitable for nesting during that

period), but we found no relationship between territory preference and the number of washes on a territory (Table 1). The potential location of washes is predictable from field topography at the time of territory selection, but the actual formation of washes may not be. Wash formation depends on crop type, weather, and residue amount. Where corn and soybeans are rotated annually, topographical conditions favoring wash formation within the territory must be present on both sides of the fence-row for a wash to be formed in a soybean field each year (assuming soybeans on one side of the fencerow and corn on the other). The development of washes depends on heavy rains and erosion during the period when soybean plants are small. Without such rains, potential wash sites may become as densely vegetated as the rest of the crop field. Because tillage practices differ among farm operators, the amount of crop residue within a territory may differ from one year to the next. Large amounts of crop residue slow water movement off the field, reducing the likelihood of washes being formed, whereas a lesser amount of crop residue may not prevent wash formation.

Although the amount of crop residue was related significantly to nesting success, we were unable to further define this relationship. Other factors that potentially influence nesting success (i.e., nest concealment, predation, parasitism) were not correlated with the amount of crop residue.

Adaptiveness of breeding on cultivated areas.—Territory selection is adaptive if preferred habitat characteristics are highly correlated with fitness, as measured by productivity (Hilden 1965, Verner 1975, Partridge 1978). Our results show relatively little correspondence between habitat characteristics associated with territory preference and those related to breeding productivity. We attribute this primarily to the disruptive effects of agriculture. Only the amount of crop residue was related positively to both territory selection and nesting success.

In uncultivated habitats, factors affecting nesting success and territory preferences of Vesper Sparrows are largely predictable. Nest failure is caused primarily by predators (Sutton 1960; Berger 1968; Wray et al. 1982; L. H. Walkinshaw, unpubl.), and nest predator densities probably are greatest at ecotones (Gates and Gysel 1978). Nest-site vegetational characteristics also influence nest vulnerability to predators (Wray and Whitmore 1979). Habitat changes do occur, but a given site probably provides breeding requisites for several years before vegetation development or some other factor makes it unsuitable. Over time, Vesper Sparrows have evolved behavioral responses to nest predation and predictable habitat changes.

Agriculture introduces nest losses that are not selective (i.e., either all nests are destroyed [e.g., during seedbed preparation], or nests are de-

stroyed in an unpredictable pattern) and radical “instantaneous” habitat changes (e.g., 100% of the crop residue may be buried in a day). In addition, later in the season after field operations are concluded, rapid and uniform crop development in the corn and soybean monocultures over broad areas effectively shortens the breeding season for many Vesper Sparrow pairs (few nesting sites are available). Because nest destruction by tillage operations is nonselective, there is little probability that Vesper Sparrows could adapt to this cause of mortality. Some agricultural habitat manipulations are largely predictable, but current farming methods have been used for only about 35 years and are still changing (Phillips et al. 1980). Thus, although Vesper Sparrows were pre-adapted to use disturbed land created by intensive agriculture, they may not be able to adjust to transitory farming methods.

SUMMARY

Vesper Sparrows (*Poocetes gramineus*) commonly establish territories along fencerows in Iowa corn and soybean fields, where Vesper Sparrow productivity can be below replacement levels. We evaluated the adaptiveness of selecting territories on cultivated land by: (1) identifying habitat characteristics preferred by Vesper Sparrows (as measured by male arrival date and pairing success); and (2) determining the relationship between territory preference and nesting success. Males arrived earlier and had higher pairing success on territories where fencerows contained more shrub groups and where more crop residue was retained on the fields. The relationship of number of shrub groups and crop residue to various territory requisites (song perches, nestling food, and nest-sites) is discussed, as well as the implications of site fidelity in annually cultivated cropland. Nesting success was related to the number of washes and amount of crop residue on territories; both are unpredictable from year to year. Due primarily to the disruptive effects of agriculture, preferred habitat characteristics corresponded little with those related to productivity.

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