Studies in Avian Biology No. 19:149–159, 1999.

# EFFECTS OF FIRE AND HERBICIDE TREATMENT ON HABITAT SELECTION IN GRASSLAND BIRDS IN SOUTHERN MAINE

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*Abstract.* We studied habitat selection of grassland birds nesting on a 240-hectare grassland in southern Maine. The site was commercially managed for blueberry (*Vaccinium*) production, which involved prescribed burning and herbicide spraying. These management practices profoundly affected vegetation physiognomy and influenced patterns of habitat selection of nesting species. There were clear differences in the types of habitat birds selected; four species preferred sites with both tall and short graminoid cover, whereas three species preferred sparse cover. Despite general similarities in each of these two groups, habitat selection for each species was generally characterized by a unique suite of vegetation features rather than distinct values for any particular habitat parameter.

Territory densities of five breeding species were strongly influenced by management practices at this site. Species that preferred grass cover were adversely affected by herbicide spraying; these effects persisted for two to six years, depending on the number of herbicide applications and the species. In particular, Eastern Meadowlark (*Sturnella magna*) densities had not recovered six years after spraying. In unsprayed plots, densities of six species declined with time since fire; densities of one species, Field Sparrow (*Spizella pusilla*), increased with time since fire; and densities of Eastern Meadowlarks were unaffected by time since fire.

## LOS EFECTOS DEL FUEGO Y DEL TRATAMIENTO DE HERBICIDA EN LA SELECCIÓN DE HÁBITAT POR AVES DE PASTIZAL EN EL SUR DE MAINE

*Sinopsis.* Estudiamos la selección de hábitat por aves de pastizal en un prado en el sur de Maine. Se explotaba comercialmente el sitio para la producción del arándano (*Vaccinium*), que comprendía fuegos programados y fumigación con herbicidas. Estas prácticas de manejo afectaron profundamente la fisiognomía de la vegetación e influyeron en las normas de la selección de hábitat de las especies en anidaje. Hubo diferencias claras en los tipos de hábitat que las aves seleccionaron; cuatro especies prefirieron sitios con cobertura de hierbas alta y corta, mientras que tres especies prefirieron los de cobertura escasa. A pesar de las similitudes generales en cada uno de estos dos grupos, la selección de hábitat para cada especie se caracterizó por un conjunto único de rasgos vegetativos y no por valores distintos para algún parámetro de hábitat en particular. Las prácticas de manejo en este sitio influyeron en gran medida en las densidades de los territorios de cinco especies en reproducción. La fumigación de herbicidas afectó desfavorablemente las especies que prefirieron cobertura de hierbas; estos efectos persistieron por dos a seis años, según el número de aplicaciones de herbicidas y la especie. En particular, las densidades del Pradero Común (*Sturnella magna*) no se habían recuperado seis años después de las fumigaciones. En las parcelas sin fumigación, las densidades de seis especies disminuyeron con el tiempo después del fuego; las densidades de una especie, el Gorrión Llanaro (*Spizella pusilla*), aumentaron con el tiempo después del fuego; y las densidades del Pradero Común no experimentaron cambios con el tiempo después del fuego.

*Key Words:* burn; fire; grassland birds; habitat selection; herbicide spray; Maine.

Although extensive research has sought to determine what constitutes high-quality habitat for a wide variety of bird species (e.g., Cody 1985), various limitations to observed patterns of habitat occupancy have been described (Verner et al. 1986). These include inter- and intraspecific competition (Cody 1974; Diamond 1978; Rosenzweig 1981, 1985); population density (Fretwell and Lucas 1970; Zimmerman 1971; Wiens 1977, 1985; Karr and Freemark 1983); habitat area, shape, and isolation (Robbins 1979, Whitcomb et al. 1981, Robbins et al. 1989); site tenacity (Hildén 1965, Wiens and Rotenberry 1985); predation (Roseberry and Klimstra 1970, Slagsvold 1980); and anthropogenic factors (Robbins et al. 1986, Bollinger 1988).

In addition, resource abundance is often patchy, unpredictable, and not necessarily coincident with habitat structure (Rotenberry and Wiens 1980, Cody 1985). Thus, attraction to abundant, spatially variable resources may be more important than vegetation physiognomy when individuals select habitat. Finally, in some ecosystems there may be sufficient annual variation to make habitat selection more diffuse (Rotenberry and Wiens 1980); instead of a "single optimum expression of habitat selection, there may be an optimality plateau, within which various expressions of habitat selection may be adaptively equivalent" (Wiens 1985:244).

If vegetation and resources are highly variable in certain ecosystems and the linkage between a species and its habitat is imprecise, one would generally predict a broad "optimal plateau" for the species breeding in these ecosystems. Conversely, there may be a smaller "optimal plateau" for species breeding in more stable environments (Vickery et al. 1992a).

Controlled, manipulative studies of avian habitat use in grassland or shrubsteppe systems have often been limited by the size of the experimental units, which can make it difficult to predict population responses (Best 1972, Wiens and Rotenberry 1981, Morse 1985, Wiens et al. 1986, Petersen and Best 1987). In an effort to overcome this difficulty, we selected a broader spatial and temporal scale and established permanent plots, covering a total of 120 ha, which we followed for 8 yr. Commercial management of a native shrub, lowbush blueberry (*Vaccinium angustifolium*), for berry production in southern Maine used prescribed burning and herbicide spraying to reduce competing shrubs, graminoids, and forbs. These habitat manipulations profoundly affect the vegetation structure and composition (Yarborough and Bhowmik 1989) and thus provided the opportunity to conduct a partially controlled experiment on a scale that was large enough to elucidate some of the processes by which grassland birds occupy habitat.

## METHODS

### Study Area and Habitat Manipulation

The study site, a 240-ha sandplain grassland situated on a broad glacial-marine delta with thick sand deposits, supports a xeric native flora, notably graminoids (poverty grass [*Danthonia spicata*], little bluestem [*Schizachyrium scoparium*], and sedge [*Carex pensylvanica*]), shrubs (lowbush blueberry and chokeberry [*Aronia* spp.]), and forbs (northern blazing star [*Liatris scariosa* var. *novae-angliae*], whorled loosestrife [*Lysimachia quadrifolia*], and goldenrod [*Solidago* spp.]; see Vickery et al. 1992b). The site is located in Kennebunk, York County, Maine (43°23′ N, 70°37′ W) and was managed for commercial blueberry production until 1987. During the first phase of our study (1984–1986), the site was managed on a biennial rotation; approximately 50% was mowed and burned each year (= burn-year plots). Blueberries were harvested in the portion that was burned the previous year (= production-year plots). Beginning in 1984, the herbicide hexazinone (Velpar®) was used at the rate of approximately 4 kg per ha to increase blueberry production by reducing or eliminating competing shrubs, forbs, and graminoids (Yarborough and Bhowmik 1989). Herbicide was applied in April, in the same cycle as the burning operation. In the second phase of the study (1987–1991), there was no active management for berry production.

### Experimental Design

We examined avian habitat occupancy at two different spatial scales: the scale of individual territories (1–5 ha for all species except Upland Sandpiper [*Bartramia longicauda*]) and the scale at which the habitat manipulation occurred (plot = 6–24 ha). For territories, defined as the number of males singing and defending small areas for 4 wk or more, we assessed whether each species selected particular physiognomic features by measuring nine habitat parameters for each territory. We then compared these measurements with measurements taken in unoccupied quadrats in the grassland.

We then wanted to see if densities were affected by large-scale habitat manipulations. If populations of grassland birds breeding at this site did respond to changes in habitat, we would expect changes in territory density to be reflected at the larger scale. If birds were not selecting particular features of the habitat, however, we would expect no clear relationship between territory density and blueberry management practices. To determine which, if either, of these alternatives predominated, we estimated territory density in relation to these habitat management practices. We could make this distinction because each treatment changed in space and time during the first phase of this study (1984–1986). We distinguished between breeding territory (= breeding site) fidelity and philopatry (= return to general breeding area) and recognized that use of territory density to elucidate patterns of habitat occupancy should not be equated with habitat quality (Van Horne 1983, Vickery et al. 1992c).

We placed 10 permanent plots (6–24 ha), covering 120 ha and marked into quadrats with a 50-m-interval grid, on different parts of the site. Plots were sited to fall within a particular management unit and were 50 m or more from any management border. To examine the relationship between occupancy and habitat structure, territories for each species were spot-mapped (International Bird Census Committee 1970) using at least 8 replicate censuses on 10 plots for the first 3 yr (1984–1986) of the study. We used counter-singing of neighboring males and presence on frequently used song perches to estimate the perimeter of each territory for each species during this period. A quadrat was defined as being in a male's territory if 50% or more of that territory fell within a quadrat. For Upland Sandpipers, we simply delineated high-use areas for each pair. In the second part of the study (1987–1991), we used three to six censuses to determine the number of territories per species per plot. The reduced number of censuses during this part of the study did not allow us to accurately delineate the shape and size of individual territories, but it did allow us to calculate the number of territories for each species per plot, which in turn enabled us to examine each species' pattern of habitat occupancy in this changing environment.

We followed avian occupancy patterns in three primary treatments: plots that had received zero, one, or two herbicide applications. We then followed the status of these plots for 8 yr. We were thus able to observe bird occupancy in plots all the way from burn year (N = 17) to 8 yr postburn (N = 1; Table 1). A burn-year plot was defined as a site in its first growing season immediately following a management burn. Because a burn-year plot became a production-year plot the following summer, it was impossible to follow burn-year treatment effects for more than 1 yr. For example, a plot that was burned in early spring 1984, and thus considered a burn-year plot during the 1984 breeding season, was a first-year production-year plot in 1985.

TABLE 1. NUMBER OF MANAGEMENT UNITS ON PLOTS AT KENNEBUNK, MAINE, 1984–1991

| | Herbicide application | | |
|---|---|---|---|
| Years since burn | 0 spray | 1 spray | 2 sprays |
| 0 | 8 | 6 | 3 |
| 1 | 12 | 7 | 3 |
| 2 | 4 | 3 | 3 |
| 3 | 4 | 3 | 3 |
| 4 | 4 | 3 | 3 |
| 5 | 4 | 1 | 1 |
| 6 | 1 | 1 | 0 |
| 7 | 1 | 0 | 0 |
| 8 | 1 | 0 | 0 |

If this plot was not burned in April 1986, it became a second-year production-year plot in 1986. Because early-successional habitats experience frequent disturbance regimes, we defined control plots as first-year production-year plots that had never been sprayed with herbicide (N = 12).

Vegetation cover was estimated visually for every 50- × 50-m quadrat during the first 3 yr of intensive study (1984–1986) using a modification of the Braun-Blanquet réleve method (Mueller-Dombois and Ellenberg 1974; for detailed description, see Vickery et al. 1992a). Thereafter, from 1987 to 1991, we used the same method for 30–50% of the quadrats in a checkerboard fashion. All estimates were conducted in mid-July and August, once vegetation growth had stabilized. Graminoid, forb, and shrub cover were estimated in three strata: 0–2 cm, >2–20 cm (short cover), and >20–60 cm (tall cover). Bare ground, litter, and lichen and moss were estimated in the 0- to 2-cm stratum. Because lowbush blueberry was a dominant shrub and its rhizomatous, matlike growth habit differed from that of other low shrubs, it was estimated separately in the >2- to 20-cm stratum. Vegetative cover was estimated in the following units: < 3 stems per quadrat; < 0.1%; 0.1–1%; >1–5%; >5–15%; >15–25%; >25–50%; >50–75%; and > 75%. Only vegetation parameters with more than 5% mean cover were used for analysis. Cover percentages were transformed to midpoint percentages, and these percentages were arcsin transformed for all parametric analyses (Zar 1984).

Bird species breeding at the site included Upland Sandpiper, Horned Lark (*Eremophila alpestris*), Field Sparrow (*Spizella pusilla*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Bobolink (*Dolichonyx oryzivorus*), and Eastern Meadowlark (*Sturnella magna*). Field Sparrows were present only in the second phase of the study (1987–1991), once active management at the site had ceased and the height and abundance of shrubs had increased.

Because commercial operators had been managing this site for many years, we were unable to make this a randomized experiment. Although we did not seek to influence blueberry management for avian or habitat-related reasons, we did negotiate with the blueberry managers to ensure that each permanent plot fell completely within an operational area of the management practice. Because the site was physiographically homogeneous and the vegetation prior to herbicide application was similar, we do not think failure to meet the assumption of randomness vitiated our results.

### STATISTICAL ANALYSIS

We first used the detailed spot-map data (1984–1986) to determine which habitat variables were selected by each species (except Field Sparrow) breeding at this site. We used multivariate analysis of variance (ANOVA) to determine which vegetation parameters helped discriminate occupied habitat from unoccupied areas (Wilkinson 1990). Because species-habitat relationships were examined over a 3-yr period (1984–1986), and most treatments occurred in all 3 yr, we included the potential effect of annual variation (year effect) in this analysis (see Table 2 for sample sizes).

In a separate analysis, we used Spearman rank correlation to determine if specific habitat variables were associated with each species' density at the site. We used data from the entire study period (8 yr) for this analysis. To compensate for the possibility of increased Type I error for these eight analyses (one for each species), Bonferroni adjustment of significance level was set at P = 0.00625.

To examine habitat occupancy at the broader scale at which blueberry management occurred, we used repeated measure ANOVA to test for differences between territory density in plots that had never been sprayed with herbicide versus plots that had been sprayed once or twice (Wilkinson et al. 1996). Because sample sizes were notably uneven, especially 5–8 yr postburn (Table 1), this analysis was limited to the first 4 yr after the treatment, which was the period when differences, if they existed, were greatest. We then analyzed the importance of management effects for each year by contrasting specific management effects within the same year (Wilkinson 1990). We then used Spearman rank correlation to determine if territory densities for any of these species changed over time after burn/herbicide treatment. Because we were specifically interested in learning if Grasshopper and Savannah sparrow densities changed over time in unsprayed plots, we used repeated measures ANOVA to compare the first 4 yr postburn to the 5- to 8-yr postburn period.

## RESULTS

### EFFECTS OF BURNING AND HERBICIDE SPRAYING ON VEGETATION PHYSIOGNOMY

Burning and herbicide spraying had profound effects on grassland vegetation. Herbicide spraying reduced forb and short shrub cover for 3–4 yr (Fig. 1). Short shrub cover was greatly reduced on plots that were sprayed twice and began to recover only 4–6 yr postspray. Tall shrub cover was sharply reduced for 3 yr in plots that were sprayed twice but then increased more rapidly. This appeared to be an example of "vegetative release" common in herbicide applications in commercial forestry (Walstad and Kuch 1987). Herbicide application had a positive effect on blueberry cover for 3 yr. Thereafter, blueberry cover declined, probably as a result of

TABLE 2. VEGETATION MEASUREMENTS (PERCENT COVER; MEAN ± SE) FOR GRASSLAND BIRDS BREEDING AT KENNEBUNK, MAINE, 1984–1986

| | Species | | | | | |
|---|---|---|---|---|---|---|
| | Upland Sandpiper | | Horned Lark | | Vesper Sparrow | |
| Habitat parameters | Territory | Nonterritory | Territory | Nonterritory | Territory | Nonterritory |
| N | 405 | 233 | 186 | 449 | 434 | 204 |
| Bare ground | 23.5 (0.9) | 20.6 (0.7) | 32.8 (1.2)[a,b] | 27.3 (0.7) | 31.8 (0.8)[a,b] | 23.9 (1.0) |
| Litter | 29.2 (0.8)[a,b] | 33.6 (0.6) | 33.4 (1.1) | 31.4 (0.6) | 30.9 (0.6)[a,b] | 34.2 (1.0) |
| Graminoid (2–20 cm) | 22.1 (0.8) | 21.2 (0.6) | 20.2 (0.9)[a] | 24.1 (0.6) | 21.2 (0.6)[a,b] | 32.9 (0.5) |
| Graminoid (>20–60 cm) | 20.9 (1.0) | 23.5 (0.8) | 21.5 (1.2) | 22.4 (0.7) | 20.9 (0.7) | 22.4 (1.1) |
| Forb (2–20 cm) | 15.3 (0.9) | 15.1 (0.8) | 14.9 (1.1) | 15.3 (0.7) | 15.0 (0.7) | 15.5 (1.1) |
| Forb (>20–60 cm) | 25.7 (0.9) | 27.8 (0.8) | 25.1 (1.1) | 27.7 (0.7) | 25.8 (0.7) | 28.2 (1.0) |
| Blueberry | 27.2 (1.1)[a] | 31.9 (0.8) | 31.7 (1.0)[a,b] | 29.5 (0.8) | 30.1 (0.8) | 30.4 (1.1) |
| Shrub (2–20 cm) | 15.4 (1.1) | 17.0 (0.9) | 11.6 (1.2)[a,b] | 18.5 (0.8) | 16.6 (0.8)[a] | 20.5 (0.8) |
| Shrub (>20–60 cm) | 21.7 (1.0) | 23.6 (0.8) | 17.1 (1.1)[a] | 24.9 (0.7) | 20.9 (0.7) | 23.5 (1.1) |

[a] Significant difference ($P < 0.05$) between territory and nonterritory.
[b] Significant difference ($P < 0.05$) in year effect.

increased competition with other plants (Fig. 1). Increased nutrient availability and reduced competition after fire appeared to benefit short and tall forbs in unsprayed plots (Wright and Bailey 1982, Smith et al. 1988). Tall graminoids also responded favorably to fire, but this effect was also apparent in plots that were sprayed (Fig. 1). Tall graminoids consisted primarily of little bluestem, which was the only grass species not adversely affected by spraying.

The decline in short shrubs in unsprayed plots 4 yr postburn was probably a result of successional effects; after 3 yr these shrubs grew into the tall shrub category (Fig. 1).

## PATTERNS OF HABITAT SELECTION AT KENNEBUNK

Multivariate ANOVA revealed a major division in the way species occupied habitat at this site. Savannah and Grasshopper sparrows, Eastern Meadowlarks, and Bobolinks selected sites with greater amounts of both short and tall vegetation cover, particularly graminoid cover, whereas Upland Sandpipers, Horned Larks, and Vesper Sparrows preferred sites with generally sparse cover (Table 2). Savannah and Grasshopper sparrows, Bobolinks, and Eastern Meadowlarks all selected sites with significantly greater amounts of graminoid cover (Table 2). These four species also appeared to be more discriminating in their habitat requirements, or at least territories that were occupied by these species were described by a greater number of significant habitat parameters (Table 2). Savannah Sparrows selected areas with increased short graminoid, tall graminoid, and short forb cover and less litter, blueberry, short shrub, and tall shrub cover (Table 2). Grasshopper Sparrows chose habitat with increased short graminoid, tall forb, and short shrub cover and less litter and blueberry cover. Bobolinks chose sites with increased tall graminoid, tall forb, and blueberry cover and reduced tall shrub cover (Table 2). Eastern Meadowlarks selected sites with increased short graminoid and shrub cover, both short and tall forb cover, and decreased litter and blueberry cover.

Selection of habitat by Horned Larks and Vesper Sparrows was similar. Both species chose sites with increased bare ground and reduced short graminoid and shrub cover. Vesper Sparrows also selected sites with increased litter cover, whereas Horned Larks were positively associated with increased blueberry cover (Table 2). In general, Upland Sandpipers were not highly selective but did occupy areas with sparse litter and blueberry cover (Table 2).

All seven species showed considerable year-to-year variation in the habitats they occupied. Overall, there was significant annual variation in 22 of 33 of the habitat parameters that showed differences between used and unoccupied habitat. These between-year differences ranged between 2.8 and 10.9%.

Although each species selected certain sites that were associated with particular vegetative characteristics, Spearman rank analysis revealed few clear correlations between a species' density and any habitat parameter. None of the four species associated with grass cover showed correlations with any habitat parameters. Upland Sandpiper densities were positively associated with bare ground ($r_s = 0.457$, $P < 0.005$) and were negatively associated with tall forbs ($r_s = -0.531$, $P < 0.005$) and tall shrubs ($r_s = -0.734$, $P < 0.001$). Horned Lark densities were negatively correlated with short graminoid cover ($r_s = -0.532$, $P < 0.005$) and tall forb ($r_s = -0.466$, $P < 0.005$) and tall shrub cover ($r_s = -0.637$, $P < 0.005$). Field Sparrow density was

TABLE 2. EXTENDED.

| Species | | | | | | | |
|---|---|---|---|---|---|---|---|
| Savannah Sparrow | | Grasshopper Sparrow | | Bobolink | | Eastern Meadowlark | |
| Territory | Nonterritory | Territory | Nonterritory | Territory | Nonterritory | Territory | Nonterritory |
| 283 | 355 | 319 | 318 | 261 | 377 | 121 | 517 |
| 22.1 (1.0) | 23.2 (0.6) | 23.7 (0.9) | 22.4 (0.6) | 21.8 (0.8) | 23.5 (0.7) | 24.5 (1.2) | 22.4 (0.6) |
| 28.8 (0.8)[a,b] | 33.2 (0.6) | 28.6 (0.7)[a,b] | 33.7 (0.7) | 30.8 (0.6) | 32.8 (0.7) | 26.0 (0.8)[a,b] | 33.4 (0.6) |
| 29.3 (0.7)[a,b] | 20.9 (0.6) | 24.1 (0.8)[a,b] | 20.2 (0.6) | 21.8 (0.8) | 21.3 (0.6) | 27.1 (1.1)[a,b] | 20.2 (0.5) |
| 25.7 (1.0)[a] | 21.0 (0.8) | 22.6 (0.9) | 20.9 (0.8) | 23.4 (0.9)[a] | 20.2 (0.8) | 21.4 (1.0) | 21.5 (0.7) |
| 16.8 (1.1)[a,b] | 14.5 (0.7) | 14.6 (0.9) | 15.4 (0.8) | 15.8 (0.9) | 14.7 (0.8) | 18.3 (1.3)[a,b] | 14.4 (0.7) |
| 27.4 (1.0) | 27.1 (0.7) | 28.7 (0.9)[a,b] | 26.3 (0.7) | 29.5 (0.8)[a,b] | 26.3 (0.8) | 31.2 (1.1)[a,b] | 26.2 (0.7) |
| 26.7 (1.2)[a] | 31.6 (0.8) | 26.4 (1.0)[a] | 30.3 (0.8) | 32.6 (1.0)[a,b] | 29.2 (0.9) | 26.7 (1.4)[a] | 31.0 (0.7) |
| 18.2 (1.3)[a,b] | 22.1 (0.7) | 20.1 (1.2)[a,b] | 16.1 (0.9) | 17.1 (1.1) | 15.9 (0.9) | 20.2 (1.6)[a] | 15.5 (0.7) |
| 19.7 (1.1)[a] | 22.9 (0.7) | 20.6 (0.9) | 22.9 (0.8) | 24.1 (0.9)[a,b] | 16.9 (0.8) | 20.0 (1.2) | 22.4 (0.7) |

negatively associated with bare ground ($r_s$ = −0.551, $P < 0.005$), tall graminoids ($r_s$ = −0.467, $P < 0.005$), and tall forbs ($r_s = -0.512$, $P < 0.005$) and was positively associated with litter ($r_s = 0.603$, $P < 0.005$), short graminoids ($r_s = 0.663$, $P < 0.001$), and tall shrubs ($r_s$ = 0.519, $P < 0.005$).

### EFFECTS OF HABITAT MANIPULATION ON HABITAT SELECTION PATTERNS

Herbicide use reduced densities of Savannah and Grasshopper sparrows, Bobolinks, and Eastern Meadowlarks, whereas Horned Lark densities increased with herbicide use (Table 3). Herbicide use did not affect Upland Sandpiper or Vesper Sparrow densities (Table 3). In sprayed plots, Savannah Sparrow and Bobolink densities increased with time since burning and herbicide use, whereas Upland Sandpiper and Horned Lark densities declined with time since burning and herbicide use.

#### *Burn effects*

Prescribed burning reduced burn-year densities for Savannah and Grasshopper sparrows, Bobolinks, and Eastern Meadowlarks such that, except for Savannah Sparrows, there was no difference between unsprayed and sprayed (1 or 2 herbicide applications) treatments; all four of these species showed similar declines on treated plots compared to control plots (Fig. 2). This decline persisted for only 1 yr for unsprayed plots, however (Fig. 2). Bobolink densities were highest in treated and control plots 1–2 yr post-burn.

Densities of Upland Sandpipers, Horned Larks, and Vesper Sparrows were generally greatest in the burn year or first year thereafter (Fig. 3). Horned Larks only occurred on burn-year plots in unsprayed areas (Fig. 3).

#### *Herbicide effects*

In plots sprayed with herbicide, territory densities were sharply reduced for the four species that were positively associated with graminoid cover (Fig. 2). Eastern Meadowlark densities were consistently greater in unsprayed than in sprayed plots (Fig. 2). Densities of Savannah Sparrows, Grasshopper Sparrows, and Bobolinks were also negatively affected by spraying, at least initially (Fig. 2). Depending on the spe-

TABLE 3. REPEATED MEASURES ANALYSIS OF VARIANCE FOR EFFECTS OF HERBICIDE USE ON GRASSLAND BIRD TERRITORY DENSITY AT KENNEBUNK, MAINE, 1984–1991

| | Herbicide effect | | | |
|---|---|---|---|---|
| Species | df | F-ratio | P | Response to herbicide |
| Upland Sandpiper | 2, 6 | 1.579 | ns[a] | |
| Horned Lark | 2, 6 | 5.639 | 0.035 | + |
| Vesper Sparrow | 2, 6 | 0.563 | ns | |
| Savannah Sparrow | 2, 6 | 9.451 | 0.014 | − |
| Grasshopper Sparrow | 2, 6 | 10.809 | 0.003 | − |
| Bobolink | 2, 6 | 9.454 | 0.014 | − |
| Eastern Meadowlark | 2, 6 | 28.013 | 0.001 | − |

[a] Nonsignificant ($P > 0.05$).

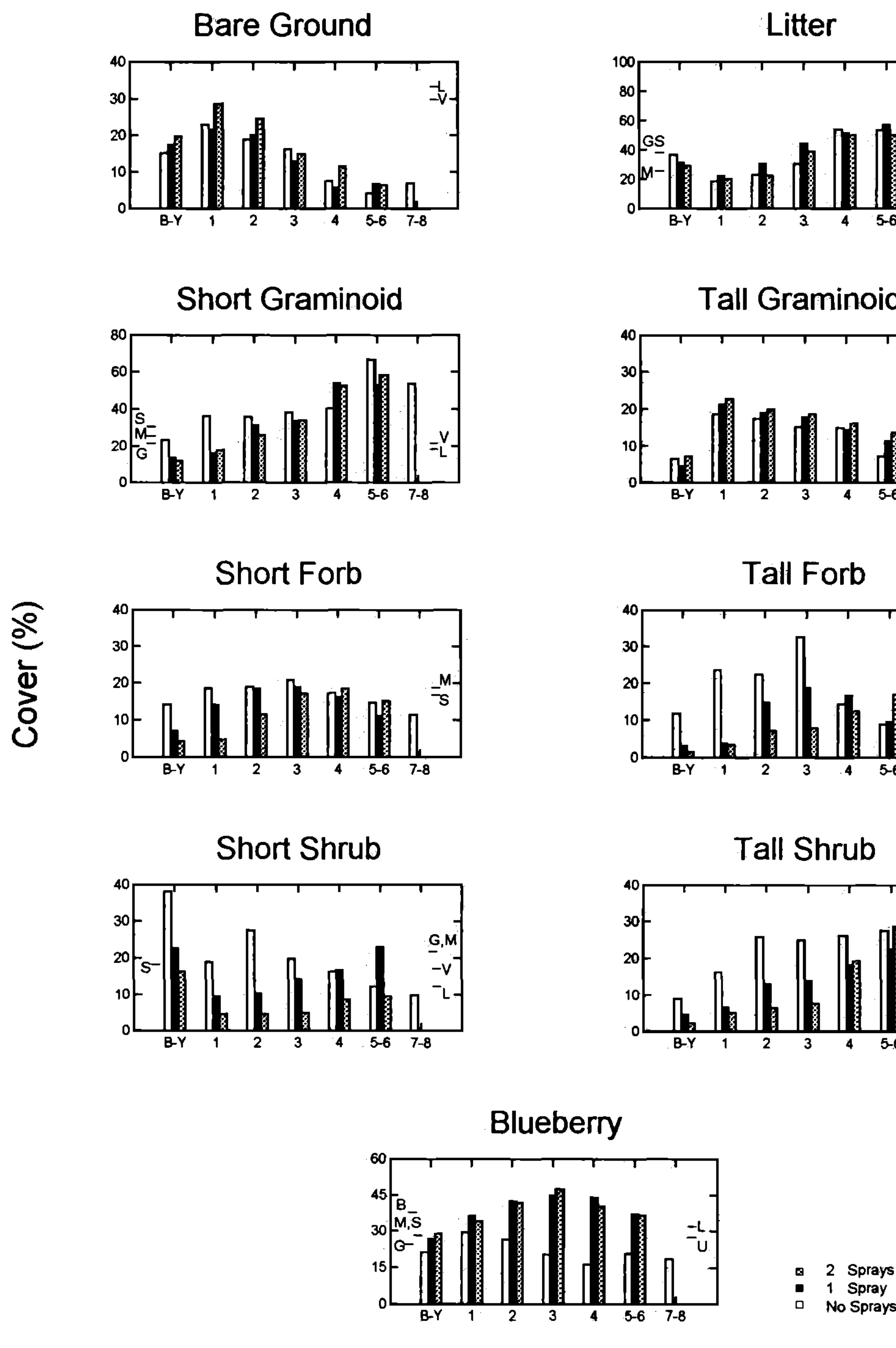


FIGURE 1. Mean cover values (percent) of nine habitat variables measured at Kennebunk, Maine, 1984–1991. Depending on the number of applications, herbicide spray reduced cover of short graminoid, short and tall forbs, and short and tall shrubs for 2–6 yr. Letters and bars represent mean cover values of significant habitat variables associated with four species that preferred extensive graminoid cover (Savannah Sparrow [S], Grasshopper Sparrow [G], Eastern Meadowlark [M], and Bobolink [B]) and three species that preferred sparser cover (Upland Sandpiper [U], Horned Lark [L], and Vesper Sparrow [V]).

cies and number of herbicide applications, these effects persisted for 2–6 yr (Fig. 2).

Eastern Meadowlark densities appeared to be negatively affected by herbicide-induced reductions in short graminoid and short and tall forb cover and increases in blueberry cover (Fig. 1). Increased litter and decreased tall forb cover in years 5–8 did not seem to affect meadowlark densities, even though the birds selected habitat with reduced litter and greater tall forb cover (Fig. 1). This suggests that this species was tolerant of changes in these two parameters but that herbicide-induced reduction in short graminoid cover, coupled with increased blueberry cover, effectively limited habitat use by meadowlarks.

Savannah and Grasshopper sparrows displayed a similar pattern. As a result of herbicide spray, especially two applications, densities were reduced to levels that were similar to, or lower than, those found in unsprayed burn-year plots (Fig. 2). In sprayed plots, it took Savannah Sparrow densities 2–3 yr to recover to control-plot levels (Fig. 2). It took Grasshopper Sparrow densities 5 yr to recover to control-plot levels after spraying (Fig. 2). The number of herbicide applications (1–2) did not seem to affect the duration of this recovery period, though Grasshopper Sparrow densities were initially greater in plots that had been sprayed only once (Fig. 2). For both species, herbicide-induced decreases in short graminoid and short shrub cover apparently limited the amount of available habitat for 2 yr postspray. An increase in litter coupled with decreases in tall forb and short shrub cover appeared to affect Grasshopper Sparrows more than 4 yr postspray.

Bobolink densities in plots that were sprayed twice did not recover to control-plot densities until 5 yr after treatment (Fig. 2). The near absence of tall forbs and tall shrubs in these plots appeared to have a negative effect on Bobolinks for 4 yr (Fig. 2). The steady decline in tall graminoids and tall forbs (years 4–8) appeared to have a negative effect on Bobolink densities in unsprayed plots (Fig. 2).

Horned Larks occurred only in plots that were burned or burned and sprayed, or in production-year plots that had been recently sprayed; they never occurred in unsprayed production-year

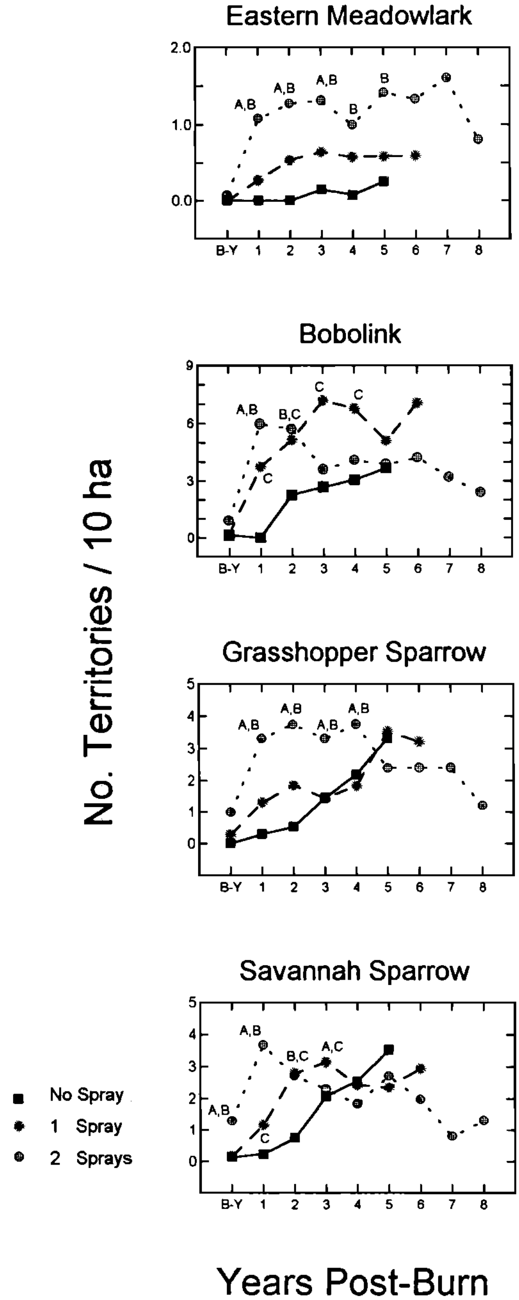


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FIGURE 2. Mean nesting densities of four species that were positively associated with graminoid cover were adversely affected by herbicide spray at Kennebunk, Maine, 1984–1991. Eastern Meadowlark densities had not recovered 6 yr after spraying. Depending on the number of herbicide applications, Grasshopper Sparrow, Savannah Sparrow, and Bobolink densities were reduced for 2–5 yr. "A" indicates difference ($P < 0.05$) between unsprayed and single-spray plots; "B" indicates difference between unsprayed plots and plots sprayed twice; "C" indicates difference between plots sprayed once versus twice. Irrespective of herbicide treatment (0, 1, or 2 applications), densities on burn-year plots differed ($P < 0.05$) from those on control plots (unsprayed 1 yr postburn). Standard errors (not shown) were less than 0.2 territories per 10 ha for all significant differences.

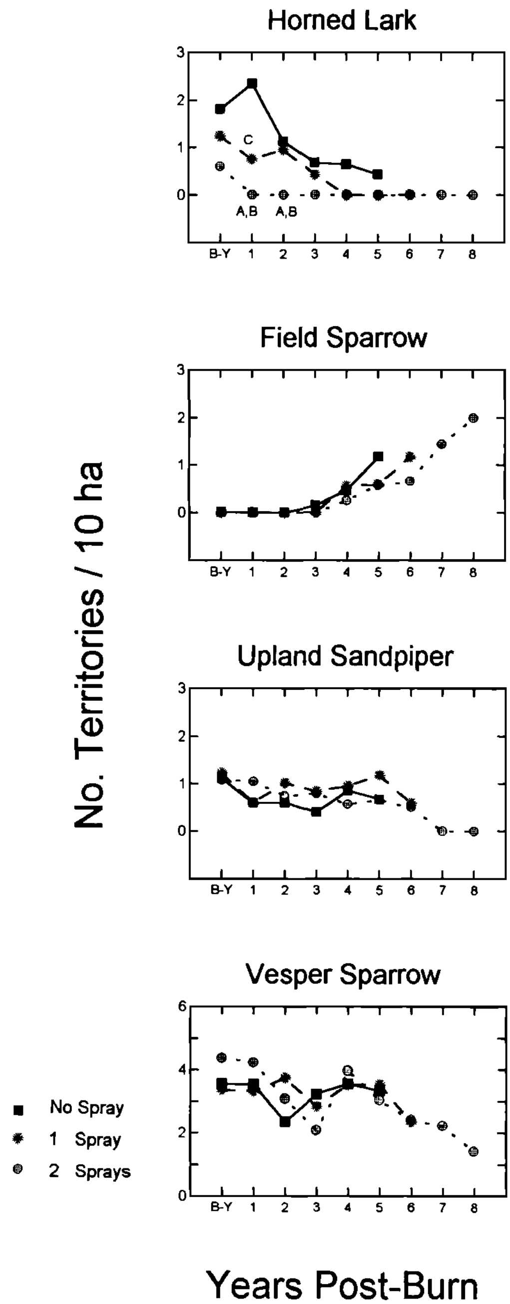


FIGURE 3. Mean nesting densities of four species that were not adversely affected by herbicide use at Kennebunk, Maine, 1984–1991. Burning and spraying benefited Horned Larks; they occurred only in plots that had been recently burned or burned and sprayed. Field Sparrows did not nest in recently burned or sprayed plots but started to occupy territories 3 yr postburn. "A" indicates difference ($P < 0.05$) between unsprayed and single-spray plots; "B" indicates difference between unsprayed plots and plots sprayed twice; ← "C" indicates difference between plots sprayed once versus twice. Standard errors (not shown) were less than 0.02 territories per 10 ha for all significant differences.

plots (Fig. 3). Not surprisingly, extensive bare ground and reduced graminoid cover provided preferred habitat for Horned Larks (Table 2). Upland Sandpipers and Vesper Sparrows were unaffected by spraying (Fig. 3).

*Successional effects*

Savannah and Grasshopper sparrow densities in unsprayed plots declined notably 4–5 yr postburn (Fig. 2). Grasshopper Sparrow densities in unsprayed plots were greater in the first 4 yr than in the latter 4 yr of the study ($F = 4.871$; $df = 1, 3$; $P = 0.031$); Savannah Sparrow densities displayed a similar pattern ($F = 3.289$; $df = 1, 3$; $P = 0.074$). Both species appeared to be adversely affected by the combination of increased litter and short graminoid cover and diminished short shrub cover 5–8 yr postfire (Fig. 1).

Upland Sandpiper, Horned Lark, and Vesper Sparrow densities generally declined as the time since the most recent fire increased (Fig. 3). In unsprayed areas, densities for all three species declined with time since the most recent burn (Upland Sandpiper: $r_s = 0.255$, $P = 0.003$; Horned Lark: $r_s = 0.230$, $P = 0.004$; Vesper Sparrow: $r_s = 0.193$, $P = 0.01$). It was likely that increased litter coupled with reductions in bare ground and increased tall shrub cover reduced habitat suitability for Upland Sandpipers (Fig. 1). The reduction in bare ground and increased litter cover and short graminoid cover appeared to reduce habitat suitability for Vesper Sparrows (Figs. 1 and 3).

Field Sparrows did not occur on recently burned or sprayed plots but occurred in low densities on plots 3 yr postburn; they increased steadily thereafter ($r_s = 0.243$, $P = 0.002$; Fig. 3). Densities were greater in sprayed plots 4–6 yr postspray than in unsprayed plots. This appeared to reflect the increased tall shrub cover, which this species prefers, in these plots (Evans 1978; Figs. 1 and 3).

## DISCUSSION

### HABITAT SELECTION BY GRASSLAND BIRDS

Grasshopper and Savannah sparrows, Bobolinks, and Eastern Meadowlarks all had similar cover values for significant, occupied habitat parameters. On average, these cover values were quite different from those for Upland Sandpipers, Horned Larks, and Vesper Sparrows (Table 2). Interestingly, the habitat for each species was defined by a unique set of significant vegetation parameters rather than any notably different measures of a shared habitat variable.

Although certain habitat parameters were closely associated with a species' occupancy of this site, there was significant between-year variation (3–10%) in cover values for more than half of these parameters. Wiens (1973) found similar variability for Grasshopper and Savannah sparrows in Wisconsin, suggesting flexibility in the habitat-selection process—an "optimality plateau" rather than a "single optimum expression of habitat selection" (Wiens 1985: 244).

The breadth and configuration of an "optimality plateau," however, may depend on the scale or resolution of the study (Wiens 1981). In our study, density was used to infer coarse-grain patterns of "acceptable" or "adequate" breeding habitat but not to make fine-grain distinctions of high-, medium-, or low-quality habitats (Van Horne 1983). Previous research at Kennebunk determined that there was less variability in vegetation cover values for highly successful territories compared with territories in general for three breeding Emberizid sparrows (Vickery et al. 1992a). Thus, a plateau that appears to be a flat tableland at a general level of resolution may in fact be more patchy and three-dimensional when examined at a finer scale.

### Effects of Burning and Herbicide Spraying

Use of prescribed burns and herbicides had profound effects on vegetation physiognomy at Kennebunk, and these changes in turn affected patterns of territory occupancy by grassland birds.

Although prescribed burning reduced densities of nesting Grasshopper and Savannah sparrows, Bobolinks, and Eastern Meadowlarks, this effect was temporary and persisted for only 1 yr. Thus, for most species, burning appeared to be a key disturbance factor that led to high densities of these species over the subsequent 2–4 yr. The general pattern at Kennebunk was similar to the response to fire by the same species in North Dakota; populations were depressed immediately after burning but had highest densities 2–5 yr postfire and then gradually declined (Cody 1985, Johnson 1997). High burn frequency was also essential in creating and maintaining breeding habitat for Horned Larks. This disturbance, however, precluded Field Sparrows from establishing territories at Kennebunk; the species was not present until the latter years of our study (1987–1991) when active management had ceased and successional effects were apparent.

Herbicide spraying had a more prolonged effect on reducing population densities for Grasshopper and Savannah sparrows, Bobolinks, and Eastern Meadowlarks. Except for Eastern Meadowlarks, which had not recovered in 6 yr, there was a general pattern of recovery that took 2–6 yr depending on the number of herbicide applications. These results follow the same general pattern found in forest systems sprayed with herbicide; avian declines are usually short-term (see Lautenschlager 1991 for review).

There is a notable difference, however, between the use of herbicides in forestry and in blueberry agriculture. In forest conifer-release programs, herbicides are usually applied only once (Lautenschlager 1991), whereas they are usually applied biennially on commercial lowbush blueberry fields. Furthermore, many blueberry fields have been sprayed four or more times in the past decade. More than 90% of Maine's commercial blueberry fields have been sprayed with herbicide (D. Yarborough, pers. comm.), whereas less than 10% of Maine's forests have been sprayed (R. A. Lautenschlager, pers. comm.). Persistent biennial use of herbicides would presumably lead to permanent depression of breeding populations for at least five of the bird species we examined. Such declines are likely to have profound effects on populations of these species, several of which are rare or regionally threatened grassland birds (Vickery 1992, Vickery et al. 1994).

## ACKNOWLEDGMENTS

The authors warmly acknowledge E. and O. Campbell and Coastal Blueberry, Inc., for permission to conduct this study on private land. Major financial support was provided to the primary author through Switzer Environmental Fellowships and Switzer Environmental Leadership Grants. Additional financial support was provided by The Nature Conservancy (Maine Chapter and Eastern Regional Office), Nongame Project of the Maine Department of Inland Fisheries and Wildlife, Maine Department of Agriculture (Board of Pesticides Control), F. I. Dupont, Inc., and Maine Audubon Society. The Massachusetts Audubon Society provided additional time and support for the project. W. Halteman provided assistance in data analysis. J. Gibbs, W. E. Glanz, J. R. Herkert, G. L. Jacobson, Jr., N. T. Wheelwright, A. S. White, J. L. Zimmerman, and an anonymous reviewer provided valuable suggestions. Critical logistical support was provided by D. Coonradt and B. Vickery. R. Denny and B. Vickery provided encouragement and support for which they are gratefully and warmly acknowledged.

## LITERATURE CITED

BEST, L. B. 1972. First-year effects of sagebrush control on two sparrows. Journal of Wildlife Management 36:534–544.

BOLLINGER, E. K. 1988. Breeding dispersion and reproductive success of Bobolinks in an agricultural landscape. Ph.D. dissertation. Cornell University, Ithaca, NY.

CODY, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, NJ.

CODY, M. L. 1985. Habitat selection in grassland and open-country birds. Pp. 191–226 *in* M. L. Cody (editor). Habitat selection in birds. Academic Press, Orlando, FL.

DIAMOND, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66: 322–331.

EVANS, E. W. 1978. Nesting responses of Field Sparrows (*Spizella pusilla*) to plant succession on a Michigan old field. Condor 80:34–40.

FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. Acta Biotheoretica 19:16–36.

HILDÉN, O. 1965. Habitat selection in birds. Annales Zoologica Fennica 2:53–75.

INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Notes 24:722–726.

JOHNSON, D. H. 1997. Effects of fire on bird populations in mixed-grass prairie. Pp. 181–206 *in* F. L. Knopf and F. B. Samson (editors). Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York, NY.

KARR, J. R., AND K. E. FREEMARK. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. Ecology 64:1481–1494.

LAUTENSCHLAGER, R. A. 1991. Response of wildlife in northern ecosystems to conifer release with herbicides. Maine Agricultural Experimental Station Miscellaneous Report 362, Orono, ME.

MORSE, D. H. 1985. Habitat selection in North American parulid warblers. Pp. 131–157 *in* M. L. Cody (editor). Habitat selection in birds. Academic Press, Orlando, FL.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, NY.

PETERSEN, K. L., AND L. B. BEST. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildlife Society Bulletin 15:317–329.

ROBBINS, C. S. 1979. Effect of forest fragmentation on bird populations. Pp. 198–212 *in* R. M. DeGraaf and K. E. Evans (editors). Management of north central and northeastern forests for nongame birds. USDA Forest Service Gen. Tech. Rep. NC-51. USDA Forest Service North Central Forest Experimental Station, St. Paul, MN.

ROBBINS, C. S., D. BYSTRACK, AND P. H. GEISSLER. 1986. The Breeding Bird Survey: its first fifteen years, 1965–1979. U.S. Fish and Wildlife Service Resource Publication 157.

ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103:1–34.

ROSEBERRY, J. L., AND W. D. KLIMSTRA. 1970. The nesting ecology and reproductive performance of the Eastern Meadowlark. Wilson Bulletin 82:243–267.

ROSENZWEIG, M. L. 1981. A theory of habitat selection. Ecology 62:327–335.

ROSENZWEIG, M. L. 1985. Some theoretical aspects of habitat selection. Pp. 517–540 *in* M. L. Cody (editor). Habitat selection in birds. Academic Press, Orlando, FL.

ROTENBERRY, J. T., AND J. A. WIENS. 1980. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia 47:1–9.

SLAGSVOLD, T. 1980. Habitat selection in birds: on the presence of other bird species with special regard to *Turdus pilaris*. Journal of Animal Ecology 49:523–536.

SMITH, C. T., J. W. HORNBECK, AND M. L. MCCORMACK, JR. 1988. Changes in nutrient cycling following aerial application of triclopyr to release spruce-fir. Proceedings of the Northeastern Weed Scientific Society 42:94–99.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

VERNER, J., M. L. MORRISON, AND C. J. RALPH (EDITORS). 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

VICKERY, P. D. 1992. A regional analysis of endangered, threatened, and special-concern birds in the northeastern United States. Transactions of the Northeast Section of the Wildlife Society 48:1–10.

VICKERY, P. D., M. L. HUNTER, JR., AND S. M. MELVIN. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology 8: 1087–1097.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992a. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. Auk 109:697–705.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992b. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992c. Is density an indicator of breeding success? Auk 109:706–710.

WALSTAD, J. D., AND P. J. KUCH. 1987. Forest vegetation management for conifer production. John Wiley and Sons, New York, NY.

WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125–205 *in* R. L. Burgess and D. M. Sharpe (editors). Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY.

WIENS, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah sparrows. Ecology 54: 877–884.

WIENS, J. A. 1977. On competition and variable environments. American Scientist 65:590–597.

WIENS, J. A. 1981. Scale problems in avian censusing. Studies in Avian Biology 6:513–521.

WIENS, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds. Pp. 227–251 *in* M. L.

Cody (editor). Habitat selection in birds. Academic Press, New York, NY.

WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 5:21–41.

WIENS, J. A., AND J. T. ROTENBERRY. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. Journal of Applied Ecology 22:655–668.

WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1986. A lesson in the limitations of field experiments: shrubsteppe birds and habitat alteration. Ecology 67:365–376.

WILKINSON, L. 1990. Systat: the system for statistics. Systat, Inc., Evanston, IL.

WILKINSON, L., G. BLANK, AND C. GRUBER. 1996. Desktop data analysis with Systat. Prentice-Hall, Englewood Cliffs, NJ.

WRIGHT, H. A., AND A. W. BAILEY. 1982. Fire ecology: United States and southern Canada. John Wiley and Sons, New York, NY.

YARBOROUGH, D. E., AND P. C. BHOWMIK. 1989. Effect of hexazinone on weed populations and on lowbush blueberries in Maine. Acta Horticulturae 241:344–349.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

ZIMMERMAN, J. L. 1971. The territory and its density dependent effect on *Spiza americana.* Auk 88:591–612.