

- HERRERA, C. M. 1973. Régimen alimenticio de *Tyto alba* en España sudoccidental. *Ardeola* 19: 359-394.
- JOHNSON, A. W. 1965. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Buenos Aires, Platt Establecimientos Gráficos.
- MESERVE, P. L. 1977. Food habits of a White-tailed Kite population in central Chile. *Condor* 79: 263-265.
- MORTON, S. R. 1975. The diet of the Barn Owl *Tyto alba* in southern Victoria. *Emu* 75: 31-34.
- RAPPORT, D. J., & J. E. TURNER. 1970. Determination of predator food preferences. *J. Theor. Biol.* 26: 365-372.
- SCHAMBERGER, M. L., & G. W. FULK. 1974. Mamíferos del Parque Nacional Fray Jorge. *Idesia* 3: 167-179.
- SOKAL, R. R., & F. J. ROHLF. 1969. *Biometry*. San Francisco, California, W. H. Freeman.
- THROWER, N. J. W., & D. E. BRADBURY (Eds.). 1977. Chile-California scrub atlas. Stroudsburg, Pennsylvania, Dowden, Hutchinson, and Ross.

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Short-term Change in Vegetation Structure and its Effect on Grasshopper Sparrows in West Virginia

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Numerous studies have documented the changes in bird communities that follow plant succession (e.g. Johnston and Odum 1956, Shugart and James 1973). Most studies of this kind have looked at a variety of plant communities in various seral stages and then measured their accompanying avifaunas. However, the effect of short-term change in bird populations caused by vegetation change is not widely documented. Webb et al. (1977) followed the plants and birds of 4 logged and 1 control area for 10 yr and found that over the long term only a few species were adversely affected by the logging operations and that, in fact, many were benefitted. They did not attempt to correlate the change to specific habitat variables, however.

In vegetational communities with a relatively simple structure, short-term changes in floristic composition may be pronounced. This is especially true in newly created sites such as reclaimed surface mines. After initial reclamation, successional change may be rapid (Staples 1977), and within a few years the site may have changed significantly in plant species presence, density, and diversity. If bird species do in fact select habitats based upon a predetermined search image (i.e. "niche gestalt," James 1971), and if this search image is based on a complex series of vegetation structure variables, then changes in one or more of these variables may bring about a change in avian presence and density.

The Grasshopper Sparrow (see Table 2 for scientific names) is a common breeding bird in suitable short- to middle-height grassland throughout much of temperate North America (Smith 1963). Owing to its recent population increase as a result of using reclaimed surface mines (Whitmore and Hall 1978), this species is ideal for studying vegetation-caused changes in avian density. Here I document changes in the vegetation structure of reclaimed surface mines in northern West Virginia and their effects on Grasshopper Sparrow population densities.

Three reclaimed surface mines in Preston County, West Virginia, were studied during the spring and summer of 1976-78. The mines were located at 39°37'N, 79°40'W; ranged in size from 9.1 ha to 41.5 ha; and were 3-6 yr old. Dominant species planted on the sites included tall fescue (*Festuca arundinacea*), birdsfoot trefoil (*Lotus corniculatus*), red top (*Agrostis alba*), timothy (*Phleum pratense*), and oats (*Avena sativa*). Dominant pioneers included orchard grass (*Dactylis glomerata*), poverty grass (*Danthonia spicata*), velvet grass (*Holcus lanatus*), rye grass (*Lolium perenne*), and black locust (*Robinia pseudo-acacia*) (Staples 1977, Whitmore and Hall 1978). Bird territories were delineated by using the flush technique described for grassland birds by Wiens (1969). Once territory locations were outlined, they were drawn on scale maps and absolute densities were calculated for each mine.

The center of each territory served as the starting point for two 25-m-long line transects, the directions of which were determined by a random numbers table and a compass. Six vegetation structure variables measured along these transects were selected for detailed study (Table 1).

TABLE 1. Comparison of the vegetation structure based on six key variables measured on three reclaimed surface mine grasslands in northern West Virginia in 1976 and 1978. Asterisks note significant difference between the 2 yr (* = $P < 0.05$; ** = $P < 0.01$). Values are means; SD in parentheses; n = number of sample plots.

Variable	Great Mine		Laurel Run		Fur-Fin-Feather	
	1976 $n = 20$	1978 $n = 77$	1976 $n = 18$	1978 $n = 14$	1976 $n = 13$	1978 $n = 8$
Mean effective height of vegetation (cm)	33.24 (8.13)	22.43** (14.80)	31.26 (11.99)	35.17 (9.15)	36.41 (10.30)	36.00 (13.50)
Litter depth (cm)	2.35 (2.08)	1.80 (1.53)	3.82 (2.02)	1.99 (0.65)	3.05 (2.21)	3.08 (1.00)
Forb cover (%)	27.55 (7.01)	25.43 (17.01)	26.92 (14.91)	19.39 (16.87)	26.29 (17.72)	32.38 (16.01)
Litter cover (%)	70.07 (19.75)	67.40 (21.55)	60.38 (20.20)	96.23** (3.87)	67.09 (30.31)	87.80* (5.97)
Bare ground (%)	24.22 (15.21)	30.42* (20.88)	18.59 (17.70)	3.72** (3.17)	41.92 (35.15)	10.59* (5.66)
Grass cover (%)	42.84 (12.13)	21.08** (9.37)	30.70 (20.18)	51.55** (17.71)	39.34 (23.83)	21.48* (3.91)

The percent cover variables were measured by estimating, for example, the amount of litter that the transects covered. Grass cover was measured directly at the ground to avoid the effect of the grass bending or matting. Litter depth was measured directly at 10 regular points along the transect, while mean effective height was the average height of the vegetation (grass, forb, or shrub) at each of those 10 points. The vegetation of each mine was characterized by selecting enough nonoverlapping territories to cover the mine and then tabulating their variable scores. For comparisons between years, Student t -tests were used for litter depth and mean effective height, while Wilcoxon's two-sample test was used on the percent data (Steele and Torrie 1960).

All three mines showed directional trends in avian densities (Table 2). For supportive purposes, data for all bird species breeding on these sites are presented. The Great Mine increased four-fold in breeding pairs, while the other two mines, Laurel Run and Fur-Fin-Feather, both decreased to approximately one-third of their original densities. On the Great Mine, all species save the Eastern Meadowlark increased greatly, with the Grasshopper Sparrow reaching the highest density at 79.5 pairs/100 ha. On the Fur-Fin-Feather site, three species dropped out and the remaining two, Grasshopper Sparrow and Vesper Sparrow, decreased in density. Over the 3-yr period, Laurel Run had 1 species drop out, 1 "in and out" species, 2 invaders, and 2 that remained on the site but decreased in density.

On the Great Mine, three habitat-structure variables had significant changes during the 3-yr study (Table 1). Mean effective height of the vegetation decreased ($P < 0.01$), percent bare-ground cover increased ($P < 0.05$), and percent grass cover decreased ($P < 0.01$). This corresponds to a general opening up of the vegetation. On Laurel Run, percent litter cover increased by 36% ($P < 0.01$), percent bare-ground cover decreased ($P < 0.01$), and percent grass cover increased ($P < 0.01$), while the other variables did not change significantly. The Fur-Fin-Feather site was similar to Laurel Run in that there was a large increase in percent litter cover ($P < 0.05$) and a decrease in percent bare-ground cover ($P < 0.05$), but percent grass cover decreased significantly ($P < 0.05$). This difference can be explained by the fact that on Laurel Run the bare-ground cover was decreasing due to an increase in grass density (growth) and a concomitant increase in its litter, while on Fur-Fin-Feather the bare-ground cover decreased because the grass was dying out with subsequent litter cover increasing. Moreover, the latter site was also the oldest mine, having been reclaimed in 1970 before passage of more stringent reclamation laws. Its fate is typical of many older mines in that acid eventually works to the surface and begins to kill the vegetation. Once the amount of living grass decreases to the point that it can no longer hold the litter, then bare-ground cover should increase and litter cover should decrease. Therefore, two different scenarios can explain a general decrease in open areas on these two reclaimed surface mines. Both result in a decrease in bare-ground cover and an increase in litter cover.

Apparently, the decrease in avian densities in two sites and the increase on the Great Mine was due to changes in the amount of open areas. These relationships are especially apparent for the Grasshopper Sparrow. From 1976 to 1978, 104 territories were studied (Table 3). Every territory encountered was

TABLE 2. Density (pairs/100 ha) of passerine birds breeding on reclaimed surface mines in northern West Virginia, 1976-1978. Year of reclamation and size are in parentheses.

Species	Great Mine (1974, 41.5 ha)			Fur-Fin-Feather (1970, 16.5 ha)			Laurel Run (1973, 9.1 ha)		
	1976	1977	1978	1976	1977	1978	1976	1977	1978
Horned Lark (<i>Eremophila alpestris</i>)	4.8	7.2	19.3						
Eastern Meadowlark (<i>Sturnella magna</i>)	4.8	2.4	2.4	18.2					
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)			9.6	18.2	6.1				11.0
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	19.3	21.7	57.8	6.1	12.1		54.9	22.0	22.0
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	21.7	28.9	79.5	60.6	48.5	36.4	120.9	33.0	22.0
Henslow's Sparrow (<i>Ammodramus henslowii</i>)								11.0	
Vesper Sparrow (<i>Pooecetes gramineus</i>)	4.8	16.9	50.6	18.2	18.2	12.1	22.0	11.0	
Field Sparrow (<i>Spizella pusilla</i>)									11.0
Total	55.4	77.1	219.2	121.3	84.9	48.5	197.8	77.0	66.0

analyzed quantitatively and the values for percent litter cover, percent bare ground, and percent grass cover were normally distributed about the mean (Kolmogrov-Smirnov-Lilliefors Test, $P < 0.05$; Conover 1971). Therefore, I feel that the means presented in Table 3 accurately reflect the optimum values of these variables for Grasshopper Sparrows on reclaimed surface mines in West Virginia. To make this statement, I must assume that interspecific competition for habitat has not occurred between the sparrows on these sites and that the distribution of Grasshopper Sparrows on these variable gradients is not affected by the presence of the other species. The habitat available to Grasshopper Sparrows on the Laurel Run site in 1976 did not differ significantly from the optimum for any of these variables, and hence the high density of 120.9 breeding pairs/100 ha is to be expected. By 1978, however, the site had significantly higher litter cover ($P < 0.01$), lower bare-ground cover ($P < 0.01$), and higher grass cover ($P < 0.01$) than the optimum required by Grasshopper Sparrows. Interestingly, the habitats actually selected on Laurel Run did not differ significantly from the optimum in any of the three variables (Table 3), indicating that the required habitat was present on the site but was not representative of the whole area. This means that the Grasshopper Sparrows did occupy territories on Laurel Run that were closer to their optimum in structure but that those habitat patches were not as available as during other years, hence the drop in density. This story holds true for Fur-Fin-Feather as well. As with Laurel Run, the Grasshopper Sparrows on Fur-Fin-Feather dropped in density. In 1976 the overall habitat available to Grasshopper Sparrows had significantly higher bare-ground cover than optimum ($P < 0.01$), significantly greater grass cover ($P < 0.05$), and significantly lower litter cover ($P < 0.05$). These differences could account for the relatively low density, 60.6 pairs/100 ha, in 1976. By 1978 the density had dropped to 36.4 pairs/100 ha, when bare-ground cover and litter cover were significantly lower ($P < 0.01$) and higher ($P < 0.01$), respectively, than the optimum, and grass cover did not differ significantly from the optimum. As before, the sites actually selected did not differ from the optimum, showing that the birds

TABLE 3. Optimum and actually selected means (SD in parentheses) of three variables measured on the territories of Grasshopper Sparrows. The optimum values are obtained from 104 breeding territories sampled from 1976 to 1978.

	Optimum	Actually selected on Laurel Run and Fur- Fin-Feather in 1976	Actually selected on Great Mine in 1978
Litter cover (%)	73.13 (21.72)	75.56 (21.32)	70.91 (16.43)
Bare ground (%)	24.09 (20.41)	24.24 (24.83)	23.18 (12.76)
Grass cover (%)	27.78 (20.55)	21.58 (11.27)	34.44 (18.01)

selected the same habitats from year to year, while the number of available patches of suitable habitat had decreased.

On the Great Mine, territorial Grasshopper Sparrow pairs increased from 21.7 to 79.5 pairs/100 ha. In 1976 this mine had significantly higher grass cover ($P < 0.01$) than the optimum, while the other two variables did not differ. In 1978 none of the variables was significantly different from the optimum. Moreover, none of the 1978 Great Mine variables differed significantly from the 1976 Laurel Run variables. Thus the two locations of highest Grasshopper Sparrow density had nearly identical habitats.

The data for Savannah and Vesper sparrows parallel that for the Grasshopper Sparrow, while the data for Eastern Meadowlark show the opposite. As vegetation density increased and bare areas decreased, Eastern Meadowlarks increased. This shows that species with different species-specific habitat requirements may react differently to changes in habitat structure.

Before concluding that changes in vegetation structure are responsible for these density changes, other contributing factors must be considered. While yearly fluctuations in passerine population densities are widely documented, it is unlikely that this can explain the observed results of this study. Because these study areas are in close proximity to each other (~2 km), one would expect yearly changes in avian density to follow similar patterns, not opposite as in this case. Likewise, climatic factors, differential winter survival, or man-caused effects probably are not important to this study in that their effects should be the same on each site. Differential predation rates may be important on these sites. While no obvious differences have been recorded in predator numbers and types on the mines (Wray et al. 1978), it is possible that each mine may have been subjected to a different predatory regime.

All of this seems to point to a simple conclusion, that grassland birds select a certain preferred habitat patch out of the spectrum of available types, and that when the number or availability of such patches decreases, so does the number of birds. The choice of the patches for these species appears to be directed by overall density of the ground cover. There must be enough open or bare ground to allow the birds freedom to move about, but enough cover to provide adequate nesting sites. The natural history of most of these species dictates that area be available on the ground for foraging, courtship, nest selection, etc. Apparently, these areas must be free of litter and dense living vegetation. It appears that the territories of Grasshopper Sparrows, for example, must have at least 24% bare ground.

This study looks only at rough correlations of bird density and presence with a few vegetation structure variables. From the results, one may only infer that these variables play a role in habitat selection. Manipulation experiments, such as fall burning to remove excess litter and create open areas, or carefully controlled laboratory experiments with a choice of rigidly defined habitat types offered to birds, might better document which cues are being used in the selection process. Even such controlled experiments, however, will offer insight only into the proximate factors, those features that evoke a settling response (Orians 1971) and would add little to our knowledge of the ultimate factors, those affecting the fitness of the birds. For example, the vegetation structure, a proximate factor, may dictate the thermal suitability of the microhabitat or the available food present, both of which may act as ultimate factors (Hildén 1965). In other words, detailed study of the vegetation structure may have predictive value in determining which species will inhabit a site, but cannot determine why the species is or is not there.

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LITERATURE CITED

- CONOVER, W. J. 1971. Practical nonparametric statistics. New York, John Wiley and Sons, Inc.
- HILDÉN, O. 1965. Habitat selection in birds. *Ann. Zool. Fennica* 2: 54-75.
- JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bull.* 83: 215-236.
- JOHNSTON, D. W., & E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology* 37: 50-62.
- ORIAN, G. H. 1971. Ecological aspects of behavior. Pp. 513-546 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King Eds.), New York, Academic Press.
- SHUGART, H. H., & D. JAMES. 1973. Ecological succession of breeding bird populations in northwestern Arkansas. *Auk* 90: 62-77.
- SMITH, R. L. 1963. Some ecological notes on the Grasshopper Sparrow. *Wilson Bull.* 75: 159-165.

- STAPLES, J. 1977. Vegetational succession, soil characteristics, and primary production and energetics on surface mines. Unpublished M.S. thesis. Morgantown, West Virginia, West Virginia Univ.
- STEELE, R. G., & J. H. TORRIE. 1960. Principles and procedures of statistics. New York, McGraw-Hill.
- WEBB, W. L., D. F. BEHREND, & B. SAISON. 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildl. Monogr.* 55: 6-35.
- WHITMORE, R. C., & G. A. HALL. 1978. The response of passerine species to a new resource: reclaimed surface mines in West Virginia. *Amer. Birds* 32: 6-9.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* No. 8.
- WRAY, T., P. B. WACKENHUT, & R. C. WHITMORE. 1978. The reproductive biology of passerine birds breeding on reclaimed surface mines in northern West Virginia. Pp. 333-334 in *Proc. Conf. on Surface Mining and Fish/Wildlife Needs in the Eastern United States*, Morgantown, West Virginia, December 3-6, 1978. U.S.D.I. FWS/OBS-78/81.

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The Incubation Temperature of Leach's Storm-Petrel

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The Procellariiformes are pelagic, surface-feeding seabirds, all of which nest on islands, lay a single egg, and have prolonged development periods compared with other birds. Leach's Storm-Petrel (*Oceanodroma leucorhoa*), one of the smallest species in the order, lays a 10-g egg, has an incubation period (laying to hatching) of 40-42 days (Palmer 1962), which is twice as long as that of other birds having eggs of similar size (Rahn and Ar 1974, Drent 1975), and has a nestling period (hatching to flight) of 63-70 days (Palmer 1962, Wilbur 1969). The single-egg clutch and slow postnatal growth have been related to the food supply, which is distant, patchy, and apparently unpredictable, especially when storms prevent feeding (Lack 1966, 1968). But because the embryo is provided with all its food at the beginning of incubation, food limitation cannot directly cause the prolonged period of embryonic development. To explain the long incubation periods of procellariiform birds, Lack (1968) suggested that rates of embryonic and postembryonic growth have a common genetic basis, and therefore selection of slow postnatal growth to reduce energy requirements would necessarily prolong the incubation period. This hypothesis may be rejected, however, because the growth rates of Procellariiforms do not differ greatly from those of species in other orders (e.g. Galliformes, Charadriiformes) having much shorter incubation periods (Ricklefs 1973).

Warham (1971) contended that the long incubation periods of Procellariiformes derive from low incubation temperatures, but Drent (1975) could find no evidence to support this view. According to Drent, the reported incubation temperatures of 25 species of birds varied between 34 and 38°C, with those of most species being between 35 and 36°C. Incubation temperatures of four Procellariiformes varied between 34.8 and 36.6°C, the lowest value being Drent's unpublished measurement for Leach's Storm-Petrel. Drent dismissed many extremely low values included in Warham's summary as being caused by faulty technique and by the failure to allow sufficient time for full equilibration of egg temperature after disturbance. Here we report two independent measurements of the incubation temperature of Leach's Storm-Petrel of about 32 and 33°C, the lowest yet recorded by direct, reliable measurement for any species (cf. Burger and Williams 1979).

Studies were conducted by RER on Baccalieu Island, Newfoundland, between 21 and 24 July 1978, and by HR on Kent Island, Grand Manan, New Brunswick, during the last week of June and first two weeks of July 1978. On Baccalieu Island, nest burrows were dug into steep, west-facing, grassy slopes. Temperatures were obtained using a Yellow Springs Instruments thermistor thermometer. Body temperatures were measured by extending the thermistor probe into the proventriculus of adults immediately after they were removed from the nest. Brood patch temperatures were obtained from adults removed from their nests. The birds were provided artificial nests, with a petrel egg to which a thermistor had been taped, in a box at an ambient temperature (T_a) of 15°C. The birds readily incubated the eggs. The