The Auk 109(4):706–710, 1992

IS DENSITY AN INDICATOR OF BREEDING SUCCESS?

PETER D. VICKERY,[1,3] MALCOLM L. HUNTER, JR.,[1] AND JEFFREY V. WELLS[2,4]

[1]*Wildlife Department, University of Maine, Orono, Maine 04469, USA; and*
[2]*Biology Department, University of Maine at Farmington, Farmington, Maine 04938, USA*

ABSTRACT.—A new method of measuring reproductive success was used to test Van Horne's (1983) contention that reliance on population density as a measure of habitat quality can produce misleading results. None of the three emberizine sparrows in this study showed a clear correlation between high territory density and high reproductive success. Grasshopper Sparrows (*Ammodramus savannarum*) were most successful in medium-density plots, and did poorly when territory density was low. Savannah Sparrows (*Passerculus sandwichensis*) were significantly more successful at low density, and were least successful at high density. Vesper Sparrows (*Pooecetes gramineus*) were the only species whose reproductive success was unaffected by territory density and, thus, for which density would have been a reasonable measure of habitat quality. These results lend support to Van Horne's thesis that the singular use of density may be a poor indicator of habitat quality and that additional factors should be considered. *Received 5 March 1991, accepted 10 February 1992.*

POPULATION DENSITY frequently is used as an indicator of a habitat's quality, because a greater number of individuals within a given area is generally thought to reflect larger amounts of the necessary resources to sustain a species (Van Horne 1983). By extension, it often is assumed that concentration of resources allowing a high population density also will be reflected in greater reproductive success, or other indices of fitness. Because density is easier to measure than fitness, Flood et al. (1977) and others who model habitat relationships have used density to make inferences about habitat quality, although not necessarily with a high degree of predictive success (Lancia et al. 1982, Bart et al. 1984, Maurer 1986). Van Horne (1983) questioned the singular reliance on density as an indicator of habitat quality and suggested that inferences about which habitats support individuals with the highest fitness often may be false. She suggested that, from a population-viability and management perspective, it is preferable to define habitat quality as a product of density and reproductive success. To test the hypothesis that density is a reasonable index of nesting habitat quality for three grassland sparrows, we examined the relationship between breeding densities and reproductive success for each species.

METHODS

The study site was located on a sandplain grassland in Kennebunk, York County, Maine (43°24'N, 70°59'W). We studied three emberizine sparrows: Vesper Sparrow (*Pooecetes gramineus*); Savannah Sparrow (*Passerculus sandwichensis*); Grasshopper Sparrow (*Ammodramus savannarum*). Vickery et al. (1992) provided additional information on site and methods. The site was managed for commercial blueberry production with one-half of the area mowed and burned on a biennial rotation. This management created profound year-to-year changes in the vegetation structure with a concomitant influence on habitat quality. These habitat manipulations allowed us to measure the avian response to these year-to-year changes in each plot.

To examine the relationship between territory density and reproductive success, territories were "spot mapped" (International Bird Census Committee 1970) using eight replicate censuses on eight plots (8–24 ha) for three years (1984–1986). For each species, plots were assigned to a class depending on territory density: low, ≤2.5 territories per 10 ha; medium, >2.5 to <3.5 territories per 10 ha; high, ≥3.5 territories per 10 ha. There were at least four plots for each density category. The reproductive-index rank (Vickery et al. 1992) for each territory was assigned to the appropriate density category. We then used the Kruskal-Wallis test (Conover 1980:229) to determine if there were differences in the reproductive-index rankings within each density classification.

We measured percent cover for nine vegetation features for high-success and low-success Grasshopper, Savannah and Vesper sparrows, and also measured the same parameters on the unoccupied habitat in each plot. To evaluate whether Savannah Sparrows

[3] Present address: Conservation Department, Massachusetts Audubon Society, Lincoln, Massachusetts 01773, USA.

[4] Present address: Department of Natural Resources, Field of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853, USA.

occupied a wider range of habitats than Grasshopper Sparrows, we used a sign test (Conover 1980:122) to compare differences between the mean of each of the nine vegetations parameters for high-success and low-success Savannah and Grasshopper sparrows. To examine whether density-dependent pressures might obligate some Savannah Sparrows to use obviously lower-quality habitat than Grasshopper Sparrows (i.e. patches that are more similar to unoccupied sites), we employed the sign test to compare the differences between the mean of each vegetative parameter for low-success Grasshopper Sparrow and Savannah Sparrow territories to the mean of the same vegetative parameters on the unoccupied portions of each plot (see Vickery et al. 1992).

Results

The relationship between the density of territories and reproductive success differed for each species (Fig. 1). Grasshopper Sparrow reproductive success was poorest at low density and was greatest at medium density (Kruskal-Wallis $X^2 = 6.84$, df = 2, $P = 0.033$). Savannah Sparrows displayed a very different pattern; reproductive success declined significantly as territory density increased (Kruskal-Wallis $X^2 = 10.09$, df = 2, $P = 0.006$). Vesper Sparrows showed no significant relationship between territory density and reproductive success (Kruskal-Wallis $X^2 = 1.13$, df = 2, $P = 0.568$).

Because Savannah Sparrows differed so clearly from Grasshopper Sparrows, we tested the hypothesis that Savannah Sparrows might occupy a wider range of habitats than Grasshopper Sparrows. For the nine habitat parameters, the differences between means of high-success and low-success Savannah Sparrows were greater than the corresponding means for Grasshopper Sparrows in five cases, but were less in four cases ($n = 9$, $P > 0.40$; Table 1; for complete vegetation data, see Vickery et al. 1992). The second hypothesis, that density-dependent pressures might obligate some Savannah Sparrows to occupy obviously lower-quality habitat, was not supported statistically ($n = 9$, $P > 0.40$).

Discussion

The relationship between territorial density and reproductive success was different for each of the three species. Importantly, high density did not reflect the highest reproductive success for any of the species studied. Each species' unique response to territorial density underscores the need for caution in simply using density as a measure of habitat quality. Indeed, Vesper Sparrow was the only species in this study for which density would have been an adequate index of the habitat quality.

The striking differences in patterns of reproductive success and territory density among three ecologically similar species may involve a variety of factors. As preferred habitat becomes saturated, additional potential breeders may find it equally advantageous to select secondary habitat or to continue compressing into preferred primary habitat (Fretwell and Lucas 1969). This may explain why, for Vesper Sparrows, reproductive success was fairly uniform across all three territory densities. However, such an ideal, free distribution may not be possible for all species, depending on the size, distribution and juxtaposition of patches of their preferred, secondary, and lesser-quality habitats (Wiens 1974, 1976, Maurer 1986). For example, high-success Savannah Sparrow territories may be found in low-density plots because these territories occur on discrete islands of excellent habitat that are too small to accommodate additional territories, but are also surrounded by large areas of inferior or unsuitable habitat (Huxley 1934). Plots with high densities of Savannah Sparrows may simply represent larger areas of secondary and tertiary habitat occupied by subordinates incapable of defending a large territory. The clear differences in vegetative cover between high-success and low-success territories for all three species, and the fact that multivariate analysis revealed that high-success territory formed a discrete cluster within the spot-map matrix (Vickery et al. 1992), lends support to this "spatial-effect hypothesis."

There may also be clear differences in the range of habitats these species will occupy. As grassland generalists, Savannah Sparrows are more likely to attempt nesting in a wider range of habitats (Baird 1968), including poor-quality sites, than are Grasshopper Sparrows, which are more of a habitat specialist (Smith 1968). However, data from our study did not support this hypothesis.

Social factors may also complicate the supposition that increased density will reflect greater reproductive success. Many species are highly philopatric, especially if they have been successful (e.g. Austin 1949, von Haartman 1960). Although most sparrows clearly shifted territories in response to changes in habitat

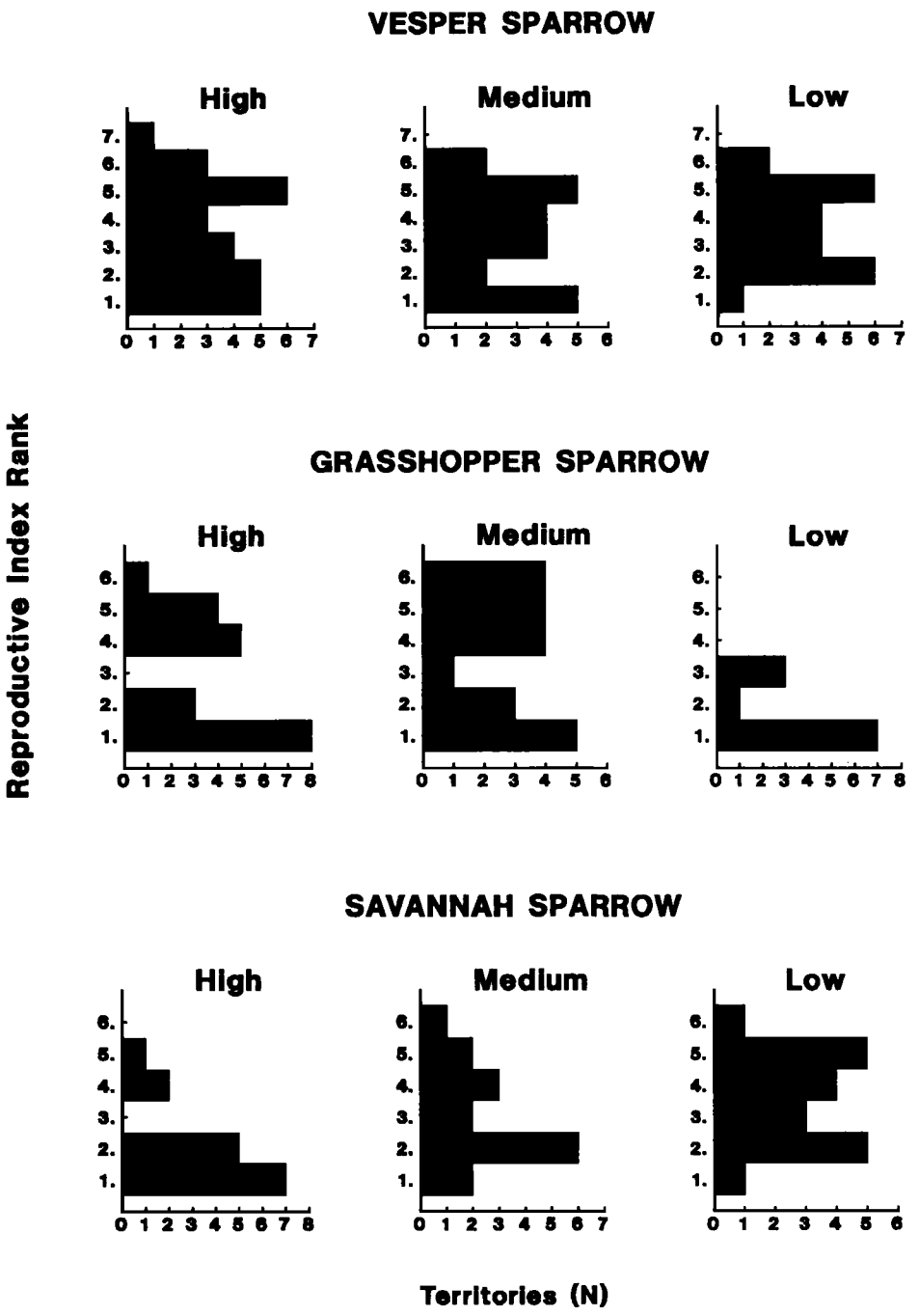

Fig. 1. Difference in reproductive success for high-, medium- and low-density of Vesper, Grasshopper and Savannah sparrows at Kennebunk, Maine, 1984–1986. Graph depicts number of territories for each rank in each density class. Density had a significant effect on Grasshopper and Savannah sparrows. Grasshopper Sparrow reproductive success was greatest at medium density, whereas Savannah Sparrow success declined as density increased. Vesper Sparrow reproductive success was similar at all three densities..

TABLE 1. Difference in mean (percent cover) vegetation parameters for high-success and low-success Grasshopper, Savannah, and Vesper sparrows on territory at Kennebunk, Maine (1984–1986).

Habitat parameters	Grasshopper Sparrow			Savannah Sparrow			Vesper Sparrow		
	Success		Difference	Success		Difference	Success		Difference
	High	Low		High	Low		High	Low	
Bare ground	24.5	20.9	3.6	21.1	24.3	3.2	21.9	23.0	1.1
Litter	24.3	27.1	2.8	32.6	26.6	6.0	27.1	27.2	0.1
Graminoid (2–20 cm)	31.5	25.9	5.6	23.3	34.0	10.1	20.9	22.7	1.8
Graminoid (>20–60 cm)	21.1	25.1	4.0	22.0	26.7	4.7	21.9	22.5	0.6
Forb (2–20 cm)	16.6	14.0	2.6	13.8	12.4	1.4	13.7	13.2	0.5
Forb (>20–60 cm)	31.4	26.1	5.3	24.9	31.3	6.4	23.3	27.1	3.8
Vaccinium	28.3	35.6	7.3	36.5	30.4	6.1	32.2	38.8	6.6
Shrub (2–20 cm)	20.5	17.1	3.4	18.3	27.1	8.8	13.6	14.9	1.3
Shrub (>20–60 cm)	26.8	21.1	5.7	21.9	25.9	4.0	24.0	23.5	0.5

quality created by the mowing and burning regime at this site, a few territories (most notably for Grasshopper Sparrows) were established in precisely the same areas as the previous year. This suggests that some individuals are highly philopatric and, as a result, are likely to be less successful (Zwickel and Bendell 1972, Wiens and Rotenberry 1985). This appears to be the case for the few Grasshopper Sparrows nesting in low-density plots.

In conclusion, the facts that three ecologically similar species occupying the same ecosystem showed such different relationships between territory density and reproductive success, and that density would have been a poor measure of habitat quality for two of these three species, lend support to Van Horne's (1983) thesis that it is probably inappropriate to rely on density as a singular measure of habitat quality.

ACKNOWLEDGMENTS

Earl and Oka Campbell and Coastal Blueberry, Inc., graciously permitted this study to be conducted on private land and are acknowledged for their cooperation. Financial support was provided by The Nature Conservancy (both the Maine Chapter and the Eastern Regional Office), the Nongame project of Maine Department of Inland Fisheries and Wildlife, the Maine Board of Pesticides Control, F. I. Dupont, Inc., and the Maine Audubon Society. The Maine Chapter of the The Nature Conservancy and Bowdoin College Biology Department provided additional office and library support. Mary Droege, Sally Rooney, Peggy O'Connell, and Barbara Vickery assisted in collecting vegetation data. William Halteman provided guidance for the data analysis. William Glanz, George Jacobson, R. A. Lautenschlager and two anonymous reviewers provided valuable suggestions. Rob Denny and Barbara Vickery are both gratefully and warmly acknowledged for their encouragement and support.

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