USE OF A NEW REPRODUCTIVE INDEX TO EVALUATE RELATIONSHIP BETWEEN HABITAT QUALITY AND BREEDING SUCCESS

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ABSTRACT.—A new method of measuring reproductive success is proposed that uses a composite of breeding-behavior observations (for behaviors that reflect different stages in the reproductive cycle) as an index of fitness. This reproductive index does not rely on discovery of nests, but is comprehensive in that it includes information on all monitored territories. The reproductive index was applied to three co-occurring grassland emberizine sparrows, two of which required special care because of their regional rarity. Ranks derived from this reproductive index were used to distinguish territories of birds of known high success (i.e. those that fledged young in at least one brood) from territories of birds with known low success (unpaired males), and were compared with findings for "spot-mapped" territories. Principal-components analyses of habitat measurements for these territory types revealed a similar pattern for all three species: spot-mapped territories overlapped broadly with nonterritory (unoccupied) plots, whereas high-success territories formed a discrete, isolated cluster within the spot-map matrix. Univariate analyses revealed that high-success territories were described by 15 vegetation features that differed ($P < 0.01$) from nonterritory values, whereas in spot-mapped territories only 8 vegetation measures differed and in low-success territories only 2 differed. The ability to distinguish high-success territories allowed us to identify a greater number of habitat features that were correlated with reproductive success. If we had relied on the spot-mapping method, we would have been unable to identify many of these important habitat features. Yet, the ability to make such discriminations is likely to be critical in the management of threatened species. *Received 5 March 1991, accepted 7 April 1992.*

THE DIFFICULTY of being able to gather detailed reproductive information about a bird

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population or community in a time-efficient manner has frequently limited avian-community research (e.g. Wiens 1973). Techniques for quantifying avian reproductive activity usually fall into two general categories. The simplest method, territory mapping, allows the researcher to define the location of individual male territories for a species or group of co-occurring species (Kendeigh 1944, International Bird Cen-

sus Committee 1970, Emlen 1971, 1977, Jarvinen and Vaisanen 1975, Reynolds et al. 1980), but is constrained by providing no information about reproductive success. The second technique, locating and following the success of individual nests, provides an accurate measure of reproductive output and rates of predation (e.g. Mayfield 1961, Brittingham and Temple 1983), but potentially is disruptive because most nests are difficult to find; in addition, it is time consuming, especially if there is an attempt to locate all nests for all territories (Bull 1981). Use of nest data, unless comprehensive or randomly derived, suffers from potential biases associated with nonrandom data collection.

The reproductive index described here is based on the assumption that behaviors indicative of different stages of the breeding cycle can be observed for all territories in question; criteria were adapted from the protocol established by the British-Irish breeding-bird atlas (Sharrock 1976). We evaluated this reproductive index on three ecologically similar grassland emberizine sparrows. One of the primary aims of our study was to determine if information derived from this reproductive index might facilitate discrimination of significant habitat features not detected by territories derived from the "spot-mapping" technique. Therefore, we used the rankings from this reproductive index to help us examine the relationship between breeding success and habitat quality.

THE REPRODUCTIVE INDEX

In order to reproduce successfully, most nidicolous male passerines must: (1) establish a territory and (2) attract a mate. At least one of the pair must: (3) build a nest, lay and incubate eggs; (4) feed nestlings; and, finally (5) feed fledglings. Although it often is difficult to observe nest building, egg laying, or incubation, it usually is possible to monitor other phases in the nesting cycle. We established a ranking system, from 1 to 5, for single-brooded species using the five phases of the breeding cycle listed above (Table 1). We also developed a similar ranking index, from 1 to 7, for double-brooded species (Table 1). For the purposes of this index, nest success was defined as fledging at least one young.

Adequate knowledge of the species under study is critical if behaviors are to be recognized and interpreted appropriately. For example, it is essential to know if a species carries food for courtship displays or just to feed young. Studies need to begin early enough in the breeding season and must be intensive

enough to follow the complete chronology of the breeding cycle. Errors of interpretation are less likely if the field observer has a clear understanding of the current activity stage for each territory. To avoid bias of uneven censusing effort (e.g. Mayfield 1961), all plots should be censused the same number of times throughout the breeding season.

Establishing ranks.—To use a reproductive index as a measure of fitness, one must determine a minimum time period that a territory needs to be occupied to be classified as rank 1. We recommend employing as a minimum the time it takes for the species under study to complete one successful clutch, from territory establishment to fledging (i.e. for emberizine sparrows, minimally four weeks). Sexual dimorphism and nonagonistic behavior towards conspecifics of the opposite sex facilitate recognition of pair establishment (rank 2). For most species it is difficult to document nest building, egg laying or incubation (rank 3), but this can vary considerably. First observations of adults carrying food are recorded as evidence of the nestling stage (rank 4), and these nestlings are assumed to have just hatched (day 1). Observations of adults carrying food to young for a period longer than the nestling stage (in our study 10 days) are used to document fledging (rank 5). The appropriate use of statistics for rank data should be considered carefully; most notably, ranks are not additive (Conover 1980, Zar 1984).

Determining equivalent census time per territory.—Bird surveys should allocate equivalent effort among all territories, but in some cases this may be difficult to quantify. Researchers studying a species whose territories are widely separated may be able to measure minutes of censusing effort per territory. However, in multispecies censuses, spending equal time per territory may not be time efficient, or feasible, given: (1) the complication of overlapping interspecific territories and simultaneous data collection of several species; and (2) the fact that it is quicker to document the unchanged status of an unpaired singing male than to determine if a known pair has begun feeding young, or has initiated a second nest (Gibbs and Faaborg 1990).

Estimating the requisite number of censuses.—Because it is possible to gain additional information with each new census, one must determine the minimum number of censuses necessary to generate a meaningful reproductive index. This number will undoubtedly vary with research goals and with habitat type; for instance, it is more difficult to observe avian behavior in dense or tall vegetation. By sequentially comparing ranks of the most recent census ($i + 1$) with those of the previous census (i), it is possible to plot the percentage of territories that have changed ranks (Fig. 1). We suggest a change of 5 to 10% as the point of diminishing information, but specific research needs will define this lower limit.

Measurement of information change on a chrono-

TABLE 1. Reproductive-index rankings for single-brooded and double-brooded species.

Rank		
Single-brooded species	Double-brooded species	Definition
1	1	Territorial male present 4+ weeks.
2	2	Territorial male and female present 4+ weeks.
3	3	Pair found nest building, laying or incubating eggs or giving distraction display.
4	4	Adults carrying food to presumed nestlings.
5	5	Evidence of fledging success. For double-brooded species, evidence of fledging success in one brood only.
	6	Evidence of fledging success in either brood, plus evidence of nestling success in other brood.
	7	Evidence of fledging success in both broods.

logical scale provides insight into the duration of the nesting period, but determination of the minimum threshold using these rank changes will be somewhat arbitrary. Calculation of the percentage of territories that have changed rank between randomly generated censuses from a random subset of the total territories under study will avoid this chronological bias and, thus, will provide greater insight into the intensity of effort required through the breeding season.

METHODS

Study species and site.—Our study focused on three species of emberizine sparrows, two of which warranted special attention and care; the Grasshopper Sparrow (*Ammodramus savannarum*) is designated as endangered in Maine and the Vesper Sparrow (*Poeecetes gramineus*) is on a list of vertebrates that may be declining in the state (Swartz 1987). The third species, the Savannah Sparrow (*Passerculus sandwichensis*), is common. These three species occupy similar habitats, but their nest concealment varies considerably: Vesper Sparrow nests were usually only partially concealed and were fairly easy to locate ($n = 38$); Savannah Sparrow nests were well hidden and moderately difficult to find ($n = 6$); Grasshopper Sparrow nests were domed, hidden in dense vegetation, and extremely difficult to find because the female flushes only when humans are very close (<1 m) to the nest (Smith 1968). We were able to find only 2 nests on 53 monitored Grasshopper Sparrow territories. Further intensive efforts to locate such well-concealed
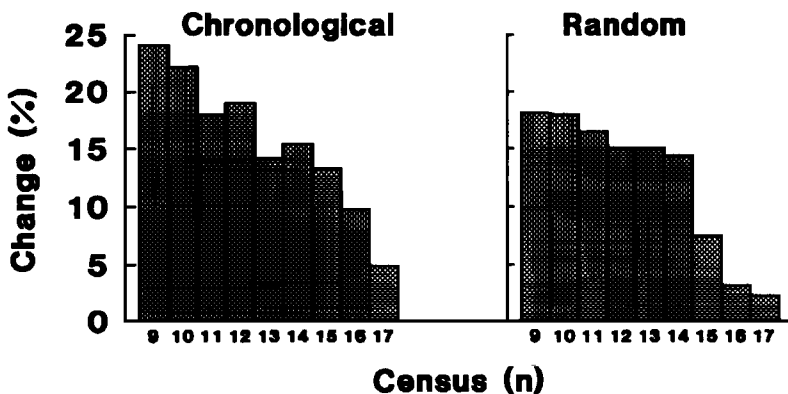

Fig. 1. Chronological histogram showing percentage of all territories whose reproductive-index rank increased after each new census. Note that the level of change diminished as the breeding season progressed. Random histogram depicts percent change in ranks after eight randomly selected censuses. Thereafter, each additional census was randomly selected (see text). Random histogram illustrates intensity of census effort required to gain adequate reproductive information and demonstrates that change in ranks diminished sharply after 14 censuses.
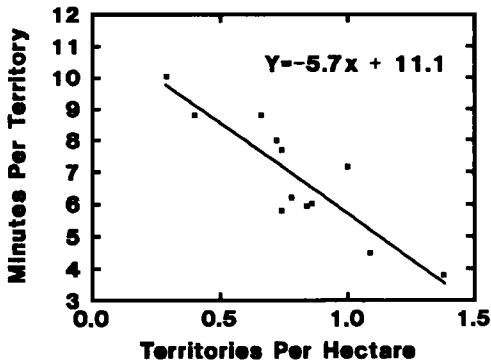
Fig. 2. Linear regression of census time per sparrow territory versus total sparrow density showed a steady decline as sparrow density increased ($r = -0.839$, $P < 0.001$).

nests would have been unacceptably disruptive for this rare species. The clear differences in detectability of nests and the care required to monitor sensitive species provided an opportunity to evaluate this new reproductive index for otherwise ecologically similar species. The study site was located on a sandplain grassland in Kennebunk, York Co., Maine (43°24′N, 70°59′W).

Census methods.—Two observers censused eight grassland plots marked with 50 × 50 m grids, totaling 120 ha, by: (1) mapping territories of all sparrows using the "spot-mapping" method (International Bird Census Committee 1970) and flushing territorial males (Wiens 1969); (2) noting behaviors indicative of breeding such as adults carrying food or fecal sacs, or giving distraction displays (Sharrock 1976); or (3) observing recently fledged young. Reproductive data were gathered on 174 territories, including the outcome of all discovered nests. Because we were uncertain of a minimum censusing threshold, plots were censused 10 to 17 times at a rate of 5.2 ± SE of 0.8 min per ha. Intervals between censuses at each plot were four to eight days. Field work was conducted each year (1984–1986) from 15 May to 25 August. Because meaningful patterns of habitat preference are not necessarily discernible from short-term data (O'Connor 1981, Van Horne 1983), we evaluated this index over a three-year period.

Because all three sparrow species can produce two broods at this site, we used a reproductive index that incorporates both broods into one index (Table 1). Males defending a site at least four weeks were classified as being on territory (rank 1). Males singing for shorter periods were excluded. Because none of the species in our study carry food for courtship display (Berger 1968, Smith 1968, Baird 1968), it was easy to interpret all food-carrying behavior. Initial observations of food carrying were registered as evidence of recently hatched nestlings (day 1). Adults carrying

food for 10 or more days, the average nestling period for these three species, were presumed to be feeding fledglings.

Because territories overlapped interspecifically, we sometimes were able to collect data on two or three species simultaneously. Thus, it was not practical to measure census time per discrete territory. Instead, we recorded census time per hectare and divided this number by overall sparrow density for the plot to provide a measure of census minutes per territory. We calculated the average census time per territory. This parameter declined as the number of territories per hectare increased ($r = -0.839$, $P < 0.001$; Fig. 2). This decline reflected decreasing transit time between territories as density increased and increasing opportunities to simultaneously census overlapping territories in denser plots. Thus, we think that effort per territory was comparable.

Because it takes several censuses to collect sufficient information to generate a preliminary reproductive index, we calculated the ranks for all territories on all plots after eight censuses, and after each additional census thereafter. We then calculated the percentage of territories whose ranks changed with each new census. There was a steady decline from about 25% of the territories changing ranks between censuses 8 and 9, to only a 5% change between censuses 16 and 17 (the latter shown in Fig. 2).

To determine an estimate of the necessary censusing effort unbiased by phenology, we selected a random sample of 100 territories from a total of 174 territories and a random sample of 8 to 17 censuses (*i*) for each of these territories. The rank for each territory then was calculated based only on these censuses. We repeated the process using another 100 random territories with *i* + 1 random censuses, calculating the percent change between ranks based on the *i* versus the *i* + 1 census (Fig. 1). From this analysis, it was clear that changes in ranks diminished sharply (to <10%) after the 14th census. Based on these two analyses, we considered 14 censuses a minimum threshold at this site, and any plots with fewer censuses were disregarded from further analyses. For plots with more than 14 censuses, only data from 14 randomly selected censuses were used in analyses.

Definition of high-success and low-success territories.— We ultimately wanted to compare habitat characteristics of spot-mapped territories, in which reproductive success was unknown, to those of two subsets: territories of known high reproductive success; and those with known low success. Therefore, we grouped territories with reproductive-index ranks of 5 to 7 into a high-success category; territories with rank 1 were assigned to a low-success group. Spot-mapped territories were generated from census data for all territories for each species.

The perimeter of each territory was outlined on a base map of each plot. Every 50 × 50 m quadrat within each plot was then assigned to one of the following

categories: high success; low success; intermediate (ranks 2–4); and nonterritory (=unoccupied areas for a particular species). All occupied quadrats, whether high, intermediate or low, were assigned to spot-mapped territories. Quadrats with less than 50% territory occupancy were classified as nonterritory plots. If two adjoining territories received the same rank (e.g. 5) and collectively occupied more than 50% of the same quadrat, that quadrat was included in the appropriate category (e.g. high success).

Habitat description.—Vegetation was estimated visually for every 50 × 50 m quadrat in each plot and for each of the three years. We used a minor modification of the Braun-Blanquet releve method (Mueller-Dombois and Ellenberg 1974; for detailed description, see Vickery et al. 1992). Shrub, forb, and graminoid cover were estimated at three strata: 0–2 cm; >2–20 cm; and >20–60 cm. Bareground, litter, lichen and moss were estimated in the 0–2 cm stratum. Lowbush blueberry (*Vaccinium angustifolium*), a dominant shrub, was considered separately from other shrubs and was estimated in the 2–20 cm stratum. Vegetation was estimated in the following units: <3 stems per subplot; <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 ranks were transformed into midpoint percentages, and these percentages were arcsin transformed for all parametric analyses (Zar 1984:239).

Statistical analysis.—Because we wanted to know if this reproductive index produced comparable results for the three species, we used a Kruskal-Wallis ANOVA (Wilkinson 1990) to test if there were differences in final ranks of the species. If there were differences, this would suggest one of two things: (1) that reproductive success among the three species was different, which we thought was unlikely (Vickery et al. 1992); or (2) that a particular species' behavior skewed the reproductive-index ranks in some fashion.

We used principal-component analysis (PCA; Wilkinson 1990) to reduce the nine habitat variables into multivariate "niche" components. The first three principal components were used to plot bivariate confidence ellipses that might help in depicting the relationship of these four territory types for each species. Because the 99%-confidence-ellipse size is affected by sample size (Wilkinson 1990:214), we standardized our habitat data set for each territory type and for each species by randomly selecting a subset of the original samples for each territory type (Grasshopper Sparrow, $n = 68$; Savannah Sparrow, $n = 39$; Vesper Sparrow, $n = 28$). There was no difference between these subsets and the original data (discriminant-function analysis, 9 tests, all $P > 0.40$). For each species we plotted principal component I against II and against III (Fig. 3); comparison of principal components II and III revealed the same general pattern as the bivariate ellipses shown.

We wished to compare: (1) the vegetation structure of these territory types (high success, low success, spot-mapped) to unoccupied habitat (nonterritory plots); and (2) vegetation measurements among territory types. Therefore, each vegetative parameter was analyzed separately using one-way ANOVA (Wilkinson 1990). This allowed us to make direct contrasts between territory types for each parameter. To reduce type I error effects, we chose a significance level of $P < 0.01$.

Finally, we wanted to learn if the three species differed in the number of habitat features associated with each type of territory; this would provide a general test of the utility of the reproductive index in this application. We used a chi-square analysis to test for interspecific differences in the number of significant vegetative parameters that characterized each of the three occupied-territory types (Zar 1984).

RESULTS

The reproductive index.—We found that 47 of 174 territories (27%) had a rank of 5 or higher, demonstrating fledging success in at least one brood (Table 2). This compared to 42% nest success at the same study area during the same period as determined from regular nest checks ($n = 60$; Vickery et al. 1992), which indicated that this index provided a reasonable measure of reproductive success. There was no difference in final ranks among the three species ($X^2 = 2.241$, df = 2, $P = 0.326$), indicating that reproductive success was comparable among species and that there did not appear to be unique behaviors that skewed the reproductive-index rankings.

Reproductive success and habitat analysis.—Principal-components analysis graphically revealed the habitat relationships among these four territory types for the three species (Fig. 3). The multivariate ellipses for spot-mapped territories and nonterritory plots overlapped broadly for all three species, indicating little separation in multidimensional "niche" space. High-success territories were generally defined by a discrete ellipse within the spot-map matrix; it was usually distantly removed from low-success and nonterritory ellipses (Fig. 3). Low-success ellipses generally were positioned between spot-map territories and nonterritory plots, but appeared to be primarily a subset of nonterritory plots.

For high-success territories, 15 of 27 habitat parameters (9 features × 3 species) were statistically different ($P < 0.01$) from those for nonterritory plots, whereas for spot-mapped terri-

VESPER SPARROW
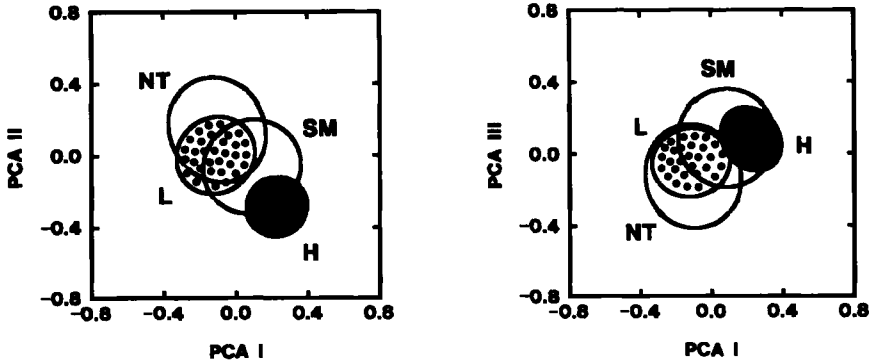
SAVANNAH SPARROW
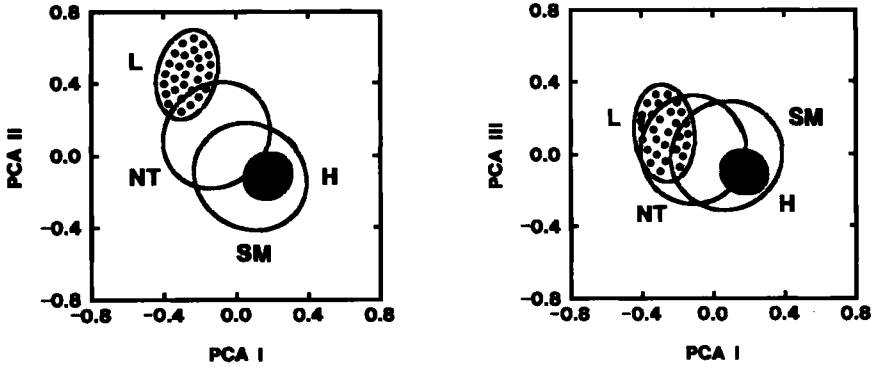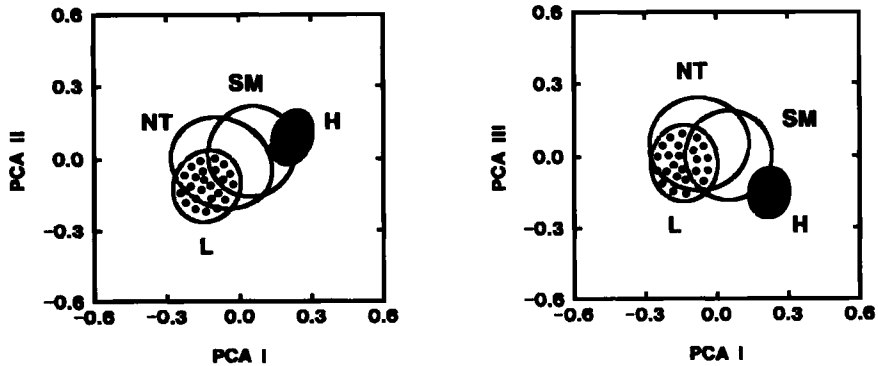

GRASSHOPPER SPARROW

Fig. 3. Principal-components analysis (99% confidence ellipses) of vegetation measures for Vesper, Savannah and Grasshopper sparrows at Kennebunk, Maine (1984–1986) represents multidimensional "niche" habitat for each territory type. H = high-success territories (black ellipses), SM = spot-map territories, L = low-success territories (speckled ellipses), NT = comparable nonterritories. Generally, broad overlap occurred between spot-map and nonterritory plots, and high-success territories formed discrete ellipses within the spot-map matrix.

tories there were 8 significant parameters, and for low-success territories just 2 (Table 3). This pattern was similar for each of the three species; high-success territories were distinguished by the largest number of parameters, and low-success by the least. The differences in the number of significant habitat parameters recorded among high-success, spot-mapped, and low-success territory types were significant ($X^2 =$ 10.22, df = 2, $P < 0.01$). Finally, although there were eight habitat features identified as significant by the spot-mapping procedure, for five of these the high-success territories differed statistically ($P < 0.01$) from spot-mapped territories (Table 3). This meant that, even when a vegetation parameter was noted as significant using the spot-mapping method, we usually were able to make additional habitat distinctions that were likely to be associated with high levels of reproductive success.

DISCUSSION

Reproductive index.—This reproductive index was comprehensive and time efficient. Also, its use was not limited to the brief early morning period of high song activity (Skirven 1981). Comparison of reproductive-success estimates with those based on other research at this site (Vickery et al. 1992) indicated that the index was a conservative but reasonable measure of reproductive success. More frequent censusing probably would have increased the records of fledging success somewhat, but the level of detail we obtained was satisfactory for the purposes of this study. Importantly, territories were distributed across all ranks, suggesting no dramatic bias per rank. The fact that there was no difference in final ranks among species indicated that all three species experienced comparable levels of reproductive success and that there were no anomalous behaviors that skewed final index ranks for any of these species.

We caution that ranks of different species probably should not be compared, or would need to be very carefully considered, because no two species will have the same likelihood of detection for each phase of the nesting cycle. For example, the ease of locating and monitoring Vesper Sparrow nests ($n = 38$) obviously altered behavioral interpretations in comparison to Grasshopper Sparrows, whose nests ($n = 2$) were very difficult to find. The observer's knowledge of a nest's status allows for a differ-

TABLE 2. Reproductive-index ranks for Grasshopper Sparrows, Vesper Sparrows, and Savannah Sparrows at Kennebunk, Maine (1984–1986).

Year	Rank						
	1	2	3	4	5	6	7
Grasshopper Sparrow (n = 53)							
1984	4	4	1	4	3	0	0
1985	7	2	0	5	3	2	0
1986	9	1	3	0	2	3	0
Vesper Sparrow (n = 71)							
1984	4	3	6	4	4	0	0
1985	3	3	2	5	10	3	0
1986	4	7	4	2	3	3	1
Savannah Sparrow (n = 50)							
1984	6	7	0	4	5	1	0
1985	2	4	2	1	1	0	0
1986	2	5	3	4	2	1	0
Total	41	36	21	29	33	13	1

ent interpretation. For example, first observations of adult Vesper Sparrows carrying food could confirm fledging for a recently emptied nest, but for Grasshopper Sparrows, whose nests had not been discovered, this primary observation only indicates the presence of nestlings.

Because it is comprehensive, this reproductive index avoids potential biases associated with nonrandomly collected nest data. Also, it does not disrupt nests of rare or endangered species. We think this reproductive index is a potentially useful tool that merits further field testing. It promises to be most useful where the scope of a study is too large to make it practical to locate all nests, or where fiscal, ecological, or conservation constraints prohibit exhaustive searches for nests.

Habitat analysis.—For all three species, principal-components analysis revealed a similar pattern; there was broad overlap between spot-mapped territories and nonterritory plots. Thus, principal-components analysis was unable to discriminate sharp distinctions in multidimensional "niche" space between habitat features of spot-mapped territories and nonterritory plots. However, high-success territories could be identified as a distinct, isolated ellipse within the spot-map matrix. Ellipses for low-success territories generally were positioned between ellipses of spot-mapped territories and nonterritory plots, but appeared to be a subset of the nonterritory ellipses. Recognizing this overall pattern, it was not surprising that high-success

TABLE 3. Vegetation measurements (percent cover) for Grasshopper, Savannah, and Vesper sparrows at Kennebunk, Maine (1984–1986). Means (SE in parentheses) given for all measurements. Sample size (*n*) of vegetation measurements for each territory type noted in parentheses following species name.

Habitat parameters	Territory type[a]			
	High success	Spot map	Low success	Nonterritory
Grasshopper Sparrow (*n* = 68, 271, 81, and 249)				
Bare ground	24.5 (1.3)	23.5 (0.9)	20.9 (1.7)	22.3 (0.9)
Litter	24.3 (0.8)[A,B]	28.5 (0.7)[C]	27.1 (1.4)	29.4 (0.7)
Graminoid (2–20 cm)	31.5 (0.6)[A]	28.3 (0.9)[C]	25.9 (1.8)[D]	18.3 (0.9)
Graminoid (>20–60 cm)	21.1 (1.1)	22.6 (0.9)	25.1 (1.6)	23.9 (0.9)
Forb (2–20 cm)	16.6 (1.3)	13.8 (0.9)	14.0 (1.8)	12.9 (1.0)
Forb (>20–60 cm)	31.4 (1.0)[A]	27.8 (0.9)	26.1 (1.8)	26.6 (0.9)
Vaccinium	28.3 (0.9)[A,B]	32.8 (1.0)[C]	35.6 (1.8)	36.0 (1.2)
Shrub (2–20 cm)	20.5 (0.8)[A]	20.0 (1.1)[C]	17.1 (2.0)	16.0 (1.2)
Shrub (>20–60 cm)	26.8 (0.9)[A]	23.7 (0.9)	21.1 (1.7)	23.0 (1.0)
Savannah Sparrow (*n* = 69, 221, 39, and 299)				
Bare ground	21.1 (1.0)	24.5 (1.0)	24.3 (2.6)	23.4 (0.8)
Litter	32.6 (0.8)[A,B]	28.0 (0.9)	26.6 (2.1)	28.7 (0.6)
Graminoid (2–20 cm)	23.3 (0.7)[A,B]	31.8 (1.1)[C]	34.0 (2.7)	27.6 (0.8)
Graminoid (>20–60 cm)	22.0 (1.1)	25.5 (1.0)	26.7 (2.4)	22.9 (0.9)
Forb (2–20 cm)	13.8 (0.8)	12.7 (1.0)	12.4 (2.5)	14.1 (0.9)
Forb (>20–60 cm)	24.9 (0.6)[A]	29.3 (1.0)	31.3 (2.1)	27.3 (0.9)
Vaccinium	36.5 (0.7)[A,B]	29.1 (1.1)	30.4 (1.9)	31.8 (1.1)
Shrub (2–20 cm)	18.3 (1.0)[A]	20.2 (1.3)[C]	27.1 (2.7)	24.5 (1.1)
Shrub (>20–60 cm)	21.9 (0.8)[A]	26.6 (0.9)	25.9 (2.1)	24.4 (0.9)
Vesper Sparrow (*n* = 124, 328, 28, and 192)				
Bare ground	21.9 (0.7)	21.9 (0.8)	23.0 (3.0)	24.5 (1.1)
Litter	27.1 (0.7)	29.5 (0.6)	27.2 (2.3)	27.9 (0.9)
Graminoid (2–20 cm)	20.9 (0.8)[A]	23.4 (0.8)[C]	22.7 (3.1)	28.9 (1.2)
Graminoid (>20–60 cm)	21.9 (0.6)	23.5 (0.8)	22.5 (3.0)	22.8 (1.1)
Forb (2–20 cm)	13.7 (0.6)	14.1 (0.8)	13.2 (3.1)	12.1 (1.1)
Forb (>20–60 cm)	23.3 (0.8)	27.6 (0.8)	27.1 (3.0)	26.7 (1.2)
Vaccinium	32.2 (0.7)[A]	39.1 (1.0)	38.8 (3.8)	43.0 (1.3)
Shrub (2–20 cm)	13.6 (0.7)[A]	16.3 (1.0)[C]	14.9 (2.3)[D]	21.1 (1.3)
Shrub (>20–60 cm)	24.0 (0.8)	22.8 (0.8)	23.5 (2.7)	24.4 (1.1)

[a] Superscripts indicate significant differences (*P* < 0.01) of percentages: (A) high success and nonterritory; (B) high success and spot map; (C) spot map and nonterritory; (D) low success and nonterritory.

territories provided more information about preferred habitat because they were described by a larger number of significant habitat parameters than were spot-mapped territories. In addition, identification of high-success territories also provided important insights about high-quality habitat by permitting a more accurate definition of physiognomic features likely to be associated with higher levels of reproductive success. Importantly, all three species displayed this pattern.

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