



USING SPATIAL POINT-PATTERN ASSESSMENT TO UNDERSTAND THE SOCIAL AND ENVIRONMENTAL MECHANISMS THAT DRIVE AVIAN HABITAT SELECTION

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ABSTRACT.—Understanding when species distributions should be ascribed to patterns in the physical habitat, rather than to the influence of social cues, is a crucial step in understanding avian habitat selection. To distinguish between these mechanisms, we assessed the point pattern of 213 Saltmarsh Sparrow (*Ammodramus caudacutus*) nests and the spatial autocorrelation of vegetation characteristics at two study sites. Our tests of aggregation at cumulative and discrete distance classes failed to detect any significant nonrandom pattern, which is consistent with the hypothesis that nest placement is random with respect to other nests. When the timing of nesting attempts was taken into account such that only previous or currently active nests were considered, there was still no evidence that females attempted to nest closer to other nests than expected given random site selection. The underlying spatial structure of the vegetation variables was somewhat patchy, but not in a way that was consistent between sites or that matched patterns in nest placement, which suggests that female Saltmarsh Sparrows do not distribute themselves within marshes according to these features. A lack of association between vegetation characteristics and the probability of nest flooding, which is the primary source of nest failure in this species, may explain the apparent lack of spatial structure. *Received 20 July 2009, accepted 10 March 2010.*

Key words: *Ammodramus caudacutus*, conspecific attraction, nest aggregation, pair correlation function, Ripley's *K* function, Saltmarsh Sparrow, spatial autocorrelation.

Uso de Evaluaciones de Patrones Espaciales Puntuales para Entender los Mecanismos Sociales y Ambientales que Conducen la Selección de Hábitat en las Aves

RESUMEN.—Entender cuándo las distribuciones de las especies deben ser atribuidas a patrones en el ambiente físico, más que a la influencia de señales sociales, es un paso crítico para entender la selección de hábitat en las aves. Para distinguir entre estos mecanismos, evaluamos el patrón de distribución puntual de 213 nidos de *Ammodramus caudacutus* y la autocorrelación espacial de las características de la vegetación en dos sitios de estudio. Nuestras pruebas de agregación en clases de distancia acumulativas y discretas no pudieron detectar ningún patrón no azaroso, lo cual concuerda con la hipótesis de que la ubicación de los nidos se hace al azar con respecto a los otros nidos. Cuando se tuvo en cuenta el momento de los intentos de anidación de modo que sólo los nidos activos previos o actuales fueron considerados, tampoco hubo evidencia de que las hembras intentaran anidar más cerca de los otros nidos que lo esperado según una selección de sitios al azar. La estructura espacial subyacente de las variables de la vegetación se presentó un tanto en forma de parches, pero no en un modo consistente entre sitios o coincidente con los patrones de ubicación de los nidos, lo que sugiere que las hembras de *A. caudacutus* no se distribuyen dentro de los pantanos de acuerdo a estas características. Una falta de asociación entre las características de la vegetación y la probabilidad de inundación de los nidos, la cual es la causa principal de fracaso de los nidos en esta especie, podría explicar la falta aparente de estructura espacial.

HOW ANIMALS SELECT habitat and distribute themselves in space has fundamental consequences for their demography, ecology, and evolution, yet our ability to predict species distributions remains mixed (Scott et al. 2002). Stamps (1994) and others (Reed 1999, Reed et al. 1999, Blumstein and Fernández-Juricic 2004) have suggested that a greater understanding of behavioral processes is

needed to improve our theoretical and practical understanding of habitat selection. If social cues are commonly used during habitat selection, responses to these cues could drive species distribution patterns and would have significant implications for both habitat selection theory and conservation practice (Stamps 1988, Ahlring and Faaborg 2006).

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Environmental parameters such as soil moisture, elevation, and slope can directly affect vegetation composition and structure, which in turn can drive faunal species occurrence (Fortin and Dale 2005). When biologically important resources are spatially autocorrelated, patterns in species distributions may occur in response to the underlying spatial structure of the environment. Such “induced” spatial patterns have quite different implications for species settlement behavior than the “inherent” structured patterns that arise from behavior such as conspecific attraction or competition (Fortin and Dale 2005). Thus, aggregated settlement patterns can occur when individuals select habitat on the basis of the presence of conspecifics or simply in response to clusters in resource distribution (Stamps 1988).

Although much progress has been made in addressing such questions in the plant and landscape ecology literature (Fortin and Dale 2005), spatial analysis of avian nest locations is much less common (Bourque and Desrochers 2006). Despite widespread interest in quantifying the ecological features of avian breeding habitat, the influence of these features on habitat selection behavior is infrequently approached from an explicitly spatial perspective (but see Bourque and Desrochers 2006, Cornulier and Bretagnolle 2006), and few studies have specifically addressed the influence of social cues in habitat selection via spatial pattern assessment (e.g., Brown and Brown 2000, Melles et al. 2009). Given the growing interest in the role of social cues in the process of avian habitat selection (e.g., Danchin et al. 1998, Ward and Schlossberg 2004, Ahlring and Faaborg 2006), these topics would benefit from being united by spatially explicit analyses.

We analyzed the spatial pattern of Saltmarsh Sparrow (*Ammodramus caudacutus*) nests and assessed mechanisms that potentially drive nest-placement decisions. The Saltmarsh Sparrow is a nonterritorial species in which individuals do not form pair bonds (Woolfenden 1956, Shriver et al. 2007, Hill et al. 2010) and females are the exclusive providers of parental care (Woolfenden 1956, Greenlaw and Rising 1994). These behavioral attributes eliminate two major social constraints that most birds face and make this species especially well suited for studies that seek to determine the role of social information cues. The breeding-season distribution of female Saltmarsh Sparrows is not well understood at the local scale, but the current consensus from the literature is that nests are clustered. For example, nesting has been referred to as semicolonial and as occurring in “hotspots” (Forbush 1929, Montagna 1942, Hill 1968, Murray 1969). Greenlaw and Rising (1994) suggested that sparrow aggregations in the marsh resulted from patchiness in nest microhabitat characteristics, whereas Murray (1969) speculated that aggregations resulted from social causes such as mate attraction. However, no study has determined statistically whether the nests of this species are clustered, which limits our ability to make inferences regarding putative mechanisms. Consequently, our main goal was to test the hypothesis that nests are distributed nonrandomly. We also consider plausible explanations for nonrandom nest-placement patterns.

Saltmarsh Sparrows occur in saltmarsh habitats that are dominated by vegetation such as Saltmeadow Cordgrass (*Spartina patens*), Saltmeadow Rush (*Juncus gerardii*), and Smooth Cordgrass (*S. alterniflora*) (Woolfenden 1956, Greenlaw and Rising 1994). Although Saltmarsh Sparrow occurrence is closely tied to vegetation type, the species’ abundance varies considerably

during the breeding season, both within and between marshes, and only a small portion of this variation can be attributed to habitat characteristics (Gjerdrum et al. 2005, 2008a). In addition, nest failure in the species is primarily attributed to tidal flooding associated with monthly high tides; individuals that are synchronized with the tide have a greater chance of successfully fledging young, regardless of nesting vegetation (Gjerdrum et al. 2005, Shriver et al. 2007). Nevertheless, establishing whether the vegetation features associated with Saltmarsh Sparrow occurrence are patchy in their distribution is an important component of understanding the birds’ nest-placement decisions. If vegetation parameters are key determinants of settlement decisions and the distribution of vegetation is patchy, one would expect that nest placement corresponds to patches of especially favorable habitat. Thus, an additional aim of our study was to determine the spatial structure of the underlying saltmarsh vegetation.

Conversely, if Saltmarsh Sparrow settlement patterns are primarily a function of conspecific attraction, females may cluster around other nests with little regard to fine-scale habitat characteristics. Under this hypothesis, the scale and location of nest aggregations would be unrelated to that of vegetation patches. Because nonrandom patterns in nest placement could result either from females using other nests as cues in their nest placement decisions or because females are attracted to nest near other actively nesting females, we used information on the temporal sequence of nest activity to assess each possibility separately.

Under the scenario in which vegetation is patchy and nest placement is clustered, our null model of random nest placement would need to be modified to specifically control for patchiness in vegetation. If nests were still clustered compared with the null expectation, the hypothesis that birds are aggregating for social reasons would be supported. However, if the settlement pattern was consistent with the null expectation, the hypothesis that females respond to similar habitat cues, but not necessarily social cues, would be supported. If we found patchiness in the vegetation, but not clustered settlement patterns, the hypothesis that nest placement is random with respect to other females, and to the specific aspects of vegetation we measured, would be supported.

METHODS

Study system.—Field research on breeding Saltmarsh Sparrows was conducted from 21 May to 24 August 2007 at two salt marshes on Long Island Sound in Connecticut: Hammonasset State Park (41°15′47″N, 72°32′55″W) and East River Marsh (41°16′24″N, 72°39′12″W). These sites were chosen because of their large size (209 ha and 289 ha, respectively), availability of suitable habitat, and high density of nesting Saltmarsh Sparrows compared with other sites (Gjerdrum et al. 2005, Elphick et al. 2009). We selected study areas of similar size within each marsh (Hammonasset: 31.5 ha; East River: 25.2 ha), using natural features of the marshes—large channels, waterways, and upland boundaries—to delineate the sites. The two marshes are ~8 km apart and lie within different watersheds separated by non-salt-marsh (suburban and forest) habitat. Our banding data show that there are occasional movements between the two sites but suggest that there is little within-season mixing of the populations (C. S. Elphick unpubl. data).

Nest monitoring.—Each study area was partitioned into four contiguous plots of approximately 6–8 ha to facilitate equal nest-searching effort across all portions of the study area. Plots were systematically searched twice weekly, with additional searching during nest-monitoring activities. Nest locations were recorded with a Garmin GPSMap76. A small flag was placed near each nest to identify the location, but at a distance of ~5 m to limit the potential for it to act as a cue to predators. Care was also taken not to trample the vegetation in the vicinity of the nest or create a trail leading to and from the nest. Nests were monitored every 2–5 days to track the outcome of the nesting attempts, and temperature data-loggers (Thermochron iButtons, Maxim, Sunnyvale, California) were used in 35 nests (16% of total) to track nest fate (cf. Gjerdrum et al. 2008b, Bayard 2010). Nests that fledged at least one chick were considered successful. Although we cannot be certain that all nests were found, most marsh vegetation is short (<0.5 m) and easy to search. Moreover, we found most nests (88%) in the building or incubation phase, which suggests that our nest searching was sufficiently thorough to detect most nest attempts early in the nesting cycle (see Gjerdrum et al. 2008a). Because most Saltmarsh Sparrows in our study population were not individually marked, the identity of the female associated with each nesting attempt was not known. Females may engage in multiple nesting attempts and, therefore, some nests in some analyses represent renesting attempts (see below). Given that the statistical tests we used are designed to detect spatial dependence among nests (i.e., clustering), the potential lack of independence among these nests is not an issue (Fortin and Dale 2005). On the basis of the timing of all nest attempts, however, a minimum of 53 females at Hammonasset State Park and 43 females at East River Marsh were sampled.

Vegetation sampling.—Vegetation sampling was conducted within 1-m² quadrats centered at each nest and at randomly located points selected using the ARCGIS, version 3.2 (ESRI, Redlands, California), random point generator. Data gathered included maximum vegetation height at each quadrat corner, thatch depth (i.e., dead plant matter underlying the vegetation) at the center of the quadrat, stem density in five 10-cm² subquadrats, and species composition (see Gjerdrum et al. 2005).

Data analysis.—To test the null hypothesis that Saltmarsh Sparrow nests were distributed randomly within the marsh, we used a combination of first- and second-order point-pattern tests. First-order tests are related to the mean number of events (i.e., nests) per unit area (intensity) and allow a crude assessment of clustering within a bounded study area. Second-order methods are concerned with the covariance structure of the number of events per unit area and allow investigation of interaction among events (Perry et al. 2006). Because different statistical approaches can yield conflicting results (Fortin and Dale 2005), we used a combination of these tests to determine the robustness of our results. All tests were computed in R (R Development Core Team 2008) using the SPATSTAT library (Baddeley and Turner 2005). Data from each marsh were analyzed separately.

We used two first-order nearest-neighbor tests as a preliminary tool to assess whether the spatial distribution of Saltmarsh Sparrow nests differed significantly from the null hypothesis of complete spatial randomness. The Clark and Evans aggregation index R is calculated as the ratio of the mean nearest-neighbor

distance (NND) for all nests to the mean NND expected for a Poisson point process of the same intensity (Clark and Evans 1954). A value of R significantly greater than 1 suggests clustering, a value significantly less than 1 suggests regularity, and $R = 1$ is the expected value for spatial randomness. We also used the nearest-neighbor distribution function (Diggle's G function; Diggle 1979) to quantify the cumulative distribution function (i.e., the distance from a randomly chosen nest to the nearest other nest; Baddeley and Turner 2005). We used 499 Monte Carlo simulations of a Poisson point-pattern process to generate a 99% confidence envelope of the function (Diggle 2003). The estimation of Diggle's G derived from the nest data set was compared with the theoretical curve of the Poisson point pattern. Values of the empirical G function above the 99% confidence envelope indicate clustering, and those below the confidence envelope indicate regularity.

A central assumption of second-order pattern analysis is that the variable under consideration has an equal probability of occurring throughout the study area. To test this assumption of homogeneity, we used the Kolmogorov-Smirnov goodness-of-fit test to compare the observed distribution of nest-location x coordinates (i.e., longitude) with the distribution expected under complete spatial randomness (Baddeley 2008).

Another important consideration in point-pattern analyses is the possibility of edge effects, and how to select an appropriate edge correction. Edge effects arise because the points lying near the edge of the study area have fewer neighbors available in all directions than points located in the middle. Many edge corrections exist, and the shape and extent of the study area can be used as a guide for choosing among them (Haase 1995, Lancaster and Downes 2004). For the sites considered here, the biological justification for using edge corrections was mixed. Some portions of the study areas' boundaries should be considered hard boundaries because Saltmarsh Sparrows do not occur in the adjacent habitat (e.g., upland edges); hence, no correction is needed. Other areas had softer boundaries, such as river edges where we have regularly observed Saltmarsh Sparrows crossing en route to adjacent areas of marsh; in this situation it is ambiguous whether a correction is warranted. Still other areas had boundaries that were completely artificial and, thus, clearly necessitate an edge correction. Consequently, we ran all analyses with and without edge corrections for irregular polygonal study areas (when such a correction was available) and report any differences between the two sets of results as a test of the sensitivity of the results to edge-related bias.

Ripley's K ($K(r)$) is a cumulative test that allows the detection of clustered point patterns at successively larger spatial scales (Ripley 1979, 1981). We used this test with Ripley's isotropic edge correction (Ripley 1988) to test for the presence of clustering among nests at distance lags of r . We used the linearized form of K , $L(r) = (K(r)/\pi)^{0.5} - r$, to aid in interpretation and to stabilize the variance (Besag 1977, Haase 1995). Here, the expected number of nests in a circle of radius r is subtracted from $(K(r)/\pi)^{0.5}$, the observed number of nests in a circle with radius r . Under complete spatial randomness, the number of nests in a circle follows a Poisson distribution and $L(r) = 0$ for all distances. Variability in user-defined distances for this test can affect the outcome of Ripley's L , so we ran each test using the default range as prescribed

by SPATSTAT. The recommended range for the distance lags was 0–163 m for Hammonasset State Park and 0–156 m for East River Marsh. We did not perform this test without an edge correction because the exclusion of a weighting factor caused the values for the observed and expected $L(r)$ to converge after very few distance lags (Lancaster and Downes 2004).

Using Monte Carlo simulation methods, we generated 499 simulations of a homogeneous Poisson process of the same average density as that found at each study area. We defined 99% confidence envelopes for the $L(r)$ function by taking the lowest and highest values of the simulated $L(r)$ for each r . Values of $L(r)$ above the upper bounds of the confidence envelope indicate clustering, and those below the lower bounds indicate regularity.

To supplement this analysis, we also used the pair-correlation function (PCF) recommended by Stoyan and Stoyan (1994), which tests for interactions between points (i.e., nests) separated by a distance r and is related to Ripley's K . The PCF can be thought of as a circle centered at a given nest, where the only nests counted are those that lie on the circle boundary, whereas Ripley's K function counts all nests that are contained within the circle. The PCF is the probability of observing a pair of nests separated by a distance r , divided by the corresponding probability for a Poisson process (Baddeley 2008). Interpretation of the PCF is similar to that of Ripley's K , in that values above the upper bounds of the confidence envelope indicate clustering.

To assess the relative importance of vegetation in influencing settlement of female Saltmarsh Sparrows, we investigated spatial autocorrelation in habitat features within the marsh. If vegetation parameters are key determinants of settlement decisions, one would expect that clusters of nests would correspond to patches of especially favorable habitat. Although vegetation substrate type is not correlated with Saltmarsh Sparrow nest fate, the birds select nest sites where the vegetation has a greater maximum height, is denser, and has a higher proportion of *Spartina patens* than non-nest locations (Gjerdrum et al. 2005). To understand how the spatial structure of marsh vegetation compares to the settlement pattern of nesting Saltmarsh Sparrows, we used Moran's I to test for spatial autocorrelation (Moran 1948) in these three vegetation features. Where multiple measurements were taken of vegetation characteristics at a point (e.g., maximum vegetation height, stem density), the mean values were used. Moran's I is used to test the null hypothesis of no systematic pattern, or spatial autocorrelation, in the distribution of a quantitative variable (Cliff and Ord 1981); positive autocorrelation (aggregation) is indicated by positive values of the coefficient, negative autocorrelation (segregation) is indicated by negative values, and nonsignificant values (randomness) are close to 0.

To explore spatial autocorrelation at different scales, each vegetation parameter was tested using different distance classes (20, 50, 100) in the freely available software SAM (Rangel et al. 2006), with greater numbers of distance classes representing a finer-scale analysis. Each distance class was defined such that an approximately equal number of pairs of points were considered in each distance class (T. Rangel pers. comm.). Significance of Moran's I was tested for each distance class using a randomization procedure (Fortin and Dale 2005). Vegetation data for nest locations and randomly located points were analyzed both separately and in a combined data set. To account for non-independence

among distance classes, significance for each class was assessed using a sequential Bonferroni correction ($\alpha = 0.05$, $k = 1-20$, $1-50$, $1-100$) (Legendre and Legendre 1998). Moran's I values were then plotted as a correlogram against k distance classes to aid in interpretation (Fortin and Dale 2005). Only those values of the coefficient that were significant at the α/k level were used to interpret spatial structure (Fortin and Dale 2005). A positive, significant Moran's I value was taken as an indication of a patch of similarly structured vegetation, whereas a negative, significant value indicating dissimilar vegetation characteristics was interpreted as a space between patches (Amico et al. 2008).

The question of whether female Saltmarsh Sparrows use similar cues in their settlement decisions, irrespective of the exact nature of the cues used, was addressed in the tests of spatial randomness presented above. However, in these analyses, a focal nest's nearest neighbor could be a nest that was active before, during, or after the focal nest was initiated, or even a female's previous nesting attempt. We therefore conducted further tests, taking into account the order of nest establishment. We used an iterative procedure of nearest-neighbor tests to analyze the distribution of nests according to their initiation dates throughout the breeding season. We estimated initiation dates for each nest assuming 12 days of incubation and a 10-day nestling period, and using observations of laying, hatching, or fledge dates (Greenlaw and Rising 1994). When hatching and fledge dates were unknown because of early nest failure, we used a modification of the formula that Gjerdrum et al. (2005; originally from Martin et al. 1997) used to determine when incubation started: Initiation date = {date found – [(incubation period – number of days observed) ÷ 2]} – number of eggs in clutch. We determined end dates for each nest using the following criteria: (1) the last date the nest was observed active prior to nest failure, (2) the last date the nest was active according to iButton temperature data (available for 35 nests), and (3) the estimated fledge date based on a 10-day nestling phase and positive evidence of fledging.

To test whether female Saltmarsh Sparrows build nests closer to previously established nests than expected under complete spatial randomness, we calculated the NND for each nest, using only nests that were initiated on or before the focal nest's initiation date as potential neighbors. Each nest's NND was computed from a distinct data set that included only nests (number of neighbors = n) that could have served as a cue during nest placement (including, potentially, a female's own previous nesting attempt). We then simulated random placement of n points in the marsh, using the "nncross" and "runifpoint" commands in SPATSTAT (Baddeley and Turner 2005) to generate a unique, random simulation for each focal nest. The distance from each real nest to its nearest neighbor in the simulated-point data set was calculated. A paired t -test was used to compare the NNDs from the previously-active-nest data set with the NNDs of the random-point data set. Although testing whether females nest closer to previously active, successful nests than to previously active, failed nests is an important indicator of the use of social cues in nest-site selection (e.g., public information, *sensu* Valone and Templeton 2002), the synchronous nature of nest activity in the species made this analysis unfeasible. The majority of nesting attempts in the early part of the season were failures, whereas a second round of nesting that culminated in mid-July yielded many successful attempts. As a

result, only the females nesting very late in the breeding season had both failed and successful nests to use as cues; this sample was too small for a separate analysis.

To test whether females are attracted to settle near simultaneously nesting females, we also calculated the NND for each nest using only active nests as potential neighbors. We defined the active-nest data set for each nest as the set of nests that were active at the time of the focal nest's initiation date. Again, a distinct data set of active neighbors was created for each nest (number of neighbors = q), and the nearest-active-neighbor distance was calculated. A simulation of randomly located points was performed for each nest, using the number of active neighbors, q , as the basis for the number of points to be simulated. The distance from each nest to its nearest neighbor in the simulated-point data set was calculated. The NNDs from the active-nest data set were compared with the NNDs of the random-point data set using paired t -tests.

RESULTS

A total of 130 and 83 Saltmarsh Sparrow nests were found and monitored at Hammonasset State Park and East River Marsh, respectively (Fig. 1). None of the first- or second-order tests conducted showed strong evidence for clustered nesting. Clark and Evans aggregation indices revealed mild aggregation at the global level for both marshes (Hammonasset, $R = 0.89$; East River, $R = 0.88$) when a cumulative-distribution-function edge correction was used. When no edge correction was applied, the results were even more suggestive of a random pattern (Hammonasset, $R = 0.97$; East River, $R = 0.98$). Consistent with the conclusion that there was little clustering, comparison of Diggle's G function with the 99% confidence limits of the Poisson point-process null model failed to reveal a departure from complete spatial randomness at either study area (Figs. 2A, B). Finally, the assumption of homogeneity required for second-order analyses was met at both marshes (Kolmogorov-Smirnov: Hammonasset, $D = 0.08$, $P = 0.31$; East River, $D = 0.13$, $P = 0.12$). Comparison of the empirical $L(r)$ function with the 99% confidence intervals for the null hypothesis also revealed a lack of departure from spatial randomness at both study marshes, in all distance classes (Fig. 2C, D), as did results from the pair-correlation function test (Fig. 2E, F).

The level of spatial autocorrelation detected in the three salt-marsh vegetation variables differed between marshes and among variables, and depended on the type of points considered (Table 1). Of the 54 tests of spatial autocorrelation conducted (2 sites \times 3 vegetation variables \times 3 distance classes \times 3 point subsets), 44% (24 of 54) yielded no significant autocorrelation. The best support for patchiness in vegetation features was found for vegetation density (15 of 18 tests), and the least support was found for mean maximum vegetation height (4 of 18 tests). Significant spatial autocorrelation (i.e., patchiness) was detected at distances ranging from 15 to 90 m, depending on the number of classes and vegetation features considered. Although all point combinations yielded a similar number of significant tests—all points (9 of 18), nests only (10 of 18), and random (8 of 18)—the nature of spatial autocorrelation detected in each data set was sometimes inconsistent (e.g., spatial autocorrelation was strongest for maximum vegetation height at Hammonasset State Park and for percent *S. patens* at East River

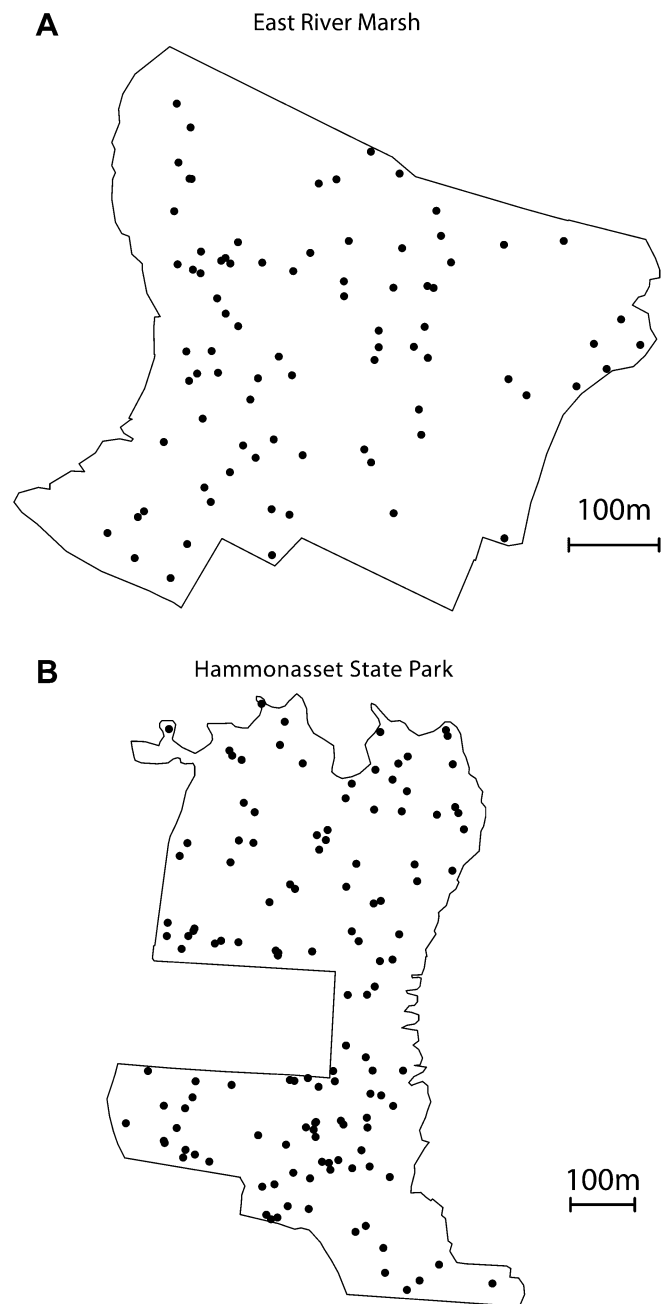


FIG. 1. Map of Saltmarsh Sparrow nest locations used in point-pattern analyses. Nests are from the 2007 breeding season at the (A) East River Marsh and (B) Hammonasset State Park study sites in Connecticut.

Marsh). Vegetation features at East River Marsh tended to exhibit more patchiness than those at Hammonasset State Park, and this patchiness persisted under all combinations of distance classes, point types, and vegetation parameters considered, with the exception of vegetation height. Vegetation features at Hammonasset State Park differed in their degree of patchiness, depending on the number of distance classes used and on whether nest locations, random locations, or all locations were considered.

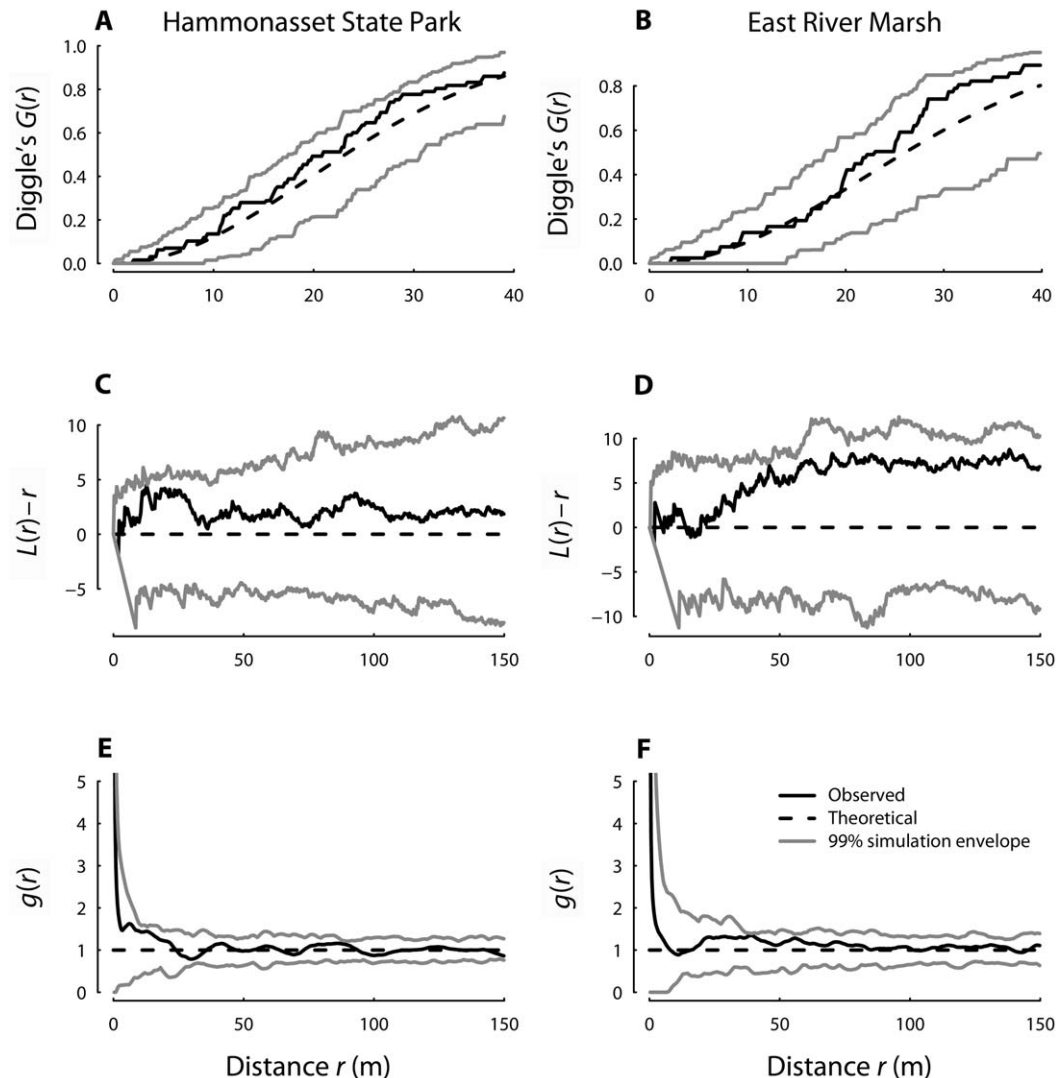


FIG. 2. (A, B) Comparison of Diggle's cumulative distribution function G , (C, D) Ripley's K (transformed to L), and (E, F) the pair-correlation function for Saltmarsh Sparrow nests at two Connecticut salt marshes. Solid black lines represent values for the point patterns (observed), dashed black lines represent the expectation under complete spatial randomness (theoretical), and gray lines represent the 99% confidence interval based on 499 randomizations of a Poisson point process. Values above the upper bounds of the confidence interval indicate clustering at distance r , and values below the lower bounds indicate regularity.

If female Saltmarsh Sparrows built their nests close to other current or previously established nests, this could be attributable to shared preference for a habitat characteristic (possibly unmeasured) rather than social cues. Females, however, did not place their nests in relation to previously active nests in a way that was significantly different from random placement (Hammonasset: t -test = 0.24, df = 127, P = 0.81; East River: t -test = -1.29, df = 80, P = 0.20), nor did simultaneously nesting females show evidence of aggregation in their nest placement. The distances between actively nesting nearest neighbors were not significantly different from the distances expected under random nest placement (Hammonasset: t -test = 0.67, df = 127, P = 0.50; East River: t -test = 0.18, df = 80, P = 0.86).

DISCUSSION

Although quantitative analysis of species distributions is now common at the landscape scale (Scott et al. 2002), it remains an underused tool for understanding settlement patterns and mechanisms of habitat selection at the local scale (Melles et al. 2009). Similarly, as our understanding of the potential role of social cues in avian habitat selection grows (e.g., Ahlring and Faaborg 2006), many have come to realize the importance of incorporating this information into models of species distributions, but they have lacked the data to do so (Blumstein and Fernández-Juricic 2004). Quantitative analysis of settlement patterns provides a tool to address these issues by allowing assessment of alternative hypotheses in advance of performing experimental tests.

TABLE 1. Results of Moran's I -tests of spatial autocorrelation for three vegetation features associated with Saltmarsh Sparrow nests. Each variable was evaluated using 20, 50, and 100 distance classes and three subsets of point vegetation data: all points, nests only, and random points only. The significance of Moran's I coefficients for each distance class was evaluated at the α/k level ($\alpha = 0.05$, $k = 1-20, 1-50, 1-100$). When significant spatial autocorrelation was detected at a given distance class, the median distance (m) of that class is reported; "NS" indicates that the result was not significant. When significant spatial autocorrelation was detected for multiple distance classes, the range of the median distance of the closest and farthest distance classes is reported, along with the maximum P value associated with those classes.

	Hammonasset State Park						East River Marsh					
	All points		Nests only		Random points		All points		Nests only		Random points	
	Distance	P	Distance	P	Distance	P	Distance	P	Distance	P	Distance	P
Vegetation height												
20 distance classes	NS		95	0.004	NS		NS		NS		NS	
50 distance classes	NS		23	0.018	NS		NS		NS		NS	
100 distance classes	15	0.020	15	0.034	NS		NS		NS		NS	
Percent <i>Spartina patens</i>												
20 distance classes	NS		NS		37	0.046	33–80	<0.004	NS		34	<0.001
50 distance classes	NS		NS		NS		21–90	<0.030	NS		21–82	<0.010
100 distance classes	NS		NS		NS		14	0.002	12	0.023	36–58	<0.018
Vegetation density												
20 distance classes	38	0.040	38	0.002	NS		33–150	<0.011	29	<0.001	34	<0.001
50 distance classes	23	<0.001	23	0.006	NS		21–90	<0.017	18–45	<0.002	21–52	<0.003
100 distance classes	NS		15	0.012	51	<0.001	14–46	<0.012	12–40	<0.014	14–58	<0.050

Despite a long history of anecdotal references to the "patchy local distributions" of Saltmarsh Sparrows (Greenlaw and Rising 1994), tests of aggregation at cumulative and discrete distance classes did not detect any significant nonrandom pattern in Saltmarsh Sparrow nests at either of our study sites. This finding is consistent with the view that nest placement is random with respect to other nests within suitable habitat. These tests addressed the similarity of nest-placement choices made by individual females, rather than directly shedding light on the mechanisms behind those choices. When the timing of nesting attempts was taken into account such that only previous or currently active nests were considered, however, there was no evidence that female Saltmarsh Sparrows attempted to nest closer to other nests. Although some patchiness in the underlying vegetation features of Saltmarsh Sparrow breeding habitat was identified, there was no evidence that females aggregated in response to this patchiness, and the degree of vegetation patchiness varied depending on the marsh and the variable considered. If we had detected aggregations in Saltmarsh Sparrow nests, incorporating vegetation patchiness into our null models would have been an essential step in determining whether aggregations were attributable to a shared preference for a habitat characteristic or to the use of social cues (e.g., Melles et al. 2009). Given the lack of evidence for aggregation, however, such tests were not warranted in our study.

Our findings are seemingly at odds with early studies of Saltmarsh Sparrows and indeed our own perception that sparrows aggregate in certain areas of the marsh. C. W. Townsend (in Forbush 1929) and Murray (1969), among others, also thought that Saltmarsh Sparrows congregate in certain areas of the marsh, leaving seemingly suitable habitat unoccupied. It is difficult to compare these early anecdotal reports of aggregation with the patterns observed in the present study, in part because we lack detailed information regarding Saltmarsh Sparrow populations and their

habitat at the time of these historical studies. Whether or not early reports of Saltmarsh Sparrow aggregations reflect a truly alternative distribution pattern to that of today's Saltmarsh Sparrows is not clear. One possible explanation for this discrepancy is that changes in Saltmarsh Sparrow population density or habitat availability have resulted in a change in settlement patterns. Similarly, we cannot be certain whether the patterns observed at our study marshes in one breeding season are representative of most years or sites. Our study marshes contain large populations and are considered relatively high-quality marshes; different patterns may occur in low-quality marshes where suitable marsh habitat is limited and Saltmarsh Sparrow density is low. Annual changes in settlement patterns are unlikely, however, given that vegetation composition and hydrology are fairly consistent on a year-to-year basis. Moreover, our anecdotal observations in multiple years and in multiple marshes provide no reason to believe that there was anything atypical about the data used here. A final possibility, and the one that we find most plausible, is that it is simply difficult for humans to distinguish among spatial patterns without careful quantitative analysis. Saltmarsh Sparrow nest densities differ considerably across marshes (Gjerdrum et al. 2008a), and it is possible that females nesting in proximity to one another are more noteworthy in our minds, especially if this behavior conforms to our expectation of clustered settlement patterns (i.e., confirmation bias; Nickerson 1998). These sensory weaknesses, coupled with biases in nest search-image that field workers inevitably develop (Rodewald 2004), highlight the need to conduct quantitative analyses of point patterns, rather than relying on the subjective nature of human perception.

Despite a lack of evidence to support the influence of conspecific cues in Saltmarsh Sparrow nest placement, it is plausible that some combination of social cues and habitat features are important factors in the habitat-selection process at a larger spatial scale.

Montagna (1942) reported that Saltmarsh Sparrow surveys in apparently suitable marshes sometimes yielded few or no individuals, yet Saltmarsh Sparrows were abundant in Long Island Sound marshes at the time of his research. More recently, Gjerdrum et al. (2008a) evaluated the performance of habitat-based Saltmarsh Sparrow distribution models using field data from 30 study plots. Although the habitat models did moderately well in explaining Saltmarsh Sparrow abundance and nesting activity within study plots, they were poor predictors of Saltmarsh Sparrow activity in cross-validation tests and at new sites, which suggests that habitat features alone are insufficient to explain Saltmarsh Sparrow distributions. Both of these studies indicate that cues at the landscape level could be more important than local nest-placement cues for habitat selection in this species. If the density of conspecifics in a potential habitat area is a critical factor in individual settlement decisions, conspecific attraction at the marsh level would be an important mechanism driving Saltmarsh Sparrow distributions. Exactly where females nest within a given marsh may be less important.

The nature of nest failure in this species is such that fine-scale differences in elevation and vegetation at nest locations may be largely irrelevant. Nest failure is primarily caused by flooding events associated with monthly high tides (>60% of all failures; DeRagon 1988, Shriver 2002, Gjerdrum et al. 2005); females that nest synchronously with the tide have a greater chance of successfully fledging young (Shriver et al. 2007), regardless of nest vegetation characteristics (Gjerdrum et al. 2005). Given these results, one would like to know whether nests that succeed (or fail because of flooding, predation, etc.) are more clumped than is expected by chance. For example, if nests that succeed are clustered, it would suggest that either the processes driving nest fate, such as predation or tidal flooding, do not act uniformly across the habitat or that there is some benefit to nesting in groups. This analysis could be achieved by “marking” each nest in accordance with its fate and performing a bivariate or multitype version of the point-pattern analyses outlined here (for methods, see Baddeley 2008; also see Gießelmann et al. 2008). However, because such tests would need to be conducted for simultaneously nesting females (i.e., to detect spatial associations between temporally coincident failures) rather than the entire nest data set, we lacked the sample sizes necessary for each nest-fate type to perform these analyses.

Animal ecologists often express concern about the degree to which habitat-selection studies fail to predict species occurrence (Garshelis 2000, Jones 2001), and these failures have been attributed to a range of factors (Scott et al. 2002). The scale or extent of the study may be inappropriate (Maurer 2002, Trani 2002), behavioral interactions are often ignored (Stamps 1988, Smallwood 2002), and the failure to consider the hierarchical structure of the habitat-selection process may play a role (Wiens 1989, Battin and Lawler 2006, Gjerdrum et al. 2008a). The spatially explicit approach presented here addresses the behavioral aspect of this issue and allows researchers to generate and test specific hypotheses of habitat-selection mechanisms using a commonly collected type of data. Ultimately, understanding when the absence of Saltmarsh Sparrows at the landscape level should be ascribed to a deficiency in the physical habitat rather than to a lack of social cues remains a crucial step in understanding habitat selection in this and many other species.

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LITERATURE CITED

- AHLERING, M. A., AND J. FAABORG. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? *Auk* 123:301–312.
- AMICO, G., D. GARCIA, AND M. A. RODRIGUEZ-CABAL. 2008. Spatial structure and scale-dependent microhabitat use of endemic “tapaculos” (Rhinocryptidae) in a temperate forest of southern South America. *Ecología Austral* 18:169–180.
- BADDELEY, A. 2008. Analysing spatial point patterns in R. *In* Workshop Notes, version 3. CSIRO, Australia. [Online.] Available at www.csiro.au/resources/pf16h.html.
- BADDELEY, A., AND R. TURNER. 2005. SPATSTAT: An R package for analyzing spatial point patterns. *Journal of Statistical Software* 12:1–42.
- BATTIN, J., AND J. J. LAWLER. 2006. Cross-scale correlations and the design and analysis of avian habitat selection studies. *Condor* 108:59–70.
- BAYARD, T. S. 2010. Testing the role of social cues in Saltmarsh Sparrow habitat selection decisions. Ph.D. dissertation, University of Connecticut, Storrs.
- BESAG, J. 1977. Contribution to the discussion of Dr. Ripley’s paper. *Journal of the Royal Statistical Society, Series B* 39:193–195.
- BLUMSTEIN, D. T., AND E. FERNÁNDEZ-JURICIC. 2004. The emergence of conservation behavior. *Conservation Biology* 18:1175–1177.
- BOURQUE, J., AND A. DESROCHERS. 2006. Spatial aggregation of forest songbird territories and possible implications for area sensitivity. *Avian Conservation and Ecology* 1. [Online.] Available at www.ace-eco.org/vol1/iss2/art3/.
- BROWN, C. R., AND M. B. BROWN. 2000. Nest spacing in relation to settlement time in colonial Cliff Swallows. *Animal Behaviour* 59:47–55.
- CLARK, P. J., AND F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- CLIFF, A., AND J. ORD. 1981. *Spatial Processes: Models and Applications*. Pion, London.
- CORNULIER, T., AND V. BRETAGNOLLE. 2006. Assessing the influence of environmental heterogeneity on bird spacing patterns: A case study with two raptors. *Ecography* 29:240–250.
- DANCHIN, E., T. BOULINIER, AND M. MASSOT. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. *Ecology* 79:2415–2428.

- DERAGON, W. R. 1988. Breeding ecology of seaside and sharp-tailed sparrows in Rhode Island salt marshes. M.S. thesis, University of Rhode Island, Kingston.
- DIGGLE, P. J. 1979. Statistical methods for spatial point patterns in ecology. International Cooperative Publishing House, Fairland, Maryland.
- DIGGLE, P. J. 2003. Statistical Analysis of Spatial Point Patterns, 2nd ed. Arnold, London.
- ELPHICK, C. S., T. BAYARD, S. MEIMAN, J. M. HILL, AND M. A. RUBEGA. 2009. A comprehensive assessment of the distribution of Saltmarsh Sharp-tailed Sparrows in Connecticut. Final report to the Long Island Sound License Plate Program and the Connecticut Department of Environmental Protection. University of Connecticut, Storrs.
- FORBUSH, E. H. 1929. Land birds from sparrows to thrushes. Pages 61–64 in *Birds of Massachusetts and Other New England States*, part 3. Massachusetts Department of Agriculture, Norwood.
- FORTIN, M.-J., AND M. R. T. DALE. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, United Kingdom.
- GARSHELIS, D. L. 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. Pages 111–164 in *Research Techniques in Animal Ecology: Controversies and Consequences* (L. Boitani and T. K. Fuller, Eds.). Columbia University Press, New York.
- GIESSELMANN, U. C., T. WIEGAND, J. MEYER, M. VOGEL, AND R. BRANDL. 2008. Spatial distribution of communal nests in a colonial bird: Benefits without costs? *Austral Ecology* 33:607–613.
- GJERDRUM, C., C. S. ELPHICK, AND M. RUBEGA. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: The importance of nest habitat, timing, and study site differences. *Condor* 107:849–862.
- GJERDRUM, C., C. S. ELPHICK, AND M. A. RUBEGA. 2008a. How well can we model numbers and productivity of saltmarsh sharp-tailed sparrows (*Ammodramus caudacutus*) using habitat features? *Auk* 125:608–617.
- GJERDRUM, C., K. SULLIVAN-WILEY, E. KING, M. RUBEGA, AND C. S. ELPHICK. 2008b. Egg and chick fates during tidal flooding of saltmarsh sharp-tailed sparrow nests. *Condor* 110:579–584.
- GREENLAW, J. S., AND J. D. RISING. 1994. Sharp-tailed sparrow (*Ammodramus caudacutus*). In *The Birds of North America*, no. 112 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- HAASE, P. 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *Journal of Vegetation Science* 6:575–582.
- HILL, C. E., C. GJERDRUM, AND C. S. ELPHICK. 2010. Extreme levels of multiple mating characterize the mating system of the Saltmarsh Sparrow (*Ammodramus caudacutus*). *Auk* 127:300–307.
- HILL, N. P. 1968. *Ammodramus caudacutus caudacutus* (Gmelin): Eastern sharp-tailed sparrow. Pages 795–812 in *Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies*, part 2 (O. L. Austin, Jr., Ed.). U.S. National Museum Bulletin, no. 237.
- JONES, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* 118:557–562.
- LANCASTER, J., AND B. J. DOWNES. 2004. Spatial point pattern analysis of available and exploited resources. *Ecography* 27:94–102.
- LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical Ecology, 2nd ed. Elsevier, Amsterdam, The Netherlands.
- MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HOCHACHKA, P. ALLEN, AND W. JENKINS. 1997. BBIRD Field Protocol. Biological Resources Division, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.
- MAURER, B. A. 2002. Predicting distribution and abundance: Thinking within and between scales. Pages 125–132 in *Predicting Species Occurrences: Issues of Accuracy and Scale* (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Hafler, M. G. Raphael, W. A. Wall, and F. B. Samson, Eds.). Island Press, Washington, D.C.
- MELLES, S. J., D. BADZINSKI, M.-J. FORTIN, F. CSILLAG, AND K. LINDSAY. 2009. Disentangling habitat and social drivers of nesting patterns in songbirds. *Landscape Ecology* 24:519–531.
- MONTAGNA, W. 1942. The sharp-tailed sparrows of the Atlantic coast. *Wilson Bulletin* 54:107–120.
- MORAN, P. A. P. 1948. The interpretation of statistical maps. *Journal of the Royal Statistical Society, Series B* 10:243–251.
- MURRAY, B. G., JR. 1969. A comparative study of the Le Conte's and sharp-tailed sparrows. *Auk* 86:199–231.
- NICKERSON, R. S. 1998. Confirmation bias: A ubiquitous phenomenon in many guises. *Review of General Psychology* 2:175–220.
- PERRY, G. L. W., B. P. MILLER, AND N. J. ENRIGHT. 2006. A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology* 187:59–82.
- RANGEL, T. F. L. V. B., J. A. F. DINIZ-FILHO, AND L. M. BINI. 2006. Towards an integrated computational tool for spatial analysis in macro-ecology and biogeography. *Global Ecology and Biogeography* 15:321–327.
- R DEVELOPMENT CORE TEAM. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. [Online.] Available at www.R-project.org.
- REED, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13:232–241.
- REED, J. M., T. BOULINIER, E. DANCHIN, AND L. W. ORING. 1999. Informed dispersal: Prospecting by birds for breeding sites. Pages 189–259 in *Current Ornithology*, vol. 15 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.
- RIPLEY, B. D. 1979. Simulating spatial patterns: Dependent samples from a multivariate density. *Applied Statistics* 28:109–112.
- RIPLEY, B. D. 1981. *Spatial Statistics*. Wiley, New York.
- RIPLEY, B. D. 1988. *Statistical Inference for Spatial Processes*. Cambridge University Press, Cambridge, United Kingdom.
- RODEWALD, A. D. 2004. Nest-searching cues and studies of nest-site selection and nesting success. *Journal of Field Ornithology* 75:31–39.
- SCOTT, J. M., P. J. HEGLUND, M. L. MORRISON, J. B. HAFLER, M. G. RAPHAEL, W. A. WALL, AND F. B. SAMSON, Eds. 2002. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, D.C.
- SHRIVER, W. G. 2002. Conservation ecology of salt marsh birds in New England. Ph.D. dissertation, State University of New York, Syracuse.
- SHRIVER, W. G., P. D. VICKERY, AND T. P. HODGMAN. 2007. Flood tides affect breeding ecology of two sympatric sharp-tailed sparrows. *Auk* 124:552–560.

- SMALLWOOD, K. S. 2002. Habitat models based on numerical comparisons. Pages 83–96 *in* Predicting Species Occurrences: Issues of Accuracy and Scale (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, Eds.). Island Press, Washington, D.C.
- STAMPS, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–347.
- STAMPS, J. A. 1994. Territorial behavior: Testing the assumptions. Pages 173–232 *in* Advances in the Study of Behavior, vol. 23 (P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and M. Milinski, Eds.). Academic Press, New York.
- STOYAN, D., AND H. STOYAN. 1994. Fractals, Random Shapes and Point Fields: Methods of Geometrical Statistics. Wiley, New York.
- TRANI, M. 2002. The influence of spatial scale on landscape pattern description and wildlife habitat assessment. Pages 141–156 *in* Predicting Species Occurrences: Issues of Accuracy and Scale (J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, Eds.). Island Press, Washington, D.C.
- VALONE, T. J., AND J. J. TEMPLETON. 2002. Public information for the assessment of quality: A widespread social phenomenon. *Philosophical Transactions of the Royal Society of London, Series B* 357:1549–1557.
- WARD, M. P., AND S. SCHLOSSBERG. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–525.
- WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- WOOLFENDEN, G. E. 1956. Comparative breeding behavior of *Ammodramus caudacuta* and *A. maritima*. University of Kansas Museum of Natural History 10:45–75.

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