Incorporating Social Information to Improve the Precision of Models of Avian Habitat Use

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INCORPORATING SOCIAL INFORMATION TO IMPROVE THE PRECISION OF MODELS OF AVIAN HABITAT USE

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Abstract. Correlations between habitat measures and animal distributions are not always applicable outside the study area that generated them. In such cases, the particularities of these correlations likely arise because only use of the local habitat has been quantified, rather than actual habitat selection, as the distribution models do not account for the behavior of animals in choice. The addition of covariates accounting for selection strategies could improve the precision and accuracy of correlative models of habitat use, but this conjecture has received little empirical attention. To evaluate this possibility, we re-assess previously developed habitat-use models for abundance of males of three grassland birds by explicitly including two measures of selection behavior: the “propensity to aggregate” and “propensity to use social information.” Habitat-use models for Nelson’s Sharp-tailed Sparrow (Ammodramus nelsoni) were not improved by either behavioral variable. However, models for two other species, the Bobolink (Dolichonyx oryzivorus) and Savannah Sparrow (Passerculus sandwichensis), improved substantially through reduced prediction error (assessed with cross-validation) and were much more likely to be an appropriate model (by reducing the deviance of the fitted models). These results indicate that habitat-selection models can be an improvement over correlative habitat-use models. In our case, these improvements were limited to two species in which individuals use their conspecifics as cues of local habitat quality. However, numerous other measures of selection behavior can be included to improve upon certain habitat-use models, particularly when those models depart unexplainedly from optimality theory.

Key words: aggregation, conspecific attraction, habitat selection, producer–scrounger game, social information

Introducción. Las correlaciones entre algunas medidas del hábitat y las distribuciones de los animales no siempre son aplicables fuera del área de estudio en donde fueron generadas. En esos casos, las particularidades de dichas correlaciones probablemente aparecen debido a que sólo se ha cuantificado el uso del hábitat a nivel local y no la selección real de hábitat, ya que los modelos de distribución no consideran el comportamiento de los animales en la selección. La adición de covariables que consideran las estrategias de selección podría mejorar la precisión y exactitud de los modelos correlativos de uso de hábitat, pero esta conjetura ha recibido poca atención empírica. Para evaluar esta posibilidad, reevaluamos modelos de uso de hábitat desarrollados previamente para la abundancia de los machos de tres especies de aves de pastizales incluyendo de forma explícita dos medidas del comportamiento de selección: la “propensión a agruparse” y la “propensión a utilizar información social”. Los modelos para Ammodramus nelsoni no mejoraron con la inclusión de ninguna de las variables de comportamiento. Sin embargo, los modelos para otras dos especies (Dolichonyx oryzivorus y Passerculus sandwichensis) mejoraron sustancialmente mediante la reducción en el error de predicción (evaluado mediante validación cruzada) y presentaron una probabilidad mucho mayor de ser modelos adecuados (reduciendo la desviación de los modelos ajustados). Estos resultados indican que los modelos de selección de hábitat pueden representar una mejora en comparación con los modelos correlativos de uso de hábitat. En nuestro caso, la mejora se limitó a los casos de dos especies en las que los individuos usan a sus conspecificos como señales de la calidad del hábitat a nivel local. Sin embargo, muchas otras medidas del comportamiento de selección podrían considerarse para mejorar algunos modelos de uso de hábitat, particularmente cuando esos modelos se desvían de la teoría de optimidad de forma inexplicada.

INTRODUCTION

Patterns of animal distribution are the product of the environment, chance, and endogenous reactions of animals to these factors. Distribution patterns are usually interpreted from a perspective of use versus availability to infer habitat selection (e.g., “resource selection functions”; Manly et al. 1993). However, models such as resource-selection functions have limitations; they are unpredictably sensitive to sampling design (Keating and Cherry 2004) and require the researcher to...
know something about why and how a population’s distribution is limited (Boyce and McDonald 1999). In some cases, models may accurately predict an animal’s distribution across a broad geographic range, such as when they describe processes that are clearly density-dependent (e.g., Morris 1987, 1990, Morris et al. 2004). Conversely, some models may be less spatially robust, particularly when the processes that regulate distribution are not well known (Petit et al. 2003). Shortcomings of such models are apparent when animals aggregate in patterns different from those of their measured resources (e.g., Greene and Stamps 2001, Tarof and Ratcliffe 2004, Nocera et al. 2009). Sometimes what appears to be excellent habitat is underused while what appears to be mediocre habitat is used (Stamps 2001, Shochat et al. 2002, Battin 2004).

Although part of the problem may be how we define “habitat” and “quality,” some models may be less robust because they take for granted the animal’s actual behavior in selecting a site (Kramer et al. 1997). Furthermore, the adaptive significance of such behavior is rarely considered in interpretation of models (Clark and Shutler 1999). The quantifications from resource-selection functions and other similar models (e.g., compositional analyses, Bingham and Brennan 2004) tend to depict only habitat “use,” because animals are observed using a patch of habitat, but they may not entirely represent “selection,” because the animal’s behavior in choosing the habitat is not observed (Johnson 1980, Kramer et al. 1997). This important distinction is often ignored in animal-habitat studies (Hall et al. 1997). In general, when we observe an animal in a particular place, we assume it made the choice to be there. However, what limits our attempts to model selection of habitat adequately is that we usually do not know what its options were or what strategy it followed when making its choice(s). As a rule of thumb, we could more simply consider habitat-use models as those that describe where and how many individuals there are in relation to habitat conditions, while habitat-selection models attempt to illustrate the choices animals make (Boyce and McDonald 1999). Most habitat-use models implicitly invoke optimality theory, so that when we observe an animal occupying a place, we assume that occupancy indicates an attempt to maintain or improve its fitness (Hildén 1965, Fretwell and Lucas 1970). Although animals may still be attending to individual fitness, some social behaviors can lead to complex distribution patterns that seem to defy the predictions of optimality theory (Kramer et al. 1997, Ridley et al. 2003, Arlt and Pärt 2007), such as traditionality in mating sites (Warner 1988), local inhibition (Slaa et al. 2003), local enhancement (Buckley 1996, Giraldeau 1997), or patterns of choice that vary by year (Schooley 1994, Haila et al. 1996). All these processes result from habitat-selection behavior of the animal and would not be described adequately by habitat-use models. Because distribution patterns are the additive result of individuals’ behavior (Goss-Custard and Sutherland 1997, Pöysä et al. 1998), some habitat-use models should therefore improve if they account for selection behavior (Kramer et al. 1997). There is an empirical basis for this suggestion; for instance, habitat-use models can be improved dramatically by incorporating spatial autocorrelation (e.g., Augustin et al. 1996). However, the processes generating the autocorrelation are generally unknown (Legendre 1993), and, therefore, the course of actually selecting habitats remains uncharted.

It is extremely difficult to manipulate, or account for, all options available to animals that are selecting a habitat; this level of knowledge would normally be restricted to laboratory experiments. Nonetheless, field-based models of habitat use will improve if at least some aspect(s) of selection behavior are included as covariates (Camponizzi et al. 2008). We suggest that some candidate covariates could account for the predominant strategies an animal uses to identify suitable habitat (Goss-Custard and Sutherland 1997), constraints on the selection process (Morrison 2001, Martin et al. 2008), and/or habitat types critical for certain behaviors (e.g., Zollner et al. 2000, Bos and Carthew 2003).

Such theorized improvements are starting to receive qualitative support. For instance, Zollner et al. (2000) built standard habitat-use models for the swamp rabbit (Sylvilagus aquaticus) but then applied these models to sites associated with specific behaviors, which highlighted markedly different models. Lindenmayer et al. (2003) acknowledged an apparent lack of fit for models of several Australian vertebrates and speculated the differences might be attributable to conspecific attraction. Camponizzi et al. (2008) reviewed similar cases. It is also possible that these patterns resulted from information transfer among heterospecifics (Seppänen et al. 2007). Bowler and Benton (2005) reviewed evidence to show that accounting for behavior can improve models of dispersal, to which they added that in many groups animals make decisions based on their internal state. This suggestion is important, as sites (e.g., for foraging, nesting, or movement) are often selected in a state-dependent way (Nonacs 2001, Stillman et al. 2002, Jonsen et al. 2003). Hence, there is a need to empirically illustrate the benefits of applying such suggestions, as in the case of improving habitat-use models by considering selection strategies. This is an important gap to fill because the proximate behavioral causes of habitat selection, and their ultimate consequences for fitness, are essential to our understanding of a species’ ecology and evolution, and thus its conservation and management (Stamps 1991, Clark and Shutler 1999, Morrison 2001).

To reveal how certain habitat-use models can be improved by accounting for selection strategies explicitly, as opposed to the implicit attribution of autocorrelation, we examine breeding-site selection by males of three species of migratory grassland birds: the Bobolink (Dolichonyx oryzivorus), Savannah Sparrow (Passerculus sandwichensis), and the Acadian race of Nelson’s Sharp-tailed Sparrow (Ammodramus nelsoni subvirgatus; hereafter Nelson’s Sparrow). These three species are useful for elucidating the contributions of behavior to habitat-use models.
because they represent a gradient in sociality: the Bobolink is more gregarious and social (Martin and Gavin 1995), the Savannah Sparrow is also gregarious but sometimes found breeding as single pairs (Wheelwright and Rising 1993), and Nelson’s Sparrow is more nonsocial (Greenlaw and Rising 1994). The levels of conspecific attraction of the Bobolink and Nelson’s Sparrow are also markedly different (Nocera et al. 2006).

In our analyses, we account for the predominant strategy males of each species use in regard to conspecifics by measuring their propensity to aggregate. We also examine differences in information use by settlers of different age classes, which requires some introductory explanation. After initially assessing habitat features (Hildén 1965), inexperienced settlers (first-time breeders) can collect further information on many aspects of habitat quality by observing the settlement decisions of others (Stamps 1988, 1991, Serrano et al. 2004, Nocera et al. 2006) or evaluating their performance in breeding the previous year (Doligez et al. 2002, Danchin et al. 2004). In so doing, they are “scrounging” habitat information from others to help them make a decision about settlement. In contrast, some studies show that, older, more experienced breeders tend to ignore information from conspecifics and rely more on their own experience with a habitat (Serrano et al. 2001, Slaa et al. 2003, Nocera et al. 2006, 2009; however, see Hahn and Silverman 2006). These older individuals are thus likely to be producers of the habitat-quality information used by younger settlers. This interplay of information transmission from experienced to inexperienced settlers can be viewed as a simple solution for a stable producer–scrounger game (Barnard and Sibly 1981, Barta and Giraldeau 2001, Doligez et al. 2003). So, to account for these two different strategies of information use, we also quantify the ratio of younger (≤1 year) and older (>2 years) males with home ranges, per neighborhood (see Methods), and use this in new models as a proxy for the solution of the simple stable producer–scrounger game.

To determine if the addition of either or both selection-strategy variables improves predictive power, we compare the performance of existing habitat-use models with and without them. We predicted that models for the two more social species should improve when propensity to aggregate was included. Furthermore, although some species may not aggregate, young birds still need to gather habitat information, which may be done most quickly by observing conspecifics. We therefore predicted that incorporating ratios of age classes (as a proxy for a producer–scrounger game) should improve the baseline habitat-use models for each species studied.

METHODS

STUDY SPECIES AND SITES
We studied behavior of the Bobolink, Savannah Sparrow, and Nelson’s Sparrow in selecting breeding sites in hayfields of the western Annapolis Valley, Nova Scotia, Canada (centered on 44° 45’ N, 65° 30’ W). Male Bobolinks tend strongly to choose territories on the basis of presence of conspecifics (Martin and Gavin 1995, Nocera et al. 2006, 2009). Male Savannah Sparrows are less likely to choose territories by this criterion (Wheelwright and Rising 1993, Nocera et al. 2009). Nelson’s Sparrows are less gregarious and do not defend a territory but reside within “home ranges” (Greenlaw and Rising 1994). Each species arrives on the breeding grounds over a short period in May and completes its nesting cycle within 8 weeks (Nocera et al. 2005). For simplicity, we hereafter refer to Bobolink and Savannah Sparrow territories and the breeding areas occupied by Nelson’s Sparrow, as “home ranges.”

Our study was conducted from May to August, 2002–2004 at four diked marshes supporting numerous hayfields: Belleisle (210 ha), Upper Belleisle (116 ha), Queen Anne (180 ha), and Pea Round (142 ha). Mixtures of timothy (Phleum pratense), meadow fox-tail (Alopecurus pratensis), bluegrass (Poa spp.), and reed canary grass (Phalaris arundinacea) typify the hayfields at Queen Anne, Belleisle, and Upper Belleisle. The same mixtures of grasses are planted on Pea Round, with the addition of alfalfa (Medicago sativa).

No fields at our study sites were grazed, planted in crops other than forage, or received any pesticides during the study. Although hay harvest severely limits reproduction and habitat use by these species in other regions (Bollinger et al. 1990, Dale et al. 1997), at our study sites (except for some fields at Pea Round) the hay harvest was delayed until after 1 July to allow time for nesting and brood rearing (Nocera et al. 2005).

HABITAT-USE MODELS
We had previously used Poisson regression to determine how changes in the abundance of males were related to variables representing four broad categories of habitat features (vegetation, prey, management, and physiography) (Nocera et al. 2007). Table 1 lists the best models and the direction of the relationships. The abundance of male Bobolinks was associated primarily with variables related to vegetation (cover, forbs, alfalfa, and cordgrass) and the abundance of hemipteran prey. The abundance of male Nelson’s Sparrows was related to physiography (ditches) and the abundance of orthopteran prey. The abundance of male Savannah Sparrows was associated primarily with the abundance of prey of three orders of insects and the height and density of grass. Here, we briefly discuss the methods (see also Nocera et al. 2007) pertaining only to independent variables in those best models (Table 1).

We sampled the abundance of males at 52 stations, placed >175 m from each other across the four study sites. At each station, we conducted 5-min point counts (Hutto et al. 1986) of birds within a 50 m radius, between 30 min after sunrise and 10:00 AST (weather permitting: wind <25 km hr⁻¹, no precipitation). Each station was sampled 10–12 times per year. All point-count data were summarized as mean abundance to minimize the inflationary effects of floaters (Betts et al. 2005).

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TABLE 1. Best models describing habitat use by male Bobolinks, Savannah Sparrows, and Nelson’s Sparrows (from Nocera et al. 2007). Sign preceding the predictive variable indicates direction of the relationship to abundance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Best habitat-use model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bobolink</td>
<td>+ % vegetative cover + abundance of Hemiptera − % forbs − presence of alfalfa − presence of <em>Spartina</em></td>
</tr>
<tr>
<td>Nelson’s Sparrow</td>
<td>+ length of ditch + abundance of Orthoptera − abundance of Diptera − abundance of Chilopoda − abundance of Stylommatophora − height/density of grass</td>
</tr>
<tr>
<td>Savannah Sparrow</td>
<td>+ abundance of Orthoptera − height/density of grass</td>
</tr>
</tbody>
</table>

During May of each year, at four locations within 50 m of each count point, we measured grass height and density with a visual-obstruction pole (Robel et al. 1970) and quantified percent vegetation cover and forb cover within a 0.25-m² frame. We also recorded presence of alfalfa and slough cordgrass (*Spartina pectinata*), known to be important cover features for the Bobolink (Martin and Gavin 1995) and Nelson’s Sparrow (Greenlaw and Rising 1994), respectively. We quantified terrestrial invertebrates as the catch per unit effort from pitfall trapping; two pitfall traps (plastic cups 15 cm deep filled with 3–5 cm of soap and water) were deployed at each station and checked weekly. We also sampled, once per week, for aerial invertebrates by sweeping a sailcloth net through the grass canopy along a 10-m transect east and west of the count points. All captured specimens were identified to order, or further when possible. We also quantified the length of ditches within 50 m of each count point (measured from aerial photos, scale 1:10,000). At each site, ditches are approximately 75–150 m apart, so the grain size at which we mapped home ranges still allowed us to detect clusters of home ranges on this fairly regularly spaced resource.

AGE-RELATED STRATEGIES OF INFORMATION USE
Each of the three species can breed at the age of 1 year (Pyle 1997), so we define males as young if ≤1 year and as older if ≥2 years old. Previous studies have shown that older males of some species may select home ranges on the basis of their own experience (producing information for onlookers), while younger naïve males may tend to select home ranges on the basis of habitat information scrounged from others. To quantify this producer–scrounger game and apply it to our habitat-use models, we calculated the number of young and older breeding males in each cluster of home ranges (“neighborhood”; see Nocera et al. 2009) in each year (n = 12 neighborhoods per year per species). As per Nocera et al. (2009), we delineated neighborhoods by calculating an index of cluster size (Perry et al. 2002) while incrementally increasing our search window until we found an area size that maximized the index of cluster size and yielded a statistically significant difference from complete spatial randomness.

We captured the birds with mist nets and banded them with a standard U.S. Fish and Wildlife Service metal leg band and a unique combination of colored celluloid leg bands. During the breeding season, no criteria are known to identify the age classes Savannah and Nelson’s Sparrows at a resolution finer than hatch-year versus adult (Pyle 1997). Therefore, we limit our observations of these two species to 2003 and 2004, during which we knew the ratio of young to older males from whether they were banded as adults or hatch-year birds the previous year. For the Bobolink, plumage criteria for age classes have been developed (Pyle 1997, Nocera 2005) but are sometimes ambiguous. So, we likewise limit our observations to males of known age in 2003 and 2004, with the addition of a small number whose age was known by plumage in 2002.

AGGREGATIVE STRATEGIES
To determine whether our study species selected habitats because they were attracted to conspecifics (resulting in aggregations), avoided conspecifics (resulting in overdispersion), or did neither (resulting in a regular spatial pattern), we quantified the spatial patterns of marked males as another variable to add to our habitat-use models.

To determine the locations and sizes of home ranges, we resighted color-banded males (n = 61 Bobolinks, 68 Savannah Sparrows, and 69 Nelson’s Sparrows) during point counts and daily observations. Whenever we resighted a bird, we noted its identity and date of observation and mapped its location.

We used a derivative of Lloyd’s (1967) index of patchiness (IP) to measure aggregation (intensity of spatial clustering) of those home ranges, and we include it as a covariate (calculated for each neighborhood for each year) in our models. The IP is scale-independent and usually depicts the ratio of mean crowding to mean density (e.g., Reich 2004); here we supply instead the ratio between the variance (s²) and mean (𝜇) of the distance (measured in 50-m increments) between center points and a third attribute of spatial size (“area-referenced data”; Perry et al. 2002), which we here assign as the mean number of home ranges per neighborhood (η; note this is an adjustment to the equation as used in Nocera et al. 2009), so that

\[
IP = \frac{\bar{d} + \frac{s^2}{\bar{d}} - 1}{\eta}
\]

It is important to note that because IP is a measure of presence/absence patterns and not derived from abundance, in our analyses it is sensitive only to location and home-range size. IP values of 1 indicate random dispersion, values <1 indicate overdispersion, and values >2 indicate the number of times more crowding individuals face than if they were distributed in a Poisson manner. We calculated IP with the program PAS-SAGE (Rosenberg 2001).
REASSESSMENT OF MODELS

We compared the fit of habitat-use models developed by Nocera et al. (2007; Table 1) with and without the two proxy variables for selection strategy, age ratios and IP. We chose to retain the original models, rather than rebuild them, because we did not want to supersede the apparent proximate importance of the habitat features identified by those models. In other words, we sought not to overshadow the contribution of habitat (and its resources) to settlement decisions, only to make our understanding of the process stronger by assessing the contribution of behavior only. We therefore revisited the original regressions to produce a new competing set of models: (1) the original habitat-use only model, (2) the original habitat-use + IP, (3) the original habitat-use + age ratio, and (4) the original habitat-use + IP + age ratio. We did not include an interaction between IP and age ratio.

We compared deviances (divided by degrees of freedom) to discriminate among the regression models for each species and to determine if any improvement is made by additional variables. To demonstrate a model’s precision (a model may be more accurate but no more precise than another), we used delete-one cross-validation to calculate an accumulated prediction error (APE; Rissanen 1986) for each model. We evaluated APE through the minimization of

\[ \sum_{i=1}^{n} L[x_i, \hat{x}^{-1}(\rho)] \]

where, for each model i, \( \hat{x}^{-1}(\rho) \) (1 of 1000 cross-validations) forecasts the fit of the subsequent iteration \( x_i \). \( L \) is a function that measures how well the model \( (\rho) \) fits the data. For the purposes of this study, we consider a reduction in APE of >25% to represent a substantial increase in precision. We compared models and calculated APE in R (v. 2.6.2; R Development Core Team 2008).

RESULTS

AGE RATIOS

We estimated the age of 277 male Savannah Sparrows captured during the study. All neighborhoods combined, older males were outnumbered by younger males each year: 1:2.8 in 2003, 1:2.3 in 2004. In 74 Nelson’s Sparrows the ratio of older to younger was similar: 1:2.2 in 2003, 1:2.4 in 2004. In 101 Bobolinks, the ratio was 1:1.9 in 2002, 1:2.1 in 2003, and 1:2.5 in 2004.

PROPENSITY TO AGGREGATE

In all years, spatial clustering of home ranges of the Savannah Sparrow was strong, as indicated by high mean IP values (15.9 ± 4.1 in 2003, 26.1 ± 8.0 in 2004; here and throughout, means are presented ± SD). Bobolinks tended to cluster even more strongly, with IP values of 67.6 ± 12.4 in 2002, 77.8 ± 14.6 in 2003, and 41.0 ± 9.1 in 2004. Nelson’s Sparrows were not clustered but distributed more regularly, as indicated by an IP of −3.1 ± 1.7 in 2003 and −3.3 ± 1.5 in 2004.

MODEL SELECTION AND FIT

With the IP and age ratio added, we re-evaluated four regression models for each species (Table 2). For the Bobolink and Savannah Sparrow values of residual deviance were lowest for the global models (habitat use + IP + age ratio), indicating that adding IP and age ratio improved the model’s fit greatly. For both species, the original models incorporating habitat use only were clearly inferior; the residual deviance was ~10 times greater, indicating an ill-fitting model (Table 2). The non-saturated model (habitat use + age ratio) was also a contender for the best model that described Bobolink abundance, indicating some uncertainty in model selection.

For Nelson’s Sparrow, the set of best-fit models was very different (Table 2). The habitat-use-only model carried the lowest deviance value. The next lowest deviance value was for the model habitat-use + IP, which differed by only a fraction from that of the habitat-use-only model, indicating it is also plausible, and that selection of a model is somewhat uncertain. It is important to note that no models containing the age ratio were supported for this species.

MODEL PRECISION

For the Bobolink (Fig. 1a) and Savannah Sparrow (Fig. 1b), APE closely tracks the ranks of the models in Table 2. Cross-validated data, however, show substantial overlap for the habitat-use-only and habitat-use + IP models, indicating little difference in precision (Fig. 1a, b). In the global model (habitat use + IP + age ratio) of both species, the variability around the median is greatly reduced. The global model is more precise than the next model; there is no overlap with APE variability (Fig. 1a, b). We detected only one outlier (Fig. 1a, model 3), indicated by a satellite line and dot outside the box-and-whisker plot. The reverse is seen for Nelson’s Sparrow (Fig. 1c), as
both models containing the age ratio performed poorly. The median APE of the two models is similar. The habitat-use-only and habitat-use + IP models performed better but were also very similar, as the median and range of APE are not detectably different.

**DISCUSSION**

The inclusion of the two variables representing habitat-selection strategies (aggregation versus scattering and a difference by age class in use of information) greatly increased the fit and precision of models of abundance of our two more social species, the Bobolink and Savannah Sparrow. For these species, the top model included both variables, substantiating previous work (Nocera et al. 2009) showing the two age classes (males younger than 1 year and those 2 years or older) tend to aggregate. Our results for these species support the prediction that including selection strategies into models of habitat use describes abundance patterns better. An important next step is to test this prediction at other sites, with and without the two variables for habitat-selection behavior. Additionally, it would be worthwhile to examine the role of heterospecific interactions (e.g., heterospecific copying as reported by Seppänen and Forsman 2007); perhaps some of the patterns we observed were related to heterospecific dynamics we did not quantify.

Models of the abundance of Nelson’s Sparrow, a less social species, did not improve when the two variables were included, counter to one of our predictions. We reasoned that young males of each study species should evaluate habitat by observing the territories older birds chose, yet in all models for Nelson’s Sparrow that contained the age ratio, the fit and precision were strikingly reduced. The model of habitat use with IP was as adequate as the habitat-use model alone, indicating the males are no more aggregated than the habitat they occupy, which in our study area tends to be linear (e.g., unmowed ditches) and not clumped. Perhaps habitat is the only limiting force behind Nelson’s Sparrow’s abundance distribution, not behavior. Another possibility is that the birds refrained from aggregating because of the species’ polygynandrous mating strategy; perhaps males avoid each other to reduce cuckoldry.

Our model-improvement predictions were therefore correct in two of three cases, raising two important points: (1) habitat-selection strategies vary by species, and likely within a species, and (2) habitat-use models sometimes describe abundance adequately but at other times are unwittingly poor.

The propensity to aggregate toward conspecifics is an easily measured habitat-selection strategy that, all else being equal, is a behavioral basis for spatial autocorrelation (Campomizzi et al. 2008, Betts et al. 2009). However, a bird’s settling near conspecifics signifies that it was possibly using the presence of other individuals as a “location cue” of habitat quality (Danchin et al. 2004). The performance of other males

![FIGURE 1. Box-and-whisker plots of accumulated prediction error (APE; Rissanen 1986) for models of the abundance of males of the (a) Bobolink, (b) Savannah Sparrow, and (c) Nelson’s Sparrow. Model notation (x axes) is as follows: model 1 = habitat use only, 2 = habitat use + index of patchiness (IP), 3 = habitat use + age ratio, and 4 = habitat use + IP + age ratio. APE (y axes) was calculated through leave-one-out cross-validation; a reduction in APE indicates a more precise model. The boxes indicate the limits of the middle half of the cross-validation data, and the line inside is the median. The whiskers represent variability around the median in the remaining 50% of the data.](image-url)
interference is strong. Nonetheless, any interference among a quantification of the threat of predation (e.g., ratio of relevant producers to scroungers (or, in our case, older to younger birds). Although the aggregations we observed were driven by behavioral mechanisms associated with age, mechanisms among which information use is very likely to be important, we recognize that other behaviors, such as competitive ability, previous reproductive experience (success or failure), and reproductive potential, can also be age-dependent and could be considered.

We suggest that our prediction failed to apply to Nelson’s Sparrow because this species evaluates information other than location cues. Of the three species we studied, its breeding is the least synchronous (Nocera et al. 2005), so presumably the birds have more time to gather public information. In this polygynandrous species, multiple paternity within nests is extreme (Greenlaw and Rising 1994, Shriver 2002), indicating the possibility of a longer breeding period, giving the birds further opportunities to gather public information; the use of public information by this species remains to be tested. The regular distribution of male Nelson’s Sparrows’ home ranges suggests they follow an ideal free distribution (Fretwell and Lucas 1970); however, a regular spatial pattern could also be explained by interference; animals avoid one another when interference is strong. Nonetheless, any interference among Nelson’s Sparrows must be indirect because they do not defend a territory, allowing individuals free access to resources. We suggest that habitat-selection patterns of Nelson’s Sparrow may instead be related to heterospecifics that can act as information sources and/or interfering competitors; these predictions could be tested experimentally (e.g., Thomson et al. 2003, Betts et al. 2010).

When a habitat-use model has been developed for a species, a reasonable estimation of a habitat-selection strategy to be included as a covariate should improve its fit. The model’s precision should also be estimated (Campomizzi et al. 2008), and if the model is not made more precise, the hypothesized strategy is either wrong or is being overshadowed by other processes. If we had limited our assessment of Bobolink and Savannah Sparrow abundance to habitat-related variables only, our best model would have been substantially less likely to be an appropriate approximation (Table 2). By accounting for these species’ potential selection strategies, we explored the behavioral nature of spatial autocorrelation and enhanced the base habitat-use model, allowing us to track actual habitat selection more closely. It is worth noting that the extra variables we added to our models were of rather low resolution; 52 count points were distributed among approximately 12 neighborhoods, so at many stations the age ratio and IP were the same. We predict that adding variables of greater resolution should overcome this limitation and further enhance the reliability of habitat-selection models.

We recognize that obtaining variables with greater resolution may not always be possible. Indeed, the method we describe requires substantial a priori information on the local system under study (e.g., territory sizes, distributions, age ratios). Such information is rarely readily available, and in such cases we suggest the next best thing may be to consider proxies for approaches based in game theory, which instead require more general knowledge of intra- and interspecific interactions. In our case, we reasoned that the interaction between older and younger prospecting birds should resemble a producer–scrounger game; to represent this, we therefore simply included age class as a variable in our models. The ratio of producers to scroungers (or, in our case, older to younger prospectors) is just one of many evolutionarily stable strategies resulting from applications of game theory (Maynard-Smith 1982). There are likely many opportunities to include variables that represent frequency-dependent evolutionarily stable strategies, so long as there is a precedent (e.g., from the literature) to believe that a particular game may be relevant to a system. For another example, Mitchell and Angilletta (2009) illustrated how, in a “thermal game,” the distribution of a prey species among habitat patches of differing quality can be a response to the threat of predation. That study found that the evolutionarily stable strategy was for prey to distribute itself randomly when faced with very effective predators; a quantification of the threat of predation (e.g., ratio of relevant
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LITERATURE CITED


ROSENBERG, M. S. 2001. PASSAGE. Pattern analysis, spatial statistics, and geographic exegesis, version 1.1 (release 2.3). Department of Biology, Arizona State University, Tempe, AZ.


