1-2013

Evaluating The Roles Of Visual Openness And Edge Effects On Nest-Site Selection And Reproductive Success In Grassland Birds

Alexander C. Keyel

Allan M. Strong

Noah G. Perlut
University of New England, nperlut@une.edu

J. Michael Reed

The Auk 130(1):161–170, 2013

EVALUATING THE ROLES OF VISUAL OPENNESS AND EDGE EFFECTS ON NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS IN GRASSLAND BIRDS

Alexander C. Keyel,[1,4] Allan M. Strong,[2] Noah G. Perlut,[3] and J. Michael Reed[1]

[1]*Department of Biology, Tufts University, 163 Packard Avenue, Medford, Massachusetts 02155, USA;*
[2]*Rubenstein School of Environmental and Natural Resources, University of Vermont, 347 Aiken Center, Burlington, Vermont 05405, USA; and*
[3]*Department of Environmental Studies, University of New England, 11 Hills Beach Road, Biddeford, Maine 04074, USA*

Abstract.—In some species, habitat edges (ecotones) affect nest-site selection and nesting success. Openness, or how visually open a habitat is, has recently been shown to influence grassland bird density and may affect nest-site selection, possibly by reducing the risk of predation on adults, nests, or both. Because edge and openness are correlated, it is possible that effects of openness have been overlooked or inappropriately ascribed to edge effects. We tested the roles of edges and visual openness in nest-site selection and nesting success of two grassland passerines, the Bobolink (*Dolichonyx oryzivorus*) and Savannah Sparrow (*Passerculus sandwichensis*), in the Champlain Valley, Vermont. We also evaluated the sensitivity of our results to alternative definitions of edge on our landscape. Bobolink (n = 580) and Savannah Sparrow nests (n = 922) were located on seven hay fields and three pastures from 2002 to 2010. Both species avoided placing nests near edges and in less open habitat compared with expectations based on random placement. When the effects of openness and edge were separated, less open habitats were still avoided, but edge responses were less clear. These results were robust to different definitions of habitat edge. We found no strong relationships between either openness or edges and reproductive success (numbers of eggs and fledglings, percentage of eggs producing fledglings, and nest success), although there may be an edge-specific openness effect on timing of reproduction (clutch completion date). Our results support openness as an important factor in nest-site selection by grassland birds. *Received 9 March 2012, accepted 9 November 2012.*

Key words: antipredator, Bobolink, *Dolichonyx oryzivorus*, fragmentation, habitat selection, openness, *Passerculus sandwichensis*, reproductive success, Savannah Sparrow.

Evaluacion del Papel de La Apertura Visual y los Efectos de Borde en la Selección de Sitios de Anidación y el Éxito Reproductivo en Aves de Pastizal

Resumen.—En algunas especies, los bordes del hábitat (ecotonos) afectan la selección desitios de anidación y el éxito reproductivo. Recientemente se ha demostrado que el grado de apertura (qué tan abierto es un hábitat visualmente) podría afectar la selección del sitio de anidación, posiblemente al reducir el riesgo de depredación de los adultos, los nidos o ambos. Dado que la apertura y el efecto de borde están correlacionados, es posible que los efectos de la apertura hayan sido pasados por alto o descritos inapropiadamente como efectos de borde. Probamos el rol del efecto de borde y de la apertura en la selección del sitio de anidación y en el éxito reproductivo de dos paserinos de pastizal, *Dolichonyx oryzivorus* y *Passerculus sandwichensis*, en el valle de Champlain, Vermont. También evaluamos la sensibilidad de nuestros resultados a definiciones alternativas de borde en nuestro paisaje. Los nidos de *D. oryzivorus* (n = 580) y de *P. sandwichensis* (n = 922) se localizaron en siete campos de heno y tres pastizales entre 2002 y 2010. Ambas especies evitaron ubicar los nidos cerca a los bordes y en hábitats menos abiertos, comparado con lo esperado si la ubicación fuese al azar. Cuando se separaron los efectos del borde y de la apertura, los hábitats menos abiertos siguieron siendo evitados, pero las respuestas al borde fueron menos evidentes. No encontramos una relación fuerte entre la apertura o el efecto de borde del hábitat y el éxito reproductivo (número de huevos y volantones, porcentaje de huevos que producen volantones y éxito de anidación), aunque podría haber un efecto de la apertura específica del borde en la sincronización de la reproducción (fecha de terminación de la nidada). Nuestros resultados apoyan la idea de que la apertura es un factor importante en la selección del sitio de anidación por parte de las aves de pastizal.

Hildén (1965) made the observation that the nesting behavior of some species appeared to depend on the openness of habitat, and there is a strong theoretical basis for why that may be. For instance, some species depend on open habitat as part of their antipredator escape tactics (e.g., Lima 1993) because species in open areas may be better able to detect predators (e.g., Amat and Masero 2004) and may be less detectable by predators (e.g., Andersson et al. 2009). Early detection of predators can substantially

[4]E-mail: skeyel@gmail.com

The Auk, Vol. 130, Number 1, pages 161–170. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2012.12039

increase a prey species' chances of surviving (Kenward 1978) and of driving off nest predators (Klomp 1954). In addition to direct predation, perceived predation risk can be affected by the openness of the habitat (e.g., Lima and Valone 1991). Recent work has suggested that increased openness or factors related to openness may increase grassland bird occupancy and density (Bakker et al. 2002, Renfrew and Ribic 2002, Grant et al. 2004, Winter et al. 2006, Keyel et al. 2012). Openness can also affect nest placement. In results based on a surrogate measure, Burrowing Owls (*Athene cunicularia*) avoided nest sites within 50 m of trees or perches (Uhmann et al. 2001).

We evaluated nest placement and success by two ground-nesting, grassland obligate species, Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*), in relation to habitat openness. We hypothesized (1) that both species would select more open locations for their nests, because this may lower adult predation risk; and (2) that this result would be more biologically informative than a measure of distance to edge. An alternative rationale is that if nest success is greater in more open habitat, these species may select more open locations to reduce the likelihood of losing their clutches. On the basis of research on Northern Lapwings (*Vanellus vanellus*; Klomp 1954), we also hypothesized that nests in more open locations would have lower rates of failure and higher fledging success than nests in more closed locations. Finally, in a predator removal study, birds in areas with reduced nest predation risk laid larger clutches (Fontaine and Martin 2006). Therefore, we hypothesized that increased reproductive allocation would result in a greater number of eggs laid in more open locations because of a potential decrease in perceived predation risk. Our objective was to evaluate multiple possible mechanisms that could lead to nesting preferentially in open sites by examining nest placement and nesting success.

Wooded edges, especially those with tall trees, can reduce openness, so evaluating openness can be confounded by potential edge effects. Consequently, it was necessary to examine the correlation between openness and distance to edge, and test whether any effects ascribed to openness could be explained by distance to edge. In the course of evaluating edges, our research group derived very different definitions of edge, and these definitions were influenced by different perspectives on the grassland bird literature and varying amounts of direct experience with the study sites. This could be a problem with a variety of field settings and species perceptions. For example, Paton (1994) found wide discrepancies in the way researchers classified edges for forest patches; edge discrepancies might be responsible for some interstudy differences in reported edge effects within species. Hence, we analyzed our nesting data using two alternative digitizations of edges at our study sites.

METHODS

Study site, study species, and nest searching.—We worked in the Champlain Valley of Vermont and New York, an area that includes 146,000 ha of managed grasslands (National Agricultural Statistics Service 2010). We sampled seven hay fields and three pastures in Hinesburg and Shelburne, Vermont (fields within 44°20.2′–44°24.5′N and 73°9.1′–73°16.6′W). Field size range was 13.2–38.3 ha (mean 21.1 ha), and the vegetation was composed of a mixture of cool-season grasses and forbs (for details on vegetation, see Perlut et al. 2006). The 10 study fields represent the four most common grassland treatment types in the Champlain Valley (Perlut et al. 2008). Early-hayed fields (n = 2) were harvested between 27 May and 11 June and, generally, again in early to mid-July. Middle-hayed fields (n = 3) were harvested between 21 June and 10 July. Late-hayed fields (n = 2) were harvested after 1 August, after birds had ended their reproductive season. Rotationally grazed pastures (n = 3) were fields in which cows were rotated through a matrix of paddocks every 7–10 days, depending on the paddock and growing conditions. Each paddock was thereby given a multiple-week "rest" between grazing events.

From 2002 to 2010, fields were searched for Bobolink and Savannah Sparrow nests from mid-May to late July. We found nests through behavioral observations and by flushing incubating birds off nests by swishing bamboo stakes as we walked through the fields. We visited each nest every 1 to 2 days between 0500 and 1400 hours (EST) until it either produced fledglings or failed. Global positioning system (GPS) locations were recorded with a Garmin Etrex Legend, and dates of clutch completion, numbers of eggs, and numbers of fledglings were recorded, as described in Perlut et al. (2006).

In order to contrast responses to openness and responses to edges, it is necessary to have study species that potentially respond to both. Both of our study species have been shown to respond negatively to edges (e.g., O'Leary and Nyberg 2000, Bollinger and Gavin 2004), and Bobolinks have been shown to respond positively to openness (Renfrew and Ribic 2002, Keyel et al. 2012). Thus, these two species provide an excellent study system for untangling the effects of openness and edges.

Openness.—Openness was measured in October–November 2010 using an approach similar to that taken by Keyel et al. (2012). Keyel et al. provided a means of quantifying openness independently of distance to edge that can be compared in a consistent manner and applied within and across fields. The method is visually based and, consequently, is something that an individual animal could directly assess. The one way in which our methods differed from those of Keyel et al. (2012) is that they averaged values from a single transect to calculate an openness index value for the entire field, whereas we quantified openness in a grid across the entire field to assess variation in openness within a field. Our methods did not differ at survey points within the field. We determined openness values for previously collected nest locations and for random points (see below) using a contour map of openness values for each field. To create the contour map, each field was covered with a grid of points 50 m apart, placed using Hawth's tools in ARCGIS, version 9.3. Grid points were loaded onto a Trimble Juno SC GPS unit with TERRASYNC, version 4.2. At each grid point (when the GPS indicated that we were <2 m from the point and the GPS error was <6 m), the angle to the horizon was measured in four directions, each direction perpendicular to a field edge (Fig. 1). A sample grid is illustrated in Figure 2, including the directions to the field edge for a sample point. The four measurements were averaged for each point and subtracted from 90° to provide an index of openness that increases with increasing openness. At some grid points, there was a tall stand of trees or a tall structure not captured by the perpendicular angle measurements that nevertheless affected visual openness of a point. If the openness value for these obstructions

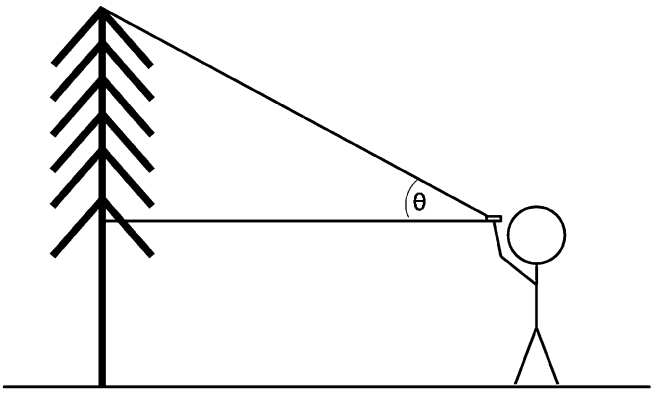

FIG. 1. Openness of Bobolink and Savannah Sparrow nest locations was quantified in Vermont by measuring the angle to the visual horizon above a plane at eye level. In many cases this was to a field edge, but in some cases it was to a small rise or to a distant horizon. Note that the final angle measures were subtracted from 90° to give an index that increases with increasing openness.

was >2° more than the openness value for the nearest perpendicular measurement, an additional measurement was taken to the top of the obstruction and included in the average (but only if this inclusion served to decrease overall openness). Openness values from the systematic grid were exported into ARCGIS, and inverse distance weighting (k = 6 nearest neighbors, power = 2) was used to create an interpolation surface for each field (2 × 2 m cells) within 25 m of measured points (Fig. 2). The accuracy of the interpolation was checked against openness values measured at nest sites; root mean squared error (RMSE) was 0.85 (n = 124 nests), with a maximum observed error of 3.8°. Based on a subset of data (n = 43 nests, 1 field), ordinary kriging did not provide a better fit to the data than did inverse distance weighting, so it was dropped from consideration. Values from the interpolation were assigned to nest locations and to random points.

Edges.—We used two edge-data sets. The first edge-data set (ED 1) included two edge types, roads and woods (forest and hedgerows were combined as one edge type), and ignored wetland edges, based on the assumption that these edge types do not affect grassland birds' nesting location or nesting success (e.g., wetland areas <400 m were not considered patch boundaries by Bakker et al. 2002). Also, in this data set, if a wooded edge (e.g., a line of trees) bordered a road, the edge was digitized as a wooded edge, because Fletcher and Koford (2003) found this to be the more disruptive edge type. However, a recent analysis of edge effects using the same fields (D. Perkins et al. unpubl. data) found that wetland edges were associated with nest placement by Bobolinks, which suggests that this edge type could not be safely ignored. Consequently, the edge file used by D. Perkins et al. acted

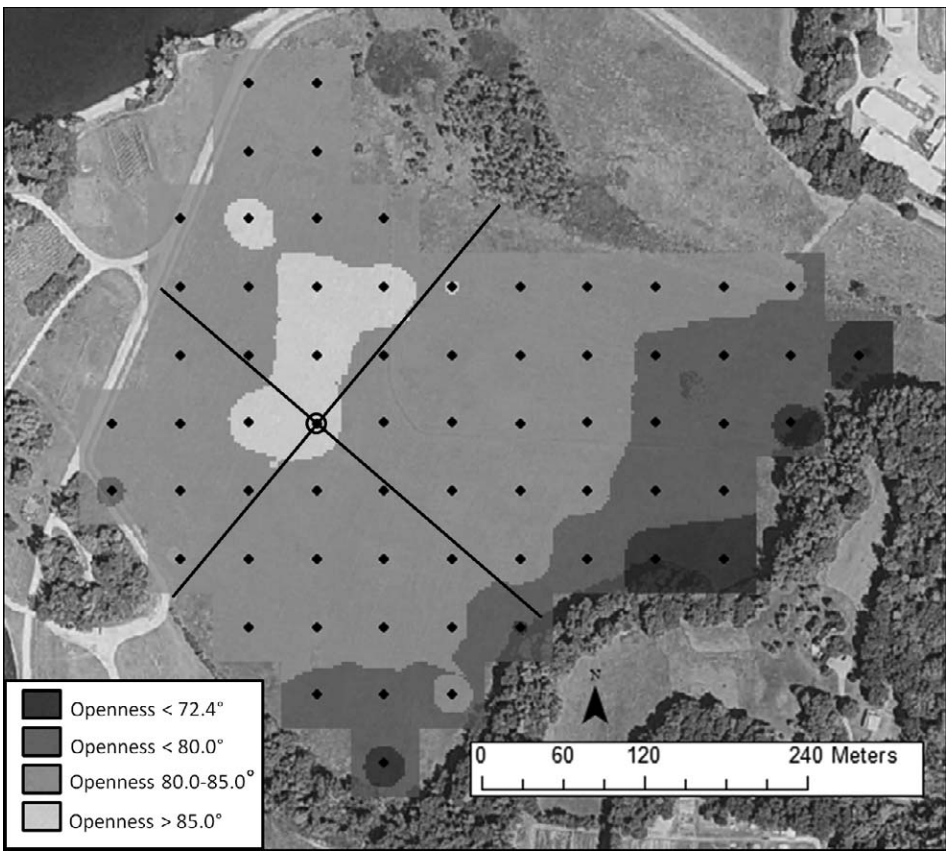

FIG. 2. An example of openness in one study field in Vermont. Openness was measured at systematic points placed 50 m apart (black points). Four measurements to the horizon were taken perpendicular to one another, and approximately perpindicular to the field edges (dark lines – open circle indicates an example survey point). The resulting interpolated openness values for one field are shown here as a raster overlaid on a 2007 U.S. Geological Survey aerial orthophotograph. Systematic points that fell in marsh or forested habitat were not surveyed and are not depicted here.

as our second edge-data set (ED 2). It contained six edge types: forest, hedgerow, road, agriculture (management-defined boundary between pasture and hay field, not digitized in ED 1), human development (due to a difference in definitions, human development was never the closest edge type to a nest in ED 1), and wetland. In contrast to ED 1, this data set gave priority to roads where roads and hedgerows co-occurred. All edges for both data sets were digitized for each field, based on a combination of aerial photographs and ground-truthing. Distance to nearest edge was calculated for nests and for random points for both data sets in ARCGIS.

Data analysis.—Observed nest distributions were compared with random locations to determine whether openness or edge influenced nesting location using Monte Carlo tests (Manly 2007). Random points were generated in ARCGIS using Hawth's Tools, and the number of random points was proportional to field area. Random points were included only in areas that were searched for nests and for which interpolated openness values could be computed.

Two sets of tests were performed to examine the role of openness and edges on nesting location. First, to test whether nests were placed randomly, the average openness of all nest locations for each species (580 nests for Bobolinks and 922 nests for Savannah Sparrows) was compared with averages obtained from sets of randomly placed (dimensionless) points in the landscape. A *P* value was calculated by examining how many sets out of 1,000 had the same or more extreme averages than those of the grassland bird species (sets of 580 points for Bobolinks, sets of 922 points for Savannah Sparrows). Second, to further untangle potential openness and edge effects, we grouped observed nests into categories based on distance-to-edge and openness, and compared these results with those obtained by chance. Nest data and 10,000 random points were grouped by distance to nearest edge (50-m intervals) and by openness category (<80°, 80–85°, >85°). Openness categories were selected to provide intuitive and simple breakpoints with a sufficient number of points in each category. The observed distribution of nests for each species in relation to openness and distance-to-edge was then compared with the expected distribution of nests based on the random points, using a chi-square test that we corrected for continuity using Emigh's (1980) correction when applicable (i.e., df = 1; Zar 1999), because Yates's correction is known to be too conservative. Openness and proximity to wooded edges were correlated (ED1, $r = 0.62$; ED2, $r = 0.51$); however, sufficient independent variation allowed their effects to be examined separately. We used an approach similar to partial correlation analysis (Zar 1999) and tested to see whether edge effects on nest location were present when there was high openness (>85°), and whether openness effects were present when close to edges (distance to nearest edge <50 m). To directly test the role of wooded edges, the data set was then restricted to nests and random points for which a wooded edge was the nearest edge. Thus, instead of 10,000 random points, 580 Bobolink nests, and 922 Savannah Sparrow nests, the sample sizes were, respectively, 8,781, 494, and 810 in ED 1; and 5,239, 294, and 561 in ED 2. The analyses were repeated with these subsets.

Timing of reproduction (clutch completion date) and reproductive success (numbers of eggs and fledglings produced, percentage of eggs from which birds fledged, including nests that failed and then excluding nests that failed, and nest survival) were examined in relation to openness and distance to edges using GLMM in SAS (SAS/STAT, version 9.2; SAS Institute, Cary, North Carolina). Clutch completion date was used instead of nest initiation date because many of the nests (although less than the majority) were found during the nestling stage, where there could have been brood reduction or egg loss, and consequently clutch completion date could be estimated more accurately and consistently. Except for the analysis of clutch completion date, nests that failed because of haying were excluded from the analysis. First, we conducted mixed model regressions between the variable of interest (e.g., number of eggs) and the independent variable(s), with year and management type included as random effects (analyses without the random effects did not qualitatively change the results; data not shown). We examined openness and distance to nearest edge (for ED 1 and ED 2) individually, and, for ED 2, we looked at openness and distance-to-edge in combination with edge type, including an interaction term. Finally, we looked at a model with both openness and distance-to-edge for each edge set (in the case of ED 2, edge type was also included in the model). All these models had the same random effects. Management type (early-cut, middle-cut, late-cut, pasture) has already been analyzed in detail (Perlut et al. 2006) and was statistically controlled for, as was year (included as random effects), in our analyses. We used logistic exposure analysis (Shaffer 2004) (SAS, PROC GLIMMIX, using method = laplace) to evaluate the relationship between nest survival and the above independent variables, including management type and year as random effects. One assumption of logistic exposure is that nest failure is homogeneous for given values of modeled covariates. Consequently, we included the number of days after clutch completion as a covariate to capture any stage or time-specific changes in nest-failure rate. Date was also included in the full model, but because this variable did not lower the overall AIC_c (Akaike's information criterion corrected for small sample sizes), it was not evaluated further (results not shown). Models were compared using AIC_c, with unnested models $\leq 2\ \Delta AIC_c$ considered equally supported (Burnham and Anderson 2002). In the case of nested models, addition of a variable may result in a model $\leq 2\ \Delta AIC_c$ from the simpler model with no appreciable improvement in model explanatory power. These models were not considered equally supported (Burnham and Anderson 2002, Arnold 2010). To evaluate model fit, we also calculated pseudo-r^2 for every model according to Magee (1990), where pseudo-$r^2 = 1 - e^{((-2/\text{nsize}) * (\text{likefull} - \text{like0}))}$. Here, e is the mathematical constant, "nsize" is the sample size, "likefull" is the likelihood of the model examined, and "like0" is the likelihood of a model containing only the intercept. Note that if the likelihood of the intercept-only model is greater than the likelihood of the full model, the pseudo-r^2 will be negative. All parameter estimates are reported ± SE.

RESULTS

Nests were not distributed randomly with respect to edge or openness. Our analyses of Bobolink and Savannah Sparrow nests revealed that they were placed away from edges more than expected by chance, and in more open locations than expected by chance (ED 1, all $P < 0.001$). The minimum observed openness was 69.0° for Bobolinks and 73.6° for Savannah Sparrows. When all edge types were pooled, both Bobolinks and Savannah Sparrows

TABLE 1. Results of tests of whether Bobolinks and Savannah Sparrows avoided edges and used open habitat more than expected by chance using chi-square analysis with respect to two edge-data sets (ED 1 and ED 2 [a]). In no case was there a significant preference for edges or non-open habitat. Nest data were collected in Vermont from 2002 to 2010, and openness data were collected in 2010.

Species	Bobolink			Savannah Sparrow		
Analysis	*n*, df	χ^2	*P*	*n*, df	χ^2	*P*
All edge types pooled						
ES1 edge	580, 3	292.9	<0.0001	922, 3	401.2	<0.0001
ES2 edge	580, 2	366.0	<0.0001	922, 2	437.7	<0.0001
ES1 openness	580, 2	152.7	<0.0001	922, 2	526.4	<0.0001
ES2 openness	580, 2	144.8	<0.0001	922, 2	461.0	<0.0001
Only wooded edges						
ES1 edge	494, 3	190.7	<0.0001	810, 3	385.5	<0.0001
ES2 edge	294, 2	155.4	<0.0001	561, 2	450.7	<0.0001
ES1 openness	494, 2	127.3	<0.0001	810, 2	564.3	<0.0001
ES2 openness	294, 2	103.1	<0.0001	561, 2	813.3	<0.0001
Only nests <50 m from wooded edge						
ES1 openness	102, 2	23.4	<0.0001	151, 2	286.9	<0.0001
ES2 openness	65, 1 [b]	16.2	<0.0001	90, 1 [b]	90.4	<0.0001
Only nests >85° openness and nearest a wooded edge						
ES1 edge	109, 3	9.7	0.02	305, 3	8.8	0.03
ES2 edge	46, 2	2.9	0.24	218, 2	9.2	0.01

[a] ES 1 included only woods and road; ES 2 included forest, hedgerow, road, agriculture, human development, and wetland edges.
[b] Expected values for >85° were too small, so we analyzed <80° and >80° and applied a correction for continuity (Emigh 1980).

avoided both edges and non-open habitat (Table 1). We tested whether our openness results were an artifact of proximity to wooded edges; note that the same concern would not exist when the closest edge is a road, wetland, or agricultural field, which do not affect openness values. When we evaluated the subset of nests whose closest edge was forest or hedgerow, we again found that Bobolinks and Savannah Sparrows avoided edges and used open habitat beyond expectation (Table 1). When we considered only nests within 50 m of the edge, Bobolinks and Savannah Sparrows still used open habitat more than expected (Table 1 and Fig. 3). Limiting the sample to nests with >85° openness, we observed edge avoidance by both Bobolinks and Savannah Sparrows in ED 1, but only by Savannah Sparrows in ED 2 (Table 1; note the smaller sample size for Bobolinks in ED 2). Thus, both openness and edge appeared to independently influence the placement of Bobolink and Savannah Sparrow nests.

Despite finding avoidance of less open habitat by both species in nest placement, statistical models of reproductive success had very little explanatory power (very low R^2) for number of eggs laid, number of fledglings, or percent fledging for either Bobolinks or Savannah Sparrows (Tables 2 and 3). For most of the dependent variables, the intercept-only model was the "best" model according to AIC_c. There was a relationship between openness and clutch size for Bobolinks and Savannah Sparrows that differed by edge type. For Bobolinks, later clutches were in more open locations, although the magnitude of the slope varied with edge type. By contrast, for Savannah Sparrows, the direction of the slope varied (Table 3; note that in many cases SE exceeds the parameter estimate). We found weak evidence (again note the low R^2) based on AIC_c that openness influenced nest survival (Table 2); for Bobolinks, the relationship was negative (increased openness was associated with decreased nest survival, $\beta_{openness} = -0.141 \pm 0.063$, $\beta_{covariate\ (days\ since\ clutch\ completion)} = -0.0816 \pm 0.019$, $\beta_{intercept} = 16.341 \pm 5.318$), and for Savannah Sparrows the relationship was positive ($\beta_{openness} = 0.069 \pm 0.041$, $\beta_{covariate\ (days\ since\ clutch\ completion)} = -0.060 \pm 0.015$, $\beta_{intercept} = -1.464 \pm 3.391$).

DISCUSSION

On the basis of our results, visually open fields were more likely to be selected as nesting habitat by Bobolinks and Savannah Sparrows than were relatively less open fields. Even though openness and distance-to-edge were correlated, openness explained independent variation in nesting location. This suggests that a novel component of habitat selection by these species is captured by the visual openess metric. Our results for Bobolinks are consistent with previous literature at the patch level (Renfrew and Ribic 2002, Keyel et al. 2012) and at the landscape scale (e.g., Coppedge et al. 2001, Bakker et al. 2002, Shustack et al. 2010). Renfrew and Ribic (2002) observed a role of topography; Bobolinks occurred at higher densities in upland pastures than in lowland pastures surrounded by tall trees. In a separate population of Bobolinks, Keyel et al. (2012) examined openness for patches and observed an occupancy threshold at 72.4°, with higher occupancy above the threshold. This threshold successfully predicted nest locations of both Bobolinks and Savannah Sparrows in this study for 1,501 of 1,502 nests (all but one Bobolink nest). Our results for Savannah Sparrows are novel, in that we know of no prior studies that examined patch-level openness in this species.

Generally, we observed no strong effects of openness or distance-to-edge on measures of nest success. Most R^2 values were low, indicating poor-fitting models with low explanatory

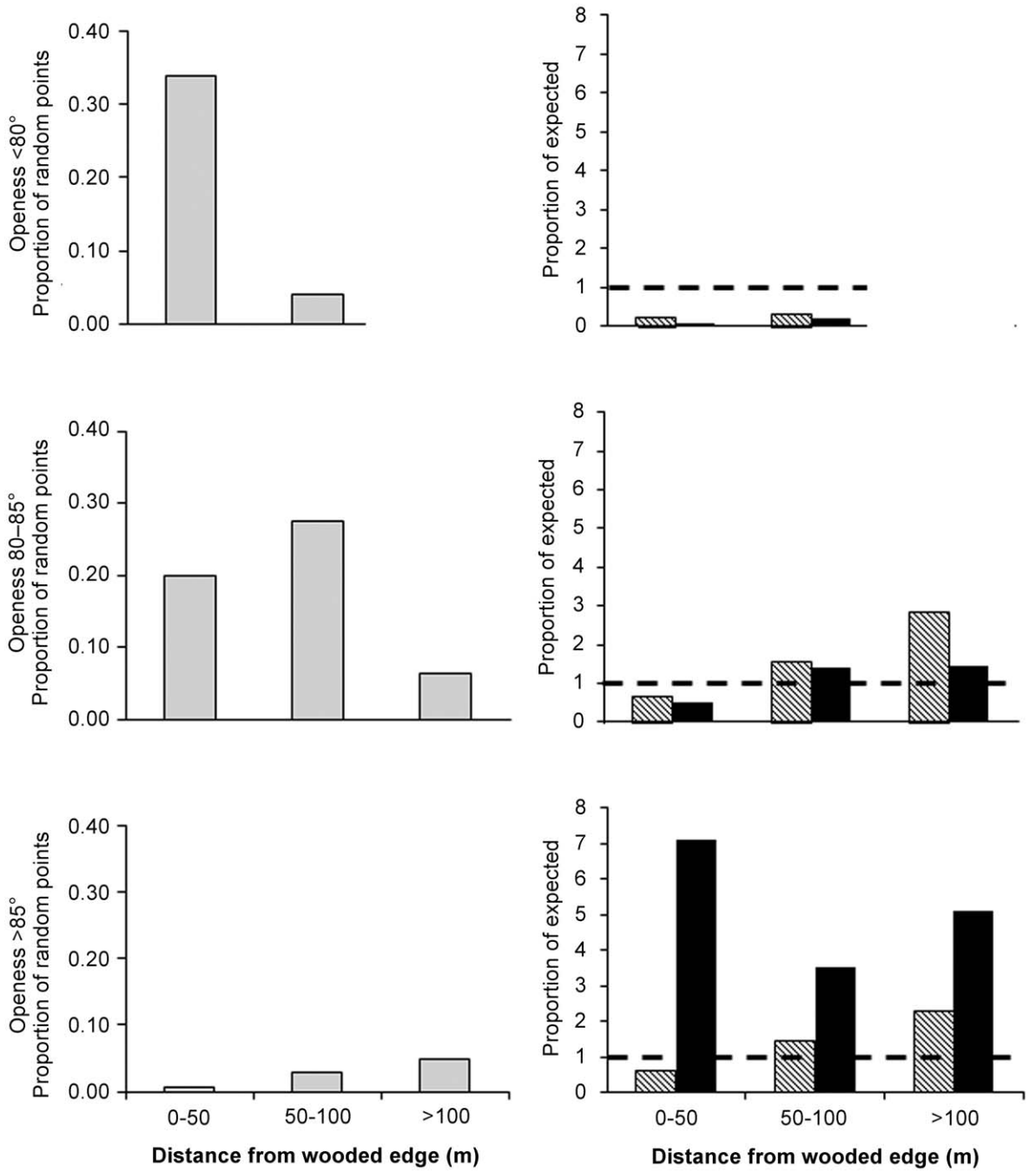

FIG. 3. Left panels (gray) display the proportion of random points expected in each category for edge-data set 2 (based on 5,239 random points apportioned to fields proportional to field area). Right panels show the observed proportion of Bobolink (hatched bars) and Savannah Sparrow (black bars) nests divided by the observed proportion of random points (there were no random points >100 m from the edge with openness <80). If nests were distributed randomly, the proportion of expected would be 1 (dashed line), with proportions <1 showing avoidance and >1 showing attraction. Only nests that were closest to forest or hedgerow are included here. Nest data were collected in Vermont from 2002 to 2010, and openness data were collected in 2010.

power. Contrary to our expectation, clutch completion date averaged later in more open habitat for Bobolinks, especially for forest edge types (but note the high SEs on the parameter estimates). Although a model containing openness was selected as the best model for Savannah Sparrows, when the interactions were explored, no clear patterns between openness and clutch completion date were revealed. There are other examples of factors affecting nest placement without affecting reproductive success (reviewed by Chalfoun and Schmidt 2012). For example, Wallander et al. (2006) found that Northern Lapwings avoided

TABLE 2. Comparison of openness and distance-to-edge for reproductive parameters in Bobolinks and Savannah Sparrows for several different models containing openness and distance-to-edge based on ΔAIC_c (best model indicated in bold). Two sets of digitized edges are included (ED 1, 2 edge types, and ED 2, 6 edge types; see text for details). Year and management type were included as random effects. "B" and "S" in the header refer to sample sizes for Bobolinks and Savannah Sparrows, respectively. Nest data were collected in Vermont from 2002 to 2010, and openness data were collected in 2010.

	Date clutch completed (B = 402, S = 559)		Clutch size (B = 493, S = 748)		Number fledging (B = 493, S = 748)		Percentage fledging (B = 493, S = 748)		Percentage fledging [a] (B = 291, S = 355)		Nest survival (B = 369, 3099; S = 490, 3673) [b]	
Model	ΔAIC_c	R^2 [c]	ΔAIC_c	R^2 [c]	ΔAIC_c	R^2 [c]	ΔAIC_c	R^2 [c]	ΔAIC_c	R^2 [c]	ΔAIC_c	R^2 [c]
Bobolink												
Intercept	47.7	0.00	**0.0**	**0.00**	3.5	0.00	**0.0**	**0.00**	**0.0**	**0.00**	21.1	0.00
Openness	40.4	0.02	5.7	<0.01	3.2	0.00	2.8	<0.01	4.3	<0.01	**0.0**	**0.01**
ED 1 distance to edge	48.5	0.00	11.7	<0.01	13.0	<0.01	12.7	<0.01	13.3	<0.01	4.9	0.01
ED 2 distance to edge	50.5	<0.01	11.5	<0.01	13.4	<0.01	13.0	<0.01	13.2	<0.01	5.6	0.01
Openness | ED 2 edge type [e]	**0.0**	**0.11**	22.4	<0.01	**0.0**	**0.01**	26.5	<0.01	41.8	<0.01	8.7	0.01
ED 2 distance to edge | ED 2 Edge type[e]	34.4	0.02	54.6	<0.01	40.2	<0.01	67.2	<0.01	80.8	<0.01	0.4	0.01
Openness, ED 1	45.8	0.00	16.8	<0.01	12.3	<0.01	15.0	<0.01	17.8	<0.01	3.1	0.01
Openness, ED 2 distance to edge, ED 2 edge type	22.0	0.06	23.2	<0.01	7.4	<0.01	22.4	<0.01	36.2	<0.01	2.9	0.01
Intercept, date clutch complete	—		—		—		—		—		3.8	0.01
Savannah Sparrow												
Intercept	54.4	0.00	**0.0**	**0.00**	**0.0**	**0.00**	**0.0**	**0.00**	**0.0**	**0.00**	14.9	0.00
Openness	54.3	0.00	6.4	<0.01	4.8	<0.01	7.4	<0.01	6.5	<0.01	**1.4** [d]	**0.01**
ED 1 distance to edge	59.9	<0.01	12.5	<0.01	11.1	<0.01	13.8	<0.01	13.3	<0.01	4.1	<0.01
ED 2 distance to edge	59.8	<0.01	12.1	<0.01	10.1	<0.01	12.7	<0.01	13.8	<0.01	4.1	2.30
Openness | ED 2 edge type [e]	**0.0**	**0.09**	31.5	<0.01	7.4	<0.01	37.0	<0.01	37.6	<0.01	0.0	0.01
ED 2 distance to edge | ED 2 edge type [e]	33.4	0.03	67.8	<0.01	39.4	<0.01	70.2	<0.01	73.6	<0.01	3.8	0.01
Openness, ED 1	58.7	<0.01	18.5	<0.01	15.2	<0.01	20.4	<0.01	20.4	<0.01	2.3	0.01
Openness, ED 2 distance to edge, ED 2 edge type	23.1	0.05	27.8	<0.01	16.3	<0.01	35.1	<0.01	33.9	<0.01	2.8	0.01
Intercept, date clutch complete	—		—		—		—		—		2.1	<0.01

[a] For nests that produced at least one fledgling.
[b] Number of nests followed by total number of nest-check intervals. Nest interval was the unit of analysis.
[c] Pseudo-R^2 calculated per Magee (1990). Note that by definition R^2 is zero for intercept-only models and can be negative for models if the –2 log likelihood of the model is less than the –2 log likelihood of the intercept.
[d] Because this model is a simpler version of the lowest model and is $\leq 2*K$ ΔAIC_c, where K is the number of additional parameters in the more complicated model, it is considered the most competitive model (Burnham and Anderson 2002:131, Arnold 2010).
[e] The | notation means that the model had both main effects and the interaction in the model.

raised human-made structures such as fences, which were used as perches by a major egg predator. However, distance to these structures was unrelated to nest success. This is unexpected on the basis of Klomp's (1954) observation that most attacks by avian nest predators (crows) were repelled aerially outside of the territory, and that Northern Lapwings did not attack perched predators (in trees). We point out that a pattern of avoidance with no pattern of nest success does not rule out the possibility of a threshold response in Northern Lapwing nest placement, whereby birds do not nest unless the habitat is sufficiently distant from human structures. Alternatively, predation could be compensatory, whereby increased defense against one predator is masked by increased nest failure because of other predators (Ellis-Felege et al. 2012).

Selection operates on evolutionary time scales and over a species' entire range. Chalfoun and Schmidt (2012) summarized 14 ecological–evolutionary hypotheses for why nest success and factors that affect nest-site selection might be decoupled. For example, predators or parasites in one part of a species' range may exert selection pressure but be absent from or choose different prey in a given study system (e.g., Brown-headed Cowbirds [*Molothrus ater*] are present in the northeast and a frequent grassland-bird nest parasite, but did not parasitize any nests during our study). Thus, it is possible that with different predator–parasite guilds, openness may confer expected benefits to nest success, but we did not observe any such benefits in our 9 years of nest data.

Two potential concerns might be raised about our openness measures. First, our openness measurements were made in the fall. We think that this is not a real concern, because the openness measure depends on the height of surrounding vegetation and topography, which do not change substantially seasonally. Although deciduous trees lose their leaves in autumn, the branches remain to indicate the height of the tree crown. The difference in height due to leaves is negligible because it is within the measurement error for the angle measurement (A. C. Keyel pers. obs). Related to this concern, nest data were collected over

TABLE 3. Parameter estimates ± SE for the most competitive non-intercept mixed models given in Table 2. Because the openness*edge type model was selected, all parameter estimates are given, even those with SE that exceeds the parameter estimate.

Model and parameters		*n*	Parameter	Intercept [a]	R^2 [b]
Bobolink	Forest	121	0.59 ± 0.54	38,829 ± 336	0.23
Clutch completion	Hedgerow	91	0.18 ± 0.35	38,857 ± 334	0.00
Openness | Edge Type [c]	Road	73	0.38 ± 0.72	38,845 ± 337	0.02
	Agriculture	24	1.19 ± 2.20	38,955 ± 367	0.14
	Developed	11	1.05 ± 9.65	38,572 ± 4,369	0.46
	Wetland	82	0.06 ± 0.86	38,874 ± 341	0.02
Savannah Sparrow	Forest	296	0.12 ± 0.57	38,873 ± 336	0.00
Clutch completion	Hedgerow	36	1.11 ± 2.99	38,784 ± 415	0.11
Openness | Edge Type [c]	Road	90	–0.06 ± 0.93	38,884 ± 342	0.02
	Agriculture	50	0.32 ± 1.84	38,844 ± 9,692	0.06
	Developed	16	–0.89 ± 3.39	38,951 ± 408	0.24
	Wetland	71	–0.73 ± 1.24	38,941 ± 350	0.04
Bobolink	Forest	144	–0.040 ± 0.093	5.9 ± 7.8	<0.01
Number Fledging	Hedgerow	90	–0.036 ± 0.099	5.5 ± 8.2	<0.01
Openness | Edge Type [c]	Road	80	–0.32 ± 0.19	29.4 ± 15.6	0.02
	Agriculture	35	0.14 ± 0.42	–9.8 ± 35.5	0.01
	Developed	14	–0.86 ± 1.27	74.1 ± 107.0	0.17
	Wetland	130	–0.06 ± 0.14	6.7 ± 11.6	<0.01

[a] Intercept for clutch completion day is given as number of days since 1 January 1900.
[b] Pseudo-R^2 calculated per Magee (1990).
[c] The | notation means the model had both main effects and the interaction in the model.

9 years, whereas openness was measured at the end of this time, because the nest data were originally collected for different purposes (e.g., Perlut et al. 2006, 2008). We believe that our openness estimates are unaffected by this time discrepancy, because the surrounding structural vegetation remained relatively constant over the study period (A. M. Strong pers. obs.). Regardless, these sources of error would be expected to weaken any observed relationships instead of producing spurious relationships. A second potential concern is that the openness metric we used is based on a person's height, and not the height of a bird. Grassland birds often perch high in the vegetation and could potentially assess openness at multiple heights while flying. More importantly, trigonometrically, observer height would have a strong influence only close to an edge that is approximately the same height as the observer.

Responses to openness versus distance-to-edge may suggest different underlying mechanisms in nest-site selection. Although edge effects may take many forms (Saunders et al. 1991), one mechanism is that edge-based predators move a specified distance into patch interiors, and that nests within this range are at greater risk of nest failure (e.g., Winter et al. 2000; reviewed by Lahti 2001, Batáry and Báldi 2004; but see, e.g., Grant et al. 2006, in which most depredation is by interior specialists). This mechanism may apply especially to ground-based edge predators, or to those using aural or olfactory cues. By contrast, an affinity for openness might suggest a relationship with predation risk based on either predator or prey visual cues. Species that select open habitat may be able to better detect and escape incoming aerial predators and, therefore, decrease predation risk. Fewer perches in open habitat may make it more difficult for avian predators to hunt. Thus, open-country specialists such as Northern Harriers (*Circus cyaneus*) and Short-eared Owls (*Asio flammeus*) (Wiggins et al. 2006, Smith et al. 2011) must compensate for the lack of perches and potential for early detection by prey.

The edge avoidance that we observed in the present study of nest placement by Bobolinks and Savannah Sparrows is consistent with the results of previous studies (e.g., Bobolink: Bollinger and Gavin 2004, trend in Renfrew et al. 2005; Savannah Sparrow: O'Leary and Nyberg 2000, Renfrew et al. 2005, but see mixed edge responses in Davis et al. 2004) and is treated in greater depth by D. Perkins et al. (unpubl. data). The lack of detection of edge avoidance by Bobolinks in ED 2, when we controlled for openness, was likely an artifact of the reduced sample sizes in this data set. In the present study, we found that despite differences in edge identification and classification, our results for nest placement and reproductive success were remarkably similar.

Management implications.—Bobolink and Savannah Sparrow nest densities were reduced in areas with openness values <80° (Fig. 3). Consequently, fields (or portions of fields) most suitable for Bobolinks and Savannah Sparrows will have openness values >80° (Figs. 2 and 4 illustrate these angle measurements in real landscapes). Openness values can be used as a GIS layer to assess the portion of a field that is likely to be suitable for Bobolinks or Savannah Sparrows (Fig. 4). It is unclear to what extent our results can be generalized to other species, but of 16 Eastern Meadowlark (*Sturnella magna*) nests found on our study fields, all were in locations above an openness value of 79.5°. This suggests that other species may be even more sensitive to openness than Bobolinks and Savannah Sparrows. Carefully designed, manipulative experiments are warranted to clarify the role of openness for grassland birds.

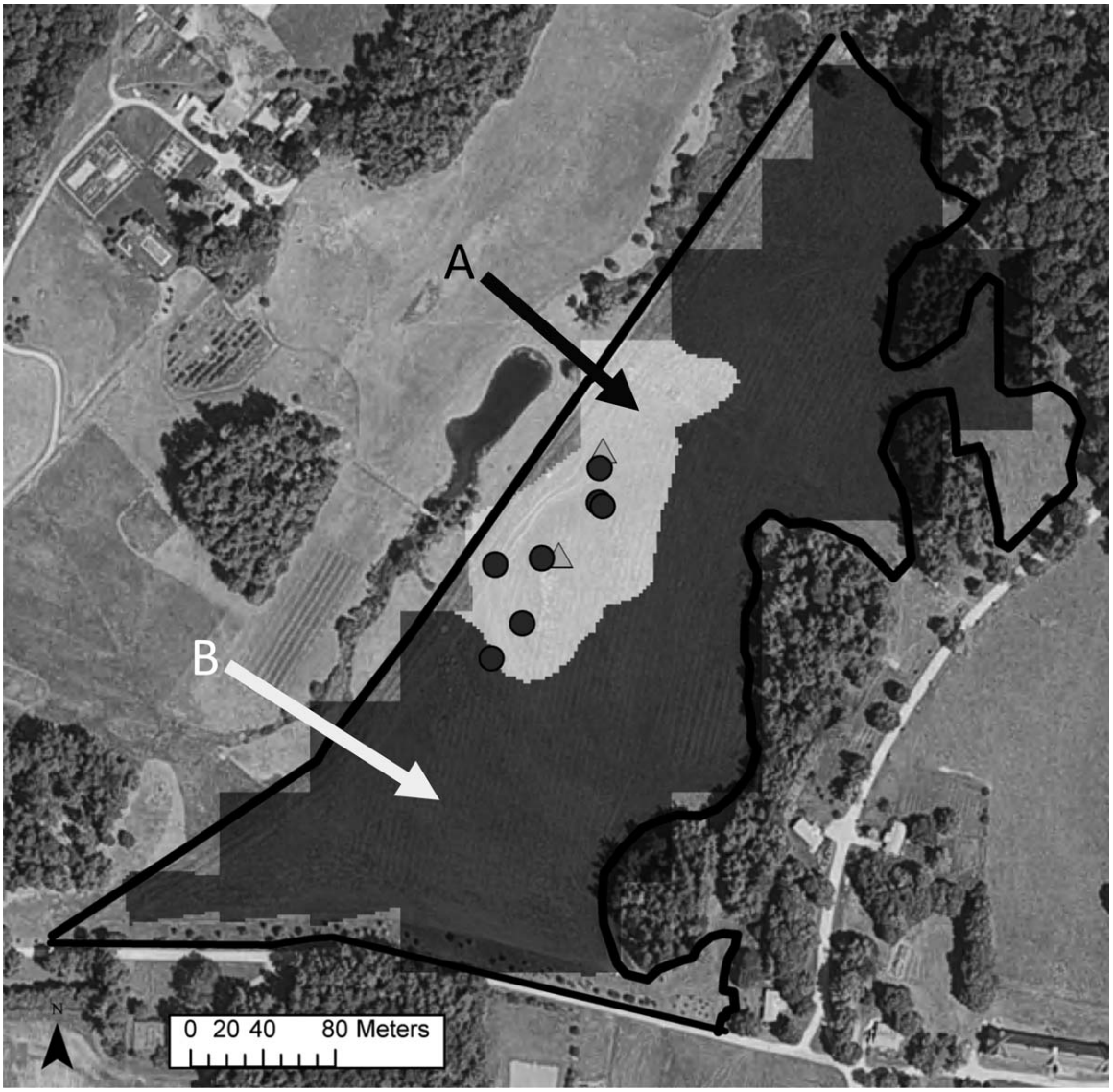

Fig. 4. Predicted suitable habitat, based on openness compared with observed nest locations (circles = Savannah Sparrows, triangles = Bobolinks). (A) The light area is pasture with openness values >80°, and (B) the dark shaded area has openness values <80°.

Acknowledgments

The authors thank D. Perkins (University of New England) for GIS work, D. Marshall for statistical advice, F. Sutti for field assistance, P. Florance for use of Tufts' Juno GPS and Trupulse laser rangefinder, L. Pepall and C. Carle (Tufts University) for administrative support, P. & L. Pastel for food and lodging, and the Reed/Romero lab group for constructive feedback. We thank M. T. Murphy, D. Johnson, and three anonymous reviewers for constructive comments on the manuscript. This research was funded in part by a National Science Foundation Graduate Research Fellowship to A.C.K. We thank Shelburne Farms and the Galipeau, Ross, Thibeau, Maile, and Stern families for generous access to their land. We thank the Galipeau family for additional financial support.

Literature Cited

Amat, J. A., and J. A. Masero. 2004. Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. Animal Behaviour 67:293–300.

Andersson, M., J. Wallander, and D. Isaksson. 2009. Predator perches: A visual search perspective. Functional Ecology 23:373–379.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74:1175–1178.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Batáry, P., and A. Báldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology 18:389–400.

Bollinger, E. K., and T. A. Gavin. 2004. Responses of nesting Bobolinks (*Dolichonyx oryzivorus*) to habitat edges. Auk 121:767–776.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Chalfoun, A. D., and K. A. Schmidt. 2012. Adaptive breeding-habitat selection: Is it for the birds? Auk 129:589–599.

Coppedge, B. R., D. M. Engle, R. E. Masters, and M. S. Gregory. 2001. Avian response to landscape change in fragmented southern Great Plains grasslands. Ecological Applications 11:47–59.

Davis, S. K. 2004. Area sensitivity in grassland passerines: Effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121:1130–1145.

Ellis-Felege, S. N., M. J. Conroy, W. E. Palmer, and J. P. Carroll. 2012. Predator reduction results in compensatory shifts in losses of avian ground nests. Journal of Applied Ecology 49:661–669.

Emigh, T. H. 1980. A comparison of tests for Hardy-Weinberg equilibrium. Biometrics 36:627–642.

Fletcher, R. J., Jr., and R. R. Koford. 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. Auk 120:799–810.

Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428–434.

Grant, T. A., E. Madden, and G. B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: Implications for breeding grassland birds. Wildlife Society Bulletin 32:807–818.

Grant, T. A., E. M. Madden, T. L. Shaffer, P. J. Pietz, G. B. Berkey, and N. J. Kadrmas. 2006. Nest survival of Clay-colored and Vesper sparrows in relation to woodland edge in mixed-grass prairies. Journal of Wildlife Management 70:691–701.

Hildén, O. 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53–75.

Kenward, R. E. 1978. Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. Journal of Animal Ecology 47:449–460.

Keyel, A. C., C. M. Bauer, C. R. Lattin, L. M. Romero, and J. M. Reed. 2012. Testing the role of patch openness as a causal mechanism for apparent area sensitivity in a grassland specialist. Oecologia 169:407–418.

Klomp, H. 1954. De terreinkeus van de Kievit, *Vanellus vanellus* (L.). Ardea 42:1–139.

Lahti, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365–374.

Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: A survey of North American birds. Wilson Bulletin 105:1–47.

Lima, S. L., and T. J. Valone. 1991. Predators and avian community organization: An experiment in a semi-desert grassland. Oecologia 86:105–112.

Magee, L. 1990. R^2 measures based on Wald and likelihood ratio joint significance tests. American Statistician 44:250–253.

Manly, B. F. J. 2007. Randomization, Bootstrap and Monte Carlo Methods in Biology, 3rd ed. Chapman & Hall/CRC, Boca Raton, Florida.

National Agricultural Statistics Service. 2010. The Census of Agriculture. U.S. Department of Agriculture. [Online.] Available at www.agcensus.usda.gov/.

O'Leary, C. H., and D. W. Nyberg. 2000. Treelines between fields reduce the density of grassland birds. Natural Areas Journal 20:243–249.

Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology 8:17–26.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: Behavioral responses and management strategies. Ecological Applications 16:2235–2247.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2008. Regional population viability of grassland songbirds: Effects of agricultural management. Biological Conservation 141:3139–3151.

Renfrew, R. B., and C. A. Ribic. 2002. Influence of topography on density of grassland passerines in pastures. American Midland Naturalist 147:315–325.

Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. Auk 122:618–636.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5:18–32.

Shaffer, T. L. 2004. Logistic-exposure analyses of nest survival. U.S. Geological Survey, Northern Prairie Wildlife Research Center Online. [Online.] Available at www.npwrc.usgs.gov/resource/birds/nestsurv/index.htm.

Shustack, D. P., A. M. Strong, and T. M. Donovan. 2010. Habitat use patterns of Bobolinks and Savannah Sparrows in the northeastern United States. Avian Conservation and Ecology 5:11.

Smith, K. G., S. R. Wittenberg, R. B. Macwhirter, and K. L. Bildstein. 2011. Northern Harrier (*Circus cyaneus*). *In* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Available at bna.birds.cornell.edu/bna/species/210.

Uhmann, T. V., N. C. Kenkel, and R. K. Baydack. 2001. Development of a habitat suitability index model for Burrowing Owls in the eastern Canadian prairies. Journal of Raptor Research 35:378–384.

Wallander, J., D. Isaksson, and T. Lenberg. 2006. Wader nest distribution and predation in relation to man-made structures on coastal pastures. Biological Conservation 132:343–350.

Wiggins, D. A., D. W. Holt, and S. M. Leasure. 2006. Short-eared Owl (*Asio flammeus*). *In* The Birds of North America Online (A. Poole, Ed.). Cornell Lab of Ornithology, Ithaca, New York. Available at bna.birds.cornell.edu/bna/species/062.

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. Journal of Wildlife Management 70:158–172.

Zar, J. H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

Associate Editor: D. H. Johnson