

Testing the role of patch openness as a causal mechanism for apparent area sensitivity in a grassland specialist

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Abstract Area sensitivity, species being disproportionately present on larger habitat patches, has been identified in many taxa. We propose that some apparently area-sensitive species are actually responding to how open a habitat patch is, rather than to patch size. We tested this hypothesis for Bobolinks (*Dolichonyx oryzivorus*) by comparing density and occupancy to a novel openness index, patch area, and edge effects. Bobolink density and occupancy showed significant relationships with openness, but logistic models based on an openness occupancy threshold had greater explanatory power. Thresholds remained approximately consistent from June through August, and shifted to be more open in September. Variance partitioning supported the openness index as unique and relevant. We found no relationships between measures of body condition (body mass, body size, circulating corticosterone levels) and either openness or area. Our findings have implications for studies of area sensitivity, especially with regards to inconsistencies reported within species: specifically, (1) whether or not a study finds a species to be area sensitive may depend on whether small, open sites were sampled, and (2) area regressions were sensitive to observed densities at the largest sites, suggesting that variation in these fields could lead to inconsistent area sensitivity responses.

Responses to openness may be a consequence of habitat selection mediated by predator effects. Finally, openness measures may have applications for predicting effects of habitat management or development, such as adding wind turbines, in open habitat.

Keywords Habitat fragmentation · Grassland bird · Stress · Tipping point · Wind energy

Introduction

Area sensitivity is defined as a species being absent or occurring in lower densities in smaller habitat patches as compared to larger habitat patches, assuming the small patches are large enough to support a species' territory (Robbins et al. 1989; Horn and Koford 2006). Despite a long history of documenting area sensitivity (e.g., Bond 1957; Moore and Hooper 1975; Robbins et al. 1989; Bender et al. 1998; Parker et al. 2005), the mechanisms that drive it for many species are not understood (Ribic et al. 2009a). Area sensitivity is widespread across animal taxa and ecosystems, although across studies that evaluate the same species, area sensitivity is not consistently reported (e.g., Bender et al. 1998; Connor et al. 2000; Johnson and Igl 2001; Bayard and Elphick 2010). A variety of mechanisms that might cause area sensitivity have been proposed, such as edge effects, conspecific attraction, and island biogeography (Foster and Gaines 1991; Beier and Noss 1998; Hokit and Branch 2003; Ribic et al. 2009b; Fletcher et al. 2007; Fletcher 2009), but few mechanisms have been tested. Furthermore, different mechanisms may cause area sensitivity in different species; for example, food limitation is likely a mechanism in the forest-dwelling ovenbird (*Seiurus aurocapillus*) (Burke and Nol 1998), but there is

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no evidence of food limitation in grassland-breeding birds (e.g., Wiens and Rotenberry 1979).

Another possibility for widespread but inconsistent patterns of area sensitivity among and within species is that species are not responding to area per se, but to something correlated with area. A variety of alternatives have been proposed, such as core area (as defined by distance from habitat edge) (Temple 1986), perimeter to area ratio (e.g., Helzer and Jelinski 1999; Bakker et al. 2002), edge sensitivity (e.g., Fletcher et al. 2007), and total habitat available in a landscape (e.g., Bakker et al. 2002; Davis 2004; Ribic et al. 2009a; Shustack et al. 2010). One correlated variable proposed as a cause of area sensitivity is openness (here as a binomial assessment of open or not; Renfrew and Ribic 2002). Although the amount of open habitat present in a landscape has been evaluated (e.g., Coppedge et al. 2001; Bakker et al. 2002; Van Der Vliet et al. 2008), openness has not been quantitatively evaluated at a patch level. Openness is a measure of how much of an animal's visual field is not occluded by ground, vegetation structure, or human-made structures in abutting habitat. It is a function of local ground contours (the top of a hill is more visually open than is the base of the hill), the height and structure of adjacent habitat, and distance to the adjacent habitat. Consequently, openness is affected by area and some edge effects. How open a patch of habitat is has been shown to influence site occupancy by birds (e.g., Klomp 1954; Hildén 1965; Milsom et al. 1985; Uhmman et al. 2001; Renfrew and Ribic 2002; Van Der Vliet et al. 2008), and by ungulates (e.g., Gerard and Loisel 1995; Attum 2007), with animals avoiding sites with low openness. One biological argument for why animals respond to openness is to increase predator detection and avoidance—for species relying on visual cues for predator detection, individuals in relatively open habitat should be able to detect and avoid an advancing predator more readily than do individuals in relatively closed habitat (Klomp 1954). Conversely, predators are better able to detect prey from tall perches (Andersson et al. 2009), and open landscapes may deny predators these perches. Additionally, some species' predator escape tactics require open habitat, e.g., Horned Larks (*Eremophila alpestris*) (Lima 1993). Consequently, openness may be an important factor in determining distributions of species either through increased predator detection, crypsis, or ability to escape from predators.

We tested the role of field openness as a proximate mechanism for apparent area sensitivity in Bobolinks (*Dolichonyx oryzivorus*), a grassland passerine. Bobolinks are declining across much of their range due to habitat loss and fragmentation, and area sensitivity could be contributing to this decline (e.g., Vickery et al. 1994). Area sensitivity has been reported for Bobolinks in some studies

(Vickery et al. 1994; Helzer and Jelinski 1999; Johnson and Igl 2001; Renfrew and Ribic 2002), but not in others (Ribic and Sample 2001; Bakker et al. 2002; Ribic et al. 2009a). This suggests that, while area may play a role in habitat selection, a different measure that is related to area but has a different underlying mechanism, such as openness, might better explain Bobolink habitat selection. We developed multiple measures of openness to determine which provided the greatest explanatory power for Bobolink site occupancy and density. We (1) examined linear, non-linear, and threshold relationships between openness and Bobolink density and compared them to area, edge effects, and an edge effects model (based on Sisk et al. 1997); (2) as responses to area and openness can change across seasons (Apollonio et al. 1998; Martin and Catterall 2001), we examined the relationship between these variables and Boboblink density during breeding and three post-breeding times; and (3) we tested whether area or openness were indicators of habitat quality. Specifically, we tested whether body condition, as measured by body mass, fat score, size, and stress responses (e.g., Homan et al. 2003; Romero 2004) increased with either patch area or openness. Stress response was measured in terms of baseline and stress-induced circulating corticosterone (CORT) levels as well as response to an adrenocorticotrophic hormone (ACTH) challenge (Romero 2004).

Materials and methods

Study location

We conducted our research from June to October 2009 and May to June 2010 in late-cut and uncut hayfields (grass/forb mixtures) within a primarily wooded matrix in eastern and central Massachusetts, USA (42°12'–42°53'N, 71°58'–70°50'W). Bobolinks are known to nest in hayfields, and can reach higher densities there than in native prairie (e.g., Bollinger and Gavin 1992). Habitat patches were delineated by roads, woods, pasture, or other habitat types (sensu Horn and Koford 2006). Fields used in June were removed from the study in subsequent months if they were hayed; opportunistically, we were able to add additional fields in July. Median patch sizes in June, July, August, September, and October were 3.6, 3.0, 2.4, 3.6, and 3.2 ha, respectively (min: 0.6 all months, max: 49.0, 49.0, 10.6, 10.6, 10.6, respectively). Sample sizes were 41, 45, 35, 18, and 15 fields, respectively (see Online Resource 1 for means and individual patch sizes and locations). We excluded sites smaller than 0.5 ha as mean Bobolink territory size from the nearest reported location (New York, ~400 km away) was 0.49 ha (Martin and Gavin 1995). Fields were chosen to represent a range of patch sizes and

were selected using a geographic information system (GIS) to avoid bias from selecting fields known to contain Bobolinks. The National Land Use Cover Data 2001 (Homer et al. 2004) was intersected with the MassGIS OpenSpaces layer (MassGIS 2008) using ArcGIS 9.3 to provide a list of candidate grasslands, which were checked for suitability. Research was conducted with landowner permission. Additional fields were added based on conversations with landowners; however, known presence of Bobolinks was not a consideration in field selection. All selected patches and edges were digitized from 2005 July orthophotos (MassGIS 2008) to obtain edge and area measurements.

Bird surveys

Male Bobolink density was measured during breeding time in June 2009 via line transect surveys and distance sampling (Bollinger et al. 1988; Buckland et al. 2001). Depending on field size, up to five 100-m transects were laid out at least 80 m apart. Pilot data from 2008 suggested that detection probability declined sharply after 40 m; hence 80-m spacing would prevent overlap in the key portion of the detection function. Furthermore, although counting the same animal on separate transects does not violate assumptions of the distance sampling analysis (Buckland et al. 2001), care was taken to avoid double counts within a transect. Transects were placed perpendicular to the nearest field edge in case there was a density gradient caused by edge effects (Buckland et al. 2001; Fletcher and Koford 2003; Fletcher 2005). Two individuals, one observer (A.C.K.) and one recorder, slowly walked each transect, stopping as necessary for distance assessment. Transect lengths were measured with a hip chain or GPS (Garmin Etrex Legend GPS, WGS 1984 datum). Surveys were performed between 0630 and 0915 hours (EDT) and were not performed in wind speeds above 16 km h^{-1} , in heavy fog, or during precipitation. Observations of Bobolinks were placed into 20-m bands out to 100 m (Bollinger et al. 1988). A Trupulse 360B laser rangefinder was used to check uncertain distance assessments. Bird density was estimated with a global detection function with the Program Distance 6.0.2 (Thomas et al. 2010); see Online Resource 1 for more details. Data were inspected to ensure a good fit of the detection function ($\chi^2 = 0.53$, $P = 0.91$).

After the breeding season, Bobolinks form flocks (July–October), so line transect surveys with distance sampling are not an effective survey method. In addition, male Bobolinks molt into basic plumage after breeding and resemble females. Consequently, for July–October surveys, all Bobolinks encountered were counted, regardless of age or sex. In July and August, when Bobolinks were still easily detected when present, fields were surveyed by two

observers walking through the fields. In September and October, when Bobolinks are more cryptic, birds were surveyed using a 50-m rope dragged between two observers in non-overlapping transects. Since the entire site was sampled with the rope drag, the survey window was expanded to 0630–1000 hours in September and to 0700–1100 hours in October. The total number of birds was divided by site area to avoid detecting area sensitivity due to passive sampling (Connor and McCoy 1979).

Site measures

Area was measured and $\ln(\text{area})$ and perimeter to area ratio were calculated from GIS data. We evaluated 12 edge variables: lengths of total edge at a site, perimeter, interior edge (e.g., from forest islands in the site), wooded, road, agricultural, residential, and “other” edges, percents of residential, wooded and non-wooded/non-residential edges, and wooded edge-to-area ratio. Of the edge variables, only total edge and perimeter were significantly correlated with Bobolink density, and these two measures were strongly correlated ($r^2 = 0.97$), so only total edge was retained in our main analysis. As Bobolinks have lower population densities near forest edges (Fletcher and Koford 2003), we modeled the expected edge effects for each patch using an edge effects model (EEM) based on the effective area model of Sisk et al. (1997). In this model, density is standardized to 1.0 in core habitat and is reduced near edges based on proximity to edge (categorical distances, 0–75 and 76–150 m from the edge) and edge type (e.g., wooded, road). Edge effects are based on Fletcher and Koford 2003; details are given in Online Resource 1. If openness is only capturing a response to wooded edges, then the EEM is expected to outperform the openness index. Note that this modeling approach does not incorporate our field data—it is a predictive model based on previously measured edge effects in Bobolinks.

Measuring openness

We evaluated 11 different openness measures (described in Online Resource 1), and selected the best one (most correlated with Bobolink density) as our openness index. The index value was obtained by taking measurements at points every 50 m along a transect set across the longest axis of a site (not the diagonal), plus a final point at the far edge of the field (end of the transect, Fig. 1a). In some instances, the site curved, in which case our transect bent to match the site curvature. At each point, an angle measurement to the horizon was taken (measured at eye level, $\sim 1.7 \text{ m}$) in the direction of the axis that was being walked plus 3 additional measurements offset at 90° intervals (Fig. 1b). Inclination was taken to the horizon; generally this was the

field edge, but in some instances this was to the top of a rise in the field or to a distant hill not connected to the site. As necessary, readings were adjusted off the 90° mark (i.e., at the first and last points on the transect, if the edges were angled instead of perpendicular to the transect and a strict 90° reading would put multiple readings close, e.g., within 5 m of one another). Inclination and angle were measured using a TruPulse 360B laser rangefinder and data were entered into a Trimble Juno SC GPS with Terrasync Professional 4.0. The four angle measurements were averaged for each point, and then averaged across all points to give a single index value for each field. This final number was subtracted from 90° so that the openness index increased with increasing openness. In some fields, there were points when the four angles to the horizon did not adequately capture the openness of that point, e.g., if the openness of field edges were uneven and the measurement overestimated openness for a field edge by $>2^\circ$. In these instances, an additional reading was taken and included in the average only if this did not cause the point to be more open. In a simplified example, if edge one's reading was 10° and edge two's reading was 5° and there was a large tree on the second edge that was 15° , we used 10° as the average measurement for that point $[(10 + 5 + 15)/3]$ instead of $7.5^\circ [(10 + 5)/2]$. If however, the first edge was 50° we used $27.5^\circ [(50 + 5)/2]$ rather than $23.3^\circ [(50 + 5 + 15)/3]$. These adjustments had only slight effects on the patch averages, and did not change any patterns reported below.

Body condition

In 2010, we used mist-nets and playback to capture male Bobolinks on their territories at fields across a range of sizes and openness. We measured body mass, natural wing chord, and circulating corticosterone (CORT) at three time

points prior to, and a fourth after, injection with adrenocorticotropic hormone (ACTH), a hormone that stimulates the release of CORT. Each time point can be uniquely informative, while the ACTH challenge was done to compare an animal's CORT response to restraint with the maximal response an animal could mount (e.g., Romero 2004). CORT concentrations were determined by radioimmunoassay (RIA; Wingfield et al. 1992). See Online Resource 1 for details. Research conformed to AALAC guidelines and was approved by the Tufts University Institutional Animal Care and Use Committee.

Statistical analyses

Linear regressions were carried out using REG and MIXED procedures and logistic regressions in the LOGISTIC procedure in SAS 9.2; CORT data were analyzed using repeated measures ANOVA in the MIXED procedure with site included as a random effect. Variance partitioning was used to assess to what degree openness and area explain unique variation (Whittaker 1984). In variance partitioning, the variation explained by a fully parameterized model (i.e., one containing all variables of interest) is compared to the full model minus an individual variable. This is repeated for each variable in the model. This allows an assessment of how much explained variation is uniquely due to a given variable and how much explained variation could be explained by more than one variable. This is important for correlated variables, as the unique contribution of one variable cannot be ascribed to the other. For a clear explanation of the technique with an example, please see Lawler and Edwards (2006). AICc was used to compare regression models; models within $\Delta AICc$ of two of the best model were considered to be equally supported (Burnham and Anderson 2002). Residuals were examined to ensure that regression

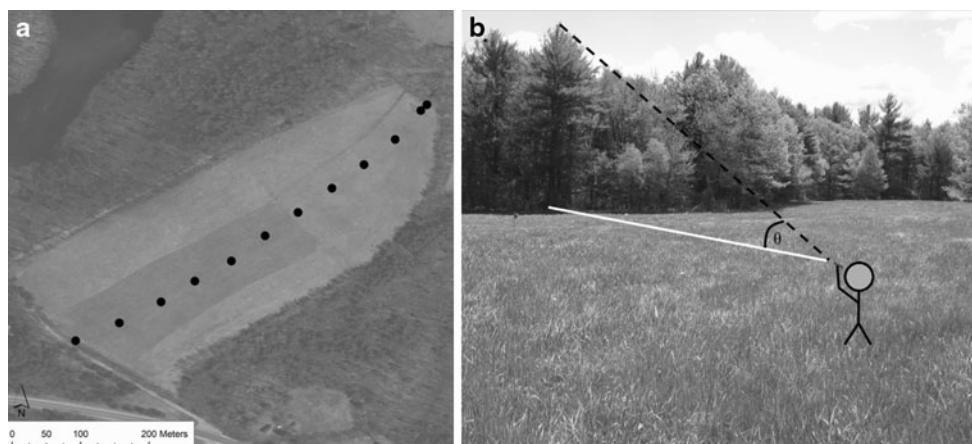


Fig. 1 **a** Openness transect, showing the survey points (black dots) at 50 m intervals and at the starting and ending edges at the large field from Moore State Park, Paxton, MA, USA. **b** Angle to the horizon

was measured from eye level to the visual horizon. This measure was taken with an inclinometer in 4 directions 90° apart and as perpendicular to the field edges as possible

model assumptions were met, and we determined leverage coefficients for all points. Outlying points on the x axis have the ability to exert a strong influence (strong leveraging) on the strength and slope of the overall regression (Sokal and Rohlf 1995). Moran's I (Moran 1950) is a common test for spatial autocorrelation, and can be evaluated using different distance classes, and choice of distance class can affect whether or not spatial autocorrelation is detected (Fortin and Dale 2005). We evaluated spatial autocorrelation at the minimum distance (default setting) in ArcGIS 9.3, and found no significant spatial autocorrelation in observed Bobolink densities or in model residuals.

We evaluated linear and non-linear fits between June male Bobolink density and patch openness using TableCurve 2.0 (using the 'all simple models' option) and found that a linear relationship with a straight-line was the most parsimonious fit (unpublished data). Data were also analyzed using both continuous and binomial (presence/absence) changepoint tests (Siegel and Castellan 1988) and these results were compared to the linear fit. Continuous and binomial changepoint tests identified the same threshold values, but as plots of the relationship suggested a binomial relationship, only results from the binomial changepoint test are presented below. An r^2 was calculated for the binomial threshold models by converting from a χ^2 , corrected for continuity (Emigh 1980), from a 2×2 contingency table based on presence/absence and before/after the threshold (Rosenthal and Rubin 1982). The September data had a small sample size for χ^2 and the results should be viewed with this in mind.

Results

Bobolink density and occupancy showed significant linear and logistic relationships with openness, respectively, but logistic models based on a openness occupancy thresholds identified by binomial changepoint tests had greater explanatory power (Table 1). Specifically, our analyses suggest that Bobolinks in our study area were absent below a certain value of openness, and present above that threshold; above the threshold there appeared to be no relationship between Bobolink density and degree of openness (Figs. 2 and 3). Thresholds remained approximately consistent from June to August, and shifted to greater openness in September (Fig. 3). No Bobolinks were present on any of the 15 fields surveyed in October. Area models were poorer predictors of Bobolink occupancy and density outside of the breeding season and were ranked lower than openness models based on AICc (Table 1). There was some support for area in combination with openness based on AICc; however, the overall increase in model explanatory power was generally small or not uniquely explained by area (Table 1, except for August and September linear models, which do not explain

as much variation as logistic models). While our openness index was significantly linearly correlated with other predictor variables (all $P < 0.001$), including area ($r^2 = 0.26$) and $\ln(\text{area})$ ($r^2 = 0.60$) (Table 2), these independent variables were not equivalent when examining Bobolink density and occupancy (Fig. 3; Table 1). Even though openness and area are correlated, variance partitioning of the logistic regression models (Whittaker 1984) show that openness consistently explained more pure variation, i.e., variation explained uniquely by the variable of interest—than did area (Table 1; June: 20 vs. 8%; July: 28 vs. 1%; August: 30 vs. 2%; September: 1 vs. 0%). A similar pattern was observed for linear models; however, area explained equal or more variation in August and September, but only when other variables, e.g., openness, were present in the model. Openness did not explain much pure variation in September because the full model was over-parameterized (only three fields where Bobolinks were present); however, openness alone was sufficient to describe Bobolink occupancy.

There was no continuous relationship between either openness or area and body condition measures: corticosterone levels (Openness: $F_{1,54} = 1.18$, $P = 0.28$; Area: $F_{1,54} = 0.50$, $P = 0.48$), wing chord (Openness: $F_{1,22} = 0.01$, $P = 0.92$; Area: $F_{1,22} = 1.54$, $P = 0.23$), and body mass (Openness: $F_{1,22} = 1.14$, $P = 0.30$; Area: $F_{1,22} = 0.50$, $P = 0.49$). The lack of openness or area relationships with Bobolink CORT levels was not due to an inability of Bobolinks to mount a CORT response. Bobolink CORT levels increased significantly over time with restraint ($F_{2,54} = 55.5$, $P < 0.0001$), and in response to ACTH ($F_{1,32} = 3.97$, $P = 0.05$) (Fig. 4).

Our analyses of leverage coefficients suggest one reason why studies might report differences in observed area sensitivity. In our area and edge effects model (EEM) regressions, there were two outlying points on the high end of the x axis, and the regression was highly sensitive (strong leverage coefficients) to them (Fig. 2); their removal changed the r^2 value for both area and for the EEM from 0.18 to 0.06. This was not corrected by \ln -transforming area, as the r^2 was still reduced from 0.16 to 0.07. In contrast, removing the single point with a high leverage coefficient from our openness regression caused a trivial increase in the r^2 (by 0.001). We also identified two open sites with small areas; removal of these points also strongly affected our area regression, increasing r^2 from 0.18 to 0.27.

Discussion

Openness versus apparent area sensitivity

The potential role of psychological factors in habitat selection by birds has been acknowledged or alluded to for

Table 1 Bobolink (*Dolichonyx oryzivorus*) occupancy (logistic) and density (linear) as a function of the openness index (OI), area (A), ln area (LA), total edge (TE), and edge effects model (EEM) for uncut hayfields

Month	Model	Logistic			Linear		
		R^2	ΔAICc	Pure ^a	R^2	ΔAICc	Pure ^a
June ($n = 40$)	OI	0.33***	0	0.20	0.20***	0	0.06
	OI + A	0.34**	2.0	–	0.21**	2.0	–
	OI + EEM	0.33**	2.4	–	0.22**	1.3	–
	A	0.20**	4.9	0.08 ^a	0.13*	3.0	0.03 ^a
	LA	0.19**	5.1	– ^a	0.12*	3.7	– ^a
	TE	0.16*	6.1	0.02	0.13*	3.3	0.01
	EEM	0.15*	6.7	0.02	0.18**	1.0	0.03
	Full	0.42*	10.4	–	0.25	8.0	–
July ($n = 43$)	OI	0.58****	0	0.28	0.16**	0.7	0.05
	OI + A + EEM	0.63****	1.7	–	0.20*	3.26	–
	OI + EEM	0.59****	1.9	–	0.19**	1.3	–
	OI + TE	0.59****	1.9	–	0.17*	2.2	–
	OI + TE + EEM	0.62****	2.6	–	0.23*	1.6	–
	Full	0.63****	10.3	–	0.25*	6.4	–
	LA	0.29***	13.8	– ^a	0.08	4.3	– ^a
	TE	0.26**	14.9	0.00	0.03	6.7	0.03
	A	0.23**	16.1	0.01 ^a	0.08	4.4	0.01 ^a
	EEM	0.08	21.6	0.03	0.17**	0	0.01
	Full	0.55****	0	0.30	0.15*	1.0	0.11
August ($n = 35$)	OI + LA	0.60****	0.5	–	0.18*	2.2	–
	OI + A	0.59****	0.8	–	0.23*	0.3	–
	OI + TE	0.59****	1.2	–	0.15	3.4	–
	OI + A + TE	0.60***	3.5	–	0.29**	0	–
	LA	0.22*	10.7	– ^a	0.04	5.3	– ^a
	TE	0.16*	12.2	0.00	0.06	4.5	0.05
	Full	0.61**	12.5	–	0.30	5.8	–
	A	0.13	13.0	0.02 ^a	0.01 ^b	6.3	0.11 ^a
	EEM	0.13	13.1	0.00	0.02	6.1	0.01
	Full	1.00****	0	0.01	0.18	0	0.10
September ($n = 18$)	OI + A	1.00***	3.4	–	0.30	0.5	–
	TE	0.27	13.0	0.00	0.03 ^b	3.0	0.04
	EEM	0.17	14.3	0.00	0.04	2.9	0.02
	LA	0.11	15.0	0.00	0.008	3.5	– ^a
	A	0.07	15.5	0.00 ^a	0.001 ^b	3.6	0.12 ^a
	Full	1.00**	24.3	–	0.35	13.3	–

OI was treated as binomial (before or after threshold) for logistic models and continuous for linear models. Bivariate models and models within 2 ΔAICc of either the best logistic or linear model are shown, but all possible combinations were examined. ΔAICc cannot be compared between seasons or between linear and logistic models. Effect sizes are in Online Resource 2

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, **** $P \leq 0.0001$

^a Unshared variation for individual variables from variance partitioning. Not calculated for models containing multiple variables

^b Pure variation for area and ln area was calculated together

^c Pure variation can exceed bivariate R^2 if the variable explains more variation when another variable is present

many years, and includes both inherited and learned preferences (e.g., Lack 1933; Hildén 1965; Harris and Reed 2002). One factor, response to openness, has been suggested as a mechanism for habitat selection by birds

(Klomp 1954; Hildén 1965; Van Der Vliet et al. 2008), and we proposed that it could drive apparent area sensitivity. Here, we have shown that an index based on visual perception of the landscape immediately adjacent to a

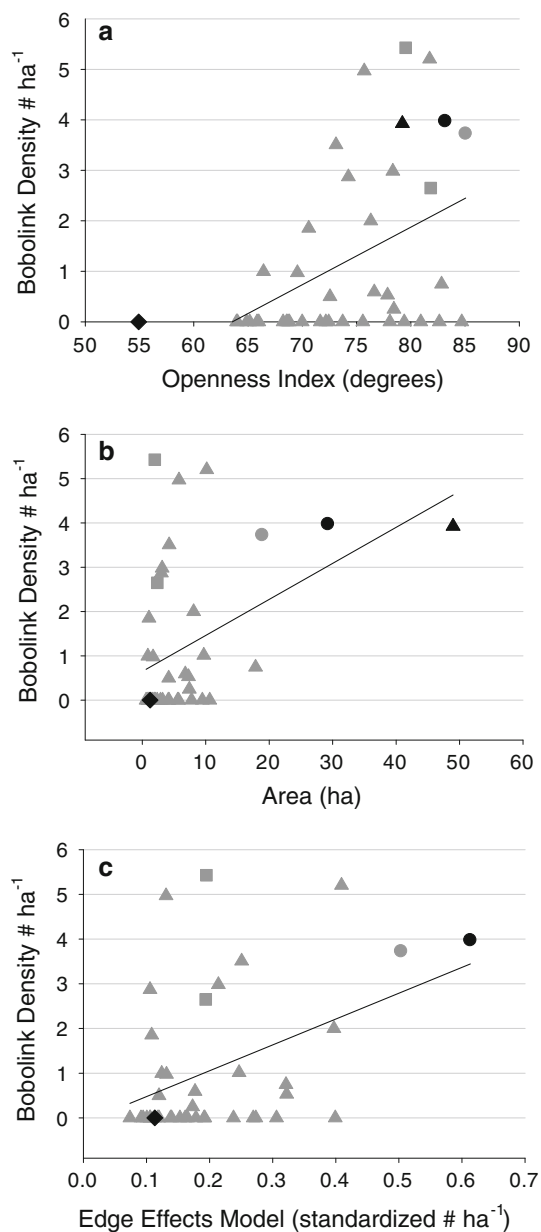


Fig. 2 Openness (a) provided a better fit to male Bobolink (*Dolichonyx oryzivorus*) density than did area (b) or the edge effects model (EEM) (c). Also, the openness regression was less sensitive to individual points than were the other regressions. The *black diamond* denotes a point with a high leverage coefficient for the openness regression (it is depicted in all 3 graphs for comparison), the *black triangle* and *black circle* denote points with high leverage coefficients for area, and *circles* (gray and black) denote points with high leverage coefficients for the EEM. *Gray squares* on each graph indicate two small open sites that when removed increase the r^2 of the area regression. The site indicated by the *black triangle* was not included in the EEM because it was unsuitable for that analysis (the field abutted grazed habitat—this did not strongly affect the openness or the area, but made the edge definition ambiguous and inconsistent with the rest of the patches)

habitat patch, openness, provides greater explanatory power for site occupancy and population density of Bobolinks than does physical patch size, and that this index

also outperforms edge metrics. Furthermore, the effect of openness persisted across dramatic changes in Bobolink behavior associated with seasonal changes in breeding status, while no consistent area effects were detected. Although we did not examine the consistency of the openness threshold value across years, the threshold values observed in 2009 were consistent with those observed at a sub-set of our sites in 2008 (June: 72.2°, $P < 0.05$; August 71.7°, $P < 0.01$, unpublished data). To our knowledge, no prior attempt to quantitatively link openness as a visual measure to area sensitivity has been made. Consequently, we present the hypothesis that apparent area sensitivity in Bobolinks is a function of how open a field is rather than how large it is, and provide a viable means to quantify openness.

Openness, like perimeter to area ratio or percent of habitat in a landscape, is generally collinear with area because patch area can be a major component of the measure itself. In contrast, there are other variables, such as within-patch vegetation structure, that might be correlated with area, but do not contain area as a physical component determining the measure itself. Although openness, area, and many of our other variables were significantly correlated (all $r^2 \leq 0.60$), they were not interchangeable. Specifically, these correlated variables differed strikingly in their explanatory power for male Bobolink density and site occupancy, especially when a threshold relationship was considered. This was reinforced by the variance partitioning analysis, where openness explained additional variation beyond any shared variation with area (Table 1). Consequently, species that are openness sensitive would appear to be area sensitive if they were in a closed landscape. Only in open landscapes would these species be predicted to lack area sensitivity. Occupancy patterns consistent with this prediction have been observed at a landscape (rather than the patch) scale in other species. Sedge Wrens (*Cistothorus platensis*) and Clay-colored Sparrows (*Spizella pallida*) are more likely to be present in small patches in landscapes containing >60% grassland compared to large patches in landscapes with <60% grassland; Bobolinks in this study, however, did not show this pattern (Bakker et al. 2002). The lack of a response by Bobolinks may have been due to the greater amount of open habitat in their study system. In our study, two small very open sites strongly influenced the fit of the relationship between area and grassland bird density, supporting or removing apparent area sensitivity (see Online Resource 3 for photographs of a small open site and a small closed site). While Bakker et al. (2002) found responses to amount of grassland in the landscape, open non-grassland habitat was important in our study—one of the small open sites was bordered by saltmarsh, and the other by mixed agricultural fields. Thus, whether or not a study finds grassland species to be area sensitive could

Fig. 3 Total Bobolink density was better explained by a binary (presence/absence) openness threshold (**b, d, f**) than by area (**a, c, e**), and remained relatively consistent across months (**b** vs. **d** vs. **f**). Thresholds are shown as *solid vertical lines*; the *dashed vertical line* (**b**) indicates the openness threshold for June (based on data shown in Fig. 2a); r^2 values refer to threshold models and were calculated by converting from 2×2 contingency table corrected for continuity. *Regression lines* are shown for significant regressions. Note that sample sizes and observed Bobolink densities changed between months

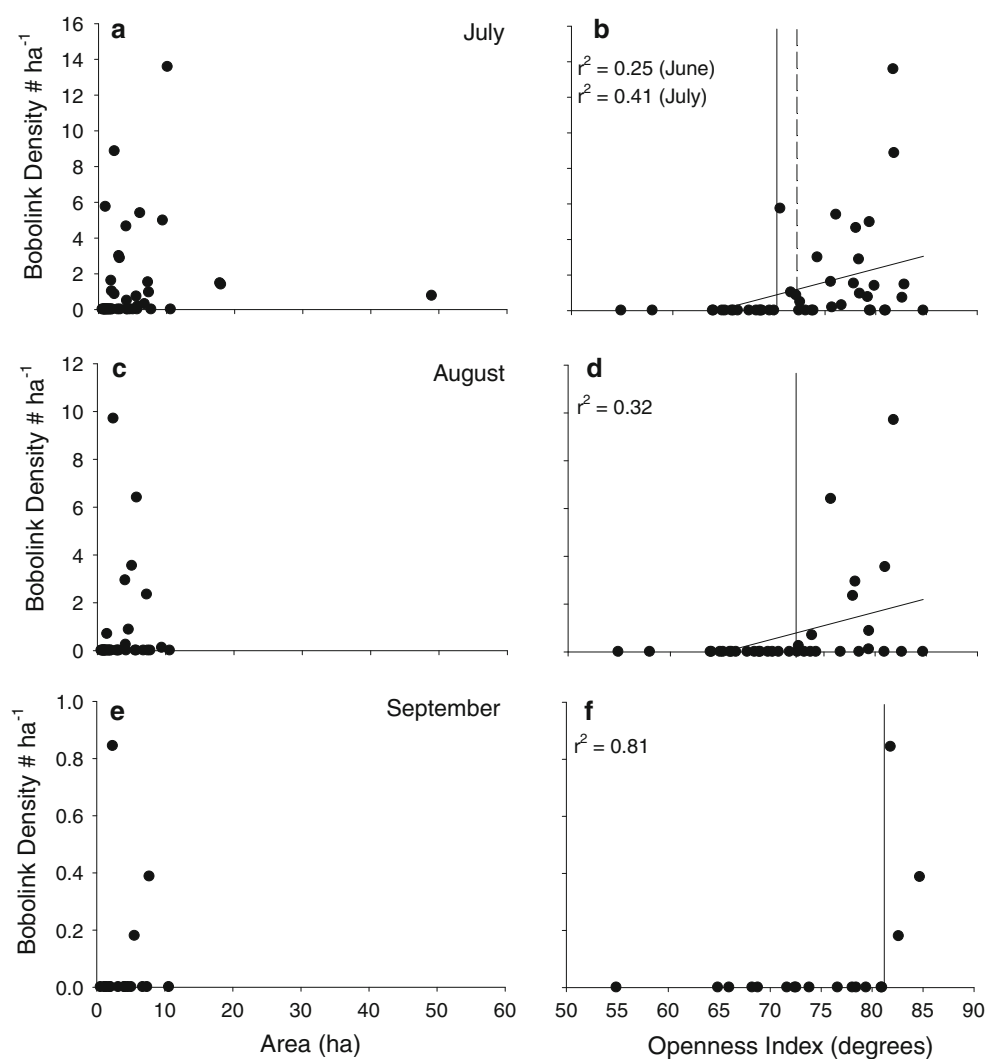


Table 2 Bivariate correlations show the openness index to be significantly correlated with the other independent variables used in this study

Measure	r	r^2	P	N
Area	0.51	0.26	0.0002	48
Ln (area)	0.77	0.60	<0.0001	48
Perimeter area ratio	-0.77	0.60	<0.0001	48
Total edge	0.67	0.45	<0.0001	41
Edge effects model	0.70	0.49	<0.0001	41

depend on whether or not small, open sites were included in the sampling design.

Statistical considerations

Inconsistencies in whether a species displays area sensitivity may also be due to the statistical approaches taken. While we observed a significant linear relationship

between openness and Bobolink density, we believe that it is an artifact of the observed threshold relationship. That is, the threshold relationship provided a stronger explanation of observed variance, and no significant linear relationship was observed when examining only data before or after the threshold. Uhmman et al. (2001) also found a threshold relationship between openness and occupancy for Burrowing Owls (*Athene cunicularia*); thus, many species may respond to openness in a threshold rather than linear manner. In contrast, most studies of area sensitivity test for linear or logistic relationships between density or occupancy and area (but see, e.g., Winter et al. 2006). If a threshold relationship exists, studies including sites only above or below the threshold might not find area sensitivity, but those spanning the threshold would. Even if a linear relationship exists, our area regression was very sensitive to the bird density values of the two largest fields (outlying points). This does not appear to be an artifact of our range of field sizes, as some previous studies of area sensitivity in grassland birds include area ranges similar to

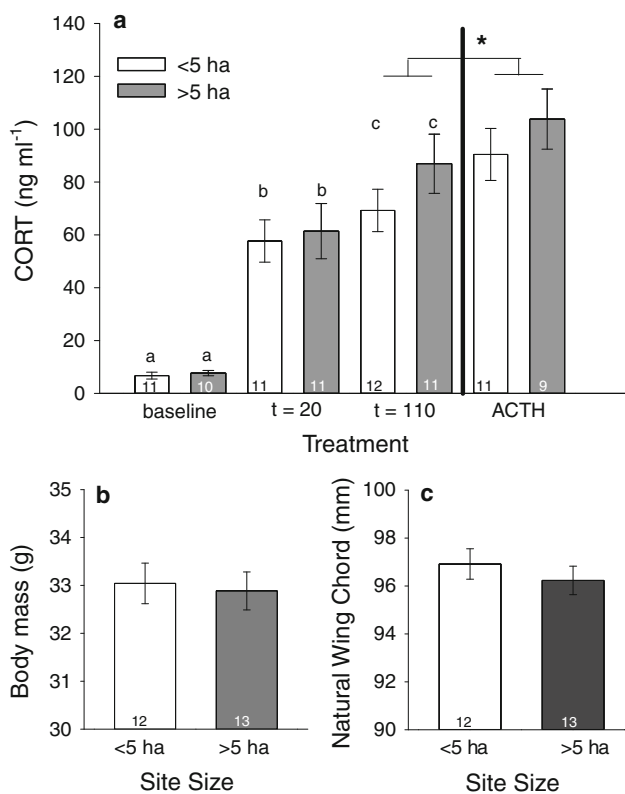


Fig. 4 Male Bobolink corticosterone (CORT) levels significantly increased over time (t , in min) and with injection of adrenocorticotropic hormone (ACTH) (a). Letters denote significant differences ($P \leq 0.01$; repeated measures ANOVA), * indicates that ACTH resulted in a significant increase in CORT relative to $t = 110$ ($P = 0.05$). There was no significant difference between sites < 5 ha and sites > 5 ha ($P = 0.48$). There were no significant differences (all $P > 0.30$) in body mass (b) or wing chord (c). Sites are grouped into < 5 ha ($n = 5$) and > 5 ha ($n = 4$) to ease visual interpretation of results; number of birds sampled given in the respective bars

ours (e.g., Helzer and Jelinski 1999), and the effect persisted when area was log-transformed. This suggests that chance values at the largest sites may determine whether or not a study finds a significant effect of area. However, some studies of area sensitivity of grassland birds avoid this potentially confounding factor by analyzing occupancy, using logistic regression, rather than density (e.g., Helzer and Jelinski 1999; Bakker et al. 2002). Logistic regression is insensitive to the values of especially large or small fields (Hosmer and Lemeshow 2000), so this confounding factor would not explain all reported intraspecific variation in area sensitivity.

While the results of linear models in Table 1 evaluate density, and so account for unequal survey effort, our logistic regression analysis examines occupancy, and therefore has a greater chance of detecting Bobolinks on large fields relative to small fields. We note that this bias would serve to strengthen an area effect relative to openness, so our result that openness explains more variation is

perhaps conservative. Although there was unequal survey effort, it was not systematically biased along an openness gradient, as small fields could also have high openness values. Furthermore, by using variance partitioning, effects due to unequal sampling due to area would be partitioned either with area or with the shared variation, leaving the pure variation explained by openness corrected for unequal sampling effort. Consequently, we advise against taking our area results from the logistic regression as unbiased, but this does not affect our conclusions relative to openness.

Management implications

If openness is in fact a causal factor determining patch selection by Bobolinks, then this could be a mechanism whereby afforestation (Norment 2002) would negatively impact grassland birds more than expected from habitat loss alone. Similar conclusions have been reached by other authors who focused on the landscape scale and concluded that fields in open landscapes should receive priority for conservation (Coppedge et al. 2001; Bakker et al. 2002; Davis 2004; Shustack et al. 2010). Here, we provide an approach that can be applied to patch-level decisions. If our observed patterns extend to other grassland species, fields could be managed to increase openness (e.g., removing trees adjacent to, or within, fields). The openness index may guide decisions as to when to retain shelter-belts or isolated trees; if fields are well below or above the openness threshold, retaining these features may not be detrimental to the grassland species and could facilitate other management goals (e.g., Johnson and Beck 1988; Fischer et al. 2010). In contrast, fields near the openness threshold may benefit from active management. We do caution that managing for openness may only be effective near the openness threshold and that our identified thresholds should not be taken as precise prescriptions.

Openness and body condition

We might expect some measurable difference in body condition between animals at closed or small sites if openness or area is a measure of habitat quality for Bobolinks. This could occur by larger or more open sites attracting higher-quality individuals, or by allowing individuals to maintain a better body condition. However, we observed an openness threshold where a patch is either suitable or not suitable. Hence, for two patches above the openness threshold, there is no evidence that the more open patch is more suitable (i.e., has birds in better body condition). This suggests that not only is openness a better predictor than area, but that the relationship is an occupancy threshold rather than a density relationship. This

occupancy threshold is strongly supported by the absence of a linear relationship between body condition and either openness or area. Lack of effect of patch size on adult body condition measures has been reported elsewhere for forest birds (wing chord and body mass in Ovenbirds, Bayne and Hobson 2002; heterophyl/leucocyte ratio in Eurasian Treecreepers *Certhia familiaris*, Suorsa et al. 2004), but Suorsa et al. (2003), in the only other study to date to look at CORT relative to patch size, reported higher stress-induced corticosterone levels in nestling Eurasian Treecreepers in smaller forest patches.

Openness and potential predator effects

In conclusion, our results are consistent with the hypothesis that openness is a proximate factor affecting Bobolink density, with the possible ultimate factor being predator avoidance. Perceived predation risk has been proposed to influence habitat selection by birds (Lima 1993), and this has been documented for grassland species (Lima and Valone 1991; Suhonen et al. 1994). Klomp (1954) observed that Lapwings (*Vanellus vanellus*) were better able to defend their nests against avian predators in more open habitats farther from wooded edges. Similarly, migrating Buff-breasted Sandpipers (*Tryngites subruficollis*) avoid fields with human-built obstructions such as farmsteads and hedgerows, and waders (Charadrii) in coastal pastures avoided fences and stone walls, which the authors suggest is due to avoiding fields where there are perches for predators (Wallander et al. 2006; Jorgensen et al. 2007). In lizards, the degree of openness can influence predation risk, which has led to evolution of different morphologies related to escape behavior (e.g., Goodman 2009). Behavioral avoidance (e.g., as measured by telemetry) of human-built constructs, such as avoidance of powerlines by prairie-chickens (*Tympanuchus* spp.), may be related to loss of openness and increased predation risk (Manville 2004; Lammers and Collopy 2007; Pruett et al. 2009). Consequently, for primarily open habitats (e.g., grasslands, wetlands, shrublands), the degree to which predators might shape responses to openness bears further examination.

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