

SPATIAL RESPONSES OF BOBOLINKS (*DOLICHONYX ORYZIVORUS*) NEAR DIFFERENT TYPES OF EDGES IN NORTHERN IOWA

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ABSTRACT.—Habitat edges are well-studied components of fragmented landscapes, yet factors mediating edge effects remain unclear. We report how different types of edges surrounding patches may affect spatial distributions of Bobolink (*Dolichonyx oryzivorus*), a declining, area-sensitive songbird that breeds in grasslands. We expected Bobolinks to be less abundant near edges, and we investigated a set of alternative hypotheses for explaining that spatial pattern: (1) passive displacement, in which individuals do not avoid edges but use edges as boundaries for territories; (2) habitat gradients, in which individuals respond to habitat structure gradients near edges; (3) territory size, in which size of territories increases near edges; and (4) active avoidance, in which individuals actively avoid edges by positioning territory boundaries away from edges. To examine those hypotheses, we surveyed Bobolinks in grassland habitats near 34 edges of three different edge types (agriculture, road, and woodland) in northern Iowa, 1999–2000. Bobolink density was lower near woodland edges than near other edge types, and density increased as a function of distance from edge for all edge types. There was no evidence for a habitat gradient close to edges, but there was some evidence for habitat structure differing among edge types. Territory size increased near roads, decreased near woodlands, but did not change near agricultural edges. Territory positioning was consistent with active avoidance near woodland edges, and to a lesser extent road edges, but positioning was only consistent with passive displacement near agriculture edges. We conclude that land use surrounding patches can have variable effects on territorial dynamics and habitat use of this area-sensitive species. Linking edge avoidance with fitness is needed to understand the demographic consequences of those responses for species in fragmented landscapes. Received 22 August 2002, accepted 22 April 2003.

RESUMEN.—Los bordes de los hábitats son componentes bien estudiados de los paisajes fragmentados, pero los factores que determinan los efectos de borde son aún poco claros. En este estudio documentamos cómo diferentes tipos de borde alrededor de parches pueden afectar la distribución espacial de *Dolichonyx oryzivorus*, un ave canora cuyas poblaciones están disminuyendo y es sensible al área. Esperábamos que *D. oryzivorus* fuera menos abundante cerca de los bordes, e investigamos una serie de alternativas para explicar dicho patrón espacial: (1) desplazamiento pasivo, en la que los individuos no evitan los bordes pero los usan como límites de sus territorios; (2) gradientes de hábitat, en la que los individuos responden a gradientes en la estructura del hábitat cerca de los bordes; (3) tamaño de territorio, en la que el tamaño de los territorios aumenta cerca de los bordes; y (4) evitación activa, en la que los individuos evitan activamente los bordes ubicando los límites de sus territorios lejos de éstos. Para examinar estas hipótesis, hicimos censos de *D. oryzivorus* en pastizales cerca de 34 bordes de diferentes tipos (áreas agrícolas, carreteras y bosques) en el norte de Iowa en 1999 y 2000. La densidad de *D. oryzivorus* fue menor cerca de bordes de bosque que de bordes de otro tipo, y la densidad aumentó como función de la distancia a bordes de todos los tipos. No hubo evidencia que indicara gradientes de hábitat cerca de los bordes, pero hubo indicaciones de diferencias en la estructura del hábitat entre los diferentes tipos de borde. El tamaño de los territorios aumentó cerca de las carreteras, disminuyó cerca de bosques y no cambió cerca de áreas agrícolas. La ubicación de los territorios fue consistente con la idea de evitación activa cerca de los bordes de bosque y en un menor grado en bordes de carretera, pero la ubicación de los territorios fue consistente sólo con desplazamiento pasivo cerca de los bordes de áreas agrícolas. Concluimos que el uso del suelo en los parches circundantes puede tener efectos variables sobre la dinámica territorial y el uso de hábitat en esta especie sensible al área. Para entender las consecuencias demográficas de estas respuestas para las especies en paisajes fragmentados, es necesario conectar la evitación de los bordes con la adecuación biológica de los individuos.

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HABITAT LOSS GENERALLY leads to increased habitat fragmentation, resulting in smaller patches, increased isolation, and increased proportion of edge habitat in landscapes. Aspects of fragmentation can affect both habitat selection and demography of migratory birds (e.g. Winter and Faaborg 1999, Woodward et al. 2001). For example, many species of migratory birds are area sensitive, being less abundant or less likely to occur in small patches (Robbins et al. 1989, Herkert 1994), and nesting success of migratory birds can also be lower in small patches (Johnson and Temple 1990, Winter and Faaborg 1999). Area sensitivity was initially documented in breeding forest birds (e.g. Whitcomb et al. 1981, Ambuel and Temple 1983, Robbins et al. 1989) but has recently become very apparent in grassland bird communities, in which most obligate grassland-nesting species have been documented to be area sensitive in at least some parts of their breeding ranges (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999, Johnson and Igl 2001; but see Horn et al. 2000). However, observed regional variation of area sensitivity within species (Johnson and Igl 2001, Bakker et al. 2002) not only limits robust conservation strategies but also our understanding of the processes of habitat selection in those species.

One proposed mechanism for area sensitivity is edge avoidance (Burke and Nol 1998, Johnson and Igl 2001), in which species tend to be less abundant or less likely to occur near edges. That effect could be exacerbated in small patches because of high proportions of edge habitat relative to interior habitat, leading to area sensitivity in fragmented landscapes (but see Bollinger and Switzer 2002). If birds do avoid edges, then that behavior could offset potential negative edge effects on nesting success, where nest predation and brood parasitism can increase near edges (e.g. Johnson and Temple 1990, Paton 1994). But not all types of edges cause similar effects (Suarez et al. 1997, Winter et al. 2000). If birds respond differently to different edge types, then some variation in area sensitivity within species might be explained. Yet lower densities near edges can be explained by several factors (Ortega and Capen 1999), so a clear understanding of edge avoidance near different edge types will be critical for evaluating the importance of edges on the distributions of area-sensitive species.

We examine how different edge types may affect spatial distributions of Bobolinks (*Dolichonyx oryzivorus*) breeding in northern Iowa. Bobolinks are polygynous, Neotropical migratory passerines that have exhibited severe population declines in recent years (Peterjohn and Sauer 1999). Bobolinks have been documented as being area sensitive throughout much of their range (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999, Johnson and Igl 2001). On the basis of previous accounts (Helzer 1996, Bock et al. 1999), we expected Bobolink density to be lower near edges, and we investigate four potential hypotheses that could explain that spatial pattern: passive displacement, habitat gradients, territory size, and active avoidance.

Passive displacement.—Passive displacement can occur near edges, in which individuals do not avoid edges, but use edges as a boundary for territories (Kroodsma 1984, King et al. 1997, Ortega and Capen 1999). Assuming relatively circular territories, that would lead to apparent patterns of avoidance on the basis of density data, typically within about half of the diameter of an average territory. That type of random settlement has explained density patterns in some systems (King et al. 1997), but not in others (Ortega and Capen 1999).

Habitat gradients.—Habitat gradients can occur near edges, and individuals could simply respond to a habitat structure gradient that can occur near edges (Gates and Gysel 1978, Kroodsma 1984). Habitat gradients observed in some systems extend up to 130 m into the interior of a patch (e.g. Chen et al. 1992). However, that hypothesis has generally not explained avian distribution near forest edges (Kroodsma 1984, Ortega and Capen 1999).

Territory size.—Territory size of individuals can increase near edges, but individuals could potentially still use edge habitat. Overall, that would lead to low densities near edges. That pattern has been observed for Ovenbirds (*Seiurus aurocapillus*) breeding near roads in New England forests (Ortega and Capen 1999). Variation in territory size can be due to variation in habitat quality, where territory size increases with lower food availability (Smith and Shugart 1987).

Active avoidance.—Finally, birds can actively avoid edges by distributing territory boundaries away from edges. That is often thought to

be due to increased predation risk near edges, either to nests (Gates and Gysel 1978, Burke and Nol 1998) or to adults (Pulliam and Mills 1977, Lima and Valone 1991).

We examine those hypotheses by combining survey data on Bobolink densities, information on territory dynamics, and habitat sampling near three common edge types occurring in grasslands of northern Iowa.

METHODS

Study area.—Grassland birds were surveyed near 34 distinct edges of three edge types (agriculture, road, and woodland) in 23 grassland patches in northern Iowa, 1999–2000 (Fig. 1). Thirty survey plots (10 of each edge type) were surveyed in 1999; however, 4 of those were altered after the 1999 breeding season, making those sites unsuitable for future surveys. In 2000, those four areas were replaced with new plots near edges, thus continuing to survey birds near 30 edges per breeding season. Grasslands included restored grasslands and native tallgrass prairies under state and federal management. Restored grasslands contained both warm-season and cool-season grass plantings. Warm-season plantings were typically switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*), or mixtures of both; whereas cool-season plantings were typically smooth brome

(*Bromus inermis*) or brome and alfalfa (*Medicago sativa*) mixtures. Other common plants included orchard grass (*Dactylis glomerata*), red clover (*Trifolium pratense*), and wild parsnip (*Pastinaca sativa*). Prairies contained a high diversity of native warm-season grasses and forbs. Common species included big bluestem, little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), switchgrass, goldenrod (*Solidago* spp.), sunflower (*Helianthus* spp.), and milkweed (*Asclepias* spp.).

Edge types considered were three of the most common grassland edge types in northern Iowa. Agriculture edges contained corn or soybean fields adjacent to grassland habitat. For road edges, only sites with two-lane gravel roads that had row crop agriculture on the side of the road opposite to the grassland habitat were used to standardize that edge type. Although that design does not isolate road effects, comparing road edges to agriculture edges demonstrates the relative effect of roads on bird distribution. Woodland edges were ≥ 30 m wide and were closed canopy deciduous woodland adjacent to grassland habitat. At most, only one replicate of each edge type was considered in each field. Overall, we surveyed 10 agriculture, 12 road, and 12 woodland edges. Five agriculture, 5 road, and 2 woodland plots were located on native prairies (all predominately warm-season grasses); whereas 5 agriculture (four cool-season, one warm-season plantings), 7 road (four cool-season, three warm-season plantings), and

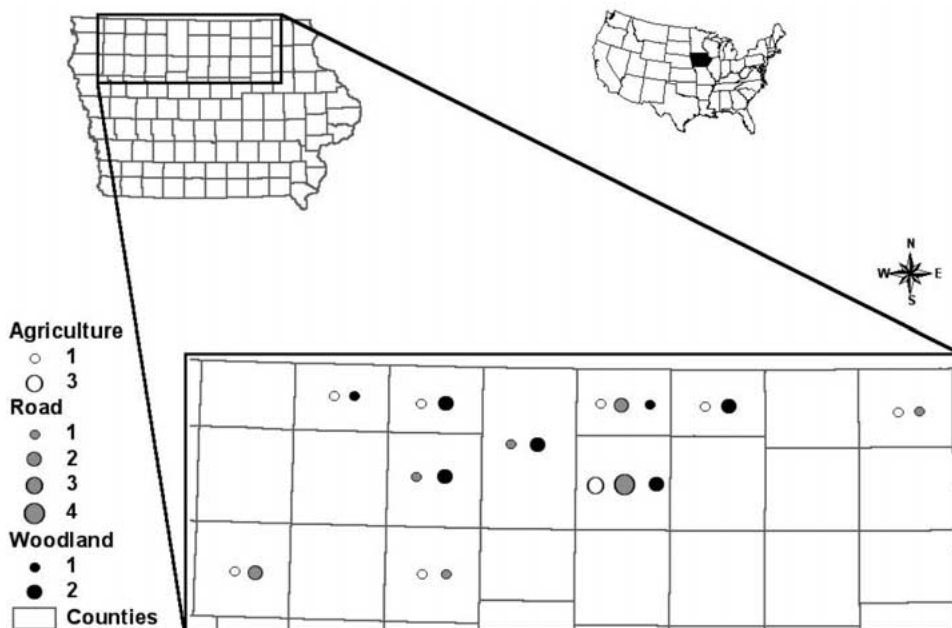


FIG. 1. Locations of grassland habitats near three different types of edges surveyed per county in northern Iowa, 1999–2000. Numbers denote the number of edges surveyed per county for each edge type.

10 woodland plots (seven cool-season, three warm-season plantings) were located on restored grasslands. Because Bobolink densities in those two habitat types tend to be similar in northern Iowa (Fletcher and Koford 2002), data were pooled across habitat types when testing for edge effects.

Bird surveys.—Birds were surveyed in grassland habitat near edges using fixed-width transects running parallel to edges to estimate an index of Bobolink density as a function of distance from edge. Each edge survey plot was placed at least 100 m from any other edge in the study site to minimize effects from other edges. We based that buffer on previous research by Helzer (1996), who found that densities of Bobolinks were lower within ~75 m of edges in Nebraska. Each edge survey plot contained three transects: one 25 m from the edge, one 75 m, and one 125 m from the edge. Transects varied in the total distance, from 100 to 400 m along the edge, to maximize total area sampled, but transect distances were constant within plots. For each survey, the observer randomly picked the order to survey transects. During each survey, the observer walked transects at a steady pace, recording all birds seen within 25 m of the transect midpoint. Observers recorded species, sex, direction (edge or interior side of transect), and distance of each bird from transects. Care was taken not to count the same individual more than once. Surveys were conducted between sunrise and 4 h after sunrise, when breeding birds are most active. Surveys were repeated three times during the breeding season, from 15 May until 6 July, 1999–2000. Each year two observers conducted surveys, and each site was surveyed by each observer at least once.

Territory mapping.—During the 2000 breeding season, we mapped territories for male Bobolinks within the survey plots at all sites between 15 May and 15 June, the approximate duration of Bobolink territoriality in that region. Male Bobolinks typically have multipurpose, nonoverlapping territories during the breeding season, where courtship, feeding, and rearing young occur (Martin and Gavin 1995). The “flush” technique was used to map territories during one visit to each survey area (Wiens 1969; see also Wittenburger 1980, Bollinger and Gavin 1989). To map territories, an observer systematically traversed the edge survey plot until observing a male Bobolink. The observer then approached the male until he flushed to a different perch, recording the universal transverse mercator coordinates of each location using a global positioning system (GPS). A minimum of 20 locations ($\bar{x} = 23.1 \pm 2.2$ SD; range: 20–33) was collected for each territory (Wiens 1969, Wittenburger 1980). That process was repeated for all males observed during the mapping visit within the boundaries of plots. Number of locations collected per territory did not differ among edge types (agriculture: 22.9 ± 3.0 , road: 23.2 ± 1.8 , woodland: $23.2 \pm$

1.8 ; $F = 0.33$, $df = 2$ and 42 , $P = 0.72$). Maximum error of the GPS unit based on deviations of readings from known locations was 11.6 m ($n = 141$; $\bar{x} = 4.1 \pm 2.3$ m). Territories were quantified using 95% minimum convex polygons. Information on territory dynamics (e.g. distance of territories to edge) was determined using a geographic information system and aerial photographs taken in 1998–2000.

Habitat measurements.—Vegetation along transects was measured each year to determine if vegetation changes in relation to the edge, and how habitat gradients may affect spatial distributions of Bobolinks. Stratified random sampling was used to estimate habitat structure. Each survey plot was stratified into six 25 m intervals from the edge. Within each interval, five sampling points were randomly chosen. At each sampling point, we recorded vertical density of vegetation, vegetation height, litter depth, and canopy coverage. Vertical density was quantified by measuring the height of visual obstruction at 4 m in each cardinal direction from a Robel pole at a height of 1 m (Robel et al. 1970). Maximum height of standing vegetation and litter depth were measured at the location of the Robel pole. Canopy coverage was assessed on the basis of nonoverlapping percentages using a Daubenmire quadrat (Daubenmire 1959). Canopy coverage categories included total (live and dead vegetation), grass, forb, standing dead vegetation, litter, and bare ground.

Statistical analyses.—Bobolink distribution patterns were quantified by grouping detections into six 25 m intervals from the edge (0–25, 26–50, 51–75 m, etc.). Although individuals likely used more than one distance interval, those intervals allow for high resolution in examining the spatial patterns near edges and our model structure accounted for that potential lack of independence (see below). Those estimates were not corrected for detectability; however, elsewhere we have documented that Bobolinks have high detectability up to 50 m from observers and that uncorrected density estimates are similar to corrected estimates (Fletcher and Koford 2002; see also Rotella et al. 1999). Because multiple surveys of the same site were not independent, we averaged those surveys into one estimate (mean number of detections of males ha^{-1}) for each interval at each site as an index of Bobolink density (density hereafter).

Estimates derived from survey data (using 2000 data only) were compared with estimates derived from territory mapping to determine the relative consistency between techniques in estimating edge avoidance. Using territory mapping data, we estimated the number of territories per hectare, d_i , for each 25 m interval by determining the proportion of each territory that fell within each distance interval, i :

$$d_i = \frac{\sum_{j=0}^n t_j}{A_i}$$

where t_i is the proportion of the territory in distance interval i for individual j (where

$$\sum_{i=1}^6 t_i = 1,$$

unless territory boundaries range outside of the survey area), n is the total number of individual territories mapped within i , and A_i is the area (hectares) of distance interval i . The two types of estimates were then compared using Spearman's rank correlation.

Density index was analyzed using a mixed-model incomplete block design with density as the response variable, site as the block (and random effect), edge type, distance from edge (distance intervals), and edge type \times distance as explanatory variables, and year as a split-plot repeated measure (Littell et al. 1996:88–92). Because distance intervals are not independent, we considered distance from edge as a repeated measure within plots. Four covariance structures were explored to explain that repeated measure (autoregressive order one, compound symmetric, unstructured, and variance components; Littell et al. 1996). However, we report results from an autoregressive order one covariance structure, which assumes that closer intervals are more correlated than intervals farther apart (i.e. the covariance structure is $\sigma^2 \rho^x$, in which x is the number of distance intervals between observations; Littell et al. 1996), because that structure made the most biological sense and consistently was the best fit to the data (i.e. it had the lowest Akaike's Information Criterion, adjusted for sample size; Burnham and Anderson 1998). The total distance of the survey transect (100–400 m) was used as a weighting factor. For distance effects, we were interested in nonzero slopes, and if slopes were heterogeneous among edge types, which were tested by using the midpoint of each distance interval as a continuous variable. Bobolink density was natural-log transformed to improve homogeneity of variance and normality.

To test for habitat gradients as a function of distance from edge, we used the same mixed-model framework with repeated measures for year and distance used above, but with habitat metrics as response variables (e.g. litter depth). Habitat measurements were transformed as needed prior to the analysis to improve normality and homogeneity of variance.

For investigating territory size near edges, the distance from the habitat edge to the center of each territory was calculated (*sensu* Ortega and Capen 1999). We then used a similar mixed-model analysis with repeated measures as above, but with territory size as the response variable, distances from territory centers to edges within plots as repeated measures, and number of territories mapped per hectare for each survey plot as a covariate, because increasing bird density can lead to decreasing territory size regardless of the spatial locations of territories (Smith and Shugart 1987). Number of locations used to estimate territory

size was also included as a covariate to control for potential effects of sampling intensity.

Passive displacement and active avoidance were investigated by estimating the mean and 95% confidence intervals of the distance from the habitat edge to the nearest border of all territories defined as "edge" territories. Edge territories were defined as those in which no other territorial locations from different males fell between the central portion of territories and the edge habitat. That confidence interval was estimated in the mixed-model framework, again using the number of territories mapped per hectare for each survey area as a covariate. If confidence intervals for that distance estimate approach zero near edges, then estimates would be consistent with birds only settling by means of passive displacement. However, if confidence intervals are displaced away from edges, then estimates would be consistent with active edge avoidance.

RESULTS

In 1999, we recorded 329 observations of Bobolinks along transects (69.6% males; $n = 229$), whereas in 2000 we recorded 358 observations (62.5% males; $n = 224$). In both years, Bobolinks were the most common bird observed on transects, being over twice as dense as other common species observed. In 2000, we mapped 63 territories on our study plots: 22 near agricultural edges, 19 near road edges, and 22 near woodland edges. Density as a function of distance from edge for survey data and the number of territories per hectare (d_i) were highly correlated (Spearman's $\rho = 0.61$, $n = 180$, $P < 0.0001$). Variation between those two measures likely reflects factors such as temporal variation, spatial bias of locations within territories, and measurement error while conducting surveys and mapping territories.

Spatial density.—Overall, Bobolink density was lower near woodland edges than other types of edges (Table 1); density was 2 \times greater near agriculture edges and 1.5 \times greater near road edges than density near woodland edges (Fig. 2A). We explored whether that effect could be explained by differences between habitat types (restored or prairie), or grass plantings (cool-season or warm-season grasses). There was no evidence for density being different between habitat types ($F = 0.41$, $df = 1$ and 21, $P = 0.53$) or grass type ($F = 0.33$, $df = 1$ and 21, $P = 0.57$). Density increased as a function of distance from edge for all edge types (i.e. a distance effect was observed but no distance \times edge type interaction; Table 1, Fig. 2B). There

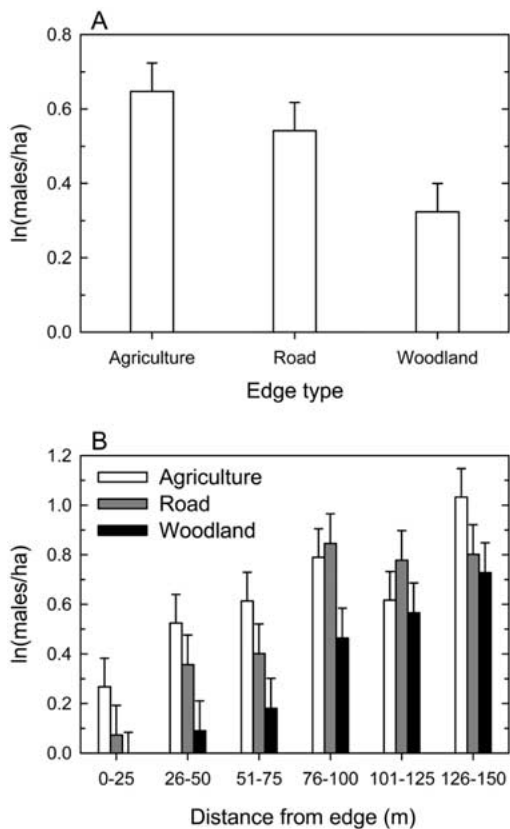


FIG. 2. Least-squares estimates of Bobolink density (mean number of detections of males ha^{-1} , 1 SE) in grasslands (A) near three different edge types, and (B) as a function of distance from edge for three edge types, northern Iowa, 1999–2000.

was no evidence for year effects ($F = 1.80$, $df = 1$ and 286 , $P = 0.18$) or any interactions with year effects ($F \leq 2.6$, $df = 1-2$ and 286 , $P \geq 0.11$).

Habitat structure.—Habitat structure differed among edge types, primarily for litter depth and total vegetation cover (Table 1). Litter depth was lowest near woodland edges and greatest near agriculture edges, whereas total cover was greatest near agriculture edges and least near road edges (Fig. 3). Although there was some evidence for habitat structure being different among edge types, there was no evidence for a habitat structure gradient as a function of distance from edge or for an interaction of distance and edge type for any habitat variable considered (Table 1; Fig. 3). There was no evidence for year effects ($F \leq 2.05$, $df = 1$ and 286 , $P > 0.15$) for any variable, except for vegeta-

tion height being greater in 1999 ($F = 8.80$, $df = 1$ and 286 , $P = 0.003$) and weak evidence of standing dead vegetation cover being greater in 2000 ($F = 3.68$, $df = 1$ and 286 , $P = 0.056$). Yet there was no evidence for interactions of year effects with edge type or distance from edge ($F \leq 2.11$, $df = 1-2$ and 286 , $P > 0.12$).

Territory size.—Average territory size was similar among edge types (agriculture: 0.34 ± 0.05 ha; road: 0.34 ± 0.05 ha; woodland: 0.35 ± 0.05 ha; Table 1). In testing whether territory size varied as a function of distance from edge, there was evidence of an interaction between edge type and distance from edge (i.e. nonparallel slopes; Table 1). Territory size increased near road edges ($F = 9.35$, $df = 1$ and 24 , $P = 0.005$), decreased near woodlands ($F = 4.13$, $df = 1$ and 24 , $P = 0.053$), and showed no evidence for a pattern near agricultural edges ($F = 1.69$, $df = 1$ and 24 , $P = 0.207$), which is consistent with the territory-size hypothesis near roads, but contrary to the hypothesis for woodlands (Fig. 4). Territory size was negatively correlated with number of territories mapped per hectare (a covariate) in our survey plots ($F = 9.87$, $df = 1$ and 24 , $P = 0.0044$) size but was not correlated with number of locations collected during mapping ($F = 0.00$, $df = 1$ and 24 , $P = 0.953$).

Passive displacement–active avoidance.—Overall, 38 territories mapped near 25 edges qualified for investigating whether territory positioning was consistent with passive displacement or active avoidance (i.e. sites with edge-defined territories): 14 near agricultural edges, 12 near road edges, and 12 at woodland edges. Of those, eight territories mapped near agricultural edges fell within 10 m of the habitat edge, two near road, and only one near woodland edges. None of the territories crossed the edge boundary into the surrounding habitat. On the basis of confidence interval estimation for the distance from the habitat edge to the nearest border of edge territories, Bobolink territory positioning was not consistent with active avoidance of agriculture edges and was only marginally consistent with active avoidance of road edges (Fig. 5). However, that evidence for road avoidance is within the measurement error of the GPS unit (see above), so inference is limited. Bobolink territory positioning was consistent with active avoidance of woodland edges. Because many territories near agriculture edges abutted the edge but did not extend into the agriculture habitat,

TABLE 1. Summary of linear mixed-model analyses testing density (detections of males ha⁻¹) of Bobolinks, habitat structure, and territory size variation of Bobolinks as a function of edge type and distance from edge, northern Iowa, 1999–2000.

| Response variable | Edge type | | Distance from edge | | Type × distance | |
|--|------------------------------------|-------|--------------------|--------|-----------------|-------|
| | F ^a | P | F ^b | P | F ^c | P |
| | Edge avoidance | | | | | |
| Density (males ha ⁻¹) ^d | 5.60 | 0.026 | 57.16 | <0.001 | 0.38 | 0.692 |
| | Habitat gradient hypothesis | | | | | |
| Vegetation height (cm) ^d | 0.29 | 0.755 | 0.00 | 0.955 | 0.45 | 0.653 |
| Vertical density (dm) ^d | 0.15 | 0.867 | 0.07 | 0.804 | 0.06 | 0.940 |
| Litter depth (cm) ^d | 6.48 | 0.018 | 0.03 | 0.876 | 2.70 | 0.121 |
| Total cover (%) ^e | 7.23 | 0.013 | 0.00 | 0.959 | 1.89 | 0.207 |
| Grass cover (%) ^e | 0.45 | 0.652 | 0.38 | 0.552 | 0.26 | 0.778 |
| Forb cover (%) ^e | 0.66 | 0.539 | 0.12 | 0.737 | 1.36 | 0.305 |
| Litter cover (%) ^e | 2.55 | 0.133 | 0.48 | 0.508 | 0.26 | 0.778 |
| Dead cover (%) ^e | 2.20 | 0.167 | 2.20 | 0.123 | 1.78 | 0.224 |
| Bare ground (%) ^e | 2.77 | 0.115 | 0.84 | 0.385 | 0.57 | 0.585 |
| | Territory size hypothesis | | | | | |
| Territory size (ha) ^e | 3.45 | 0.167 | 1.57 | 0.239 | 6.45 | 0.006 |

^adf = 2 and 9, except for territory size, in which df = 2 and 3.

^bdf = 1 and 9, except for territory size, in which df = 1 and 10.

^cdf = 2 and 9, except for territory size, in which df = 2 and 24.

^dNatural log transformed for analysis.

^eArcsine square root transformed for analysis.

passive displacement alone was occurring and probably best explains density patterns near agriculture edges. Overall, the number of territories mapped per hectare (the covariate) was correlated with the distance of territories to the habitat edge ($F = 5.06$, $df = 1$ and 13 , $P = 0.042$), where Bobolinks tended to settle closer to habitat edges in areas of high densities.

DISCUSSION

Although other research has documented some evidence of edge avoidance on the basis of nest placement (e.g. Johnson and Temple 1986), we provide the first evidence to our knowledge for variable avoidance of different kinds of edges by territorial birds. Other recent studies in grasslands have documented strong negative effects of habitat edges on local breeding bird distributions (Johnson and Temple 1986, Reijnen et al. 1996, Bock et al. 1999, Hughes et al. 1999, Bajema and Lima 2001, Bakker et al. 2002), yet none of those studies investigated both the importance of different edge types and alternative explanations for spatial patterns of distribution. The variability in edge avoidance among different types of edges suggests that land use surrounding patches can play an important role in avian distribution within patches

and should be considered in conservation and restoration strategies.

Mechanisms for spatial patterns.—Although some studies have found habitat gradients associated with edges (e.g. Chen et al. 1992, Malcolm 1994), we found no consistent change in habitat structure occurring near edges that reflected the observed change in Bobolink density. The only evidence we found for habitat differences was for overall differences among edge types for total vegetation cover and litter depth, which tended to be greater near agriculture edges and less near road edges (total cover) or woodland edges (litter depth), yet neither of those factors was correlated with Bobolink density ($r < 0.07$; $P > 0.20$). Therefore, it is unlikely that those patterns explain the overall pattern of Bobolink density being lower near woodland edges, and habitat structure cannot explain patterns as a function of distance from edge. However, it is possible that some unidentified gradient, such as species composition, did occur near edges. Most research focusing on habitat gradients has occurred in forested landscapes, which might be more likely to contain distinctive gradients on the basis of increasing subcanopy layers near edges. Habitat gradients near edges in grasslands, if they do indeed occur, are likely to be more subtle than those occurring in forested landscapes.

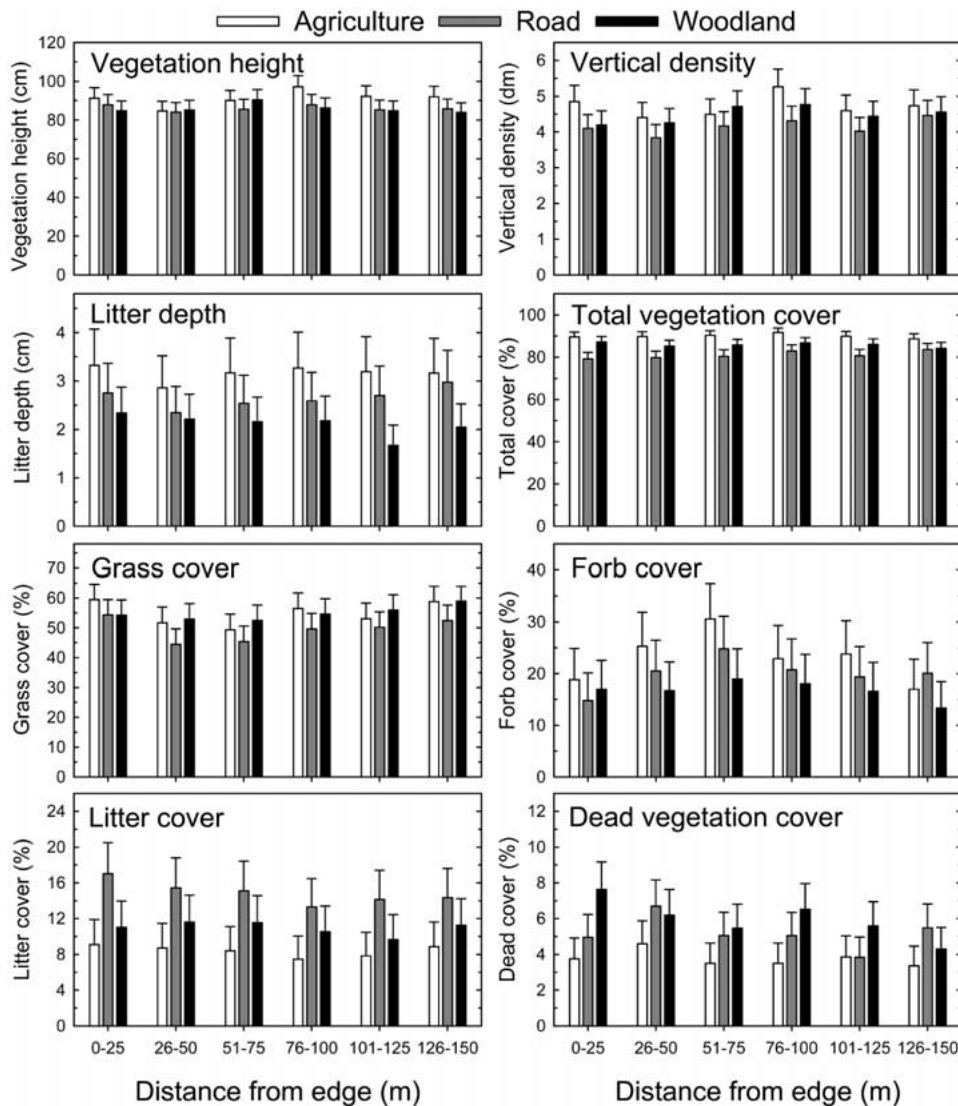


FIG. 3. Habitat structure (least-squares means + SE) in grasslands as a function of distance from edge near three different edge types, northern Iowa, 1999–2000. Note that scales are different on the y axis for each variable. Only canopy cover variables representing >5% coverage are included. Raw estimates are reported; however, vegetation height, vertical density, and litter depth were natural log transformed for analysis, whereas other variables were arcsine square root transformed for analysis.

Bobolink territory size increased near roads, which is consistent with the territory-size hypothesis (see also Ortega and Capen 1999), but showed a weak tendency to decrease near woodland edges, counter to the territory-size hypothesis. Territory size in birds has often been correlated with two factors: (1) food availability (e.g. Smith and Shugart 1987), in which size increases with decreasing food resources; and (2)

intraspecific territorial intrusion pressure (i.e. “intraspecific-competition hypothesis”; Smith and Shugart 1987), in which individuals defend areas as large as possible, but size is limited based on intraspecific competition and intrusion pressure with other individuals in the same area (Smith and Shugart 1987). Because intrusion pressure may be lower near edges (Stamps et al. 1987), territory size could increase.

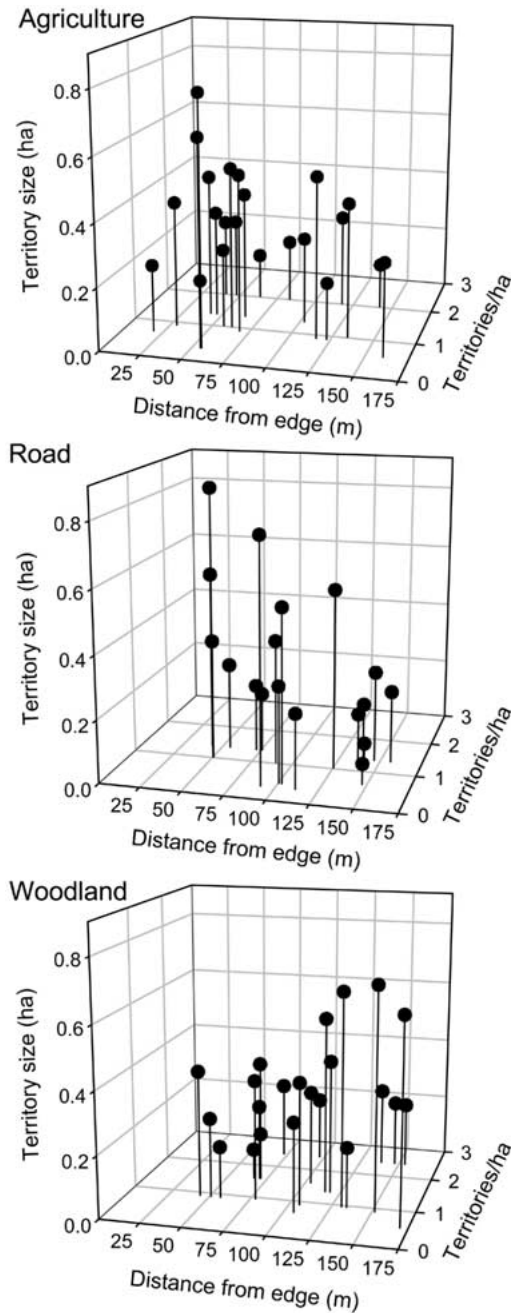


FIG. 4. Bobolink territory size (ha) as a function of distance from edge and the number of territories mapped per hectare in grasslands near three different edge types, northern Iowa, 2000.

Neither of those factors has been investigated in Bobolinks. If food availability governs those patterns, then habitat quality (based on food

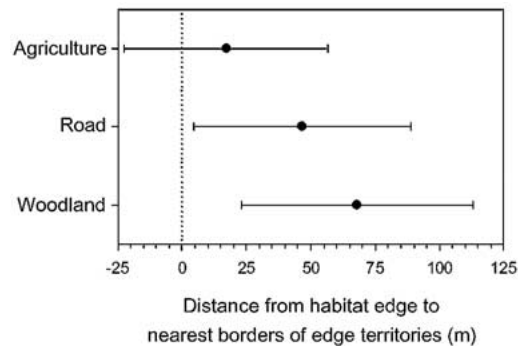


FIG. 5. Territory placement of Bobolink edge territories (least-squares means \pm 95% confidence intervals) in grasslands near three different edge types, northern Iowa, 2000. Edge territories were defined as those in which no other territorial locations from different males fell between the central portion of territories and the edge habitat.

availability) may be lower near road edges but higher near woodlands. Some research suggests that food availability may decline in small forest fragments (e.g. Burke and Nol 1998; but see Huhta et al. 1999). Neither hypothesis is consistent with patterns near woodland edges, unless a tradeoff is occurring between food availability and predation risk.

Territory positioning in Bobolinks near woodland edges was consistent with active avoidance. Potential mechanisms of active avoidance include interspecific competition, predator-escape strategies, and low site fidelity near edges. Ambuel and Temple (1983) suggested that changes in bird communities in small forest fragments in Wisconsin were more influenced by increased interspecific competitors from surrounding habitat types than habitat structure or isolation. However, interspecific competition is generally not thought to be an important component affecting habitat use by breeding grassland bird communities (e.g. Wiens 1977). Research on wintering grassland birds suggests that some species avoid woody cover because of predator-escape strategies and increased predation risk on adults (Pulliam and Mills 1977, Lima and Valone 1991), but the influence of predation risk on adults during the breeding season is unknown. Bobolinks are known to have high site fidelity in areas with high reproductive success (Bollinger and Gavin 1989). If nesting success is generally lower near woodland edges (Johnson and Temple 1990), then Bobolinks may have

lower site fidelity near woodland edges than in the interior of grasslands.

Methods for estimating edge avoidance.—Using transect surveys, we documented that Bobolink density was lower near all edge types than near the interior of grasslands, but territory mapping yielded a different interpretation of the spatial dynamics occurring near edges, particularly for birds occurring near agricultural edges. Villard (1998) argued that some survey techniques, such as point counts, are unsuitable for testing edge avoidance, and that other methods, such as spot-mapping and data on nest placement, are more appropriate. The survey technique we employed showed a strong positive correlation with territory mapping, which suggests that some survey techniques, if properly implemented, can indeed provide useful information about edge avoidance. However, inferences on survey data alone should be limited because survey data do not provide information on some factors addressed here. Although information on nest placement is critical for linking edge avoidance and edge effects on reproduction, nest placement alone might not be the best indicator for edge avoidance in single-brooded passerines, such as the Bobolink, if nest success is lower near edges. If nests fail more frequently near edges, re-nesting may occur more often, leading to high nest densities near edges (Flaspohler et al. 2001). Territory mapping does provide useful information about dynamics of edge avoidance, but that technique still does not provide a complete picture. Ultimately, timing of settlement near edges would be important for understanding and estimating edge avoidance (Bollinger and Switzer 2002). For example, Huhta et al. (1999) found that early arriving Pied Flycatchers (*Ficedula hypoleuca*) tend to occupy nest boxes away from edges, whereas nest boxes near edges are only occupied once interior boxes are full. For Bobolinks, however, settlement and nesting phenology are very synchronous (Wittenberger 1980, Fletcher 2003), limiting the value of settlement timing in understanding edge avoidance in that species.

Conservation implications.—Edge avoidance can have several consequences on understanding bird distributions and managing for species of concern. Because Bobolinks responded differently to different edge types, using a simple perimeter–area ratio or core–area framework (*sensu* Laurance and Yensen 1991, Helzer and Jelinski 1999) for predicting distributions and

managing for that species could overlook key information that might improve conservation strategies. Instead, incorporating landscape configuration, such as how suitable patches are juxtaposed by different habitat types (Watts 1996, Bakker et al. 2002, Fletcher and Koford 2002), will be critical for modeling edge patterns and addressing edge effects at landscape scales. Indeed, Fletcher and Koford (2002) found that edge density in Iowa landscapes predicted grassland bird density better than landscape composition, and that Bobolink density was negatively correlated with grassland–agriculture edge density. Although results here suggest that agricultural edges are less influential on distributions than other edge types, agricultural edges could have strong negative consequences if effects from multiple edges within fragments are additive or synergistic (Malcolm 1994). Moreover, if edge effects are synergistic, then edge avoidance might explain patterns of area sensitivity in fragmented landscapes (Fletcher 2003; but see Bollinger and Switzer 2002).

We documented that at local scales, Bobolinks responded most strongly to woodland edges, both compressing territories and actively avoiding woodlands. That pattern in Bobolinks might not be unique for grassland birds. Although we did not map territories of other species near edges, surveys revealed that five of eight common bird species tended to have lower densities near woodland edges (Fletcher 2003). In addition, many grassland birds have been documented to avoid woodland areas (Johnson and Temple 1986, Helzer 1996, Hughes et al. 1999, Bakker et al. 2002), have lower nest success (Johnson and Temple 1990), and experience population declines with the influx of woody vegetation (Coppedge et al. 2001). To minimize negative effects on declining grassland birds, management of grassland patches will need to prevent woody encroachment within patches, as well as decrease the amount of woodland vegetation surrounding patches.

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