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Multiple edge effects and their implications in fragmented landscapes

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Summary

1. Habitat edges are thought to explain much of the negative effects arising from habitat fragmentation; however, progress has been limited in extrapolating edge effects to different situations because ecologists still do not understand if and how multiple edges interact within fragments. It also remains controversial whether edge effects govern patch-size effects, such as area sensitivity, observed in many migratory songbirds.

2. I examined how multiple edges within fragments may intensify edge responses by investigating spatial distributions of an area-sensitive songbird that breeds in temperate grasslands of North America, the bobolink (*Dolichonyx oryzivorus* Linnaeus). I tested whether bobolinks avoid edges and whether avoidance is stronger near two edges (double-edge plots) than near only one edge (single-edge plots). I subsequently linked bobolink distributions to landscape maps that vary in the amount of habitat and degree of fragmentation to explore some potential implications of multiple edges on patch- and landscape-level distributions.

3. Multiple edges appeared to influence the magnitude of observed edge effects, in which the probability of bobolink occurrence was four times lower in double-edge plots and two times lower in single-edge plots than in the interior of grasslands. Within single-edge plots, the probability of occurrence increased with increasing distance from edge. Within double-edge plots, the probability of occurrence increased as a function of the nearest and next-nearest distances from edges. Multiple edges also appeared to increase the extent of edge effects, or distance of edge influence, which was estimated to be approximately 11–33% greater in double-edge plots than in single-edge plots, depending on the next-nearest distance from edge.

4. Extrapolating local bird distributions to landscape models suggests that edge effects can have strong influences on large-scale distributions and that models incorporating multiple edge effects are different to simple nearest-edge models only in highly fragmented landscapes, regardless of landscape composition. Furthermore, edge effects can lead to patch-size effects similar to empirical patterns of area sensitivity observed in this species. I conclude that edge effects can be intensified when multiple edges collide, a feature that permeates many fragmented landscapes.

Key-words: bobolink, *Dolichonyx oryzivorus*, edge effect, habitat edge, patch-size effects.

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Introduction

Habitat loss generally leads to increased habitat fragmentation, resulting in smaller patches, increased

isolation and increased proportion of edge habitat in landscapes. Habitat edges can influence a variety of population and community processes, from dispersal rates to species interactions (Paton 1994; Cadenasso & Pickett 2001), and edges are considered primary drivers for the effects of habitat fragmentation (Harrison & Bruna 1999). However, progress has been limited when extrapolating edge responses to different situations because of many poorly understood factors that

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potentially mediate edge effects, including if and how multiple edges interact within fragments (Ries *et al.* 2004). This is unfortunate, because as fragmentation increases, patch geometry tends to become more complex, resulting in many areas near multiple edges.

Most empirical research (e.g. Chen, Franklin & Spies 1995; Brand & George 2001) and models (e.g. Laurance & Yensen 1991; Sisk, Haddad & Ehrlich 1997) on edges have ignored multiple edge effects, which I define as the cumulative edge effect occurring from more than one habitat edge within a fragment (*sensu* Zheng & Chen 2000). The nature of multiple edge effects remains unknown in natural systems, yet multiple edges could influence not only the magnitude but also the extent of edge effects (i.e. the distance/depth of edge influence, DEI; Harper & MacDonald 2001). Untangling how multiple edges influence edge effects is particularly important when extrapolating edge effects to different patches and landscapes (Laurance & Yensen 1991; Malcolm 2001), and it will be critical for determining if edge effects operate at large spatial scales (Laurance 2000). In fact, a recent synthesis on edge effects suggested that multiple edge effects were a primary issue limiting extrapolation of edge responses and identified no empirical data on how multiple edges influence animals (Ries *et al.* 2004).

In practice, most research has focused on the nearest distance from an edge to describe edge effects (e.g. Laurance *et al.* 1998; Harper & MacDonald 2001), even though complex geometry permeates many landscapes. A critical framework for evaluating multiple edge effects thus requires comparing predictions from nearest-distance models to models using multiple-distance measures. Models that have been proposed for addressing multiple edge effects generally generate stronger edge effects than nearest-distance models (cf. Malcolm 1994, 1998, 2001; Zheng & Chen 2000; Fernández *et al.* 2002; Fletcher 2003), and deviations of nearest-distance models from multiple-edge models tend to be greater in small patches or in highly fragmented landscapes (Malcolm 2001; Fletcher 2003). Although few empirical data exist regarding multiple edge effects (Ries *et al.* 2004), Malcolm (1994) found that an additive edge model explained habitat structure in Amazonian fragments better than a nearest-distance model.

I investigated some potential implications of multiple edges on distributions of a migratory songbird that breeds in grasslands of the United States, the bobolink (*Dolichonyx oryzivorus* Linnaeus). Bobolinks have experienced population declines (Peterjohn & Sauer 1999; Fletcher & Koford 2003b) and have been documented to be sensitive to habitat fragmentation, by both avoiding edges (Fletcher & Koford 2003a) and being area-sensitive, or less likely to occur in small patches (Herkert 1994; Johnson & Igl 2001). Therefore, I expected that bobolinks would be less likely to occur in areas near multiple edges more so than in areas near only one edge. I tested this and subsequently linked bobolink occurrence data with landscape maps

that vary in the amount of habitat and the degree of fragmentation to explore some potential impacts of multiple edges on distributions in fragmented landscapes. Extrapolating empirical data to landscapes provides a context to determine whether incorporating multiple edges into models changes model predictions, when multiple edges might be important at large scales, and can be useful for conservation and management strategies, particularly in landscapes undergoing rapid change (Malcolm 2001; Sisk, Noon & Hampton 2002).

Methods

STUDY AREA

I surveyed breeding birds in 10 grassland sites (two to three plots per site; $n = 25$ plots; see below) scattered throughout northern Iowa, USA during 2001–02 (Fig. 1). Within this region, I selected all sites that met the following criteria: (1) sites were large enough to contain two 150×150 m plots (see below); (2) sites contained grassland habitat that bordered rowcrop agriculture edges (either corn or soybeans); (3) potential plot locations did not include any woody vegetation or wetlands; and (4) grasslands included restored grasslands or native tallgrass prairies under state or federal management. I surveyed birds on the same plots each year; however, one plot was not surveyed in 2002 because management activities caused this plot to be unsuitable for bobolinks. Restored grasslands contained warm-season and cool-season grass plantings, with common species including switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardii* Vitman) and smooth brome (*Bromus inermis* Leyss.). Prairies contained a high diversity of native grasses and forbs, including big bluestem, little bluestem (*Schizachyrium scoparium* Nash), Indian grass (*Sorghastrum nutans* (L.) Nash), switchgrass, goldenrod (*Solidago* spp.), sunflower (*Helianthus* spp.) and milkweed (*Asclepias* spp.). Bobolinks occur at similar densities in restored grasslands and tallgrass prairies in the region (Fletcher & Koford 2002).

BIRD SURVEYS

In 2001, within each site I established two plots (150×150 m; Fig. 1): one near only a single edge (single-edge plots hereafter), and one near two edges, or a corner of the site (double-edge plots hereafter). Elsewhere we documented that average territory sizes of male bobolinks near agriculture edges were 0.34 ha (± 0.05 ha; Fletcher & Koford 2003a); therefore, within each plot approximately six to seven males could occur if plots were saturated. Both plots within sites contained similar vegetation types (prairie or restored; cool-season or warm-season grasses) and were located near linear rowcrop agriculture edges. Each plot was placed at least 150 m from any other edge (other than the edges of interest) in the site to minimize effects from other edges. This buffer distance was based on Fletcher &

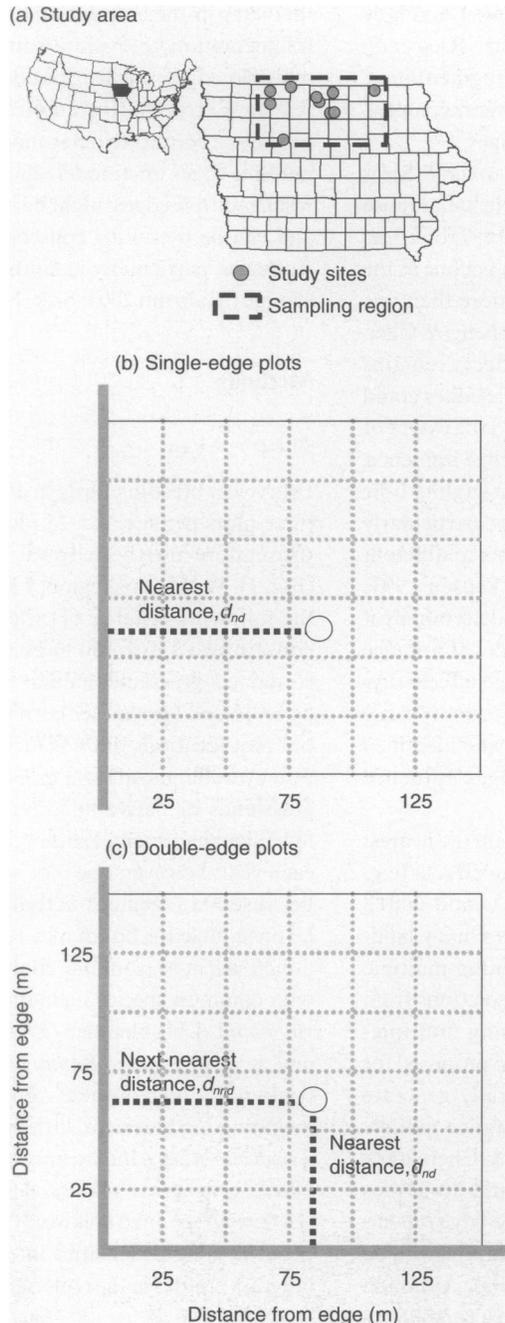


Fig. 1. Study sites ($n = 10$) and survey design used for estimating the influence of multiple edges on bobolink distribution, northern Iowa, 2001–02. (a) All sites meeting sampling criteria (managed grassland patches bordering rowcrop agriculture that could contain a single-edge and double-edge plots) within the dashed region were sampled. In each site, there were paired survey plots (150 × 150 m): (a) single-edge and (b) double-edge (corner) plots. Observations were grouped into 25 × 25 m grid cells, which allowed for nearest distance and next-nearest distance measures in double-edge plots. In 2002, interior plots, located > 200 m from any edge, were added to half of the study sites.

Koford (2003a), which suggested that edge effects on bobolink abundance occur within approximately 75–100 m from edges. Each plot contained three fixed-width line transects running parallel to the edge in single-edge plots, and parallel to a randomly selected edge on the double-edge plots, at distances of 25 m, 75 m

and 125 m from the edge. Before each survey, the observer picked the order and direction randomly to survey transects. During each survey, the observer walked transects at a steady pace, recording all birds seen within 25 m of the transect. Care was taken not to count the same bird more than once. When collecting data, observations were divided into 25 × 25 m cells within the plots. Although individuals probably used more than one cell, these cells allow for high resolution in interpreting the spatial patterns near edges, and the analysis accounted for this potential lack of independence (see below). For double-edge plots, this enabled each cell to be described by two measures for distance from edge: a nearest distance (d_{nd}) and a next-nearest distance (d_{nnd}). Surveys were conducted between sunrise and 4 h after sunrise, when breeding birds are most active. Surveys were repeated four times during the breeding season, from 20 May until 6 July, 2001–02. Each year three observers conducted surveys and each site was surveyed by each observer at least once.

In 2002, I added interior plots at five of the 10 sites. Interior plots consisted of transects that were 100 × 50 m. Each interior plot was placed at least 200 m from any edge within the site. Interior plots were sampled using the same protocol as single- and double-edge plots.

STATISTICAL ANALYSES

The study design allows for two levels of resolution for determining if multiple edges influence bird distribution. First, at the plot level, I tested for differences in male bobolink occurrence in single-edge, double-edge and interior plots. Secondly, I tested whether the distance to the nearest edge and next-nearest edge could explain male bobolink occurrence within plots. I ran three separate analyses: one at the plot-level, testing for differences in occurrence among plots, and two analyses within plot types, testing for effects of distance to the nearest edge and next-nearest edge in explaining occurrence. I evaluated occurrence using logistic regression models, adjusted for spatial correlation within plots (Littell *et al.* 1996). Site was considered a block (and random effect), and year was considered a split-plot repeated measure to accommodate non-independence between years (Littell *et al.* 1996: 88–92). For distance effects within plots, I tested whether slopes (on the logit scale) were zero by using the midpoint distance of each grid cell from the edge (12.5 m, 37.5 m, 62.5 m, etc.) as a continuous variable. This design controls for patch-level covariates, such as patch size and landscape context, by considering site as a block in the sampling design. None the less, I initially explored potential patch-size effects by including patch size as a covariate in analyses; however, there was no evidence of patch size influencing edge responses in any analysis ($P > 0.20$), so I removed it from final models. Within-season sampling was pooled by considering a cell occupied if a male bobolink was observed in the cell during at least one visit. Elsewhere we have estimated high detectability

of male bobolinks up to 50 m from observers (Fletcher & Koford 2002).

Accounting for spatial correlation is a critical issue for appropriate inference regarding edge effects as well as other ecological processes (Brand & George 2001; Keitt *et al.* 2002). Because observations in adjacent cells were not independent, I adjusted models for within-plot spatial covariance by estimating the nugget, partial sill and range parameters of the semivariogram explaining spatial correlation within plots (Littell *et al.* 1996: 303–330). Moreover, using distance as a continuous explanatory variable minimizes problems of potential pseudoreplication within plots because cells are used only in estimating a slope parameter for each plot (i.e. the plot is the effective unit of replication; Fletcher & Koford 2003a). I considered six isotropic (i.e. correlation independent of direction; Gaussian, exponential, linear, linear log, power and spherical; Littell *et al.* 1996: 305) and two anisotropic models (i.e. correlation dependent on direction; anisotropic exponential and power; SAS Institute 2001) for explaining covariance structure and compared these models to an independent errors model that did not adjust for spatial covariance. Models were compared using Akaike's information criterion, adjusted for sample size (Burnham & Anderson 1998).

I also approximated the distance of edge influence and determined if this distance changed near multiple edges. I overlapped interior estimates of occurrence with estimates derived as a function of distance from each edge within single- and double-edge plots (Laurance *et al.*

1998; Harper & MacDonald 2001). I approximated the DEI as the distance in which the interior lower confidence limit overlapped with the models (means and confidence limits) within each plot type. These approximations are not intended to provide an absolute estimate of the extent of edge effects, but they are useful for comparative purposes between the two plot types.

LANDSCAPE EDGE MODEL

To explore some potential implications of edge effects on bird distributions, I used a simulation model that linked empirical data on bobolink distributions with fragmented landscape maps. I used two types of landscape maps: (1) theoretical maps that allowed for exploring different levels of habitat loss and fragmentation (neutral landscapes; Gardner 1999) and (2) real maps of independent areas in northern Iowa, centred geographically on the survey area. Each map was a 256×256 grid of cells (25×25 m) that contained suitable habitat and unsuitable matrix, which allowed the appropriate extrapolation of empirical data to landscape maps. Therefore, landscape size was 6.4×6.4 km (41 km^2 or 4096 ha). Patches were delineated using a nearest-neighbour rule, in which patches were defined based on contiguous orthogonal clusters of cells (Gardner 1999).

I generated theoretical landscapes that varied in the amount of habitat and degree of fragmentation using the program RULE (Gardner 1999). Maps were generated with 10%, 30% and 50% suitable habitat in the landscape (Fig. 2). Fragmentation was varied by using

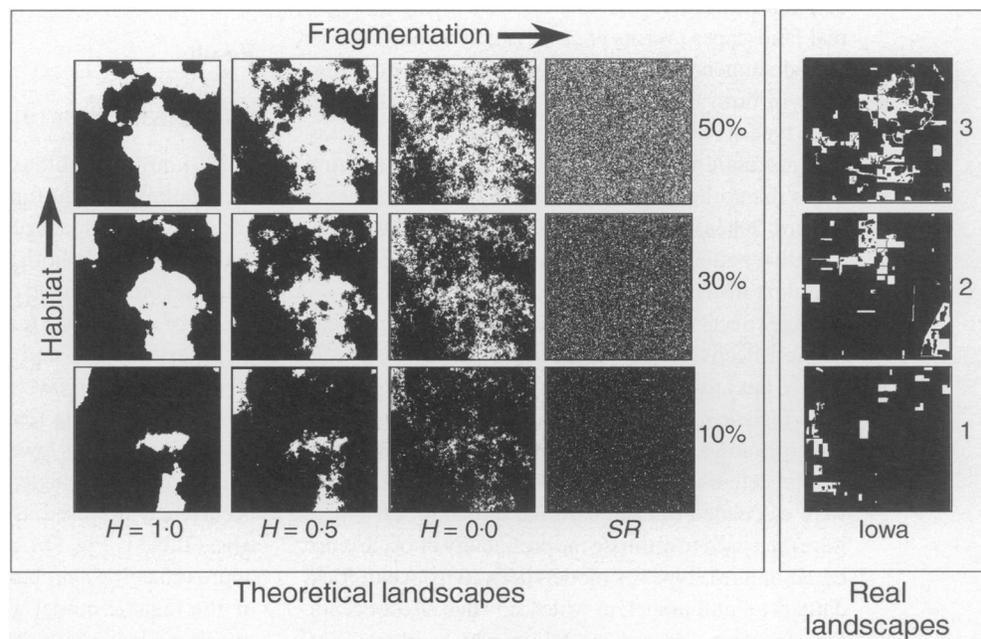


Fig. 2. An example of real and neutral landscapes used in linking multiple edge effects based on bobolink distributions to fragmented landscapes. Suitable habitat is denoted in white, unsuitable matrix is in black. For theoretical landscapes, both simple random and fractal landscapes were generated using program RULE (Gardner 1999). Fragmentation was varied by changing H , the spatial contiguity of the fractal landscape, and comparing these fractal landscapes with simple random (SR) landscapes. For each landscape type, 10 landscapes were generated and used in simulation modelling. For real landscapes, I used three simplified maps of areas within the Eagle Lake Wetland Complex, northern Iowa. To do so, I considered all grassland habitats as potentially suitable habitats, except for narrow (< 6 m) roadside ditch areas, and all other habitats as unsuitable matrix.

both simple random maps (SR) and fractal maps for each amount of habitat. For simple random maps, each cell in the landscape has an independent probability of being suitable habitat, conditional on the total amount of habitat in the landscape. For generating fractal maps, RULE uses the midpoint displacement algorithm, in which spatial contagion (or clumping) is varied based on a parameter, H , that ranges between 0 and 1 (Gardner 1999). Maps were generated with $H = 0.0$, 0.5 and 1.0. When $H = 1.0$ landscapes are more clumped (and thus less fragmented); when $H = 0.0$ landscapes are highly fragmented, and SR landscapes are an extreme form of fragmentation (Fig. 2). Twelve landscape types were generated, with 10 landscapes for each type.

In addition to theoretical maps, I used three simplified maps of real landscapes within the Eagle Lake Wetland Complex, a 162-km² area targeted for conservation and restoration strategies focused on breeding birds in north-central Iowa (43°N, 94°W; Fletcher & Koford 2002, 2003b). To do so, I considered all grassland habitats (e.g. pastures, hayfields, restored grasslands) as potentially suitable habitats (Fletcher & Koford 2003b), except for narrow (< 6 m) roadside ditch areas (Camp & Best 1993) and all other habitats as unsuitable matrix (Fig. 2). High resolution (2–3 m) vector maps were converted to raster maps with 25 × 25 m cells to link empirical data appropriately with the Iowa maps. Landscapes were the same size as theoretical landscapes and did not include any sites that were used for bird surveys. While these maps provide more realistic land use scenarios than theoretical maps, I emphasize that many issues arise when extrapolating to real landscapes (Wiens *et al.* 1993), and elsewhere we have documented that male bobolinks respond differently in both behaviour and abundance to different edge types (Fletcher & Koford 2003a). None the less, because male bobolinks respond less to agriculture edges than other edge types at local scales (Fletcher & Koford 2003a), these models probably provide conservative patterns for the negative effects of edges on bobolink distributions.

Edge effects were modelled using a similar approach to the Effective Area Model developed by Sisk *et al.* (1997), but I used the probability of occurrence (derived from logistic models) for modelling and incorporated multiple edges into the modelling process. For each habitat cell in the landscape, distances from each edge were calculated in each cardinal direction. Distances were then used to estimate the probability of occurrence based on three types of models derived from empirical data: (1) a null model, in which no edge effect occurs; (2) a nearest-distance model, in which information from only the nearest edge was used to estimate occurrence; and (3) a next-nearest-distance model, in which both the nearest and next-nearest edges were used in estimating occurrence. While some approaches allow for extrapolating beyond the number of edges investigated empirically, given certain assumptions about the

multiple edge effect process (Malcolm 1994, 2001), I did not use models that incorporated distances to all edges because empirical data only directly addressed effects from ≤ 2 edges.

I simulated distributions in landscapes for each model type by assuming that occurrence within each habitat cell was a Bernoulli process, in which a cell was occupied with a probability taken from estimates of the logistic models. The null model used the probability estimate from interior plots. The nearest-distance model used probability estimates from single-edge plots when $d_{nd} < 150$ and the interior estimate when $d_{nd} \geq 150$ m; this model is similar to previous models on edge effects (Sisk *et al.* 1997). The next-nearest-distance model used probability estimates from double-edge plots when d_{nd} and $d_{nnd} < 150$ m, single-edge estimates when $d_{nd} < 150$ and $d_{nnd} \geq 150$ m and interior estimates when d_{nd} and $d_{nnd} \geq 150$ m. From these simulations I addressed the following: (1) do different model types predict different patch- and landscape-level relative densities, and (2) do these predictions vary with the amount of habitat and degree of fragmentation? For all models I focused on predicted frequencies of occurrence for comparisons. However, these models can also be compared using predicted total population sizes by multiplying the amount of suitable habitat by the predicted frequencies of occurrence. Focusing on the total population size did not change patterns qualitatively, except that landscapes with more habitat were predicted to harbour larger populations of bobolinks, regardless of the model type used (null, nearest distance, or next-nearest distance; R. J. Fletcher, unpublished analysis).

Results

BOBOLINK DISTRIBUTIONS

In 2001, my assistants and I recorded 207 observations of bobolinks along transects (61.8% males; $n = 128$), and in 2002 we recorded 249 observations (61.0% males; $n = 152$). In both years, bobolinks were the most common bird observed on transects. Overall, the probability of occurrence for male bobolinks was greatest on interior plots and least on double-edge plots ($F_{2,13} = 8.34$, $P = 0.0047$; Fig. 3a), with mean estimates of occurrence being four times lower on double-edge plots and two times lower on single-edge plots than on interior plots. In single-edge plots, the probability of occurrence increased as a function of distance from edge (Table 1, Fig. 3b), and I estimated the DEI to be approximately 88 m, based on predicted probabilities of the logistic model within plots (60–116 m using upper and lower confidence limits of predicted values, respectively). In double-edge plots, the probability of occurrence increased as a function of the nearest (d_{nd}) and next-nearest distances (d_{nnd}) from edges (Table 1, Fig. 3c). In double-edge plots, the estimated DEI ranged from approximately 98 m to 117 m, depending the next-nearest distance from edge (27–91 m and

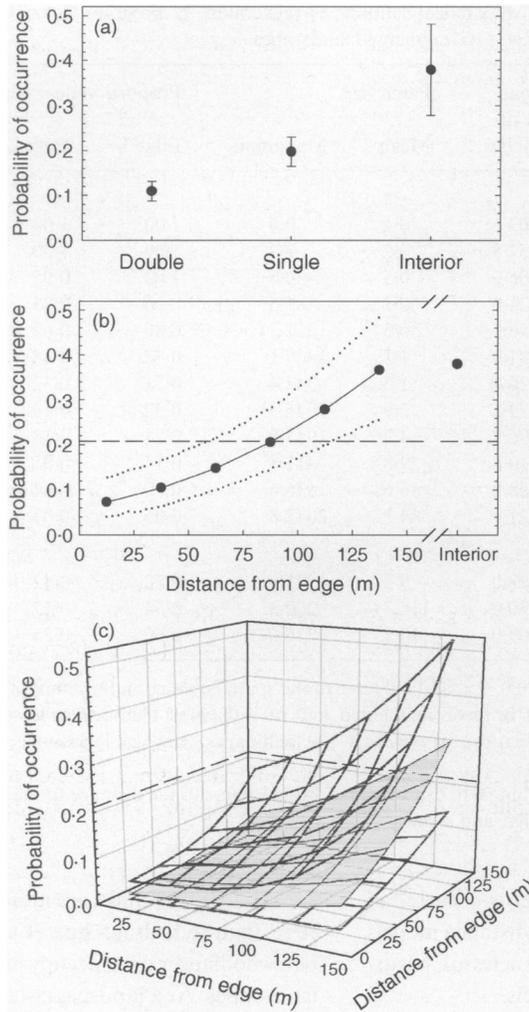


Fig. 3. The estimated probability of occurrence (per grid cell within plots; based on logistic regression analyses) for male bobolinks in double-edge, single-edge, and interior plots in northern Iowa, 2001–02. (a) The probability of occurrence ($\bar{x} \pm SE$) per cell as a function of plot type, (b) the probability of occurrence ($\bar{x} \pm 95\%$ CL) as a function of distance from edge in single-edge plots and (c) the probability of occurrence ($\bar{x} \pm 95\%$ CL) based on both nearest (d_{nd}) and next-nearest distances (d_{mnd}) from edges in double-edge plots. Note that each combination of d_{nd} and d_{mnd} occurs in two cells within plots (except when $d_{nd} = d_{mnd}$), given the symmetric nature of double-edge plots. The intersection of the lower confidence limit of the interior estimate (dashed line in b and c) and the predicted value within single- and double-edge plots approximates the DEI (*sensu* Laurance *et al.* 1998).

> 150 m using upper and lower confidence limits of predicted values, respectively). Overall, there was no evidence for year effects or interactions of edge and year effects (Table 1).

LANDSCAPE MODELS

Physical characteristics of theoretical landscapes varied in predictable ways (Table 2). The proportion of habitat within 50 m of the nearest and the next-nearest edge was much greater in highly fragmented landscapes (SR, $H = 0.0$; Table 2). At the patch level the

Table 1. Summary of logistic regression models describing male bobolink occurrence near one edge (single edge) or near two edges (double edge) in northern Iowa, 2001–02. Site was considered a random effect and year was considered a split-plot repeated measure. Models were adjusted for spatial covariance within plots by estimating the semivariogram explaining spatial correlation within plots. For both single- and double-edge analyses, the best structure (based on Akaike’s information criterion, adjusted for sample size) for estimating these parameters was a power covariance structure [$\sigma_{ij} = \sigma^2(\rho^{d_{ij}})$]

Parameter	d.f.	F	P
Single edge			
Nearest distance	1, 9	37.08	< 0.001
Year	1, 662	2.65	0.104
Year \times nearest distance	1, 662	2.22	0.137
Double edge			
Nearest distance	1, 9	14.49	0.004
Next-nearest distance	1, 9	5.74	0.040
Year	1, 687	1.60	0.206
Year \times nearest distance	1, 687	0.35	0.552
Year \times next-nearest distance	1, 687	2.63	0.105

proportion of habitat within 50 m of each edge was high for all patch sizes in highly fragmented landscapes (SR, $H = 0.0$), but in less fragmented landscapes ($H = 0.5, 1.0$) the proportion of habitat near edges declined precipitously as a function of patch size (see Fletcher 2003). The Iowa landscapes considered contained little suitable habitat ($\leq 17\%$), had generally smaller maximum patch sizes than theoretical landscapes (except for SR landscapes) and suitable habitat was closer to edges compared to most fractal landscapes (Table 2). For the landscapes considered, the proportion of habitat near the nearest and next-nearest edges was much greater than near the other edges, suggesting that the distances to the two closest edges capture most variation in edge-related spatial characteristics of habitat (Table 2).

At the patch level, the predicted frequencies of occurrence (mean number of individuals/cell) from next-nearest distance models were lower than nearest distance models for all patch sizes in the most fragmented landscapes (SR, $H = 0.0$; Fig. 4). In less fragmented landscapes, next-nearest distance models predicted slightly lower frequencies of occurrence for patch sizes approximately < 50 ha. Only in very large patches (> 150 ha) did predictions from edge-effect models approach predictions from null models (Fig. 4). Iowa landscapes exhibited similar patterns to neutral landscapes (Fig. 4).

At the landscape level, predicted frequencies of occurrence based on next-nearest distance models were lower than nearest-distance models only in the most fragmented landscapes, but this occurred regardless of the amount of habitat in the landscape (Fig. 5). With less fragmented landscapes, edge effects were still important, with edge models predicting lower frequencies of occurrence than the null model, but simple nearest-distance models were comparable to next-nearest

Table 2. Some physical characteristics of theoretical landscapes (generated by program RULE; Gardner 1999) and Iowa landscapes used in linking multiple edge effects to fragmented landscapes

Landscape type†	Percentage suitable habitat	Mean no. of patches	Patch size		Proportion near edges‡			
			Mean	Maximum	Edge 1	Edge 2	Edge 3	Edge 4
Theoretical								
SR	10	4703.6	0.1	0.6	1.00	1.00	1.00	0.96
SR	30	7551.5	0.2	2.9	1.00	1.00	0.96	0.69
SR	50	3906.0	0.5	30.7	1.00	0.95	0.74	0.32
$H = 0.0$	10	1621.8	0.2	81.5	0.96	0.85	0.68	0.41
$H = 0.0$	30	2226.5	0.5	311.3	0.86	0.67	0.45	0.21
$H = 0.0$	50	1681.9	1.1	1400.1	0.72	0.48	0.27	0.11
$H = 0.5$	10	220.4	1.5	347.4	0.51	0.32	0.17	0.06
$H = 0.5$	30	379.5	2.9	1046.3	0.32	0.18	0.09	0.03
$H = 0.5$	50	396.7	4.7	1957.8	0.24	0.13	0.06	0.02
$H = 1.0$	10	10.8	29.8	411.8	0.15	0.07	0.01	0.00
$H = 1.0$	30	28.3	36.6	1136.6	0.09	0.04	0.01	0.00
$H = 1.0$	50	21.4	84.2	2042.8	0.06	0.03	0.01	0.00
Real								
Iowa 1	3	28.0	9.5	21.9	0.82	0.42	0.15	0.03
Iowa 2	11	30.0	116.7	200.3	0.54	0.17	0.03	0.00
Iowa 3	17	109.0	110.1	236.0	0.60	0.25	0.07	0.01

†SR = simple random (most fragmented); 0.0, 0.5, and 1.0 refer to the spatial contagion (or clumping) parameter, H , of the landscape, in which 0.0 is the least clumped, or most fragmented, and 1.0 is the most clumped, or least fragmented (Fig. 2). Ten landscapes were generated for each neutral landscape type ($n = 120$ landscapes). For real landscapes, numbers refer to maps shown in Fig. 2.

‡Proportion of suitable habitat located within 50 m from an edge. Edge 1 refers to the distance to the nearest edge, edge 2 refers to the distance to the next-nearest edge, and so on.

distance models (Fig. 5). Similar patterns occurred in Iowa landscapes, with simple nearest-distance models predicting only slightly higher frequencies of occurrence than next-nearest distance models.

Discussion

MULTIPLE EDGE EFFECTS AND BIRD DISTRIBUTIONS

Edge effects can be intensified when multiple edges converge and these effects could have strong impacts on bird distributions in highly fragmented landscapes. I documented that multiple edges increased both the magnitude and extent of the edge effect on bobolink distributions. While my results were confined to a single bird species, multiple edge effects probably operate on any species influenced by habitat edges (Fletcher 2003). Harrison & Bruna (1999) suggested recently that most effects arising from habitat fragmentation were driven by edge effects. Thus, understanding the effects of habitat fragmentation will require understanding edge effects, which will ultimately require understanding how multiple edges influence edge responses. Coupled with other important factors, such as the type of edge (Fletcher & Koford 2003a) and landscape structure (Bakker, Naugle & Higgins 2002), multiple edge effects might help explain regional variation of fragmentation sensitivity within species (Johnson & Igl 2001). The relative importance of these factors probably varies depending on the scale of investigation. For instance, at

a local scale bobolinks are more sensitive to woodland edges than agriculture edges (Fletcher & Koford 2003a), but woodland edges occupy much less area in Iowa landscapes. At a landscape scale bobolinks are more sensitive to density of agriculture edge than woodland edge (Fletcher & Koford 2002), which is probably the result of the prevalence of agriculture and multiple edge effects occurring within these highly fragmented landscapes.

Although edges affected bobolink distributions, untangling the processes that underlie these patterns will improve our understanding of multiple edge effects. Some potential mechanisms for edges influencing bird distributions include changes in habitat structure, food availability and species interactions near edges (Fletcher & Koford 2003a; Ries *et al.* 2004), some of which could potentially be exacerbated near multiple edges. For example, bobolinks are known to have high site fidelity in areas with high reproductive success (Bollinger & Gavin 1989). If nesting success is generally lower near edges due to increased predation risk (Johnson & Temple 1990; Paton 1994), then bobolinks may have lower site fidelity near edges than in the interior of grasslands. In a similar area of Iowa, Kuehl & Clark (2002) found that predator activity was greater near the corners of fields than along single edges, which they attributed to predators using corners for entering and exiting grasslands. This greater activity could reduce nesting success further near multiple edges. Elsewhere we have documented that habitat structure does not change near these and other edges in

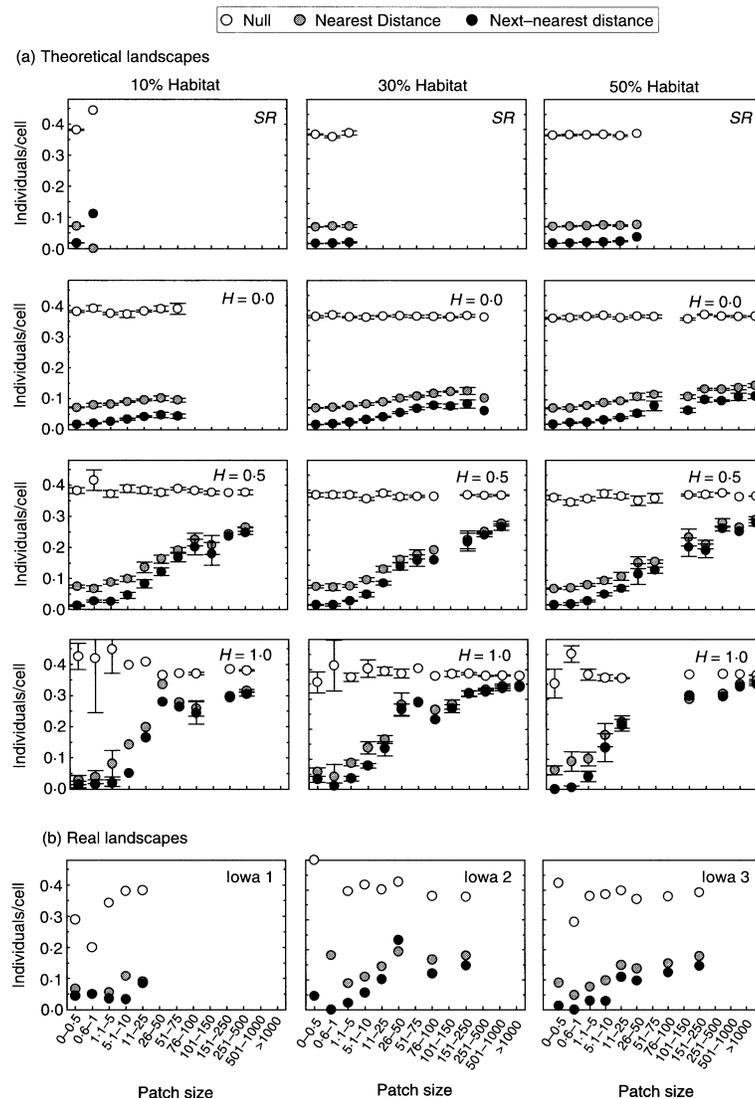


Fig. 4. The predicted patch-level frequency of occurrence (mean individuals/cell, \pm SE) of male bobolinks for three models as a function of patch size, the amount of habitat and degree of fragmentation in (a) theoretical landscapes and (b) real landscapes. Null models used interior estimates, nearest-distance models used only the nearest distance from edges in predicting occurrence (based on single edge and interior estimates), whereas next-nearest-distance models used both the nearest and next-nearest distance in predicting occurrence (based on single-edge, double-edge, and interior estimates). H denotes the relative spatial contagion, or fragmentation, of fractal landscapes (with $H = 0.0$ being less clumped, or more fragmented, and $H = 1.0$ being more clumped, or less fragmented), while SR denotes simple random landscapes. For real landscapes, numbers refer to maps shown in Fig. 2. Standard errors were estimated across landscape replicates; therefore, no standard errors were calculated for each real landscape.

Iowa grasslands (Fletcher 2003; Fletcher & Koford 2003a). Clearly, a mechanistic approach to multiple edge effects will improve predictability and the ability to link edge avoidance with fitness, which is needed to understand the demographic consequences for species in fragmented landscapes.

MODELS OF EDGE EFFECTS IN FRAGMENTED LANDSCAPES

When extrapolating edge effects to fragmented landscapes, two primary patterns emerged. First, models incorporating multiple edge effects tended to predict lower landscape-level frequencies of occurrence in only the most fragmented landscapes, regardless of landscape

composition, which was related directly to the proportion of habitat located near multiple edges. This and other recent modelling attempts (Malcolm 2001) suggest that multiple edges are probably influencing large-scale processes primarily in highly fragmented landscapes.

The second pattern that emerged was that models incorporating edge effects predicted much lower frequencies of occurrence in small patches than models that did not assume an edge effect. This was not surprising. What was surprising was the extent that this effect emerged, in which frequencies of occurrence only converged on null model predictions in very large patches (> 150 ha). Bobolinks have been reported to be area sensitive throughout much of their range (Herkert

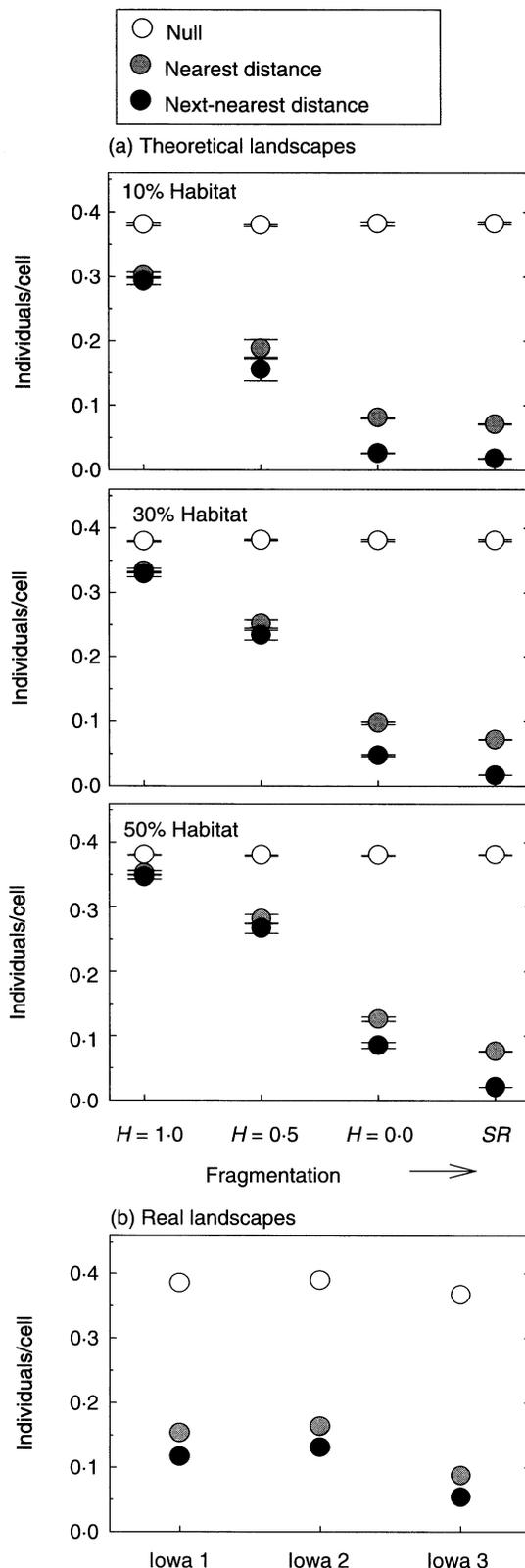


Fig. 5. The predicted landscape-level frequency of occurrence (mean individuals/cell, \pm SE) of male bobolinks for three models as a function of the amount of habitat and degree of fragmentation in (a) theoretical landscapes and (b) real landscapes. Null models used interior estimates, nearest-distance models used only the nearest distance from edges in predicting occurrence (based on single edge and interior estimates), whereas next-nearest-distance models used both the nearest and next-nearest distance in predicting occurrence

1994; Helzer & Jelinski 1999; Johnson & Igl 2001), being less likely to occur in relatively small patches, in the order of 30–60 ha (Herkert 1994; Helzer & Jelinski 1999). The models developed here suggest that observed edge effects occurring within approximately 90–120 m from edges can potentially explain higher occurrence probabilities and densities in large patches within fragmented landscapes. Although processes of edge avoidance might operate distinctly from processes of area sensitivity (Villard 1998), edge effects could none the less be a primary mechanism explaining patch-size effects (Bender, Contreras & Fahrig 1998; Johnson & Igl 2001; but see Bollinger & Switzer 2002). Indeed, Helzer & Jelinski (1999) found that perimeter–area ratios, which reflect the relative proportion of edge within patches, were better at predicting bobolink occurrence than patch size. A recent meta-analysis of patch-size effects also found that species avoiding edges exhibited increased densities in larger patches, whereas species preferring edges exhibited the opposite pattern (Bender *et al.* 1998).

My modelling approach allowed for insight into some potential large-scale implications of edge effects, yet it was not intended to estimate real distributions in fragmented landscapes. Many issues arise when extrapolating local patterns to heterogeneous landscapes (Wiens *et al.* 1993; Ries *et al.* 2004), and neutral landscapes are not intended to mimic real landscapes but instead provide an objective approach for investigating different landscape conditions that vary independently in the amount of habitat and degree of fragmentation (With & King 1997). To address implications of multiple edge effects, I modelled only effects arising from two edges within patches, because bobolink data were limited to information on two edges. While the distances to the two nearest edges captured most variation in edge configurations, particularly in the real, highly fragmented Iowa landscapes (Table 2), edge effects could be stronger in extremely fragmented landscapes if more than two edges are incorporated into the modelling process.

Two other approaches have been used for modelling multiple edge effects. Mancke & Gavin (2000) developed an edge ‘depth’ index that incorporated distances to four edges within patches, yet that approach does not isolate contributions of multiple edges within patches. Malcolm (1994), and subsequent extensions by Fernández *et al.* (2002) modelled multiple edge effects by considering the edge as a collection of points and isolating the ‘point’ edge effect. This point edge effect

(based on single-edge, double-edge, and interior estimates). H denotes the relative spatial contagion, or fragmentation, of fractal landscapes (with $H = 0.0$ being less clumped, or more fragmented, and $H = 1.0$ being more clumped, or less fragmented), while SR denotes simple random landscapes. For real landscapes, numbers refer to maps shown in Fig. 2. Standard errors were estimated across landscape replicates; therefore, no standard errors were calculated for each real landscape.

can then be integrated across the entire region of influence to estimate the 'total' edge effect (Malcolm 1994, 2001; Fernández *et al.* 2002). While that approach is robust to complex boundaries and allows for extrapolating single edge effects across all edges in a patch, in practice point edge effects can rarely, if ever, be empirically isolated and measured (Fernández *et al.* 2002), because observed effects are confounded by all nearby edge segments within a patch. Although the approach I used does not account for complex boundaries, it provides a practical and straightforward approach to isolate effects from multiple edges and allows for other covariates to be included in the modelling process.

Conclusions

Ultimately, incorporating multiple edges into a general framework on edge effects will help determine if edge effects operate on relatively large scales (Laurance 2000; Ries *et al.* 2004). In addition, conservation strategies that use edge responses in assessing impacts of habitat change (e.g. Sisk *et al.* 2002) could be refined by incorporating multiple edges into models (Malcolm 2001). As patch size decreases and fragmentation increases, ignoring issues of multiple edges becomes of paramount concern (see also Malcolm 2001). Multiple edges are also likely to be of critical importance for species that use narrow linear habitats, such as conservation corridors (e.g. Haddad & Baum 1999). Furthermore, when different types of edges converge, multiple edge effects could be complex based on the relative influence of each edge type (Fernández *et al.* 2002). As we continue to develop our understanding of habitat fragmentation, it will be valuable to determine the generality of multiple edge effects on other processes and their potential contributions to the widespread patch-size effects observed in fragmented landscapes.

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