

Spatial and temporal scales of distribution and demography in breeding songbirds:
implications of habitat fragmentation and restoration

by

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ABSTRACT

Tallgrass prairie has declined throughout the midwestern United States during the past two centuries, and migratory birds breeding in these habitats have also experienced precipitous population declines. One conservation strategy used to mitigate the effects of habitat loss and fragmentation is habitat restoration. I studied how both habitat fragmentation and restoration affect songbird populations breeding in grassland and wetland habitats in northern Iowa, 1999-2002. Most grassland birds tended to be less abundant near edges, yet birds avoided woodland edges more so than other types of edges. Edge avoidance could not be explained by changes in habitat structure. For Bobolinks (*Dolichonyx oryzivorus*), edge avoidance also increased near corners of sites, where multiple edges converged. These local patterns of edge avoidance were consistent with observed patterns of area sensitivity when scaling patterns up to fragmented landscapes using simulation modeling in neutral (randomized) landscapes. Moreover, regression modeling at landscape scales suggested that edge density metrics were better than landscape compositional metrics at explaining bird density within patches. Habitat restoration provided breeding habitat for many bird species, in which birds tended to occur at high densities in restored patches relative to other land cover types in the landscape. However, demographic data revealed a more complex pattern. In restored wetlands, reproduction was tied closely to interannual climate variation. In particular, nest predation was negatively correlated with water depth in wetlands. In restored grasslands, nest success tended to be relatively low for most species. Population projection models suggested that for Dickcissels (*Spiza americana*) and, to a lesser extent, Bobolinks, population growth rates were not high enough to be sustainable without immigration into the area ($\lambda < 1$). In addition, population growth was most sensitive to adult survival. Sensitivity to nest predation was moderate and dependent on estimates of survival, while growth was less sensitive to brood parasitism and juvenile survival. Results from this study have improved our understanding of the role of edge effects in generating spatial distributions in landscapes, how restoration ultimately affects avian populations in the Midwest, and it provides a framework for understanding songbird dynamics in fragmented landscapes.

CHAPTER 1. GENERAL INTRODUCTION

Introduction

Severe habitat loss has occurred in many ecosystems in the United States and throughout the world (Olson and Dinerstein 1998). This loss has both directly and indirectly affected ecological patterns and processes in these systems. Indeed, the most consistent threat to endangered species in the United States is habitat loss (Wilcove et al. 1998). An illuminating example includes the tallgrass prairie of North America. Historically much of the midwestern United States fell within this ecosystem, which included both native grassland habitats and scattered wetland basins (Smith 1998). However, over 99% of the tallgrass prairie ecosystem has been converted to agricultural land, hayfields, and pastures during the past two centuries, and in Iowa 99% of native prairie and 89% of native wetlands have been lost (Dahl 1990, Samson and Knopf 1994, Smith 1998). This decline has exceeded declines of any other habitat in North America (Samson and Knopf 1994). As a result of this severe habitat loss, the tallgrass prairie ecosystem is currently considered one of the most critically endangered ecosystems in the world (Olson and Dinerstein 1998).

Many species that breed within the tallgrass prairie ecosystem have also experienced precipitous declines. Based on the Breeding Bird Survey (BBS), bird populations using grassland habitats have experienced consistent widespread declines and, as a group, grassland birds have declined at a greater rate than other groups of birds in the United States (Herkert 1995, Peterjohn and Sauer 1999; see also Igl and Johnson 1997). These declines have often been attributed to severe habitat loss and fragmentation (Herkert 1994, Vickery et al. 1994, Herkert et al. 1996), but other factors, such as land-use practices (e.g., mowing of hayfields) are also having detrimental impacts (Bollinger et al. 1990, Herkert 1997). Birds using wetland habitats tend to be under-sampled by the BBS (Herkert 1995), but other evidence suggests that many wetland species have also experienced population declines (Herkert 1995, Igl and Johnson 1997). Habitat restoration is one of the only alternatives for conserving bird communities in threatened landscapes. Recently, state and federal agencies have responded by restoring some of the grassland and wetland habitats in the Midwest (Bishop et al. 1998).

My dissertation research has focused on two distinct, though interconnected, issues related to habitat loss and landscape change. First, I have investigated how habitat fragmentation affects spatial dynamics of species sensitive to fragmentation, focusing on the relative role of habitat edges. I examine two primary factors that can mediate observed edge effects on bird distributions: the type of edge (Chapter 2), and how multiple edges within fragments can interact (Chapter 3). These two factors have not been thoroughly examined for any taxon in any system and could potentially explain observed regional variation in bird distributions (Johnson and Igl 2001, Bakker et al. 2002). In addition, I investigate how local edge effects might predict patterns at larger scales (Chapters 3, 4). Second, I have used multiple perspectives to explore how habitat reconstruction and restoration—essentially the opposite of habitat loss and fragmentation—affect species distributions and dynamics (Chapters 4, 5, 6, 7). In the following chapters, I combine a variety of techniques to interpret how habitat loss, fragmentation, and restoration have affected, and continue to affect, breeding birds in Iowa. Integrating these concepts will provide a comprehensive approach to conservation.

Dissertation Organization

This dissertation is composed of eight chapters. Chapter 1 contains a general introduction and literature review. Chapters 2-7 are written as journal manuscripts; three chapters have been accepted for publication (Chapters 2, 5) or have been published (Chapter 4), and three other chapters have been prepared for publication (Chapters 3, 6, 7). Chapter 2 was recently accepted for publication at *The Auk*, Chapter 4 was published in *The Journal of Wildlife Management*, and Chapter 5 is in press at *The American Midland Naturalist*. I plan to submit Chapters 3, 7, and 8 to *Ecology*, *Oecologia*, and *Conservation Biology*, respectively. Chapter 8 contains general conclusions from my dissertation research. All sections of this dissertation were written by Robert J. Fletcher, Jr., and edited by Rolf R. Koford. All manuscript chapters have also been externally reviewed by peers and who are listed in the Acknowledgments near the end of each chapter.

Literature Review

Habitat fragmentation and species distributions.—Habitat fragmentation has been documented to affect a variety of ecological processes, from individual behavior (Belisle et al. 2001, Ricketts 2001) to species interactions (Kareiva 1987, Aizen and Feinsinger 1994) and population dynamics (Robinson et al. 1992, Donovan et al. 1995, Porneluzi and Faaborg 1999). Many of these consequences can be partitioned from a few key elements of landscapes that affect processes in diverse ways. Some prominent elements include connectivity, supplementary and complementary habitats, and edge effects (Dunning et al. 1992). Habitat edges provide an interesting opportunity to understand how different habitats can interact to govern dynamics in heterogeneous landscapes. Indeed, understanding how habitat edges and habitat boundaries affect ecological patterns and processes has become a central focus in the emerging paradigm on habitat fragmentation (Wiens 1995).

Although habitat edges have been studied intensively over the past two decades, the focus of the research has been somewhat narrow in scope (Murcia 1995). For avian populations, most research has centered on whether nest predation and brood parasitism increase near edges (reviewed in Paton 1994, Andren 1995, Hartley and Hunter 1998, McCollin 1998, Lahti 2001). Yet very little research has focused on how edges may affect spatial distributions in fragmented landscapes and the factors that can mediate these effects (but see Ortega and Capen 1999). In the absence of data, certain dogmas have emerged in the literature. One such dogma is that many neotropical migratory birds considered area sensitive, being less likely to occur in small patches, tend to also be less abundant near edges and have thus been labeled “interior” species (Whitcomb et al. 1981, Robbins et al. 1989, Villard 1998). Yet it is unclear whether the processes underlying edge avoidance and area sensitivity operate independently (Villard 1998). In grassland systems, most grassland-breeding songbirds have been documented as being area-sensitive in parts of their breeding ranges, yet there is a considerable amount of variation in the patterns observed (Samson 1980, Herkert 1994, Vickery et al. 1994, Bollinger 1995, Helzer and Jelinski 1999, Johnson and Igl 2001, Bakker et al. 2002).

Many factors could be influencing observed regional variation in fragmentation sensitivity, including landscape structure and variation in regional densities (Flather and

Sauer 1996, Johnson and Igl 2001, Bakker et al. 2002). Landscape structure could mediate area-sensitive patterns based on variation in isolation and the surrounding habitats or matrix (Donovan et al. 1997, Rodewald and Yahner 2001, Bakker et al. 2002). Regional densities could also affect patterns; at high densities all or nearly all habitat could be occupied, even though some areas might be less suitable (Horn et al. 2000, Johnson 2001, Bollinger and Switzer 2002). Other explanations for area sensitivity that might lead to variation in observed patterns include rescue and target effects (Lomolino 1990, Gotelli 1991), habitat heterogeneity (Freemark and Merriam 1986), site fidelity in large patches if breeding success is greater in large patches (Bollinger and Gavin 1989, Johnson and Temple 1990, Winter and Faaborg 1999), sampling issues (Horn et al. 2000, Johnson 2001), and edge avoidance (Burke and Nol 1998, Johnson and Igl 2001). Although edge avoidance has been hypothesized as a mechanism leading to patterns of area sensitivity in landscapes (Burke and Nol 1998, Johnson and Igl 2001), many factors can mediate edge effects, such as conspecific density (Ries and Debinski 2001), edge orientation (Chen et al. 1995), the type of edge under consideration (Suarez et al. 1997, Winter et al. 2000), and the proximity of other nearby edges (Malcolm 1994). As such, some of these local factors—particularly conspecific density, edge type, and proximity to other edges—could help to explain regional variation in spatial distributions of migrant birds. Understanding these factors will help determine if edge effects operate at large scales (Laurance 2000).

Habitat restoration and songbird populations—Because the tallgrass prairie ecosystem is currently considered one of the most critically endangered ecosystems in the world (Olson and Dinerstein 1998), one of the only alternatives for conserving this system is habitat restoration (Jordan et al. 1987). Habitat restoration can have diverse impacts on avian populations, however, and evaluating restoration can be complex. For example, at one level, restoration might attract birds to breed in these areas, with individuals quickly colonizing areas following restoration efforts (Hemesath and Dinsmore 1993). If so, a useful comparative approach for evaluating restoration might include comparing bird populations, in terms of density and diversity, in restored and native habitats (sensu Blankespoor 1980, Delphey and Dinsmore 1993, Brown and Smith 1998, Ratti et al. 2001). In addition, examining the turnover of bird populations with restoration could be useful to help interpret

future scenarios of land use change (Igl and Johnson 1995, White et al. 1998; see Chapter 5). Yet density can often be uncorrelated with fitness in populations and might provide a misleading picture of habitat quality (van Horne 1983, Vickery et al. 1992, Brawn and Robinson 1996, Hughes et al. 1999, Winter and Faaborg 1999, Vierling 1999). The efficacy of restoration might be interpreted better by estimating demographic parameters (e.g., nesting success) of populations using restored habitat (Marzluff and Ewing 2001).

Although the effects of grassland restoration on bird populations have not been thoroughly examined (but see Blankespoor 1980), certain programs placing grassland habitat back onto the landscape have been evaluated, particularly the potential contributions of the Conservation Reserve Program to bird populations (CRP; Johnson and Schwartz 1993, Reynolds et al. 1994, Igl and Johnson 1995, Best et al. 1997). CRP fields tend to have higher densities of many species of birds than cropland (e.g., Johnson and Schwartz 1993, Best et al. 1997), the primary land use that is converted to CRP grassland. Moreover, some bird populations breeding in CRP fields appear to be sustainable and making positive contributions to population growth (McCoy et al. 1999).

Documenting growth rates is not enough, however, for prescribing sound conservation strategies and determining how managers can improve restoration practices. Instead, biologists need to identify what demographic factors contribute most to population growth rates and subsequently implement strategies that have positive responses on these parameters (Sæther et al. 1996), assuming that these factors are not constrained and can be actively managed (Benton and Grant 1999, Mills et al. 1999). For example, a recent review suggested that adult survival is generally the predominant parameter influencing growth rates across a wide diversity of birds (Sæther and Bakke 2000; see also Pulliam et al. 1992, Murphy 2001). Nonetheless, fecundity is often the demographic parameter emphasized in research and management of songbirds (e.g., Johnson and Temple 1990, Robinson et al. 1995, Brawn and Robinson 1996, Smith et al. 2000). Fecundity can be influenced by different factors (e.g., nest predation, renesting rates), but only Woodworth (1999) has attempted to determine the importance of some of these factors influencing avian population growth rates, and Woodworth's modeling framework did not isolate these factors to determine the relative contribution of specific parameters to population growth rates.

Thus, a comprehensive assessment of how restoration potentially influences the density, reproduction, and population growth of declining species is needed to reliably interpret the efficacy of restoration and how restoration can be improved.

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CHAPTER 2. SPATIAL RESPONSES OF AN AREA-SENSITIVE GRASSLAND SONGBIRD NEAR DIFFERENT TYPES OF EDGES

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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 a declining, area-sensitive songbird that breeds in grasslands, the Bobolink (*Dolichonyx oryzivorus*). We expected Bobolinks to be less abundant near edges, and we investigated a set of alternative hypotheses for explaining this 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 these hypotheses, we surveyed Bobolinks in grassland habitats near 34 edges of three different edge types (agriculture, road, and woodland) in northern Iowa, USA, 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 these responses for species in fragmented landscapes.

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 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 these 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. This 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 this 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). Based on 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 this spatial pattern:

1) *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, this would lead to apparent patterns of avoidance based on density data, typically within about half of the diameter of an average territory. This type of random settlement has explained density patterns in some systems (King et al. 1997), but not others (Ortega and Capen 1999).

2) *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, this hypothesis has generally not explained avian distribution near forest edges (Kroodsma 1984, Ortega and Capen 1999).

3) *Territory size*.—Territory size of individuals can increase near edges, but individuals could potentially still use edge habitat. Overall, this would lead to low densities near edges. This 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).

4) *Active avoidance*.—Finally, birds can actively avoid edges by distributing territory boundaries away from edges. This 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 these 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.—We surveyed grassland birds 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, four of these were altered after the 1999 breeding season, making these sites unsuitable for future surveys. In 2000, we replaced these four areas with new plots near edges, 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/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.).

The edge types we 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, we only used sites with two-lane gravel roads that had row crop agriculture on the side of the road opposite to the grassland habitat to standardize this edge type. Although this design does not isolate road effects, comparing road edges to agriculture edges demonstrates the relative effect of roads on bird distribution. Woodland edges were \geq 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, five road, and two woodland plots were located on native prairies (all predominately warm-season grasses), whereas five agriculture (four cool-season, one warm-season plantings), seven road (four cool-season, three warm-season plantings), and 10 woodland plots (seven cool-season, three warm-season plantings) were located on restored grasslands. Because Bobolink densities in

these two habitat types tend to be similar in northern Iowa (Fletcher and Koford 2002), we pooled data across habitat types when testing for edge effects.

Bird surveys.—We surveyed birds 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 this buffer on previous research by Helzer (1996), who found that densities of Bobolinks were lower within approximately 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 the 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 the 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 this region. Male Bobolinks typically have multipurpose, non-overlapping territories during the breeding season, where courtship, feeding, and rearing young occur (Martin and Gavin 1995). We used the "flush" technique 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).

This process was repeated for all males observed during the mapping visit within the boundaries of plots. The 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 ± 1.8 ; $F = 0.33$, $df = 2$ and 42, $P = 0.72$). The 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.—We measured vegetation along transects each year to determine if vegetation changes in relation to the edge, and how habitat gradients may affect spatial distributions of Bobolinks. We used stratified random sampling to estimate habitat structure. We stratified each survey plot 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 based on non-overlapping percentages using a Daubenmire quadrat (Daubenmire 1959). Canopy coverage categories included total (live + dead vegetation), grass, forb, standing dead vegetation, litter, and bare ground.

Statistical analyses.—We quantified Bobolink distribution patterns by grouping detections into six 25-m intervals from the edge (0-25 m, 26-50 m, 51-75 m, etc.). Although individuals likely used more than one distance interval, these intervals allow for high resolution in examining the spatial patterns near edges and our model structure accounted for this potential lack of independence (see below). These 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 these surveys into one

estimate (mean number of detections of males/ha) for each interval at each site as an index of Bobolink density (density hereafter).

We compared estimates derived from survey data (using 2000 data only) 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 ha, d , 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_j is the proportion of the territory in distance interval i for individual j (where $\sum_{i=1}^6 t_j = 1$, 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 (ha) of distance interval i . We then compared the two types of estimates using Spearman's rank correlation.

We analyzed our density index 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. We explored four covariance structures to explain this repeated measure (autoregressive order one, compound symmetric, unstructured, and variance components; Littell et al. 1996:92-102). 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. 1996:93), because this 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 non-zero slopes and if slopes were heterogeneous among edge types, which we

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, we calculated the distance from the habitat edge to the center of each territory (*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 the number of territories mapped per ha 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). We also included the number of locations used to estimate territory size 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. We defined edge territories as those in which no other territorial locations from different males fell between the central portion of territories and the edge habitat. This confidence interval was estimated in the mixed-model framework, again using the number of territories mapped per ha for each survey area as a covariate. If confidence intervals for this 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 ha (d_i) were highly correlated (Spearman's $\rho = 0.61$, $n = 180$, $P < 0.0001$). Variation between these 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 two times greater near agriculture edges and 1.5 times greater near road edges than density near woodland edges (Fig. 2A). We explored whether this 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 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, while 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 vegetation 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 , $P = 0.207$), consistent with the territory size hypothesis near roads, but contrary to the hypothesis for woodlands (Fig. 4). Territory size was negatively correlated with the number of territories mapped per ha (a covariate) in our survey plots ($F = 9.87$, $df = 1$ and 24 , $P = 0.0044$), size but was not correlated with the 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 these, 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. Based on 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, this evidence for road avoidance is within the measurement error of the GPS unit (see Methods), 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, passive displacement alone was occurring and probably best explains density patterns near agriculture edges. Overall, the number of territories mapped per ha (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 based on 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 these studies investigated both the importance of different edge types and alternative explanations for spatial patterns of distribution. Had we limited our study to bird surveys and not considered behavioral aspects of territoriality near edges, we would have incorrectly concluded that Bobolinks strongly avoid agriculture edges. 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 these factors were correlated with Bobolink density ($r < 0.07$; $P > 0.20$). Therefore, it is unlikely that these 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 based on increasing sub-canopy 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.

Bobolink territory size increased near roads, 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. Neither of these factors has been investigated in Bobolinks. If food availability governs these patterns then habitat quality (based on food 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 due to 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, suggesting 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, renesting 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 this 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 this 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 this 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 in this study suggest that agriculture edges are less influential on distributions than other edge types, agriculture 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. This pattern in Bobolinks might not be unique for grassland birds. Although we did not map territories of other species near edges, surveys revealed that 5 of 8 common bird species tended to have lower densities near woodland edges (Fig. 6). 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 both prevent woody encroachment within patches, as well as decrease the amount of woodland vegetation surrounding patches.

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TABLE I. Summary of linear mixed-model analyses testing density (detections of males/ha) 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	
	<i>F</i> ^a	<i>P</i>	<i>F</i> ^b	<i>P</i>	<i>F</i> ^c	<i>P</i>
Edge avoidance						
Density (males/ha) ^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)	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

Figure 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.

Figure 2. Least squares estimates of Bobolink density (mean number of detections of males/ha, 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.

Figure 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, while other variables were arcsine square root transformed for analysis.

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

Figure 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.

Figure 6. Least squares estimates for density (mean number of detections of birds/ha, 1 SE) of common birds (See Chapter 5 Appendix for scientific names) in grasslands as a function of distance from edge for three edge types, northern Iowa, 1999-2000. Letters denote significance (uppercase: $P < 0.05$; lowercase: $0.05 < P < 0.1$) of explanatory variables in a mixed-model analysis, considering both distance from edge and year as a repeated measure. ^aEdge type effect, ^bDistance from edge effect, ^cEdge type \times distance from edge interaction, ^dYear effect, ^eYear \times edge type interaction, ^fDistance from agriculture edge effect (based on a

contrast), ^gDistance from road edge effect (based on a contrast), ^hDistance from agriculture edge effect (based on a contrast).

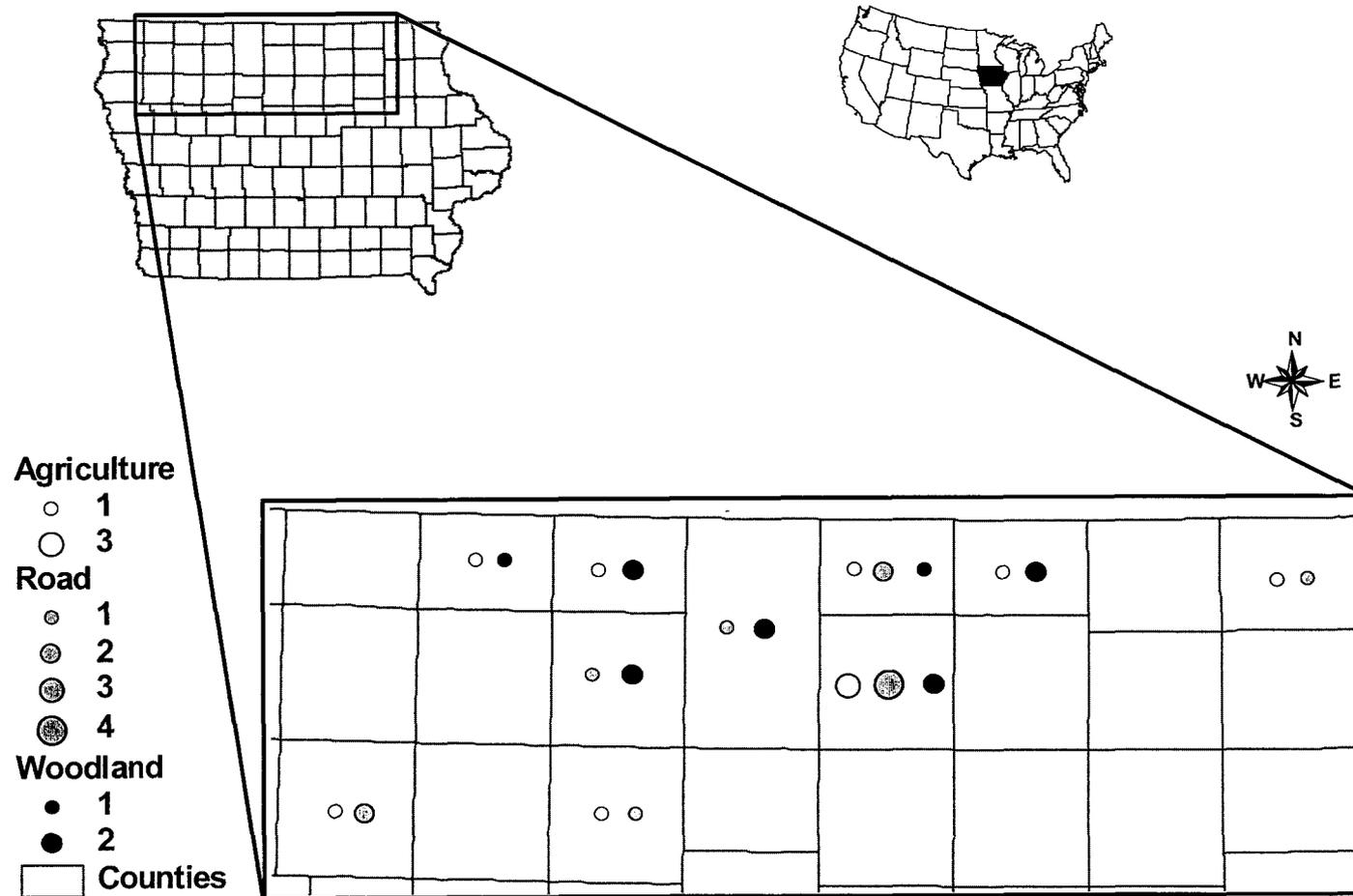


Figure 1

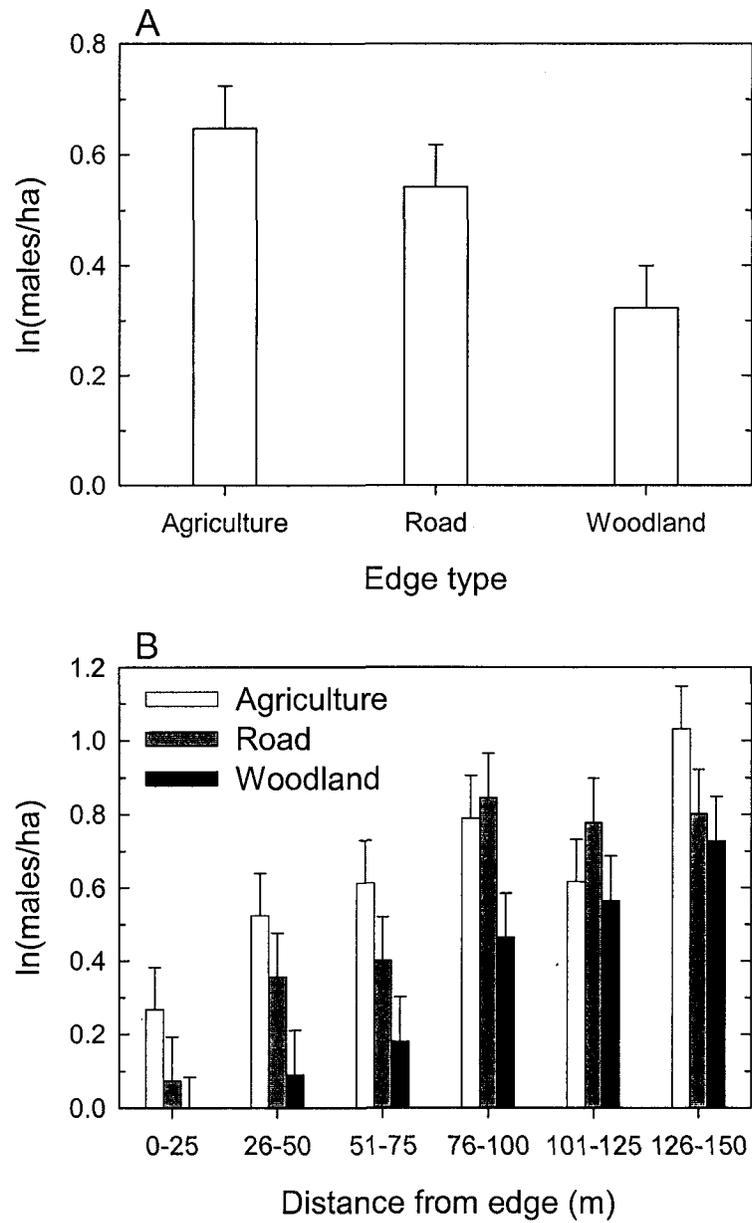


Figure 2

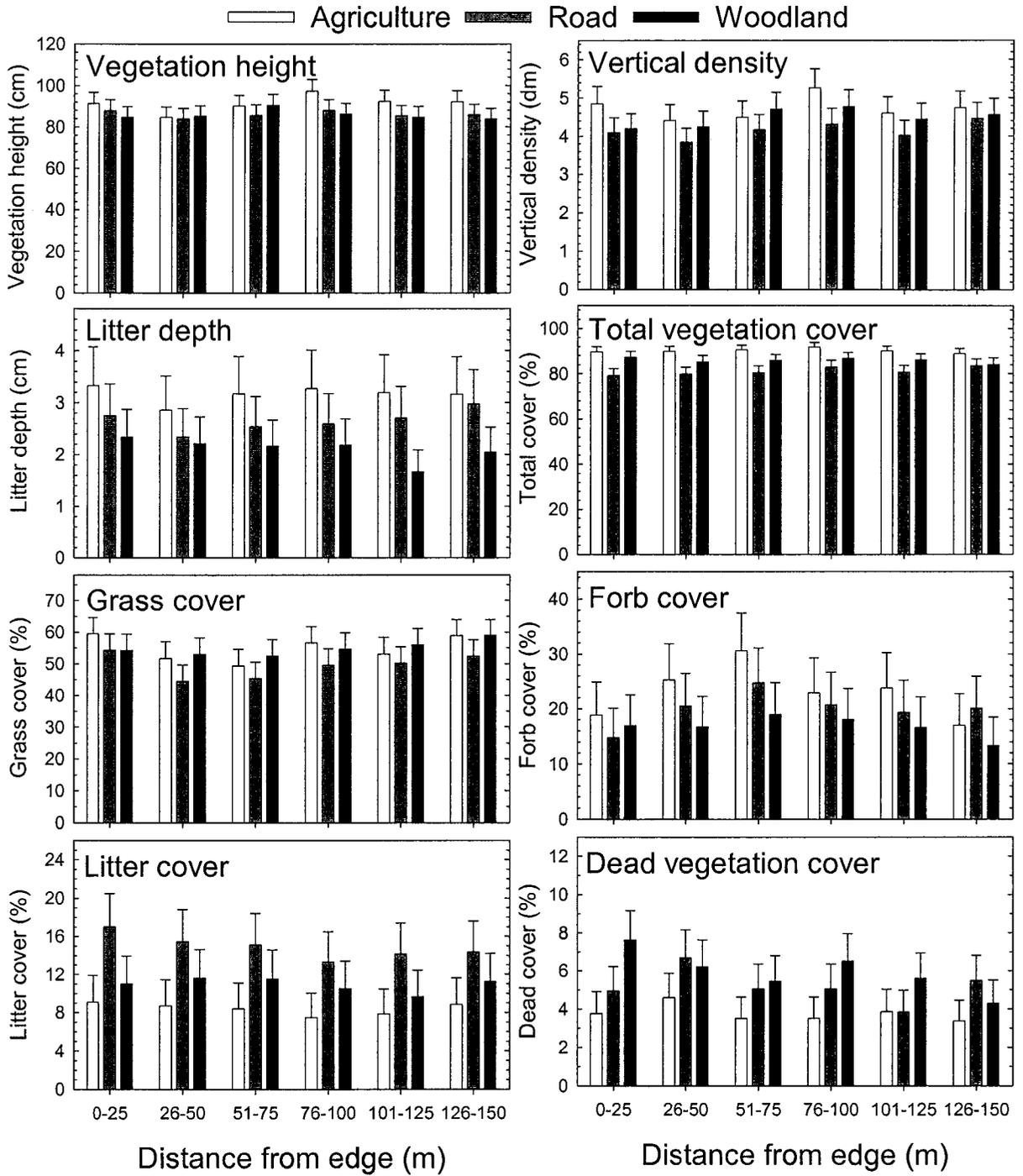


Figure 3

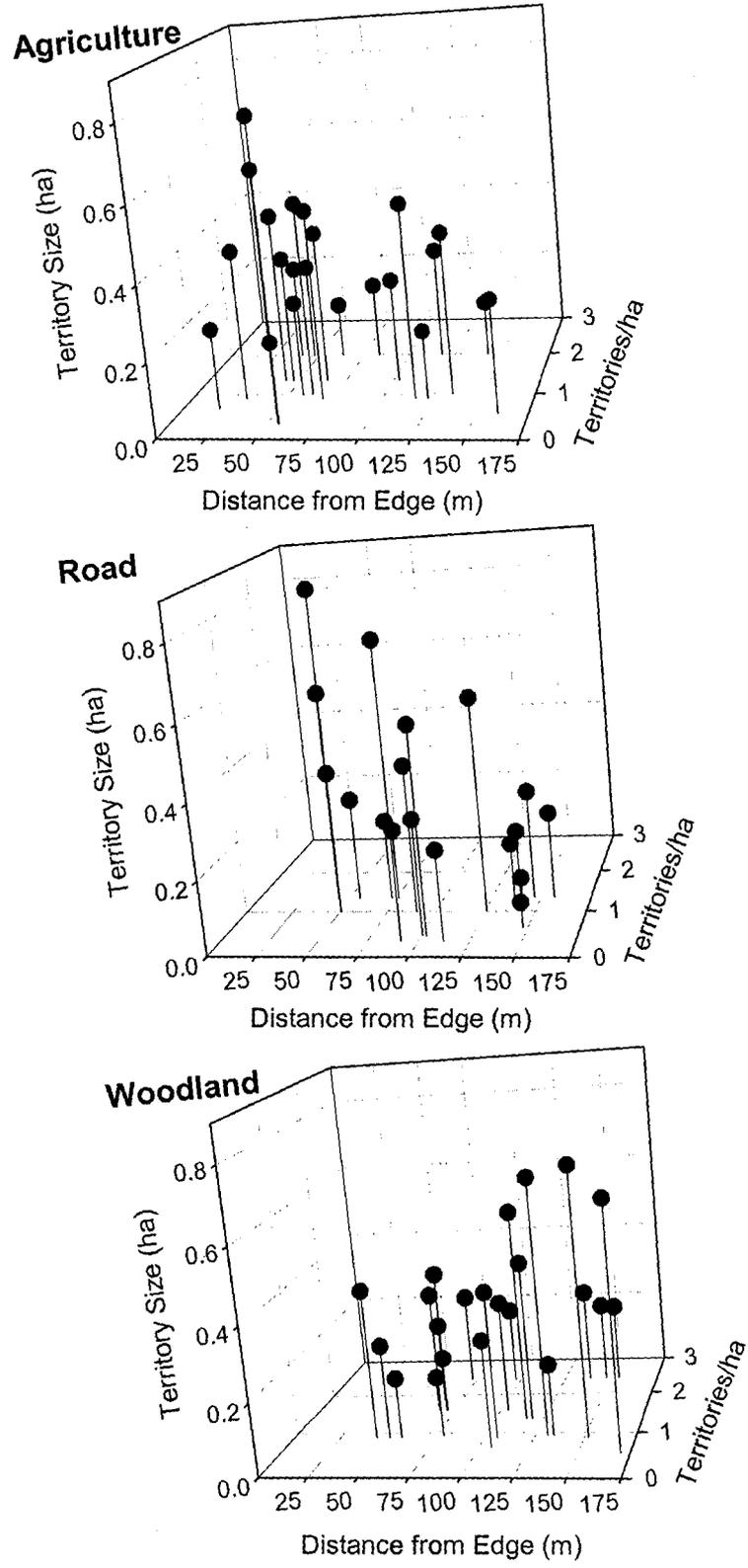


Figure 4

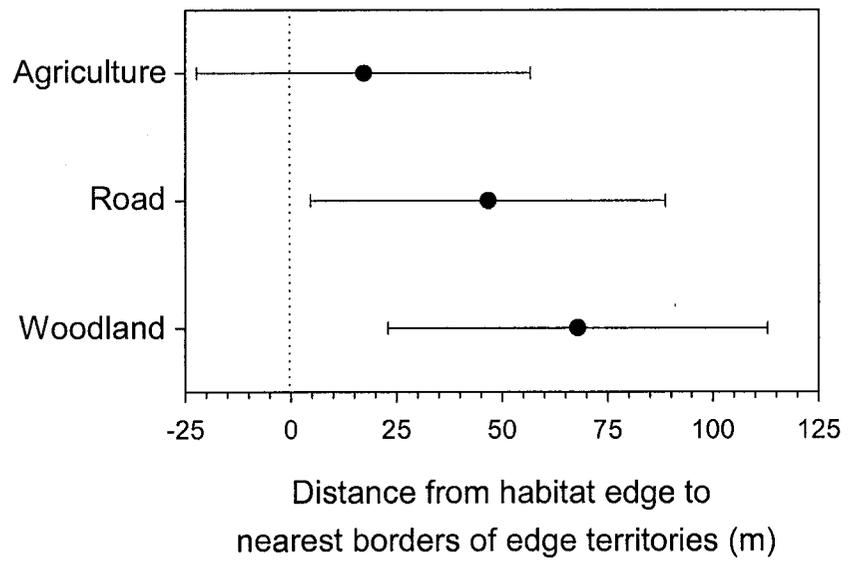


Figure 5

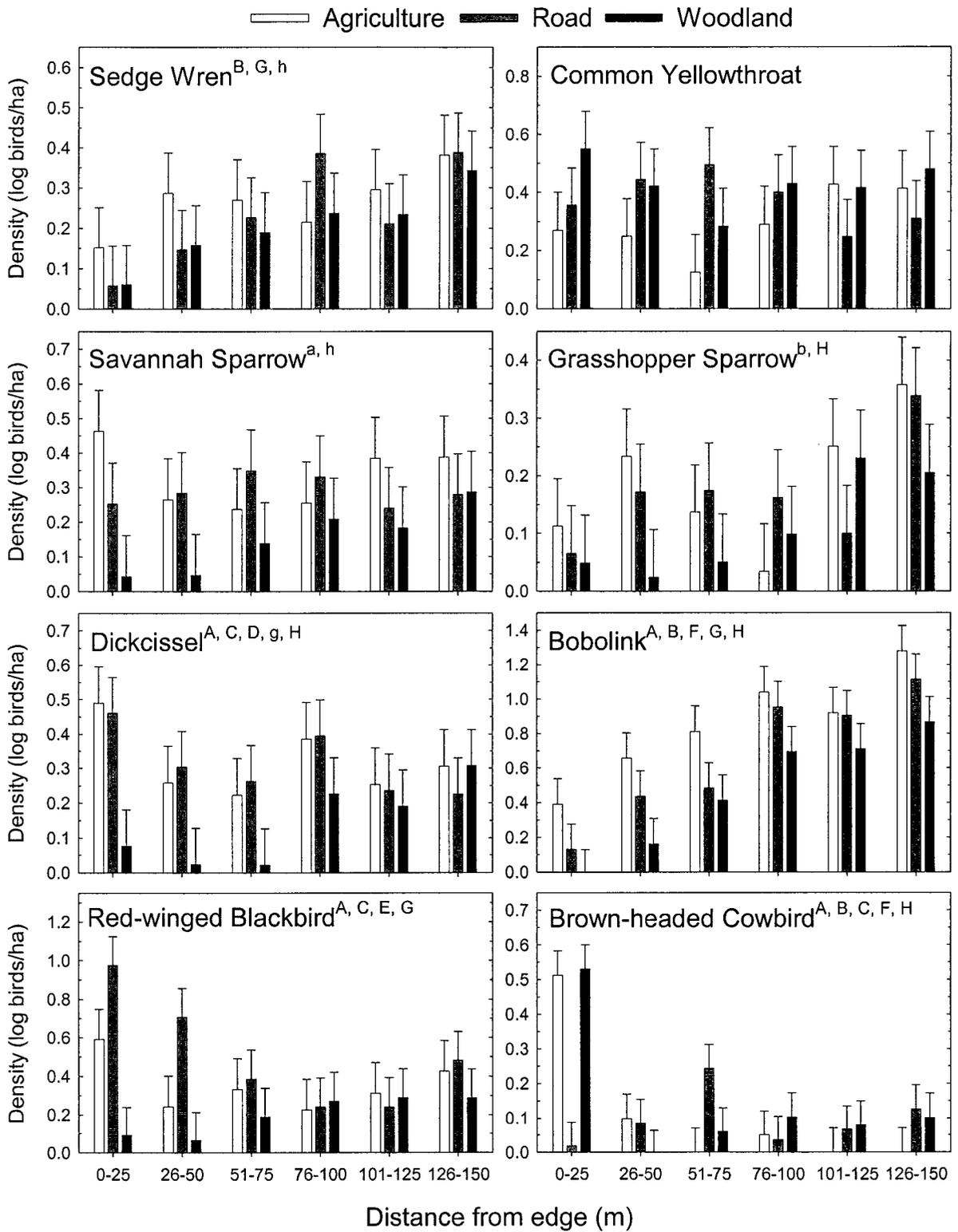


Figure 6

CHAPTER 3. THE NATURE OF MULTIPLE EDGE EFFECTS AND ITS IMPLICATIONS IN FRAGMENTED LANDSCAPES

A paper to be submitted to *Ecology*

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Abstract. Habitat edges are prominent components of fragmented landscapes. While insight on how edges can affect processes has grown in recent years, inference on edge effects has been limited in extrapolating to different situations because ecologists still do not understand if and how multiple edges interact in small fragments. We develop a model framework for interpreting multiple edge effects and examine how multiple edges may affect spatial distributions of an area-sensitive migratory songbird that breeds in temperate grasslands, the Bobolink (*Dolichonyx oryzivorus*). We expected that Bobolinks would avoid edges and that this avoidance would be stronger in plots near two edges (double-edge plots) than in plots near only one edge (single-edge plots). We test this prediction and if multiple edges influence both the magnitude and extent of edge effects. We subsequently link spatial distributions to neutral landscape models that varied in the amount of habitat and degree of fragmentation to explore the potential implications of multiple edges on patch- and landscape-level distribution in fragmented landscapes. Overall, the probability of Bobolink occurrence was lower in double-edge plots than in single-edge plots. Within single-edge plots, the probability of occurrence increased with increasing distance from edge and we estimated that the extent of the effect (i.e., the distance of edge influence, DEI) was approximately 90 m (range: 63 - 115 m). Within double-edge plots, the probability of occurrence was influenced both by the nearest distance and the next-nearest distance from edges; in both cases, Bobolink occurrence increased with increasing distance from edges. The DEI in double-edge plots ranged to approximately 100-120 m (range: 34 to >150 m), depending on the next-nearest distance from edge. Habitat structure could not explain spatial patterns of occurrence. Scaling local spatial distributions to fragmented landscape models suggests that edge effects could have strong influences on large-scale distribution and that multiple edge effects are primarily important 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. We conclude that edge effects can be exacerbated when multiple edges collide and that edge effects could be a driving force in bird distributions in highly fragmented landscapes.

Key words: area sensitivity, Bobolink, Dolichonyx oryzivorus, edge avoidance, edge effects, distance of edge influence, fractal landscapes, habitat edge, neutral landscapes, patch size effects, grassland birds

INTRODUCTION

Habitat loss generally leads to increased habitat fragmentation, resulting in smaller patches, increased isolation, and increased proportion of edge habitat in landscapes. Although much progress has been made understanding how edges can affect populations and communities, inference on edge effects has been limited in extrapolating to different scenarios because ecologists still do not understand many factors influencing edge effects, including if and how multiple edges interact in small fragments. Most empirical research (e.g., Gates and Gysel 1978, Chen et al. 1992, Laurance et al. 1998, Brand and George 2001) and models (Temple and Cary 1988, Laurance and Yensen 1991, Sisk et al. 1997, Fagan et al. 1999) on edge effects have ignored multiple edge effects, which we define as the cumulative edge effect occurring from more than one habitat edge within a fragment (sensu Zheng and Chen 2000). Of the few studies that have acknowledged the potential importance of multiple edges (Malcolm 1994, Mancke and Gavin 2000, Zheng and Chen 2000, Fernández et al. 2002), Malcolm (1994), Zheng and Chen (2000), and Fernández et al. (2002) assumed edge effects were additive, thereby assuming that multiple edges influenced the magnitude of edge effects more so than the extent of edge effects (i.e., the distance or depth of edge influence, DEI; Harper and McDonald 2001). This assumption is particularly important when extrapolating edge effects to core-area models (Laurance and Yensen 1991). Moreover, understanding the nature of multiple edge effects (i.e., the magnitude and extent) will be critical for determining if edge effects operate at large spatial scales (Laurance 2000).

We develop a model framework for interpreting the effects of multiple edges on ecological patterns and processes, placing these effects in the context of fragmented landscapes. We apply this framework to evaluate the implications of multiple edges for an area-sensitive songbird, the Bobolink (*Dolichonyx oryzivorus*), which has been documented to avoid edges (Bock et al. 1999, Fletcher and Koford 2002, 2003). We expected that distributions of Bobolinks would be impacted in areas near multiple edges more so than in areas near only one edge. We then couple these empirical data with neutral landscape models (i.e., landscape maps generated by theoretical spatial distributions that do not incorporate ecological processes, such as topography, aspect, etc.; Gardner et al. 1987, With and King 1997) that vary in the amount of habitat and the degree of fragmentation to explore the potential impacts of multiple edge effects on distributions in fragmented landscapes.

Analytical models for describing multiple edge effects

Edge effects are generally thought to resemble two types of functions (but see Murcia 1995): a negative exponential function (Laurance et al. 1998, Zheng and Chen 2000, Brand and George 2001), or a threshold function (Mancke and Gavin 2000). A negative exponential function describing an effect from one edge can be described as:

$$e_{di} = e_{max} \times \exp(-m_i \times d_i) \quad (1)$$

where e_{di} is the edge effect that occurs at distance d from edge i , e_{max} is the maximum edge effect (i.e., the effect occurring at $d_i = 0$), and m_i is the slope, or intensity, of the edge effect (Fig. 1a, b). Thus, the estimate of a parameter, β , (e.g., density) that is influenced by one edge, i , can be described as:

$$\beta_{di} = \beta_{int} - e_{max} \times \exp(-m_i \times d_i) \quad (2)$$

where β_{int} is the interior estimate of the parameter, or the estimate in the absence of edge effects. In equation 2, the edge effect is subtracted from β_{int} to reflect an effect that reduces interior estimates; however, some edge effects might increase parameter estimates and would thus be added to β_{int} (e.g., Malcolm 1994, Laurance et al. 1998). A simple additive model (using a negative exponential function) describing the influence of multiple edges (e.g., four edges in a patch; Fig. 1a) can thus be described as (cf. Malcolm 1994, Zheng and Chen 2000):

$$\beta_{xy} = \beta_{int} - \sum_{i=1}^4 e_{max} \times \exp(-m_i \times d_i) \quad (3)$$

where x and y are the coordinates for a location in 2-dimensional space. Likewise, a threshold model, similar in form to a logistic model for binary responses, can be described as:

$$\beta_{xy} = \beta_{int} - \sum_{i=1}^4 \left(\frac{\beta_{int} \times \exp(\ln(e_{max}/(\beta_{int} - e_{max})) - m_i \times d_i)}{1 + \exp(\ln(e_{max}/(\beta_{int} - e_{max})) - m_i \times d_i)} \right) \quad (4)$$

These models assume that the intensity of each edge effect varies, which is useful for estimating effects from different edge types or edge orientations (Chen et al. 1992, Suarez et al. 1997, Zheng and Chen 2000, Fletcher and Koford 2003). Yet some properties of these models are not satisfactory, particularly if edge effects reduce estimates and $\sum e_i > \beta_{int}$, predicted estimates can be outside the range of possible values. Although very little empirical data exist regarding the nature of multiple edge effects, Malcolm (1994) found that an additive edge effect model explained habitat structure in Amazonian fragments better than a nonadditive (single edge) model.

In practice, most research has focused on the minimum distance, or nearest distance, from an edge to describe edge effects (Laurance and Yensen 1991). Therefore, a critical framework for evaluating multiple edge effects requires comparing predictions from nearest-distance models to models using multiple distance measures. For example, using the above functions to generate edge effects in square patches that vary in size would produce very different patterns using nearest-distance models and additive models (Fig. 1c, d). Placed in this context, we would assume that the effect from the nearest distance to edge would have a different slope than the next-nearest distance (thus changing the function described in Fig. 1b), even if all other aspects of the edge were equivalent. These effects can then be estimated from empirical data using generalized linear models (GLM; see *Statistical Analyses*). Other approaches have been used for modeling multiple edge effects (Malcolm 1994, Fernández et al. 2002), in which observed data are fit to nonlinear functions that integrate areas near edge surfaces across a distance of edge influence. While these models are analytically tractable and satisfying, GLM allows for incorporating non-edge related factors that might influence observed patterns, such as spatial covariance, site effects, and

other structural covariates (e.g., microclimate). In particular, accounting for spatial covariance within plots has recently received attention and is considered important for appropriate inference regarding edge effects (Brand and George 2001, Harper and MacDonald 2001).

METHODS

Study area

We surveyed breeding birds in 10 grassland patches scattered throughout northern Iowa, 2001-2002 (Fig. 2). We surveyed birds on the same plots in these patches each year; however, one plot was not surveyed in 2002 because management activities caused this plot to be unsuitable for most grassland birds (including Bobolinks). 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/alfalfa (*Medicago sativa*) mixtures. 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.).

Bird surveys

At each site we set up paired plots (150 × 150 m; Fig. 2): 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). Both plots within sites contained similar habitat types (prairie or restored; cool-season or warm-season grasses). Each edge plot was placed at least 150 m from any other edge in the site to minimize effects from other edges. We based this buffer on previous research in Nebraska by Helzer (1996), who found that densities of Bobolinks were lower within approximately 75 m of 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. For each survey, the observer randomly picked the order and direction to survey transects. During each survey, the observer walked transects at a steady pace, recording all birds seen within

25 m of the transect. When collecting data, we divided observations into 25×25 m cells within the plots. Although individuals likely used > 1 cell, these cells allow for high resolution in interpreting the spatial patterns near edges and our model structure 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}). Observers recorded the species, sex, and distance of each bird from transects. Care was taken not to count the same bird twice. Surveys were conducted between sunrise and four hours after sunrise, when breeding birds are most active. Surveys were repeated four times during the breeding season, from 20 May until 6 July, 2001-2002. Each year three observers conducted surveys, and each observer surveyed each site at least once.

In 2002, we added interior transects at 5 of the 10 sites. Interior transects were 100×50 m. Each interior transect was placed at least 200 m from any edge within the study site to minimize effects from edges. Interior transects were sampled using the same protocol as single- and double-edge plots.

Habitat measurements

We measured vegetation along transects each year, once at each site between 20 June-20 July, to determine if vegetation changes in relation to the edge, and how habitat gradients may affect spatial distributions of Bobolinks. We estimated habitat structure by randomly sampling vegetation within each grid cell used for bird observations. Within each cell, 3 sampling points were randomly chosen ($n = 108$ points/plot). 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 based on non-overlapping percentages using a Daubenmire quadrat (Daubenmire 1959). Canopy coverage categories included total (live + dead vegetation), grass, forb, standing dead vegetation, litter, and bare ground.

Statistical Analyses

This study design allows for two levels of resolution for determining if multiple edges influence bird distribution. First, at the plot level, we tested for differences in bird occurrence in single-edge, double-edge, and interior plots. Second, we tested if the distance to the nearest edge and next-nearest edge could explain Bobolink occurrence within plots. For distance effects, we tested whether slopes of the probability of occurrence were zero by using the midpoint of each grid cell as a continuous variable. We considered Bobolinks to occur in cells if at least one individual was observed within the cell during at least one of the visits. We evaluated occurrence using geostatistical generalized linear mixed models for binomial data using a logit link function (Littell et al. 1996). We considered site and year as random effects to incorporate inherent variability among sites and between years. Because observations in adjacent cells were not independent, we adjusted models for spatial covariance by estimating the nugget, partial sill, and range parameters of the semivariogram explaining spatial autocorrelation within plots (Littell et al. 1996: 303-330). We considered 6 isotropic (i.e., correlation independent of direction; Gaussian, exponential, linear, linear log, power, and spherical; Littell et al. 1996:305) and 2 anisotropic models (i.e., correlation dependent on direction; anisotropic exponential and anisotropic 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 small sample size (Burnham and Anderson 1998).

We were interested in estimating the DEI and determining if this distance changed near multiple edges. To estimate the DEI, we overlapped interior estimates of occurrence with estimates derived as a function of distance from each edge within single- and double-edge plots (sensu Laurance et al. 1998, Harper and McDonald 2001). We approximated the DEI as the point in which the lower confidence limit for the interior estimate overlapped with the models (means and confidence limits) within each plot type (Laurance et al. 1998, Harper and McDonald 2001). These approximations are not intended to provide absolute estimates of the extent of the edge effect, but they are useful for comparative purposes between the two plot types.

To test for habitat gradients as a function of distance from edge, we first summarized habitat measurements into orthogonal principal components derived from the correlation matrix, because some habitat measurements were highly correlated. We used varimax rotation to improve interpretability of principal components (Hatcher and Stepanski 1994). Habitat measurements were transformed as necessary prior to the principal component analysis to improve normality and homogeneity of variance. We then used a similar mixed-model analysis adjusted for spatial covariance used above for Bobolink occurrence to test for habitat structure gradients using principal component scores for each grid cell as the response variable.

Landscape Edge Model

To explore the potential implications of multiple edge effects, we used a simulation model that linked empirical data on Bobolink distributions with fragmented landscapes to determine if incorporating multiple edge effects would change predictions of edge effects at large scales. We did not model aspects of population dynamics, such as nesting success (Donovan and Lamberson 2001, With and King 2001), because we lacked data on demographic processes. We generated neutral landscape maps that varied in the amount of habitat and degree of fragmentation using the program RULE (Gardner 1999; see also With and King 1997, 2001). Each landscape was a 256×256 grid that contained suitable habitat and unsuitable matrix. We considered each cell in the landscape to be 25×25 m to appropriately scale empirical data with the neutral landscapes. Therefore, landscape size was 6.4×6.4 km (41 km^2 or 4096 ha). We generated maps with 10%, 30%, and 50% habitat in the landscape (Fig. 3). Fragmentation was varied by using a range of fractal dimensions, D (2, 2.5, and 3), and using a simple random algorithm (*SR*) for each habitat abundance. For generating fractal landscapes, RULE uses the midpoint displacement algorithm (Saupe 1988:96-101), which creates a map of real numbers by random definitions at broad scales and successive division from broad to finer scales, interpolating values at finer scales based on broad-scale information and random perturbation (the magnitude of random perturbation is based on the parameter H , which ranges from 0 to 1, where $D = 3 - H$; Saupe 1988:96). When $D = 2$ landscapes are less fragmented, when $D = 3$ landscapes are highly fragmented. For simple random landscapes, each cell in the landscape has an independent probability, p ,

of being suitable habitat (e.g., for 30% habitat in the landscape, $p = 0.3$); simple random landscapes are an extreme form of fragmentation (Fig. 3; see also With and King 2001). A total of 12 landscape types were generated, with 10 replicate landscapes for each type. Patches were delineated using the nearest-neighbor rule, in which patches were defined based on contiguous orthogonal clusters of cells (With 1997, Gardner 1999).

Edge effects were modeled using a simple population-level approach, similar to the Effective Area Model developed by Sisk et al. (1997), but we used the probability of occurrence (derived from logistic models, see *Statistical Analyses*) for modeling and incorporated multiple edges in our modeling process. For each habitat cell in the landscape, distances from each edge were calculated in each cardinal direction. These 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 distance from edge was used to estimate the probability of occurrence, and 3) a next-nearest distance model, in which both the nearest and next-nearest distances from edges were used in estimating probability of occurrence. We did not use models that incorporated distances to all edges because our data did not allow for extrapolating effects based on > 2 edges.

We simulated bird distribution in each landscape 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, p_d , taken from probability estimates of the logistic models. The null model used the probability estimate from the interior plots. The nearest distance model used probability estimates from the single-edge plot when $d_{nd} < 150$ and the interior estimate when $d_{nd} \geq 150$ m; this model most closely resembles previous models on edge effects (Laurance and Yensen 1991, Sisk et al. 1997). The next-nearest distance model used probability estimates from the double-edge plot when d_{nd} and $d_{nnd} < 150$ m, estimates from the single-edge plot 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, we addressed the following: 1) Do different models (null, nearest distance, next-nearest distance) predict different patch and landscape-level densities?, and 2) Do these predictions vary with the amount of habitat and intensity of fragmentation?

RESULTS

Bobolink distributions

In 2001, we recorded 329 observations of Bobolinks along transects (69.6 % males; $n = 229$), whereas in 2002 we recorded 313 observations (67.4% males; $n = 211$). In both years, Bobolinks were the most common bird observed on transects, being over twice as abundant as other common species observed. Overall, the probability of occurrence for Bobolinks was greatest on interior plots and least on double-edge plots (anisotropic power covariance; $F_{2,13} = 8.89$, $P = 0.004$; Fig. 4a), with mean estimates of occurrence being two times greater on single-edge plots than double-edge plots, and mean estimates being approximately two times greater on interior plots than single-edge plots. In single-edge plots, the probability of occurrence increased as a function of distance from edge (power covariance; $F_{1,9} = 37.2$, $P < 0.001$; Table 1, Fig. 4b). In these plots, we estimated the distance of edge influence to be approximately 90 m, based on predicted probabilities of the logistic model within plots (63-115 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 edge (power covariance; d_{nd} : $F_{1,9} = 14.3$, $P = 0.004$; d_{nnd} : $F_{1,9} = 6.2$, $P = 0.035$; Table 1, Fig. 4c). In double-edge plots, the estimated distance of edge influence ranged from approximately 100 m to 118 m, depending the next-nearest distance from edge (34-90 m and > 150 m using upper and lower confidence limits of predicted values, respectively). Overall, the estimated intercept was lower and the slopes were less in double-edge plots than in single-edge plots, yet slopes for d_{nd} and d_{nnd} were similar within double-edge plots (Table 1).

Habitat structure

The first three principal components explained 64% of the variation in habitat variables measured (Table 2). The first principal component reflected a total vegetation cover and litter cover gradient, the second reflected primarily a vegetation height/density gradient, and the third reflected a grass/forb composition gradient. Overall, there was weak evidence for PC2 differing between single edge (-0.10 ± 0.29) and double-edge plots (0.09 ± 0.29 ; $F_{1,9} = 3.57$, $P = 0.092$), but no evidence for the other principal components differing between plots ($F_{1,9} \leq 0.60$, $P \geq 0.46$). Within single-edge plots, there was weak evidence for

PC2 (vegetation height and vertical density) decreasing as a function of distance from edge (Tables 3, 4), but no evidence for other aspects of habitat structure changing as a function of distance from edge. In double-edge plots, there was no evidence for habitat structure changing as a function of distances from nearest and next-nearest edges (Tables 3, 5).

Landscape models

Physical characteristics of neutral landscapes varied in predictable ways (Table 6, Fig. 5). Increased fragmentation resulted in smaller patches and a greater proportion of habitat near all edges within patches. In particular, the proportion of habitat within 50 m of the nearest and the next-nearest edge was much greater in simple random landscapes and landscapes with $D = 3$ (Table 6). At the patch level, the proportion of habitat within 50 m of each edge was high for all patch sizes in highly fragmented landscapes ($SR, D = 3$), but in less fragmented landscapes ($D = 2.5, 2$) the proportion of habitat near edges declined precipitously as a function of patch size (Fig. 5).

At the landscape level, predicted relative densities (individuals/cell) based on next-nearest distance models were lower than relative densities based on nearest-distance models only in the most fragmented landscapes, but this tended to occur regardless of the amount of habitat in the landscape (Fig. 6). With less fragmented landscapes, edge effects were still important, predicting lower relative densities than estimates derived from the null model, but simple nearest distance models were comparable to next-nearest distance models (Fig. 6).

At the patch level, relative densities (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 (i.e., simple random and landscapes with $D = 3$; Fig. 7). In less fragmented landscapes, next-nearest distance models predicted slightly lower relative densities for patch sizes approximately < 75 ha. Only in very large patches (>150 ha) did predictions from edge effect models approach predictions from null models (Fig. 7).

DISCUSSION

Edge effects can be exacerbated when multiple edges converge and these effects could have strong impacts on bird distribution in highly fragmented landscapes. We documented that multiple edges influenced both the magnitude and extent of the edge effect on Bobolink distribution, based on comparisons of observed effects in single- and double-

edge plots. These results provide the first comprehensive sketch of the nature of multiple edge effects and their potential implications in fragmented landscapes. Coupled with other important factors, such as the type of edge (Fletcher and Koford 2003) and landscape structure (Bakker et al. 2002), multiple edge effects might help explain regional variation of edge effects and fragmentation sensitivity within species (Johnson and Igl 2001). Yet, multiple edges might not only have negative effects on processes, as shown here, but could also have positive effects, particularly for species attracted to edges. For instance, Red-winged Blackbirds (*Agelaius phoeniceus*), a species that has been documented to exhibit positive associations with edges (Fletcher and Koford 2002), was more likely to occur in double-edge plots than single-edge plots in our study area (Fig. 8), though this pattern was weaker than observed patterns in Bobolinks and was more closely tied with local habitat structure (edge type: $F_{2,12} = 3.37$, $P = 0.069$; single-edge plot: nearest distance, $F_{1,9} = 2.45$, $P = 0.152$; double-edge plot: nearest-distance, $F_{1,9} = 6.33$, $P = 0.033$; next-nearest distance, $F_{1,9} = 1.40$, $P = 0.267$).

Potential mechanisms for multiple edge effects

Although edges affected Bobolink distribution, we did not document the processes that underlie these patterns. Some potential mechanisms for edges influencing spatial distributions include habitat structure, interspecific competition, predator-escape strategies, and site fidelity. Patch characteristics were unlikely to be responsible for the observed patterns because our paired design (i.e., single and double edge plots were paired within patches) accounted for this source of variability. In addition, habitat structure did not change strongly near edges (see also Fletcher and Koford 2003), but it is possible that some unidentified gradient, such as species composition, did occur near edges. 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 due to 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 edges (Johnson and

Temple 1990, Paton 1994), then Bobolinks may have lower site fidelity near edges than in the interior of grasslands. In a similar area of northern Iowa, Kuehl and 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 further reduce nesting success near multiple edges. In addition, pairing success can be lower near edges (Van Horn et al. 1995) and multiple edges could further reduce this likelihood (R. J. Fletcher, Jr., *unpubl. data*). Clearly, information linking edge avoidance and fitness is needed to understand the demographic consequences of these responses for species in fragmented landscapes.

Linking edge effects to patch and landscape patterns

When scaling edge effects to fragmented landscapes, two primary patterns emerged. First, models incorporating multiple distance measures tended to predict lower landscape-level densities in only the most fragmented landscapes, which was directly related to the proportion of habitat located near edges. Second, models incorporating edge effects predicted much lower densities than models that did not assume an edge effect. This latter point was not surprising. What was surprising was the extent to which this effect emerged as a function of patch size, in which predicted densities only converged on null model predictions in very large patches (>150 ha). 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), tending to be less abundant or less likely to occur in relatively small patches, on the order of 30-60 ha (Herkert 1994, Helzer and Jelinski 1999). These models suggest that observed edge effects occurring within approximately 90-120 m from edges can potentially explain lower densities in large patches within fragmented landscapes. Indeed, Helzer and Jelinski (1999) found that perimeter-area ratios, which reflect the relative proportion of edge within patches, were better at predicting grassland bird occurrence than habitat area.

Although processes of edge avoidance might operate distinctly from processes of area sensitivity (Villard 1998), edge avoidance could nonetheless be a driving mechanism explaining area sensitivity. Bollinger and Switzer (2002) recently addressed this issue by modeling edge avoidance processes to determine if these processes could explain area-

sensitive distributions. Results of their model suggested that edge avoidance could not explain patch size patterns of density; however their model included strong constraints on the process of settlement (e.g., individuals could not settle within 75 m of another individual and yet edge avoidance only occurred within 50 m of an edge). Moreover, in their model nest placement was not subject to minimum territory size requirements, which would increase predicted densities in small patches. Although we did not model the process of edge avoidance, we did scale observed patterns of edge avoidance and these patterns indeed manifested in strong patterns and the patch and landscape scale.

Our modeling approach allowed for insight into some potential implications of edge effects on patch-level and landscape-level dynamics, yet this approach was not intended to estimate real densities in fragmented landscapes. Many complexities arise when scaling up local patterns and processes to heterogeneous landscapes (e.g., Wiens et al. 1993). Moreover, neutral landscapes are not intended to mimic real landscapes but instead provide a rigorous and objective approach for addressing different fragmentation scenarios (With and King 1997). When addressing implications of multiple edge effects, we only modeled effects arising from two edges within patches because our empirical data was limited to information on ≤ 2 edges, yet these effects might be even stronger if >2 edges are incorporated into the modeling process. Nonetheless, our approach does illustrate some possible large-scale consequences of edge effects.

Conservation implications

Ultimately, incorporating multiple edges into a general framework on edge effects will increase our understanding of the consequences of habitat fragmentation and may help to determine if edge effects operate on relatively large scales (Laurance 2000). Future modeling attempts and empirical investigations that deal with relatively small patches should incorporate multiple edge effects and compare predictions with and without this added complexity. In addition, modeling could provide a theoretical framework to understand when multiple edge effects should be important. For example, we found that multiple edge effects are likely important only in severely fragmented landscapes and in patches less than 150 ha in size. These models could be validated in real landscapes by predicting distributions and validating these predicted distributions using surveys across landscapes.

These results and other recent research on fragmentation in grassland birds suggest that edge effects are indeed important to bird distribution (Johnson and Temple 1986, Bock et al. 1999, Hughes et al. 1999, Bakker et al. 2002), and are perhaps more influential than the composition of the landscape (Bajema and Lima 2001, Fletcher and Koford 2002). Conservation strategies that reduce the proportion of edge in the landscape (e.g., removing hedgerows, adding contiguous block habitat) will likely have positive impacts on both grassland bird distribution and reproductive success (Johnson and Temple 1990). Although agriculture edges may be less detrimental than other edge types in grasslands (Winter et al. 2000, Fletcher and Koford 2003; but see Fletcher and Koford 2002), these results suggest that even these edges can have negative consequences, particularly in highly fragmented areas where multiple edges may interact. As we continue to develop our understanding of habitat fragmentation, it will be interesting and informative to determine the generality of multiple edge effects on other processes and their potential contribution to the widespread patch size effects observed in fragmented landscapes.

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TABLE 1. Logit parameter estimates from geostatistical logistic models describing Bobolink occurrence near one edge (single edge) or near two edges (double edge) in northern Iowa, 2001-2002.

Plot type	Intercept		Nearest distance		Next-nearest distance		Goodness-of-fit†	
	β	SE	β	SE	β	SE	χ^2	P
Single edge	-2.7238	0.2931	0.0158	0.0026			617.9	0.964
Double edge	-4.3354	0.4981	0.0128	0.0034	0.0128	0.0052	430.8	1.000

†Based on deviance of each model, which is approximately Chi-squared distributed, with $N - p$ degrees of freedom (single-edge plots: $df = 683$; double-edge plots: $df = 718$); N is the number of observations and p is the number of fixed-effects parameters in the model (Littell et al. 1996:)

TABLE 2. Principal components analysis with varimax rotation of habitat characteristics measured in grasslands near one edge (single-edge plots) and near two edges (double-edge plots), northern Iowa, 2001-2002. Bold type highlights PC scores $> |0.40|$.

Output of analysis	PC1	PC2	PC3
Eigenvalue	2.9	2.0	1.4
Percentage explained	29.0	20.0	13.8
Cumulative percentage explained	29.0	49.0	62.8
Eigenvectors:			
Vegetation height (cm)	-0.231	0.768	-0.212
Litter depth (cm)	0.282	0.209	-0.139
Vertical density (dm)	-0.287	0.830	0.047
Canopy Cover (%):			
Total vegetation	-0.896	0.303	0.019
Grass cover	-0.313	0.274	-0.878
Forb cover	-0.352	0.109	0.900
Standing dead vegetation	-0.196	-0.432	-0.015
Litter	0.937	-0.174	-0.016
Bare ground	0.069	-0.265	0.019

TABLE 3. Geostatistical mixed models describing habitat structure, based on three principal components derived from vegetation characteristics, as a function of distance from edges near one edge (single-edge plots) or near two edges (double-edge plots) in northern Iowa, 2001-2002.

Parameter	Single edge				Double edge			
	β	SE	<i>F</i>	<i>P</i>	β	SE	<i>F</i>	<i>P</i>
<i>PC1: Total/litter cover</i>								
Intercept	-0.0296	0.1896			-0.0903	0.2115		
Nearest distance	-0.0002	0.0008	0.05	0.83	0.0018	0.0017	1.03	0.34
Next-nearest distance					0.0007	0.0013	0.30	0.60
<i>PC2: Vertical density</i>								
Intercept	0.0829	0.3083			0.3108	0.2904		
Nearest distance	-0.0025	0.0013	3.83	0.08	-0.0010	0.0024	0.20	0.67
Next-nearest distance					-0.0017	0.0015	1.28	0.29
<i>PC3: Grass/forb cover</i>								
Intercept	-0.0573	0.2811			-0.2911	0.2584		
Nearest distance	0.0010	0.0007	1.63	0.23	0.0026	0.0018	2.12	0.18
Next-nearest distance					0.0012	0.0008	2.02	0.19

TABLE 4. Estimates of habitat structure (SE in parentheses), based on three principal components derived from vegetation characteristics, as a function of distance from the nearest edge in single-edge plots, northern Iowa, 2001-2002.

Principal component	Nearest distance from edge (m)					
	0-25	26-50	51-75	76-100	101-125	126-150
PC1: <i>Total/litter cover</i>	0.03 (0.19)	0.02 (0.21)	-0.10 (0.22)	-0.12 (0.24)	-0.05 (0.18)	0.00 (0.13)
PC2: <i>Vertical density</i>	0.09 (0.21)	-0.05 (0.22)	-0.14 (0.23)	-0.15 (0.21)	-0.16 (0.21)	-0.24 (0.21)
PC3: <i>Grass/forb cover</i>	-0.11 (0.27)	0.12 (0.30)	-0.06 (0.27)	-0.03 (0.29)	0.03 (0.31)	0.13 (0.26)

TABLE 5. Estimates of habitat structure (SE in parentheses), based on three principal components derived from vegetation characteristics, as a function of distances from nearest and next-nearest edges in double-edge plots, northern Iowa, 2001-2002.

Next-nearest distance from edge (m)	Nearest distance from edge (m)					
	0-25	26-50	51-75	76-100	101-125	126-150
<i>PC1: Total/litter cover</i>						
0-25	-0.19 (0.25)					
26-50	0.02 (0.23)	0.09 (0.30)				
51-75	-0.16 (0.30)	-0.07 (0.31)	0.18 (0.32)			
76-100	0.09 (0.26)	0.16 (0.27)	0.13 (0.28)	-0.27 (0.27)		
101-125	-0.13 (0.22)	0.12 (0.30)	0.03 (0.30)	0.12 (0.22)	0.06 (0.28)	
126-150	-0.03 (0.26)	0.26 (0.28)	-0.05 (0.20)	0.19 (0.28)	0.28 (0.31)	0.46 (0.26)
<i>PC2: Vertical density</i>						
0-25	0.62 (0.20)					
26-50	0.89 (0.28)	0.79 (0.25)				
51-75	0.78 (0.25)	1.06 (0.33)	0.72 (0.23)			
76-100	0.60 (0.19)	0.93 (0.29)	0.85 (0.27)	1.00 (0.32)		
101-125	0.73 (0.23)	0.85 (0.27)	0.92 (0.29)	0.82 (0.26)	1.14 (0.36)	

TABLE 5. (continued)

Next-nearest distance from edge (m)	Nearest distance from edge (m)					
	0-25	26-50	51-75	76-100	101-125	126-150
126-150	0.70 (0.22)	0.72 (0.23)	0.91 (0.29)	0.79 (0.25)	0.87 (0.28)	0.96 (0.30)
<i>PC3: Grass/forb cover</i>						
0-25	-0.27 (0.25)					
26-50	-0.28 (0.24)	0.06 (0.21)				
51-75	-0.16 (0.33)	-0.13 (0.28)	0.09 (0.30)			
76-100	-0.06 (0.31)	-0.06 (0.29)	-0.01 (0.32)	0.05 (0.33)		
101-125	-0.29 (0.25)	0.13 (0.34)	0.03 (0.31)	0.05 (0.29)	0.08 (0.24)	
126-150	-0.23 (0.29)	0.13 (0.29)	0.11 (0.24)	0.04 (0.28)	0.17 (0.25)	0.06 (0.29)

TABLE 6. Some physical characteristics of neutral landscapes (generated by program RULE; Gardner 1999) used in linking multiple edge effects to fragmented landscapes. Ten replicate landscapes were generated for each landscape type ($n = 120$ landscapes).

Landscape								
percent composition	Fragmen- tation†	Number of patches	Patch size		Proportion near edges‡			
			Mean	Maximum	Edge 1	Edge 2	Edge 3	Edge 4
10	SR	4703.6	0.1	0.6	1.00	1.00	1.00	0.96
10	3.0	1621.8	0.2	81.5	0.96	0.85	0.68	0.41
10	2.5	220.4	1.5	347.4	0.51	0.32	0.17	0.06
10	2.0	10.8	29.8	411.8	0.15	0.07	0.01	0.00
30	SR	7551.5	0.2	2.9	1.00	1.00	0.96	0.69
30	3.0	2226.5	0.5	311.3	0.86	0.67	0.45	0.21
30	2.5	379.5	2.9	1046.3	0.32	0.18	0.09	0.03
30	2.0	28.3	36.6	1136.6	0.09	0.04	0.01	0.00
50	SR	3906.0	0.5	30.7	1.00	0.95	0.74	0.32
50	3.0	1681.9	1.1	1400.1	0.72	0.48	0.27	0.11
50	2.5	396.7	4.7	1957.8	0.24	0.13	0.06	0.02
50	2.0	21.4	84.2	2042.8	0.06	0.03	0.01	0.00

†SR = simple random (most fragmented); 3, 2.5, and 2 refer to the fractal dimension of the landscape, in which 3 is the least clumped, or most fragmented, and 2 is the most clumped, or least fragmented (see Fig. 2).

‡Proportion of 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.

Figure 1. A) A point within a patch (gray circle) can be described by four distances to edge, with d_1 being the nearest distance to an edge and d_4 being the furthest distance (based on distances in orthogonal directions). B) A hypothetical negative exponential edge effect function, and corresponding independent effects (e_i) occurring from each distance to edge, as represented in part A. C) The intensity of an edge effect within a rectangular patch derived from a negative exponential function, as described in part B, based on the nearest edge (left diagram) and on an additive effect from each edge in the patch (right diagram). Note that the shading in each diagram is based on the same scale, such that the intensity of the additive edge effect is greater in all portions of the patch than the effect estimated from the nearest edge. D) Relationship of edge effects per unit area within a patch as a function of patch size (in this case, all patches were square) for a negative exponential edge function based on the nearest edge and on an additive edge effect.

Figure 2. Study sites and survey plot design used for estimating the influence of multiple edges on Bobolink distribution, northern Iowa, 2001-2002. In each site, there were two survey plots (150×150 m): single-edge and double-edge plots. Observations were grouped into 25×25 m grid cells, which allowed for nearest distance and next-nearest distance measures in double-edge plots.

Figure 3. Neutral landscapes used in linking multiple edge effects based on Bobolink distributions to fragmented landscapes. Landscapes were generated using program RULE (Gardner 1999). Suitable habitat is denoted in white, unsuitable habitat (matrix) is denoted in black. Fragmentation was varied by changing D , the fractal dimension of the landscape, and comparing these fractal landscapes with simple random (SR) landscapes. For each landscape type, 10 replicate landscapes were generated and used in simulation modeling.

Figure 4. Estimated probability of occurrence (per grid cell within plots) for male Bobolinks breeding in double edge, single edge, and interior plots in northern Iowa, 2001-2002. A) The mean probability (\pm SE) of occurrence per cell as a function of plot type, B) the probability of occurrence (mean, confidence limits) as a function of distance from edge in single-edge

plots, and C) the probability of occurrence (mean, confidence limits) as a function of nearest distance and next-nearest distances from edges in double-edge plots. The intersection of the lower confidence limit of the interior estimate and the models within single and double-edge plots, shown in A and B, can approximate the distance of edge influence (DEI; sensu Laurance et al. 1998, Harper and MacDonald 2001), resulting in an approximate 90 m DEI for single-edge plots (63-115 m using upper and lower confidence limits of predicted values, respectively), and 100-118 m for double-edge plots (34-90 m and >150 m using upper and lower confidence limits of predicted values, respectively).

Figure 5. The proportion of habitat located near edges as a function of patch size for neutral landscapes used in scaling local Bobolink distributions to fragmented landscapes. Edge 1 is the proportion of habitat located within 50 m of the nearest edge, edge 2 is the proportion of habitat located within 50 m of the next-nearest edge, and so on. D denotes the fractal dimension of the landscape, while SR denotes simple random landscapes.

Figure 6. The predicted landscape-level relative density (mean individuals/cell, \pm SE) of male Bobolinks for three models as a function of the amount of habitat and degree of fragmentation in neutral 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). D denotes the fractal dimension of the landscape, while SR denotes simple random landscapes.

Figure 7. The predicted patch-level relative density (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 neutral 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). D denotes the fractal dimension of the landscape, while SR denotes simple random landscapes. Circles without error bars represent estimates from landscape types with only one patch of a given size category.

Figure 8. Estimated probability of occurrence (per grid cell within plots) for male Red-winged Blackbirds breeding in double edge, single edge, and interior plots in northern Iowa, 2001-2002. A) The mean probability (\pm SE) of occurrence per cell as a function of plot type, B) the probability of occurrence (mean, confidence limits) as a function of distance from edge in single-edge plots, and C) the probability of occurrence (mean, confidence limits) as a function of nearest distance and next-nearest distances from edges in double-edge plots. Note that the y-axis in part C is in the opposite direction than in Figure 4C to better interpret the model.

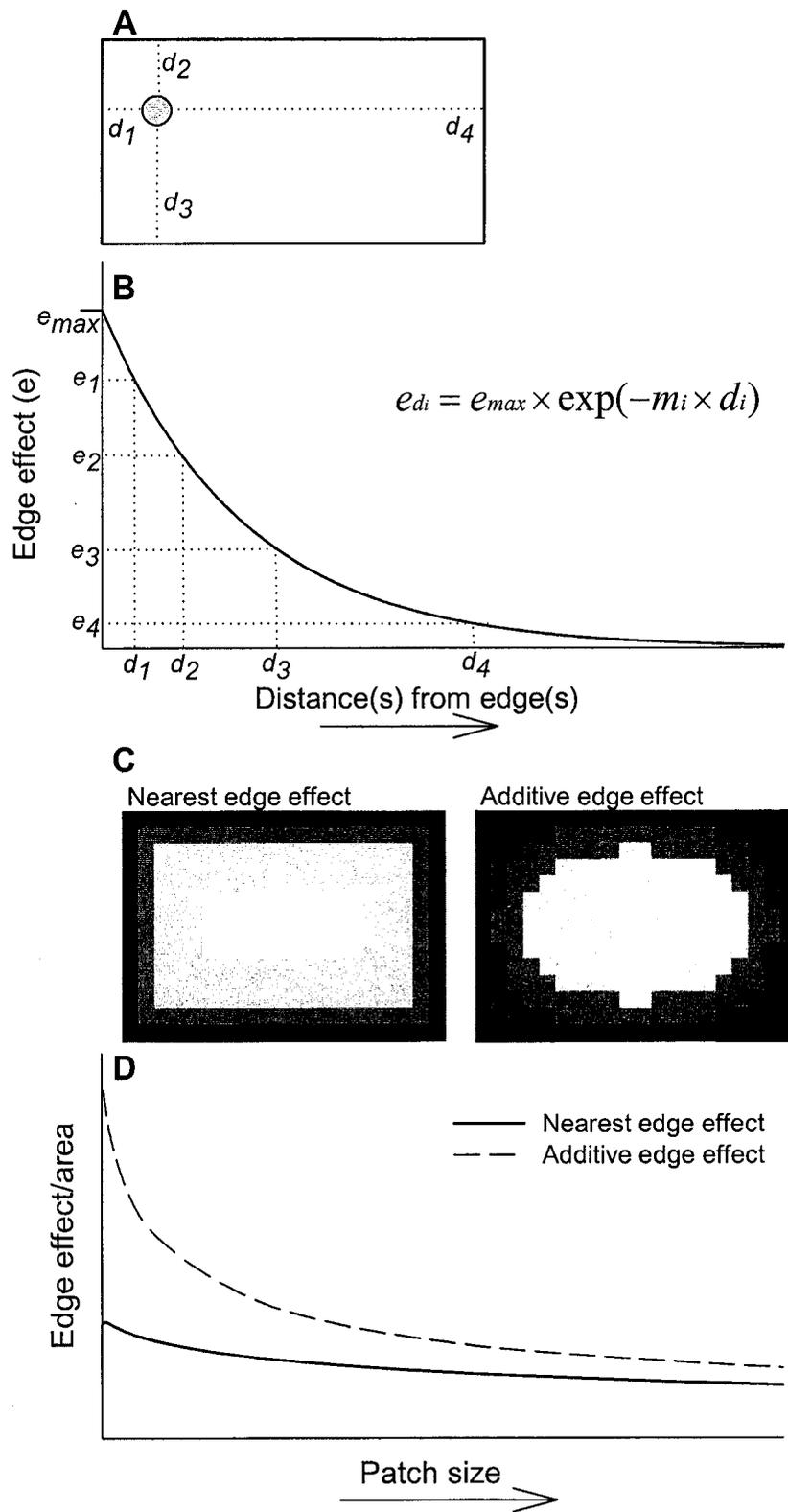


Figure 1

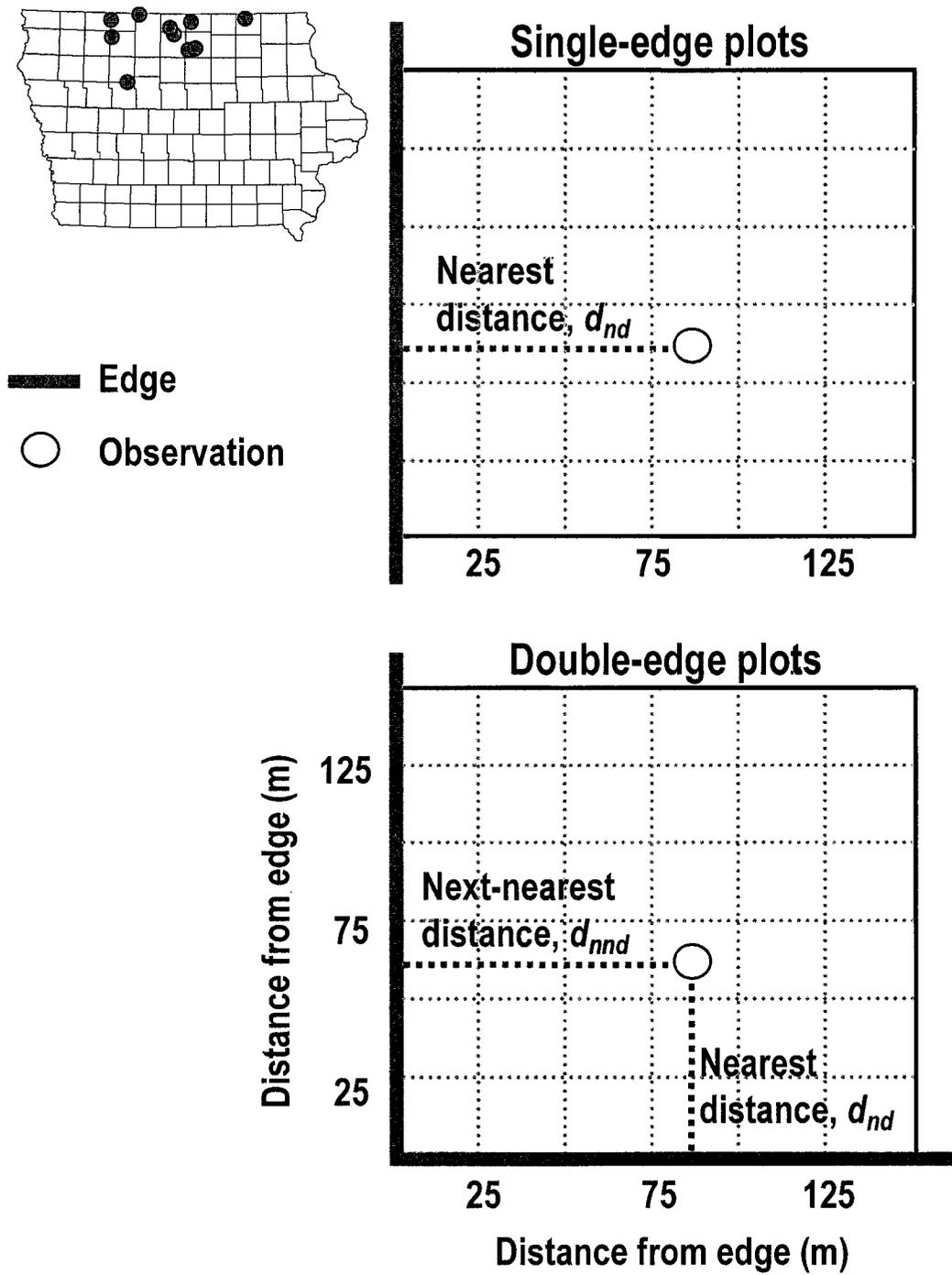


Figure 2

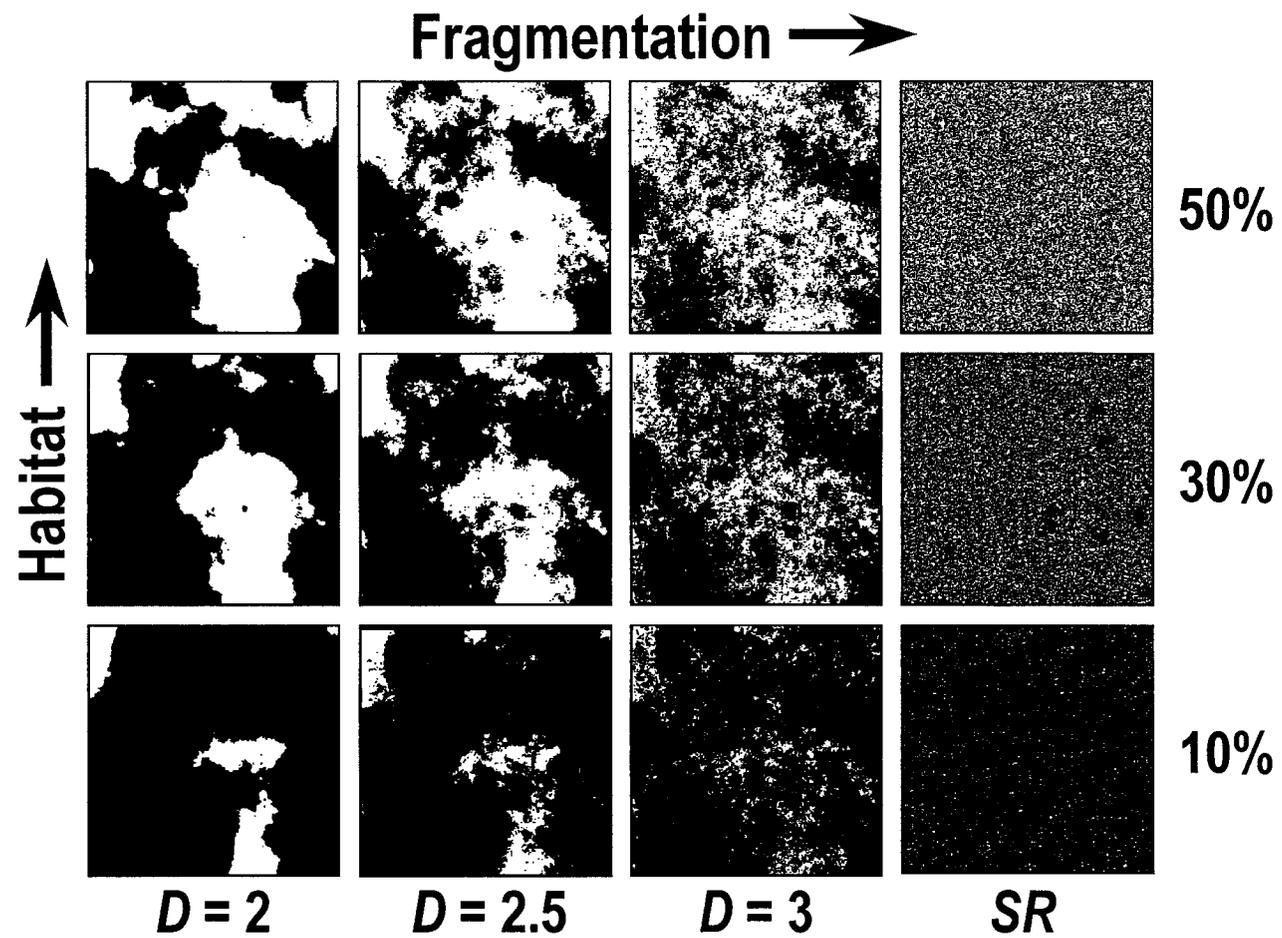


Figure 3

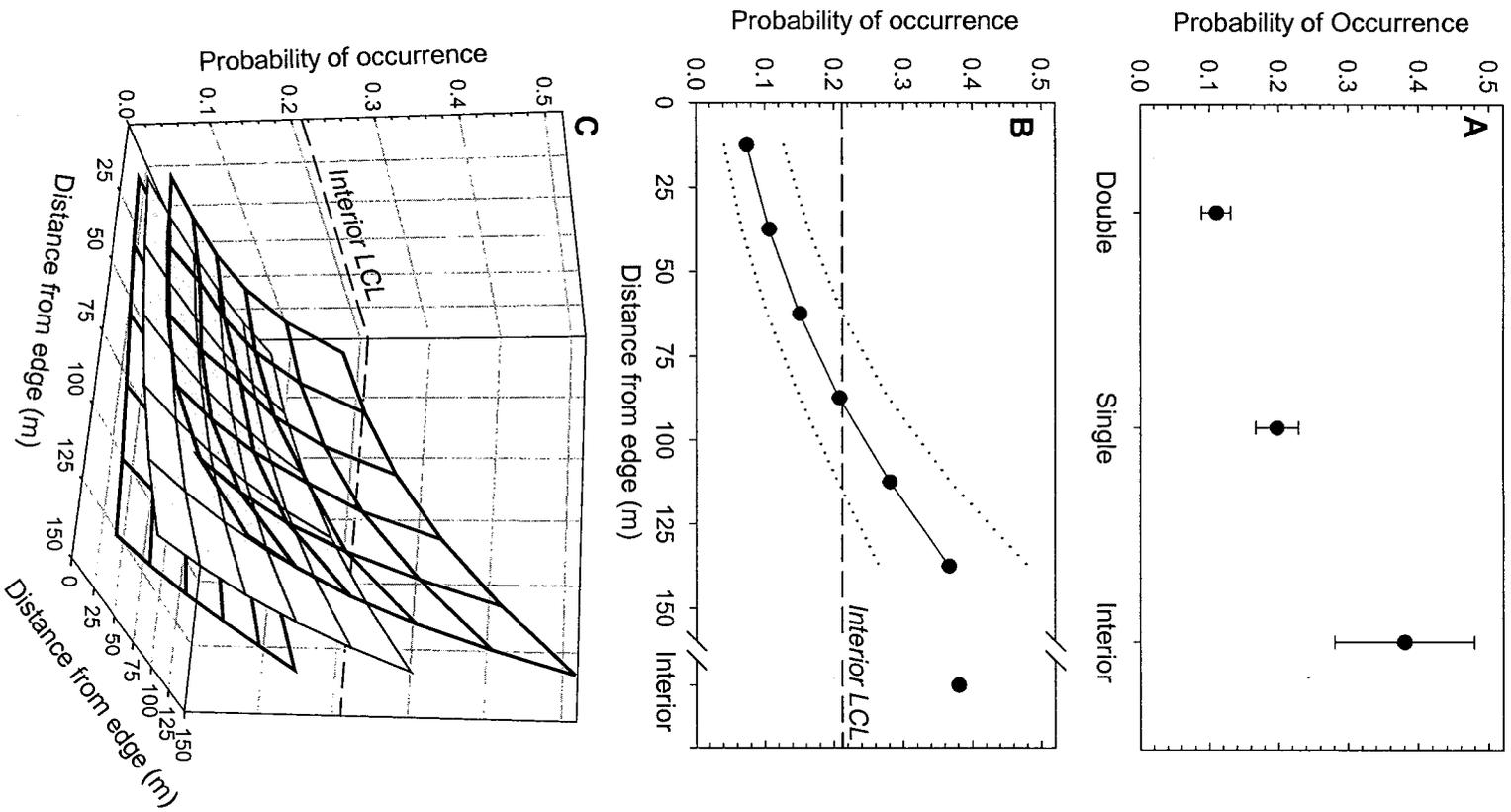


Figure 4

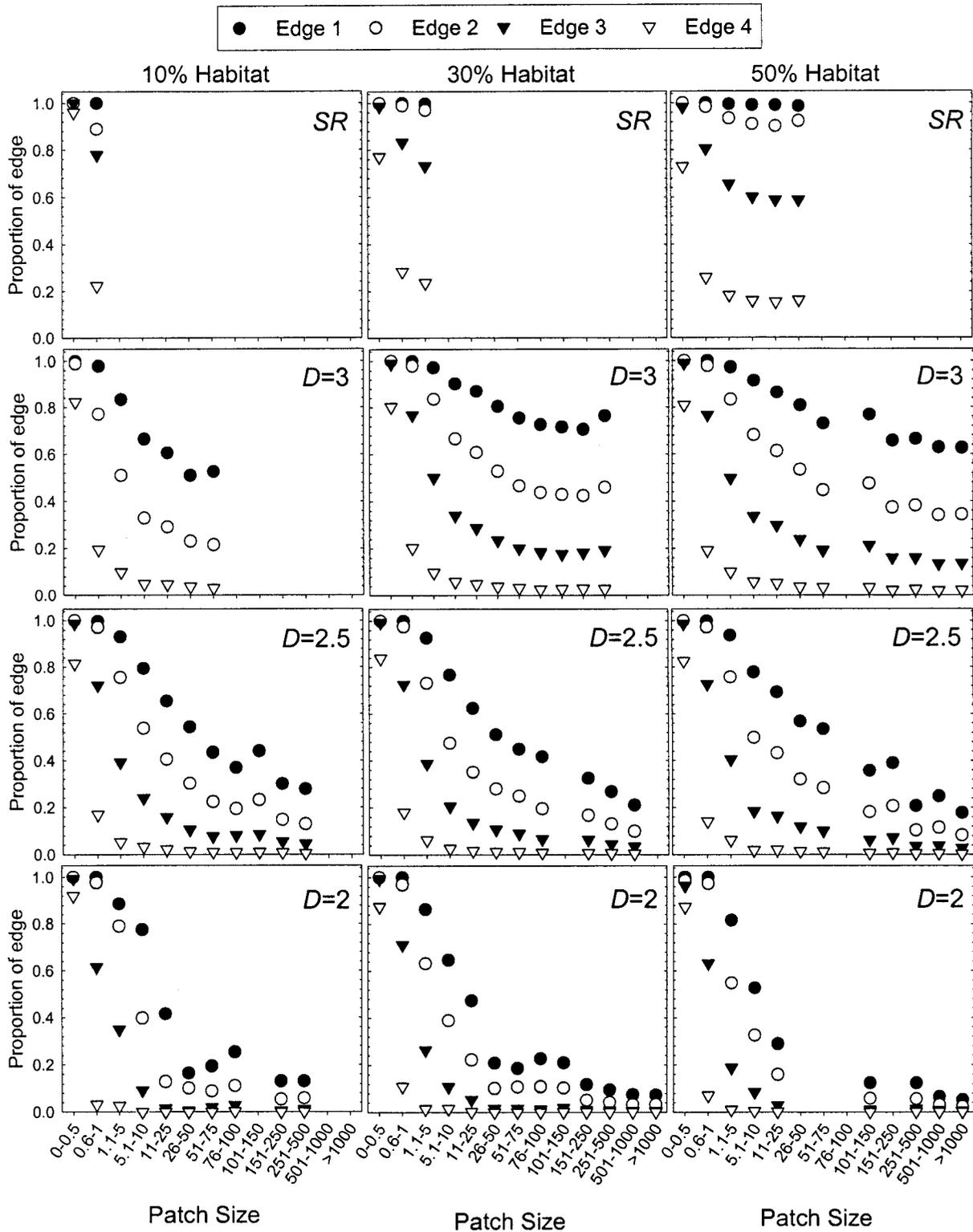


Figure 5

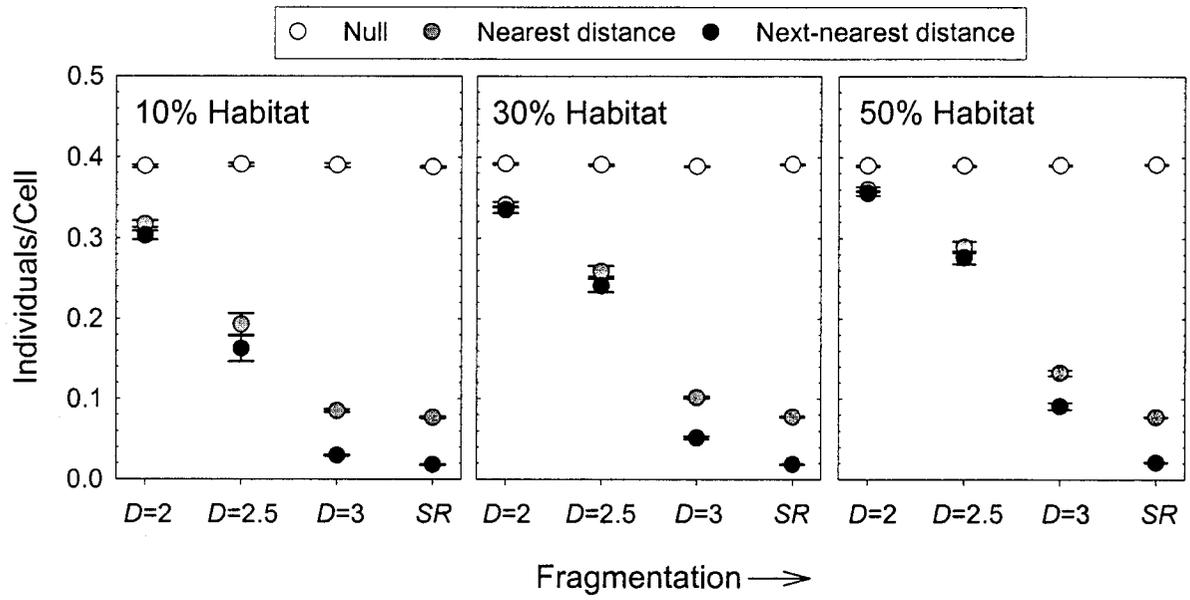


Figure 6

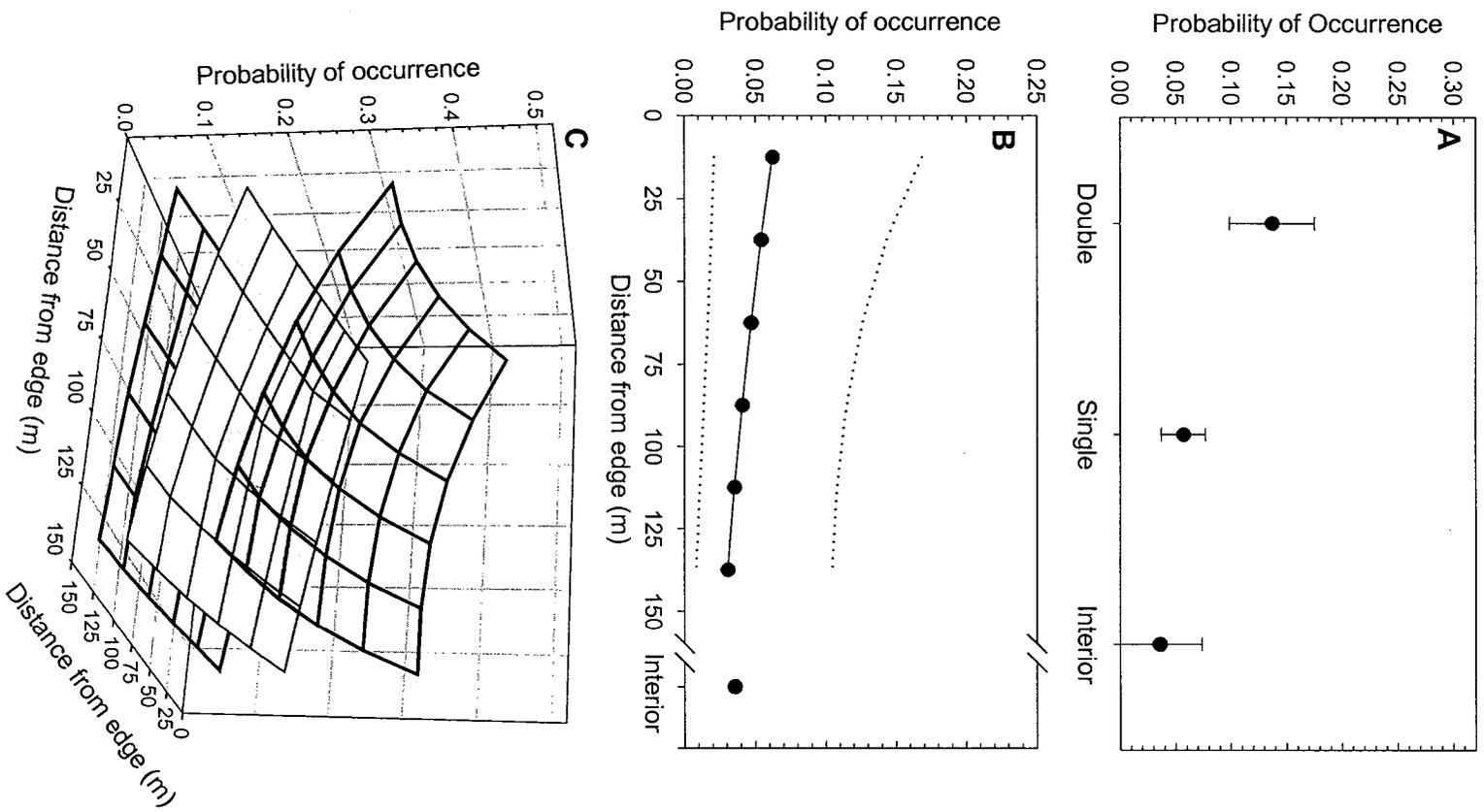


Figure 8

CHAPTER 4. HABITAT AND LANDSCAPE ASSOCIATIONS OF BREEDING BIRDS IN NATIVE AND RESTORED GRASSLANDS

A paper published in *The Journal of Wildlife Management*

Robert J. Fletcher, Jr., and Rolf R. Koford

Abstract: In the midwestern United States, less than 1 % of the original tallgrass prairie ecosystem remains. State and federal agencies have responded to this habitat loss with programs and land acquisition that have increased the amount of grassland in the landscape by restoring grassland from other land use practices. We assessed the effects of habitat restoration and the relative contribution of local habitat and landscape factors on breeding grassland birds in northern Iowa. During the 1999 and 2000 breeding seasons, we surveyed grassland birds in 10 tallgrass prairies and 10 restored grasslands that contained a wide diversity of habitat and landscape conditions. Densities of common bird species were similar between habitat types, except for grasshopper sparrows (*Ammodramus savannarum*) and savannah sparrows (*Passerculus sandwichensis*), both of which had higher densities in restored grasslands. Species richness of breeding birds was similar between habitat types. Habitat structure was different in prairies and restored grasslands; restored grasslands had less total vegetation cover and more bare ground. A nested, multiscale analysis indicated that habitat structure explained some variation in species richness and bird density of all common species, yet landscape structure improved models for species richness and for density of 4 of 8 species considered. Edge density metrics were the most common variables entering into landscape models; most species had lower densities in landscapes with high edge density. Our results indicate that restored grassland habitats contain generally similar bird communities to native prairie habitats in northern Iowa, suggesting that restored grasslands may provide similar habitat suitability for most grassland birds. In addition, both local habitat and landscape factors can be important for managing breeding grassland birds.

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Key Words: bird density, edge effects, grassland birds, habitat relationships, Iowa, landscape fragmentation, Prairie Pothole Region, restoration, tallgrass prairie

Grassland birds have experienced consistent widespread declines throughout the continental United States (Herkert 1995, Igl and Johnson 1997, Peterjohn and Sauer 1999). These declines are often attributed to severe habitat loss and fragmentation (Herkert et al. 1996). In the Midwest, over 99 % of the tallgrass prairie ecosystem has been converted to agricultural land, hayfields, and pastures during the past 2 centuries (Samson and Knopf 1994). In Iowa, for example, tallgrass prairie occupied more than 79 % of the state before settlement, yet now less than 0.1 % remains (Smith 1998). To conserve grassland communities, restoration must occur and must provide adequate resources needed by wildlife communities. Understanding processes affecting grassland bird communities will improve efforts to restore habitat for declining bird populations.

Many factors can influence habitat use of breeding migratory birds. Relationships between breeding bird abundance and local vegetation structure (habitat hereafter) have long been documented in a variety of grassland systems (Wiens 1969, Whitmore 1979, Rotenberry and Wiens 1980, Maurer 1986, Herkert 1994, Delisle and Savidge 1997). These relationships are generally coupled with nesting requirements and nesting substrates of grassland birds. More recently, ecologists have been interested in how patch attributes can influence grassland birds (e.g., Vickery et al. 1994, Delisle and Savidge 1996, Helzer and Jelinski 1999, Winter and Faaborg 1999). There is growing evidence that many species of grassland birds are area sensitive, being either less likely to occur or less abundant in small patches (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999, Winter and Faaborg 1999, Johnson and Igl 2001; but see Horn et al. 2000). However, little research has documented the relative importance of landscape structure (i.e., the composition and spatial configuration of a landscape; McGarigal and McComb 1995) on habitat use by grassland birds (but see Hughes et al. 1999, Bajema and Lima 2001, Ribic and Sample 2001). Yet in forested systems, research suggests that landscape structure can be important for habitat use of many migratory bird species (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999).

Landscape structure can influence habitat use for several reasons. Landscape structure can affect movements (Crist et al. 1992), interactions among species (Kareiva 1987), and can influence exposure to novel environments (e.g., edges). Both island

biogeography and metapopulation theory incorporate area and isolation effects to help explain occurrence and diversity of species (MacArthur and Wilson 1967, Hanski 1998). Although the theory of island biogeography has been applied to understanding habitat use of grassland birds (e.g., Samson 1980), a landscape perspective on habitat fragmentation may be more appropriate (Wiens 1995). If landscape-level processes influence grassland birds, then the amount of grassland in the landscape might be an important component for habitat use by grassland birds (Ribic and Sample 2001; but see Bajema and Lima 2001). Other aspects of landscape structure can also affect habitat use by grassland birds. For example, Bock et al. (1999) found that many species of grassland birds were less abundant in areas near suburban edge habitat.

With restoration ongoing throughout the Midwest, an important concern is whether restored areas provide suitable habitat for breeding migratory birds. Restoration typically refers to altering an ecosystem back to its initial or original state (Meffe and Carroll 1994). However, grassland restoration efforts in the Midwest typically include planting areas with few species of grasses and forbs, some of which are not endemic to the area, which we will refer to as restored grasslands (*sensu* Johnson and Igl 2001). Some ecological functions are restored, but these areas do not achieve the diversity and structure of native prairies.

We had 2 primary objectives. First, we compared avian species richness and density in restored grasslands and tallgrass prairie remnants (prairies hereafter) in northern Iowa. We evaluated these comparisons to determine whether restored grasslands were providing suitable habitat, relative to native habitat, for breeding migratory birds in northern Iowa. We then proceeded to determine what factors might explain bird density and species richness in these areas. To this end, we tested the relative importance of local habitat and landscape structure on grassland bird density using a nested, multiscale analysis.

STUDY AREA

We surveyed all restored grasslands greater than 10 ha within the Eagle Lake Wetland Complex ($n = 10$), located in Hancock and Winnebago counties, north-central Iowa (Fig. 1). The Eagle Lake Wetland Complex encompassed approximately 162 km², and contained a complex of waterfowl production areas (WPAs) and wildlife management areas (WMAs)

situated in an agricultural landscape. Most restoration occurred in the past 15 years and is ongoing in the area. Grasslands were restored primarily from agricultural areas, using several restoration techniques and plantings. 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 grass/alfalfa (*Medicago sativa*) mixtures. Other common plants in restored areas included orchard grass (*Dactylis glomerata*), reed canary grass (*Phalaris arundinacea*), red clover (*Trifolium pratense*), and wild parsnip (*Pastinaca sativa*).

Because there were no substantial blocks of native grassland habitat within or surrounding the Eagle Lake Wetland Complex, we surveyed 10 of 12 publicly owned native tallgrass prairie remnants greater than 10 ha in northern Iowa (Fig. 1). These prairies have never been tilled or developed and were characterized by a high diversity of native warm-season grasses and forbs, with some sites containing ≥ 200 plant species. Common species included big bluestem, little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), switchgrass, goldenrod (*Solidago* spp.), sunflower (*Helianthus* spp.), and milkweed (*Asclepias* spp.).

Overall, area of surveyed prairies and restored grasslands were consistent between the 2 habitat types, but there was a wide range of sizes within habitat types (prairies: $\bar{x} = 54.1 \pm 7.7$ ha; range = 10.4-96.3 ha; restored grasslands: $\bar{x} = 57.1 \pm 11.0$ ha; range = 10.8-109.3 ha).

METHODS

Grassland Bird Surveys

Surveys were conducted during the 1999 and 2000 breeding seasons. Each site was surveyed during 3 periods in each year: 20 May-5 June, 6 June-22 June, and 23 June-6 July. We used 10-min, 50-m fixed-radius point counts for surveying breeding birds (Ralph et al. 1995). Point count locations were ≥ 150 m apart. Surveys were conducted between sunrise and 4 hr after sunrise, when breeding birds are most active. Surveys were not conducted during high wind velocities (≥ 20 km/hr) or during precipitation. Each year, 2 observers

conducted surveys, and each observer surveyed each site at least once. During surveys observers recorded all birds seen or heard, including how individuals were detected (by song, visual, or call), sex of individuals, and distances of birds from the center point. Distances to birds seen were estimated using a rangefinder.

Point count locations were determined using a Geographic Information System (GIS). A grid was layered over aerial photographs of each site, with each grid cell measuring 150 × 150 m. Each cell was considered a potential sampling unit (SU), with a potential point count location at the center of each cell. We only included grid cells that were primarily grassland habitat (i.e., cells >55 % grassland with point locations >95 % grassland). We stratified potential sampling units into geographic sections of similar area (e.g., northwest, northeast, southwest, and southeast areas of the field). Sites with 12 or more SUs were stratified into 4 sections, sites with 9-11 SUs were stratified into 3 sections, sites with 6-8 SUs were stratified into 2 sections, and sites with <6 SUs were not stratified. All sites had ≥3 SUs. During each survey period, we randomly selected 1 SU in each stratum to sample. We did not repeat any individual SUs. This method provided a random sampling design yet ensured that the entire range of variability was sampled within each site. Overall, we conducted 204 distinct point counts each year: 102 in prairies and 102 in restored grasslands. The same point count locations were sampled both years.

Habitat Measurements

Each year, habitat variables were measured in prairies and restored grasslands at all point count locations to compare the breeding bird density to habitat characteristics and determine if habitat structure was different between prairies and restored grasslands. Vegetation was measured once at each location between 25 June-23 July. Although we sampled only once during the breeding season, many grassland birds stay on their breeding territories throughout the season (Wiens 1973, Whitmore 1979), and other studies have demonstrated high correlations in vegetation structure between the beginning (early May) and the end of the breeding season (mid-July; e.g., Winter and Faaborg 1999).

For each point count location, we measured vegetation using a method similar to Best et al. (1997). We measured vegetation at 4 plots within each point count area: 1 at the center

of the point, and at 3 plots located at 0°, 120°, and 240° from the center, at distances of 30 m. At each sampling point, we quantified vertical density using a Robel pole (Robel et al. 1970), by taking visual obstruction readings at 4 m in each cardinal direction from a Robel pole at a height of 1 m. We measured maximum height of standing vegetation and litter depth at the location of the Robel pole. At each sampling point, we assessed canopy coverage using a Daubenmire quadrat (20 × 50 cm) based on non-overlapping percentages (Daubenmire 1959). Canopy coverage categories included: total (live + dead vegetation), grass, forb, standing dead vegetation, litter, and bare ground.

Landscape measurements

We used aerial photographs taken in 1998 or 1999 to quantify landscape structure surrounding the study sites. The resolution of these photographs ranged from 2-5 m. Each year we ground-truthed photographs to ascertain current land use practices. We digitized the photographs using a GIS and quantified land use patterns within a 1-km radius from the center of each site. A 1-km radius exceeded the boundaries of all sites, thereby estimating local landscape structure (see also Knick and Rotenberry 1995). We chose not to investigate patterns at multiple distance buffers (*sensu* Ribic and Sample 2001), because of strong correlations among land use for different buffer distances. Although many metrics can be estimated to describe landscape structure (McGarigal and Marks 1995), for analyses we only considered 2 types of metrics: landscape composition (percent land use) and edge density metrics (m of perimeter/ha of grassland). These metrics were included because both are amenable to management practices and can have biologically significant direct and indirect effects (Dunning et al. 1992). We included 3 compositional metrics: (1) percent perennial grassland (prairies, WMAs/WPAs, pastures, Conservation Reserve Program fields, and hayfields), (2) percent woodland, and (3) percent wetland vegetation. We considered our compositional metrics to be biologically important for the following reasons: (1) the percent of grassland in the landscape might be important because of potential target and rescue effects (Lomolino 1990, Gotelli 1991), (2) the percent of wetland vegetation in the landscape could be important for species that also use wetland habitat (e.g., sedge wren [*Cistothorus platensis*]), and (3) the percent woodland in the landscape could be important because of

negative associations of grassland birds with woodland areas (Hughes et al. 1999), often thought to be due to increased predation risk near woodlands (Lima and Valone 1991). We also quantified 4 edge density metrics that helped describe the shape and structure of grassland in the landscapes: (1) total grassland edge density, (2) grassland/agriculture edge density, (3) grassland/road edge density, and (4) grassland/woodland edge density. We included these metrics because many grassland birds tend to have lower densities near some types of edges (Bock et al. 1999, Hughes et al. 1999).

Statistical Analyses

We calculated bird density (number of males/ha) for common species using the software program DISTANCE (Buckland et al. 1993). DISTANCE uses distances from the center point to individuals for calculating detection functions based on probability density functions. Models are then parameterized to determine the best fit to actual data, based on Akaike's Information Criterion (AIC; Buckland et al. 1993:75-76). An important assumption of this technique is that all birds are detected on the center point of the survey. To maximize this likelihood, we included birds observed near the center point while the observer approached each survey point location. For analyses, we grouped distance estimates into 5 equal intervals (i.e., 0-10 m, 11-20 m, 21-30 m, 31-40 m, 41-50 m). For each species with >40 observations, we compared 5 types of models to determine the best estimate of the detection function (see Buckland et al. 1993:150). Density was estimated for each year and for both years combined using a global detection function across habitat types and years. Variance was assumed to have a Poisson distribution, and 95% confidence intervals were determined using log-normal bootstrap estimates of re-sampled point counts ($n = 1000$; Buckland et al. 1993:155-158). Significant differences in bird density were inferred based on non-overlapping 95 % confidence intervals.

For analyses of species richness patterns, we randomly selected 1 point per sampling period at each site to make comparisons (total of 3 per site) because increased sampling intensity can affect apparent patterns of species richness (Connor and McCoy 1979). Species richness was defined as the number of species observed in a field that was considered to breed in grassland habitats (i.e., species that nest on or near the ground in grasses or forbs).

Habitat and landscape structure were analyzed using mixed-model, repeated measures analysis of variance models (ANOVAs), with the habitat or landscape metric as the response variable, site as a random effect, habitat type (prairie or restored grassland) as the main explanatory variable, and year as the split-plot, repeated measure (Littell et al. 1996:88-92). Because there was no evidence for measurement date affecting habitat measurements for any variables ($|r| \leq 0.2$, $P > 0.21$), we did not detrend the data. Habitat and landscape variables were transformed as needed to improve normality and homogeneity of variances; however, untransformed means and errors are reported for ease of interpretation.

We used multiple linear regression to determine the most parsimonious model to explain habitat and landscape relationships, using density (males/ha) of birds per field as a response variable. Density was natural log transformed for all analyses to improve homogeneity of variances and normality. We chose a nested, multiscale framework for developing predictive models for the following reasons. Based on prior research, we predicted that habitat structure should explain variation in species richness and relative bird density (e.g., Maurer 1986, Herkert 1994). However, we were interested in whether or not landscape structure could explain additional variation in the models. To this end, we developed parsimonious habitat models and then determined if landscape structure improved the habitat models we developed. Model selection was based on AIC_c , which accounts for small sample sizes (Burnham and Anderson 1998:51). We initially ran models using all combinations of habitat variables (not including interactions), pooling across years. Although somewhat exploratory, we used this approach because there are many studies on grassland birds that have found different relationships with habitat variables (e.g., Herkert 1994, Delisle and Savidge 1997, Madden et al. 2000). We tested the best habitat model (i.e., model with the lowest AIC_c) for any evidence of year effects and determined parameter estimates using a mixed-model analysis, with site as a random effect and year as a split-plot repeated measure (Littell et al. 1996:88-92). We then tested the best habitat model against the best habitat + landscape model (i.e., model with lowest AIC_c containing habitat variables from the best habitat model plus landscape variables) by computing the AIC_c differences, ΔAIC_c , between the two models ($\Delta AIC_c = AIC_{ci} - \min AIC_c$; Burnham and Anderson

1998:47). We only included habitat and landscape variables that were not strongly correlated with each other ($|r| < 0.7$) to minimize problems of multicollinearity (Ribic and Sample 2001). For habitat variables, vegetation height and vertical density were positively correlated ($r = 0.76$, $P < 0.001$), percent total vegetation cover and percent litter were negatively correlated ($r = -0.88$, $P < 0.001$), and percent grass cover and percent forb cover were negatively correlated ($r = -0.72$, $P < 0.001$). For landscape variables, grassland/road edge density was negatively correlated with percent grassland in the landscape ($r = -0.70$, $P < 0.001$). From these pair-wise correlations, we eliminated the variable that was most correlated with other variables, resulting in the elimination of vegetation height, percent grass cover, and grassland/road edge density from modeling analyses. This resulted in 5 habitat and 6 landscape variables used in the analysis.

For habitat models and habitat + landscape models, we assessed model selection uncertainty and determined the relative importance of each explanatory variable by first computing the "Akaike weight" of each model considered (Burnham and Anderson 1998:124). We then determined the importance of each explanatory variable by summing the Akaike weight of every model considered that included the variable in the analysis (Burnham and Anderson 1998:178-179). These importance values provide a measure of variable selection uncertainty, not reflected in Akaike weights for specific models (Burnham and Anderson 1998:140-141).

RESULTS

Restored and Native Grasslands

In 1999, we observed 23 species in prairies and 25 in restored grasslands. In 2000, we observed 25 species in prairies and 24 in restored grasslands. When pooling years, we observed 30 species in prairies and 30 in restored grasslands, with 37 total species observed in both habitat types. Accordingly, species richness of breeding birds was quite similar between prairies ($\bar{x} = 6.70$, $SE = 0.29$) and restored grasslands ($\bar{x} = 6.50$; $SE = 0.30$; $F_{1, 18} = 0.15$; $P = 0.71$). There was no evidence for year affecting species richness ($F_{1, 18} = 0.15$; $P = 0.70$), nor any evidence for a year \times habitat type interaction ($F_{1, 18} = 0.19$; $P = 0.67$).

Overall, densities of common bird species were generally similar between the 2 habitat types (Table 1), with common yellowthroats (*Geothlypis trichas*) being the most dense species in prairies each year and bobolinks (*Dolichonyx oryzivorus*) being the most dense species in restored grasslands each year. Densities of grasshopper sparrows (*Ammodramus savannarum*) were higher in restored grasslands when years were pooled and tended to show similar (though not significant) trends each year. Densities of savannah sparrows (*Passerculus sandwichensis*) were higher in restored grasslands than in prairies each year and when years were pooled (Table 1). There was no evidence for year affecting density of any species. For most species, uniform model functions with no adjustments (American goldfinch [*Carduelis pinus*], grasshopper sparrow, dickcissel [*Spiza americana*], red-winged blackbird [*Agelaius phoeniceus*]), or 1 adjustment (cosine: savannah sparrow, bobolink; simple polynomial: sedge wren) were best at explaining detectability, indicating that detectability was high within our entire fixed radius. For common yellowthroats, the detection function was best estimated using a half-normal model function with 2 cosine adjustments, indicating that detectability declined toward the perimeter of our fixed-radius plots.

Habitat structure was different between the 2 habitat types, with the main distinguishing variable being the percent total vegetation cover (Table 2), which was less in restored grasslands than in prairies. Also, there was weak evidence for percent cover of forbs and litter depth being slightly greater in prairies than in restored grasslands, and percent cover of litter and bare ground being slightly greater in restored grasslands. There was some evidence of a year effect for grass cover ($F_{1, 18} = 7.72$; $P = 0.01$), vertical density ($F_{1, 18} = 5.37$; $P = 0.03$), and litter depth ($F_{1, 18} = 5.93$; $P = 0.03$), but no evidence of year effects for other variables ($F_{1, 18} \leq 3.28$; $P > 0.05$) or year \times habitat type interactions ($F_{1, 18} \leq 2.63$; $P \geq 0.12$).

Overall, landscape structure was similar between prairies and restored grasslands (Table 2), but there was some evidence for grassland/woodland edge density being slightly greater in landscapes surrounding restored grasslands. For all landscape variables, there was

no evidence of year effects ($F_{1, 18} \leq 1.58$; $P \geq 0.22$) or year \times habitat type interactions ($F_{1, 18} \leq 2.66$; $P \geq 0.12$).

Habitat and Landscape Effects

Habitat models explained at least some variation (R^2 range: 0.06-0.40) in species richness and density for all species considered, though models for some species were weak (Table 3). The relative contribution of habitat variables differed among species, with percent total cover and vertical density most frequently contributing to the variance explained in habitat models (Tables 3, 4). Overall, there was no evidence for year effects in the habitat models for any species ($F_{1, 16-18} \leq 2.23$; $P \geq 0.15$).

Including landscape metrics substantially improved models ($\Delta AIC_c > 2$) for species richness and for densities of grasshopper sparrows, dickcissels, bobolinks, and red-winged blackbirds (Table 3). For sedge wrens and savannah sparrows, habitat + landscape models were strong competitors to habitat only models ($\Delta AIC_c < 0.10$). The relative contribution of landscape variables differed among species, with edge density metrics most frequently contributing to the additional variance explained in habitat + landscape models (Tables 3, 5). Overall, most species were negatively associated with edge density metrics and positively associated with percent grassland in the landscape (Table 5).

DISCUSSION

Restored and Native Grasslands

Both species richness and densities of common grassland birds were generally similar in restored grasslands and tallgrass prairies. However, 2 of the 3 common ground-nesting birds, grasshopper and savannah sparrows, had higher densities in restored grasslands. Both species were negatively correlated with percent total vegetation cover in habitat models, which was less in restored grasslands. These species use relatively open habitat for breeding (Wiens 1973) compared to other common species in our study area.

Overall, densities of grassland birds were high in both prairies and restored grasslands. Few studies have quantified bird density in grasslands using rigorous techniques that include estimating detection functions (but see Bollinger et al. 1988, Koford 1999, and Rotella et al. 1999). Our estimates of bird density for most species are as high or higher than

other reports that estimated density for the same species (Rotella et al. 1999, Koford 1999), suggesting that both prairies and restored grasslands in northern Iowa are suitable habitats for common grassland birds, in terms of bird density and species richness. We express caution in interpreting these results, however, because some other studies have used other techniques, such as line transects, to estimate density (Koford 1999), which could give different, potentially lower estimates than point counts (Bollinger et al. 1988).

Although the diversity of plants was much higher in prairies than in restored grasslands, habitat structure was similar for many habitat variables, with the main exception being percent total cover and percent bare ground. Lower percent total cover in restored grasslands suggests that restored grasslands had lower horizontal vegetation density (*sensu* Whitmore 1981), not reflected in other habitat variables measured. This lower density can be attributed to 3 possible reasons: (1) restored grasslands have not been planted to similar densities as vegetation density in native areas, (2) the species of plants in restored areas have less horizontal density, and (3) different management strategies in grasslands promoted lower horizontal density. Even though initial restoration efforts may not have planted vegetation at high density, most of these areas have had sufficient time for subsequent dispersal and establishment of plants. Species composition could explain differences in horizontal density, where prairies had a larger diversity of forbs than restored grasslands. This forb diversity resulted in habitat complexity not well reflected in other habitat variables measured. Although the same agencies manage prairies and restored grasslands in our study area, management strategies were slightly different. Some restored grasslands, but no prairies, were mowed after the breeding season both during and prior to our study. Immediate effects of mowing include increasing percent bare ground and litter cover, but this effect can dissipate within a few weeks after the mowing event (Frawley and Best 1991). It is unclear whether this management strategy could explain differences in horizontal vegetation density observed in prairies and restored grasslands.

A potential limitation of comparing bird communities in these prairies and restored grasslands is that prairies were scattered across northern Iowa, primarily west of the complex of restored grasslands. This was necessary because there were no prairies left in the area of

the restored complex to make comparisons. If regional gradients in avian distribution were confounding the data comparing bird density in native and restored grasslands, we would expect that the two species with higher density in restored areas would also show evidence for an longitudinal gradient in density, with densities being highest in the eastern portion of the state. However, there was no evidence for a longitudinal gradient in bird density when using Easting Universal Transverse Mercator coordinates as an explanatory variable for either species ($F_{1, 18} > 0.90$, $P > 0.35$).

Habitat and Landscape Effects

As predicted, habitat models explained some variation in species richness and relative densities of all grassland bird species considered. However, the strength of these relationships was generally weak, suggesting that other factors are also important in habitat associations of breeding grassland birds. While some have reported relatively weak habitat models (e.g., dickcissels, Winter and Faaborg 1999), others have found stronger correlations of grassland bird abundance and habitat structure (e.g., dickcissels, grasshopper sparrows; Delisle and Savidge 1997, Hughes et al. 1999). The variability of strength in habitat models between studies could be due to a variety of design-related reasons (e.g., different sampling designs, number of fields, range of variability in response and explanatory variables, etc.) or several biological reasons, including geographic range limits of species in different regions and interactions of habitat structure with other factors (e.g., Knick and Rotenberry 1995, Winter and Faaborg 1999). Although the range limits of all species we considered completely overlapped the areas we surveyed, regional variation in abundance could have affected the relationships we observed, adding unexplained variation to the habitat models.

Overall, our habitat models were fairly consistent with the nesting requirements of the species considered and with previous studies. For example, 3 of 5 above-ground nesting species—American goldfinch, sedge wren, and common yellowthroat—were positively correlated with percent total vegetation cover, which is consistent with their nesting requirements. Dickcissels, which also nest off the ground, were positively correlated with the percent forb cover, which this species commonly uses as a nesting substrate (Winter 1999). Ground-nesting species showed similar patterns. Both grasshopper and savannah sparrows

showed strong negative correlations with percent total vegetation cover (see also Rotenberry and Wiens 1980, Whitmore 1981). Furthermore, grasshopper sparrows were negatively correlated with vertical density of the habitat (see also Whitmore 1981, Herkert 1994, Madden et al. 2000).

Adding landscape variables to the analysis substantially improved models for species richness and for densities of 4 of 8 species we considered. In Wisconsin, densities of two of these species (grasshopper sparrows and bobolinks) were associated with landscape structure, though the metrics used were different than those presented here (Ribic and Sample 2001). For savannah sparrows and sedge wrens, models with landscape metrics were close competitors to habitat models (see also Ribic and Sample 2001). For American goldfinches and common yellowthroats, landscape metrics did not improve models, but these species are typically considered generalist or edge species (Herkert 1994).

Most of the species that were correlated with landscape metrics showed negative relationships with edge density metrics and weaker, positive relationships with the percent of grassland in the landscape. In previous studies, most of these species have been positively correlated with patch size and have been considered area sensitive (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999). However, Helzer and Jelinski (1999) recently argued that the perimeter-area ratio of habitat patches generally explained more variation in occurrence patterns than did patch size. Our results are consistent with Helzer and Jelinski (1999), because our edge density metrics (m of edge/ha of grassland in the landscape) are landscape-level analogs of patch-level perimeter-area ratios (m of edge/ha of grassland patch). Bajema and Lima (2001) also found that Henslow's sparrows (*Ammodramus henslowii*) were less likely to occur near edges, but were not correlated with landscape composition metrics. Other research has found that many grassland bird species tend to be less abundant or less likely to nest near edges (Johnson and Temple 1986, Delisle and Savidge 1996, Bock et al. 1999). However, none of these studies investigated effects of different edge types, which could ultimately be important to habitat use of grassland birds. Only red-winged blackbirds were positively associated with edge density. This is the only species we considered that commonly nests in agricultural habitats (Best et al. 1997) and has

been positively correlated with edges in other studies (e.g., Warner 1994). Although most species showed consistent negative correlations with total edge density, some species were more strongly associated with certain edge types and one species showed different associations with woodland edges than other edge types, suggesting that edge type may indeed be important in explaining habitat use by breeding grassland birds.

These data and other recent studies beg the question of whether landscape composition or configuration is ultimately more important in affecting breeding bird distribution. Research in forested systems suggests that forest cover (composition) is probably more important overall than forest configuration or fragmentation (McGarigal and McComb 1995, Trzcinski et al. 1999). However, there is growing evidence in grasslands suggesting that elements involving edge metrics are also very important (Johnson and Temple 1986, Delisle and Savidge 1996, Bock et al. 1999, Helzer and Jelinski 1999, Hughes et al. 1999, Bajema and Lima 2001). Although edge metrics are not spatially explicit, these metrics are typically considered configuration metrics, explaining the shape and boundaries of habitat (McGarigal and Marks 1995:33). An understanding of how and why edges may affect avian habitat use in grassland and forested systems is needed (see Donovan et al. 1997 and Ortega and Capen 1999 for examples in forested systems). If mechanisms of edge effects differ for grassland and forest birds, then insight on the relative effects of landscape composition and configuration might be gained.

We chose a "bottom-up" approach (i.e., building habitat models and then determining if landscape structure improved models) to investigating habitat associations of grassland birds because most research to date has focused on the importance of vegetation structure. However, migratory birds likely use a "top-down" approach when selecting habitat, by first selecting patches and then selecting territories or nest-sites within patches. Nonetheless, our models were qualitatively similar within species when using a "top-down" approach (i.e., building landscape models and then determining if habitat structure improved models; Fletcher and Koford; *unpublished analysis*), suggesting that our models were robust to different analysis techniques even though the strength of these relationships was generally weak.

Understanding habitat associations of breeding grassland birds is important for managing and conserving these species, but ultimately understanding demographic parameters is needed. Fragmented grasslands in the Midwest may be acting as either habitat sources or sinks for grassland birds (*sensu* McCoy et al. 1999). Because density of grassland birds may not be correlated with nesting success (Hughes et al. 1999, Winter and Faaborg 1999) and nesting success can be quite low for grassland birds (e.g., Hughes et al. 1999, Koford 1999), understanding how habitat and landscape structure affects nest success of breeding grassland birds will be critical for conserving declining bird populations.

MANAGEMENT IMPLICATIONS

These habitat associations of breeding grassland birds have 2 primary implications for management and conservation. First, restoring grasslands in agricultural landscapes can provide suitable habitat for breeding grassland birds, in terms of avian species richness and density, even if the restoration effort does not mirror native habitat conditions. Species that have undergone steep population declines (e.g., bobolink, dickcissel, grasshopper sparrow; Herkert 1995) had high densities in restored grasslands. However, there is growing evidence that density is not necessarily correlated with nesting success in grassland birds (Hughes et al. 1999, Winter and Faaborg 1999), so further study is warranted to determine if restored grasslands and native prairie remnants in severely fragmented landscapes, such as northern Iowa, act as habitat sources or sinks (*sensu* McCoy et al. 1999). Second, habitat structure is an important predictor of bird density in grasslands; however, consideration of landscape structure improves predictability in most cases. Grassland birds of management concern were negatively correlated with grassland edge density in landscapes, more so than the positive relations with amount of grassland in the landscape (see also Bajema and Lima 2001). Consequently, both the amount of grassland in a landscape and its shape or structure should be important concerns in future land acquisition, restoration, and management.

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Table 1. Density (males/ha; 95% confidence intervals) of common bird species using 10 prairies and 10 restored grasslands in northern Iowa, 1999-2000.

Species	n	Prairie						Restored grassland					
		1999		2000		Total		1999		2000		Total	
		\bar{x}	CI	\bar{x}	CI	\bar{x}	CI	\bar{x}	CI	\bar{x}	CI	\bar{x}	CI
Sedge wren	131	0.59	0.33-1.06	0.98	0.66-1.45	0.79	0.54-1.15	0.57	0.33-1.00	0.64	0.41-0.99	0.60	0.40-0.91
Common yellowthroat	190	2.11	1.10-4.04	3.24	1.69-6.23	2.68	1.41-5.08	0.98	0.48-2.00	1.09	0.55-2.18	1.04	0.55-1.96
Savannah sparrow**	65	0.05	0.01-0.16	0.09	0.03-0.26	0.07	0.03-0.17	0.70	0.38-1.30	0.63	0.35-1.15	0.67	0.38-1.17
Grasshopper sparrow*	64	0.08	0.03-0.19	0.09	0.04-0.20	0.08	0.05-0.15	0.29	0.15-0.57	0.35	0.19-0.64	0.32	0.21-0.50
Dickcissel	109	0.41	0.27-0.63	0.35	0.22-0.55	0.38	0.28-0.52	0.23	0.13-0.39	0.35	0.23-0.52	0.29	0.21-0.40
Bobolink	409	1.59	1.06-2.36	1.66	1.12-2.46	1.62	1.08-2.44	1.25	0.82-1.92	1.68	1.11-2.53	1.46	0.97-2.21
Red-winged blackbird	265	0.75	0.55-1.02	0.61	0.46-0.82	0.68	0.54-0.87	1.00	0.75-1.33	0.95	0.72-1.25	0.97	0.77-1.23
American goldfinch	43	0.16	0.06-0.42	0.24	0.09-0.61	0.20	0.09-0.47	0.11	0.04-0.34	0.03	0.04-0.15	0.07	0.02-0.21

*Non-overlapping confidence intervals between prairies and restored grasslands when years were pooled

**Non-overlapping confidence intervals between prairies and restored grasslands each year and when years were pooled

Table 2. Habitat and landscape structure of 10 prairies and 10 grasslands surveyed in northern Iowa, 1999-2000. Habitat structure determined at point count locations. Landscape structure estimated within 1-km from the center of each patch using a Geographic Information System.

Habitat/landscape variable	Prairie		Grassland		Range	<i>F</i> ^a	<i>P</i>
	\bar{x}	SE	\bar{x}	SE			
Habitat							
Vegetation height (cm)	91.7	2.2	91.6	2.8	67.5-123.1	0.0	0.868
Litter depth (cm)	3.4	0.4	2.5	0.4	0.1-6.3	3.3	0.087
Vertical density (dm)	4.6	0.2	4.8	0.3	2.8-7.8	0.2	0.628
Total cover (%) ^b	89.1	1.1	82.5	1.7	62.4-97.9	9.0	0.008
Grass cover (%) ^b	45.6	2.8	51.8	2.1	29.6-67.5	1.4	0.253
Forb cover (%) ^b	33.4	3.3	20.6	1.5	7.4-57.2	4.2	0.056
Dead cover (%) ^b	9.3	1.7	10.1	1.8	0.4-32.9	0.0	0.970
Litter cover (%) ^b	9.9	1.2	13.7	1.3	0.0-26.7	3.2	0.092
Bare ground (%) ^c	0.9	0.2	3.6	0.9	0.0-14.0	5.2	0.036
Landscape							
Grassland (%) ^c	31.8	4.5	28.4	2.3	5.0-70.9	0.1	0.745
Wetland vegetation (%) ^c	2.6	0.3	3.3	0.6	0.0-17.4	1.1	0.299
Woodland (%) ^c	2.8	1.2	2.8	0.5	0.0-17.7	0.5	0.504
Total grassland edge density (m/ha) ^d	153.4	17.5	211.6	17.1	66.3-400.8	3.0	0.100
Grassland/agriculture edge density (m/ha) ^d	47.8	8.6	74.6	9.0	10.6-182.7	2.2	0.156

Table 2. (continued)

Habitat/landscape variable	Prairie		Grassland		Range	<i>F</i> ^a	<i>P</i>
	\bar{x}	SE	\bar{x}	SE			
Grassland/road edge density (m/ha) ^d	24.9	4.0	17.1	1.7	4.2-66.2	0.3	0.568
Grassland/woodland edge density (m/ha) ^d	10.4	3.2	28.3	6.2	0.0-74.7	4.6	0.046

^aTests reported for habitat type in split-plot, repeated measures ANOVAs, with df = 1, 18

^bLogit transformed for analysis

^cArcsin square-root transformed for analysis

^dNatural log transformed for analysis

Table 3. Best habitat and habitat + landscape models (i.e., models with lowest AIC_c) for species richness and bird density (males/ha) of common species in northern Iowa, 1999-2000.

Species, Model Type	ΔAIC_c^a	R^2	Best Model ^b
Sedge wren			
Habitat	0.00	0.06	-0.485 + 1.136(PTCVR)
Habitat + Landscape	0.07	0.11	-0.427 + 1.000(PTCVR) + 0.020(WTLND)
Common yellowthroat			
Habitat	0.00	0.40	-1.546 + 2.140(PTCVR) + 1.136(PTFORB) + 0.110(LITTER)
Habitat + Landscape	1.04	0.42	-1.517 + 2.006(PTCVR) + 1.239(PTFORB) + 0.111(LITTER) + 0.018(WTLND)
Savannah sparrow			
Habitat	0.00	0.34	1.346 - 1.307(PTCVR)
Habitat + Landscape	0.08	0.41	1.534 - 1.294(PTCVR) - 0.001(EDGE) + 0.024(WTLND)
Grasshopper sparrow			
Habitat	2.75	0.20	0.825 - 0.465(PTCVR) - 0.062(VERTD)
Habitat + Landscape	0.00	0.30	0.907 - 0.493(PTCVR) - 0.061(VERTD) - 0.003(WEDGE)
Dickcissel			
Habitat	4.13	0.25	0.138 + 0.547(PTFORB) - 0.039(VERTD) + 0.044(LITTER)
Habitat + Landscape	0.00	0.37	0.358 + 0.456(PTFORB) - 0.038(VERTD) + 0.042(LITTER) - 0.001(EDGE)
Bobolink			
Habitat	9.08	0.12	0.367 + 0.082(VERTD) + 1.132(PTDVG)
Habitat + Landscape	0.00	0.34	0.602 + 0.076(VERTD) + 1.105(PTDVG) - 0.003(AEDGE)

Table 3. (continued)

Species, Model Type	ΔAIC_c^a	R^2	Best Model ^b
Red-winged blackbird			
Habitat	12.92	0.12	0.647 - 0.581(PTDVG)
Habitat + Landscape	0.00	0.44	0.393 - 0.806(PTDVG) + 0.002(EDGE) - 0.019(WOOD)
American goldfinch			
Habitat	0.00	0.20	-0.468 + 0.893(PTCVR) - 0.039(VERTD)
Habitat + Landscape	1.38	0.23	-0.397 + 0.892(PTCVR) - 0.043(VERTD) - 0.002(GRASS)
Species Richness			
Habitat	9.98	0.06	1.956 + 0.020(LITTER)
Habitat + Landscape	0.00	0.35	2.120 + 0.012(LITTER) - 0.002(AEDGE) - 0.016(WTLND)

^a $\Delta AIC_c = AIC_{ci} - \min AIC_c$

^bExplanatory variables included: LITTER = litter depth (cm), VERTD = vertical density (dm), PTCVR = total vegetation cover (%), PTFORB = forb cover (%), PTDVG = standing dead vegetation (%), GRASS = grassland in landscape (%), WTLND = wetland vegetation in landscape (%), WOOD = woodland in landscape (%), EDGE = total grassland edge density in landscape (m/ha), AEDGE = grassland/agriculture edge density in landscape (m/ha), WEDGE = grassland/woodland edge density in landscape (m/ha).

Table 4. Relative importance of habitat variables in habitat regression models explaining bird density (males/ha) and species richness in 10 prairies and 10 grasslands in northern Iowa, 1999-2000. Relative importance based on the sum of Akaike weights over candidate models in which the variable occurred. Parentheses indicate the nature of association.

Species	Habitat variables ^a				
	LITTER	VERTD	PTFORB	PTDVG	PTCVR
Sedge wren	0.30 (+)	0.50 (+)	0.40 (-)	0.33 (+)	0.55 (+)
Common yellowthroat	0.95 (+)	0.25 (+)	0.90 (+)	0.36 (-)	0.74 (+)
Savannah sparrow	0.46 (-)	0.46 (+)	0.23 (-)	0.31 (-)	1.00 (-)
Grasshopper sparrow	0.37 (-)	0.60 (-)	0.24 (-)	0.28 (+)	0.82 (-)
Dickeissel	0.93 (+)	0.45 (-)	0.59 (+)	0.28 (-)	0.40 (-)
Bobolink	0.32 (+)	0.46 (+)	0.27 (+)	0.55 (+)	0.41 (+)
Red-winged blackbird	0.24 (-)	0.36 (+)	0.36 (+)	0.80 (-)	0.28 (-)
American goldfinch	0.31 (-)	0.54 (-)	0.43 (+)	0.30 (+)	0.86 (+)
Species richness	0.58 (+)	0.27 (+)	0.47 (+)	0.28 (-)	0.35 (-)

^aSee Table 3 for codes of habitat variables

Table 5. Relative importance of landscape variables in habitat + landscape regression models explaining bird density (males/ha) and species richness in 10 prairies and 10 grasslands in northern Iowa, 1999-2000. Species included where landscape variables improved models. Relative importance based on the sum of Akaike weights over candidate models in which the variable occurred. Values in parentheses indicate the nature of association.

Species	Landscape variables ^a					
	GRASS	WTLND	WOOD	EDGE	AEDGE	WEDGE
Grasshopper sparrow	0.27 (+)	0.23 (-)	0.37 (-)	0.32 (-)	0.24 (-)	0.60 (-)
Dickcissel	0.61 (+)	0.25 (-)	0.22 (-)	0.57 (-)	0.24 (-)	0.22 (-)
Bobolink	0.30 (+)	0.21 (+)	0.24 (-)	0.27 (-)	0.92 (-)	0.23 (-)
Red-winged blackbird	0.22 (-)	0.36 (+)	0.46 (-)	0.71 (+)	0.54 (+)	0.38 (-)
Species richness	0.31 (+)	0.61 (-)	0.31 (+)	0.59 (-)	0.58 (-)	0.25 (-)

^aSee Table 3 for codes of landscape variables

Figure 1. Locations of prairies ($n = 10$) and restored grasslands ($n = 10$) surveyed in northern Iowa, 1999-2000.

Eagle Lake Wetland Complex

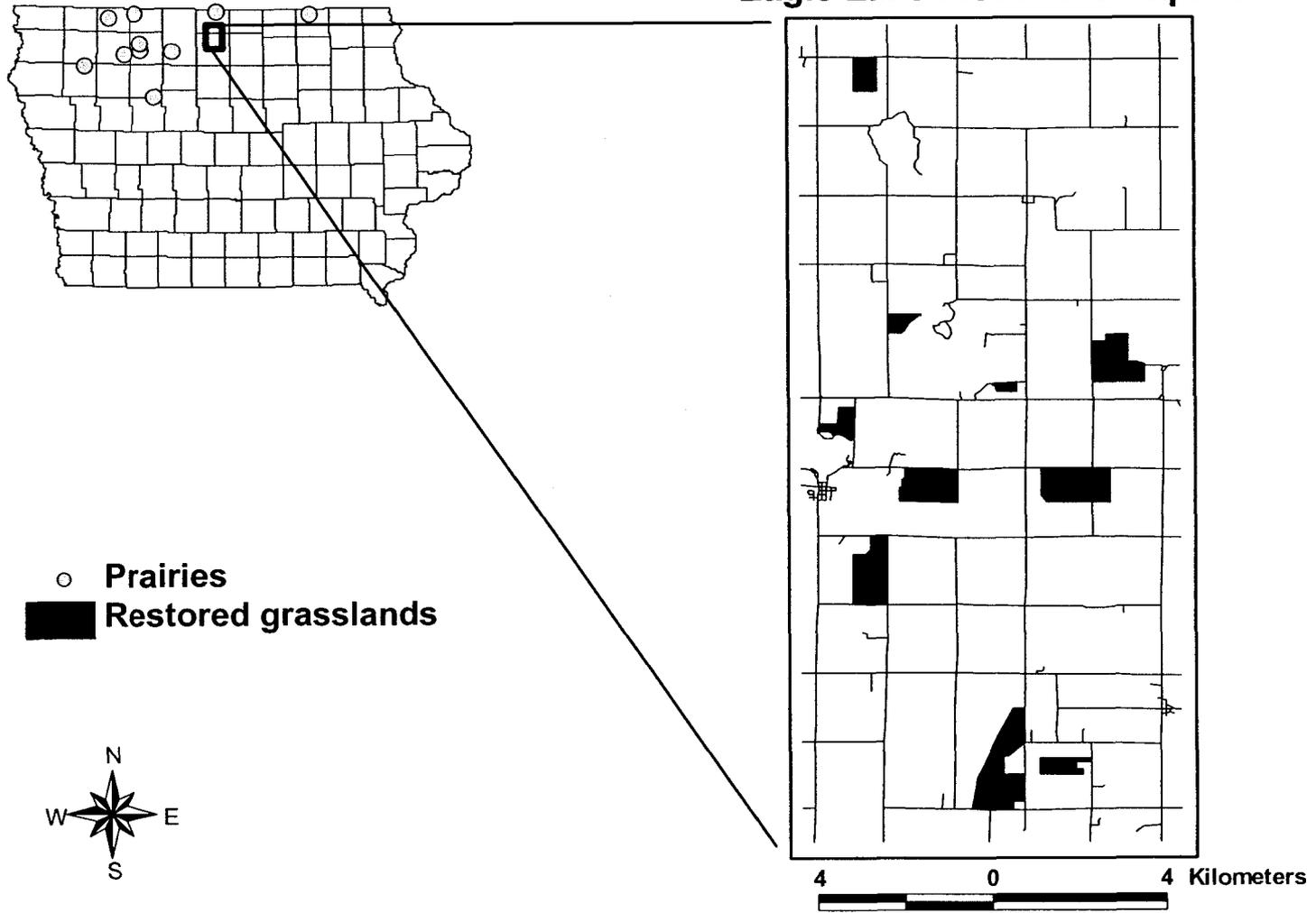


Figure 1

CHAPTER 5. CHANGES IN BREEDING BIRD POPULATIONS WITH HABITAT RESTORATION IN NORTHERN IOWA

A paper accepted by *The American Midland Naturalist*

Robert J. Fletcher, Jr., and Rolf R. Koford

Abstract.—Native tallgrass prairie and wetland habitat in the Prairie Pothole Region of the United States have declined over the past two centuries. Bird communities using these habitats have also experienced widespread declines that are often attributed to severe habitat loss and fragmentation. We estimated the change, or turnover, in bird populations in the Eagle Lake Wetland Complex, Iowa, with ongoing grassland and wetland restoration, by linking geographic information system data and bird surveys in different land cover types (hayland, pasture, restored grassland, restored wetland, and rowcrop agriculture), during the 1999-2001 breeding seasons. Habitat restoration efforts primarily converted rowcrop agriculture and pastures into grassland and wetland habitat. Based on land conversion, abundances of most species have likely increased in the area, including many species of management concern. Yet a few species, such as killdeer (*Charadrius vociferus*), have probably decreased in abundance. This estimation approach and these estimates provided a critical first step for evaluating restoration efforts; however, information on demographic parameters, such as nesting success, in restored areas is needed for understanding how restoration ultimately affects bird populations.

INTRODUCTION

Both native tallgrass prairie and wetlands in the Prairie Pothole Region of the United States have declined over the past two centuries (Dahl, 1990; Samson and Knopf, 1994). In Iowa, for example, 99% of native prairie and 89% of native wetlands have been lost (Bishop *et al.*, 1998; Smith, 1998). Based on the Breeding Bird Survey (BBS), bird populations using grassland habitats have also experienced consistent widespread declines throughout the continental United States (Herkert, 1995; Peterjohn and Sauer, 1999; *see also* Igl and Johnson, 1997) that have been attributed to severe habitat loss and fragmentation (Herkert *et*

al., 1996). Wetland birds tend to be under sampled by the BBS (Herkert, 1995), but other evidence suggests that many wetland species have also experienced population declines (Herkert, 1995; Igl and Johnson, 1997). To conserve bird communities, restoration must occur and provide adequate resources needed by avian communities. Recently, state and federal agencies have responded by restoring some of the grassland and wetland habitats in the Midwest (*e.g.*, Bishop *et al.*, 1998).

Effects of grassland and wetland restoration on bird populations are often evaluated by either: 1) comparing bird populations in native habitat to those on restored habitat (Blankespoor, 1980; Delphey and Dinsmore, 1993; Brown and Smith, 1998; Ratti *et al.*, 2001; Fletcher and Koford, 2002), or 2) comparing bird populations in restored habitat to populations on rowcrop agriculture lands (Johnson and Igl, 1995; Best *et al.*, 1997; Prescott and Murphy, 1999), which is the predominant land use in the Midwest. Bird populations are often compared between native and restored habitat to determine if restored areas are providing habitat that is similar in suitability to historical native habitat. Bird populations are often compared on rowcrop agriculture land and restored areas to determine how populations might have changed with land conversion, because habitat is generally reconstructed from rowcrop lands. Here we present a more unified approach that links geographic information systems (GIS) and recent bird surveys in different land cover types to determine the contributions of habitat restoration to local bird populations.

Our objectives were to: 1) quantify changes in land cover with habitat restoration, 2) estimate bird densities in common land cover types in the region, and 3) estimate changes in bird populations with habitat restoration. We expected grassland and wetland breeding birds would show positive changes in populations, whereas other breeding birds would not exhibit significant changes with habitat restoration. Potential scenarios of future land acquisition and restoration can be evaluated by using bird densities in common land cover types and predicting what types of land conversion will provide the greatest changes in bird populations. Estimating changes in bird populations with restoration will not only help evaluate the efficacy of past restoration efforts but will also provide a framework for evaluating future restoration efforts and restoration efforts elsewhere.

METHODS

Study area.—We quantified effects of habitat restoration within the Eagle Lake Wetland Complex, located in Hancock and Winnebago counties, north-central Iowa (43°N 94°W). The Eagle Lake Wetland Complex encompasses approximately 162 km² and contains a complex of federal waterfowl production areas (WPAs) and state wildlife management areas (WMAs) in an agricultural landscape. Areas were restored by state and federal agencies during the past 15 years, and restoration is ongoing in the complex. To estimate change, or turnover, in bird populations with restoration, we focused on the nine restored WPAs and WMAs (total area = 817.5 ha, \bar{x} = 90.8 ha, SD = 59.7 ha; range = 31.4–196.7 ha) within the complex that had been restored since 1984. All contained restored grassland and wetland habitats.

Grasslands were restored by state and federal agencies, primarily from agricultural lands, using several techniques and plantings. 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, and cool-season plantings were typically smooth brome (*Bromus inermis*) or brome/alfalfa (*Medicago sativa*) mixtures. Other common plants in restored areas included orchard grass (*Dactylis glomerata*), reed canary grass (*Phalaris arundinacea*), red clover (*Trifolium pratense*), and milkweed (*Asclepias* spp.).

Wetlands were restored by removing drainage tile lines or plugging tile lines and/or drainage ditches (sensu LaGrange and Dinsmore 1989, Delphay and Dinsmore, 1993). Some wetland basins were also excavated to increase wetland depth. Wetlands were not replanted with vegetation, but plant establishment in these areas occurred primarily from the seed bank (Galatowitsch and van der Valk, 1996). Propagules in the seed bank from drained wetlands may be viable for many years, although seed density and species richness decline over time (Wienhold and van der Valk, 1989). Dominant wetland vegetation included cattails (*Typha* spp.), bulrush (*Scirpus* spp.), and reed canary grass.

Estimating land conversion.—We calculated changes in land cover using aerial photographs of the WPAs and WMAs taken in 1983 (prerestoration) and 1999 (postrestoration). We chose 1983 as a prerestoration reference year because the earliest

restoration in the complex occurred in 1984 and this year also preceded the first sign-up for the Conservation Reserve Program (Young and Osborn, 1990). We chose 1999 as a postrestoration reference year because we initiated bird surveys during that year.

Photographs were geo-referenced and digitized using a GIS. Land-cover categories included hayland (primarily alfalfa), homesteads, linear grassland (*e.g.*, terraces, grassed waterways, roadside ditches), open water (*e.g.*, lakes, open portions of some wetlands), pasture, restored grassland (both warm-season and cool-season plantings), rowcrop agriculture (corn and soybeans), wetland vegetation, and woodland. Warm-season and cool-season plantings were not differentiated because aerial photographs did not provide sufficient resolution.

Upland bird surveys.—Surveys were conducted during the 1999-2001 breeding seasons. Each site was surveyed once in each of three periods during the breeding season: 20 May-5 June, 6 June-22 June, and 23 June-7 July. We used 10-min, 50-m fixed-radius point counts for surveying breeding birds (Ralph *et al.*, 1995) but only present data from the first 8 min to minimize differences in techniques between upland and wetland bird surveys (*see below*). Point count locations were ≥ 150 m apart. Surveys were conducted between sunrise and 4 h after sunrise. Surveys were not conducted during high winds (≥ 20 km/h) or precipitation. Each year, two observers conducted surveys, and each observer surveyed each site at least once. One of these observers surveyed birds during every year of the study, but the other observer was different each year. Observers were trained for consistency before the commencement of sampling each year. During surveys, observers recorded all birds seen or heard, including how individuals were detected (song, visual, or call), sex of individuals, and distances of birds from the center point. We did not include birds flying over points in our analyses. Distances (m) to birds seen were estimated using a rangefinder.

Point count locations were determined using a GIS. A grid was laid over aerial photographs of each site, with each grid cell measuring 150 \times 150 m. Each cell was considered a potential sampling unit (SU), with a potential point count location at the center of each cell. All sites had \geq three SUs. We stratified potential sampling units into geographic sections of similar area (*e.g.*, northwest, northeast, southwest, and southeast areas of the field). Sites with 12 or more SUs were stratified into four sections, sites with 9-11 SUs were stratified into three sections, sites with 6-8 SUs were stratified into two sections, and

sites with < six SUs were not stratified. During each sampling period, we randomly selected one SU in each stratum to sample. We did not repeat any individual SUs. This method provided a random sampling design yet ensured that the entire range of variability was sampled within each site. When sites were surveyed in more than one year, the same point count locations were sampled across years.

We surveyed birds in four upland land cover types using this protocol: hayland (primarily alfalfa; $n = 5$ sites), pasture ($n = 7$), restored grassland ($n = 8$), and rowcrop agriculture (corn and soybeans; $n = 7$). Restored grasslands were surveyed every year (1999-2001; $n = 90$ points/y). In 1999, we surveyed four pastures ($n = 30$ points) and four rowcrop agriculture sites ($n = 36$ points). However, in 2000 and 2001, we were not granted permission onto four sites surveyed in 1999 (two rowcrop and two pasture sites). We added three rowcrop agriculture ($n = 33$ points/y), three pasture sites ($n = 18$ points/y) and five hayland sites ($n = 30$ points/y) to our sampling in 2000 and 2001. Our criteria for selecting hayland, pasture and rowcrop agriculture sites were: 1) sites needed to be < 2 km of restored sites (to minimize potential landscape effects), and 2) sites needed to be > 7 ha to accommodate our sampling design.

Wetland bird surveys.—We used a slightly different protocol for surveying wetland birds than our upland survey protocol, similar to other wetland bird studies (e.g., Brown and Dinsmore, 1986; Delphey and Dinsmore, 1993; Naugle et al. 1999). We defined wetland complexes as the total number of seasonal, semipermanent, and permanent wetlands within a WPA or WMA (sensu Fairbairn and Dinsmore, 2001). We considered wetland complexes within WPAs and WMAs as independent units. Wetland surveys were conducted during the 1999-2001 breeding seasons. Each restored wetland complex was surveyed three times during similar time periods as for upland surveys: 15 May-5 June, 6-22 June, and 23 June-5 July. We conducted wetland bird surveys using 8-min, 20-m fixed-radius point counts (Delphey and Dinsmore, 1993). Count radius was smaller than in upland counts to minimize habitat heterogeneity within count circles (see also Brown and Dinsmore, 1986; Hemesath and Dinsmore, 1993; Delphey and Dinsmore, 1993; Naugle et al., 1999). Point count locations were ≥ 75 m apart. We played taped calls to detect secretive species during minutes 3-5 of each survey. We used 30-s taped calls to detect Virginia rail (see Appendix

for scientific names of common species detected), sora, least bittern (*Ixobrychus exilis*), and American bittern (*Botaurus lentiginosus*). However, we had few observations of least and American bitterns, so these species were not considered for further analyses. Surveys were conducted between sunrise and 4 h after sunrise and were not conducted during high winds (≥ 20 km/h) or precipitation.

We delineated wetland boundaries within WPAs and WMAs using aerial photographs taken in 1999 and count locations were selected using a GIS. We combined the perimeters of wetlands within a each complex (*i.e.*, WPA/WMA) into one overall length, divided the length into three equal segments, and selected one random point along each segment. Based on 1999 photos, points were centered in the emergent vegetation zone, or at the water's edge where no emergent vegetation was present (Delphey and Dinsmore, 1993). Three point count locations were surveyed in each wetland complex ($n = 7$ complexes), and each point was repeated during each time period ($n = 63$ points/y). Although wetland conditions varied among years (*see Results*), the same count locations were repeated each year. Therefore, a count location could be along the water's edge in one year but not in another year, if water levels changed across years. After each point count survey, we also measured water depth (cm) at four locations within the point count area: one at the center of the point, and at three locations 0° , 120° , and 240° from the center, at distances of 10 m.

Statistical analyses.—Because point counts within sites were not independent, we estimated bird densities (birds/ha) per site for each land cover type surveyed, averaged across years, and estimated 95 % confidence intervals for these density estimates. We weighted estimates based on the number of point counts conducted per site to incorporate increased precision with our estimates as the number of counts within sites increased. We did not correct for detectability, because of few observations of species in some land cover types (*see Appendix*). Elsewhere we documented that most species have high detectability up to 50 m from observers and that uncorrected density estimates are generally similar to corrected estimates (Fletcher and Koford, 2002; *see also* Rotella *et al.*, 1999). Lower confidence limits for density estimates were truncated to zero, because negative density cannot occur. We estimated the change in abundance for each common species with habitat restoration by

linking density estimates and changes in land cover types to determine the population change:

$$\text{Estimated change} = \sum_{i=1}^n d_i \times (A_{i, \text{postrestoration}} - A_{i, \text{prerestoration}})$$

where d_i is the density of the species (birds/ha) in land cover i , A is the total area of the land cover, and n is the number of land cover types. We estimated change using both mean density estimates and lower and upper confidence limits of density estimates. Using confidence limits is critical for incorporating precision and site variability in density estimates. This measure of change does not incorporate temporal or spatial trends in bird densities (*see* Discussion), but quantitative measures of temporal and spatial patterns of bird densities are not well-documented for the species that we considered. This measure only requires estimating bird densities in land cover types that have changed with restoration efforts. We surveyed the primary land cover types that did change with restoration; the only land cover type that we did not survey for birds that changed substantially was open water (*see* Results). For this land cover, we assumed bird density was zero, which is reasonable for all species that we considered. This assumption is conservative for evaluating restoration, because relaxing it would lead to increases in estimated changes for common bird species.

RESULTS

Overall, land acquisition and restoration converted primarily rowcrop agriculture to restored grassland, wetland vegetation, and open water land cover (Table 1). Between 1999-2001, we recorded 3322 bird observations during point counts: 1630 in restored grasslands, 740 in restored wetlands, 531 in pastures, 253 in haylands, and 168 in rowcrop fields. We observed 54 species: 29 in restored grasslands, 31 in restored wetlands, 14 in pastures, 11 in haylands, and eight in rowcrop fields. Most species had lower densities in rowcrop agriculture than other land cover types (Appendix).

We estimated changes for 20 bird species known to breed in \geq one land cover type: six species that typically nested in grasslands, six that typically nested in wetlands, and eight other species, which included species that were not grassland/wetland obligate breeders (Table 2). Based on mean estimates of change, 16 species increased with restoration and 4 decreased. However, by inspecting confidence limits, nine species exhibited significant

increases, 10 showed no change, and two decreased. Only killdeer and brown-headed cowbirds significantly decreased with habitat restoration. Eleven species have exhibited declines in the region (Table 2), based on BBS data from 1983-1999 for USFWS Region 3, which includes Iowa (route-regression analysis; Sauer *et al.*, 2001). Five of these 11 species increased with restoration.

Bird density in wetlands can vary depending on wetland conditions (Weller and Fredrickson, 1974; Igl and Johnson, 1997), which did differ among years of our study. Based on water depth measurements taken at each point count location, 2000 was significantly drier than 1999 or 2001 (1999: 21.94 ± 2.20 ; 2000: 7.08 ± 4.03 ; 2001: 27.28 ± 6.20 ; $F = 8.05$, $df = 2, 12$, $P = 0.006$). In 2000, most wetlands were relatively dry during spring migration and few wetland-nesting species settled in the restored wetlands relative to other years, whereas grassland-nesting species were more commonly observed in the relatively dry wetlands (Table 3). To incorporate this variability into our modeling approach, we also estimated changes in bird populations separately for a dry year (2000) and a wet year (2001). In general, estimates were similar between years (Table 2).

DISCUSSION

Grassland and wetland restoration inevitably provide breeding habitat for declining grassland and wetland-nesting birds. Nonetheless, estimating how restoration efforts have contributed to bird populations and communities in fragmented landscapes is not necessarily straightforward. Experimental or time-series approaches would provide strong inference for understanding temporal effects of restoration; however, most restoration efforts by state and federal agencies are done haphazardly, in which agencies opportunistically purchase land from private landowners and subsequently restore land with the resources currently available at that time. Our approach provided quantitative estimates for evaluating potential changes in bird communities based on land conversion, which could be fruitful in future restoration efforts when different scenarios are being considered. Others have used qualitative measures to evaluate landscape change (*e.g.*, species lists; White *et al.*, 1997) or have measured bird communities in different land cover types without linking bird estimates with measures of landscape change (Pidgeon *et al.*, 2001; but *see* Herkert, 1997). However, integrating standardized quantitative estimates of avian populations that incorporate measures of

precision and other information on landscape change provide stronger inference in understanding how habitat restoration or landscape change may affect bird populations.

We estimated that many species have increased with habitat restoration. Four of 6 grassland-nesting species increased, but grasshopper sparrows and western meadowlarks showed no significant change, possibly because of their high densities in pastures and high variability among sites. Grasshopper sparrows and meadowlarks both prefer relatively open habitats for breeding, like those found in pastures (Herkert, 1994; Temple *et al.*, 1999; Ribic and Sample, 2001; Fletcher and Koford, 2002). Only two of six wetland-nesting species increased significantly with restoration, possibly owing to high variability among both sites and years, or lag time in recolonization (but *see* Hemesath and Dinsmore, 1993). With continued establishment of wetland vegetation in restored wetlands, other wetland-nesting species may also increase in the area.

Even though some species exhibited an apparent increase with restoration, both killdeer and brown-headed cowbirds decreased. Killdeer tend to nest in open areas devoid of ground vegetation, such as rowcrop fields in early summer (Best *et al.*, 1997). Densities of killdeer were higher in rowcrop agriculture than other land cover types, and killdeer had higher densities in rowcrop fields than other species. Because brown-headed cowbirds had higher densities in pasture than in other land cover types, cowbirds likely decreased with restoration because of the conversion of pasture to restored grassland.

Our approach did not incorporate spatial processes that might be important in determining habitat use by birds in agricultural landscapes. For example, many species of grassland and wetland birds tend to be area sensitive, or less likely to occur or less dense in small patches of grassland or small wetland potholes (Brown and Dinsmore, 1986; Herkert, 1994; Naugle *et al.*, 1999; Winter and Faaborg, 1999; Johnson and Igl, 2001; but *see* Horn *et al.*, 2000). Other potentially important spatial factors are landscape composition and the amount of edge in the landscape (Hughes *et al.*, 1999; Bajema and Lima, 2001; Fairbairn and Dinsmore, 2001; Ribic and Sample, 2001; Fletcher and Koford, 2002). Some grassland and wetland birds may be less abundant or less likely to occur in landscapes with low amounts of grassland or wetland composition, or high amounts of edge (Naugle *et al.*, 1999; Bajema and Lima, 2001; Fletcher and Koford, 2002). Incorporating metrics that reflect these processes

could be difficult, because metrics could be conditional on regional density of the species of interest (Horn *et al.*, 2000). However, no research to our knowledge has quantified the ineluctable importance of regional density as a covariate (but *see* Johnson and Igl, 2001). In prerestoration land cover, what little grassland and wetland habitat that did occur was composed of very small patches with little to no other habitat in the surrounding areas (R. J. Fletcher and R. R. Koford, unpubl. data). Therefore, fragmentation-sensitive species may have been less likely to occur in these areas than we estimated using density estimates from larger patches.

Temporal dynamics in bird populations can potentially affect estimates of population change for two reasons: 1) bird populations can change among years based on habitat conditions, such as water depth in wetlands (Weller and Fredrickson, 1974; Igl and Johnson, 1997), and 2) some populations may be exhibiting either population increases or declines at regional scales (Herkert 1995). We incorporated yearly variability into our estimates by calculating densities for relatively wet and dry years. However, our estimates did not incorporate temporal trends in bird populations, even though most of the species we investigated have exhibited declines between prerestoration and postrestoration periods, based on BBS trends (*see also* Herkert, 1995; Peterjohn and Sauer, 1999). We did not include potential temporal factors because it is unclear if temporal trends, from data such as BBS, reflect similar changes in within-patch bird density.

Our bird density estimates for different land cover types revealed that relatively few species used rowcrop agriculture land in this landscape, and those species observed in agriculture generally had lower densities than in other land cover types. In contrast, many species had relatively high densities in both pastures and haylands (*see also* Bollinger *et al.*, 1988, Temple *et al.*, 1999). This suggests that future restoration efforts that restore grasslands from haylands and pasture will likely provide less change in avian populations than would restoring grasslands from rowcrop agriculture. Although restoring grassland from either haylands or pastures will likely provide less change in bird populations, these types of restoration efforts will ultimately be valuable, because both grazing in pastures and mowing of haylands can decrease breeding success of birds (Bollinger *et al.*, 1990; Dale *et al.*, 1997; Temple *et al.*, 1999).

Understanding how bird populations change with habitat restoration is important for managing and conserving these species, but ultimately understanding how demographic parameters may change with restoration is needed. Fragmented landscapes in the Midwest may be acting as either habitat sources or sinks for grassland birds (McCoy *et al.*, 1999). Because bird density may not be correlated with nesting success (Hughes *et al.*, 1999; Winter and Faaborg, 1999) and nesting success can be low for species breeding in agricultural landscapes (Hughes *et al.*, 1999), understanding how habitat and landscape structure affects nest success of breeding birds will be critical for evaluating habitat restoration and conserving declining bird populations.

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TABLE 1.—Land cover (ha) before (1983) and after (1999) habitat restoration in the Eagle Lake Wetland Complex, Iowa

Land cover	Prerestoration	Postrestoration	% Change
	(1983)	(1999)	
Hayland	8.2	0.0	-1.0
Open water	0.0	74.6	9.1
Pasture	67.0	0.0	-8.2
Restored grassland	0.0	530.3	64.9
Rowcrop agriculture	687.9	98.9	-72.1
Wetland vegetation	5.1	81.8	9.4
Woodland	22.3	21.7	-0.1
Other ^a	27.0	10.2	-2.1
Total	817.5	817.5	

^aIncludes all land cover types that were each < 1% of the total land cover area

TABLE 2.—Estimated change in abundance of common bird species based on land conversion from 1983-1999 in the Eagle Lake Wetland Complex, Iowa, and the Breeding Bird Survey trend (BBS; percent change per year) during this time period for USFWS Region 3 (which includes Iowa). Estimated change in abundance was calculated using density estimates (means and confidence limits) averaged across years (1999-2001), for a dry year (2000), and for a wet year (2001)

Species	Estimated change									BBS ^c
	1999-2001			2000			2001			
	\bar{x}	LCL ^a	UCL ^b	\bar{x}	LCL ^a	UCL ^b	\bar{x}	LCL ^a	UCL ^b	
Grassland-breeding birds:										
Sedge wren	360	197	522	382	161	615	187	59	315	0.4
Savannah sparrow	237	-13	548	280	0	654	92	44	18	-0.9 ^d
Grasshopper sparrow	234	91	374	183	16	327	130	-11	330	-3.1 ^d
Dickcissel	220	87	349	190	30	311	234	97	365	-1.9 ^d
Bobolink	1070	881	1266	1217	866	1607	1290	938	1656	-3.3 ^d
Western meadowlark	4	0	12	-4	-6	0	11	0	23	-1.7 ^d
Wetland-breeding birds:										
Virginia rail	19	0	45	0	0	0	19	0	50	-25.6 ^d
Sora	55	13	97	10	0	33	78	0	169	5.6
American coot	23	0	47	0	0	0	48	0	108	-12.3 ^d
Marsh wren	100	0	222	165	0	376	29	0	63	-3.9
Swamp sparrow	171	18	323	274	15	559	109	0	270	1.2
Yellow-headed blackbird	368	0	703	19	0	67	452	0	592	-9.9 ^d

TABLE 2. (continued)

Species	Estimated change									BBS ^c
	1999-2001			2000			2001			
	\bar{x}	LCL ^a	UCL ^b	\bar{x}	LCL ^a	UCL ^b	\bar{x}	LCL ^a	UCL ^b	
Other breeding birds ^c :										
Killdeer	-173	-298	-40	-157	-311	0	-126	-272	0	2.6 ^d
Horned lark	-36	-75	0	-33	-110	0	-50	-122	0	-1.4 ^d
Common yellowthroat	544	266	815	557	101	1006	547	230	816	-0.9 ^d
Vesper sparrow	-77	-166	0	-83	-275	0	-133	-297	0	-0.8
Song sparrow	121	2	248	89	0	196	124	17	250	0.9 ^d
Red-winged blackbird	1474	1229	1694	1543	916	2120	1432	1054	1686	-1.0 ^d
Brown-headed cowbird	-8	-9	-3	-64	-167	0	3	-7	31	-0.4
American goldfinch	44	0	89	52	0	137	18	0	43	0.8 ^d

^aLCL = lower confidence limit

^bUCL = upper confidence limit

^cRoute-regression analysis (Sauer *et al.* 2001)

^dP < 0.05

^eIncludes species that tend to breed in > 1 land cover type or are non-obligate grassland/wetland breeders

TABLE 3.—Density of common bird species (mean birds/ha, standard error [SE]) observed in restored wetlands within the Eagle Lake Wetland Complex, Iowa, 1999-2001. 2000 was a relatively dry year, whereas 1999 and 2001 were relatively wet

Species	1999		2000		2001	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Grassland-breeding birds:						
Sedge wren	0.13	0.13	0.63	0.37	0.00	0.00
Savannah sparrow	0.00	0.00	0.13	0.13	0.00	0.00
Grasshopper sparrow	0.38	0.38	0.38	0.26	0.00	0.00
Dickcissel	0.00	0.00	0.13	0.13	0.00	0.00
Bobolink	0.00	0.00	0.38	0.38	0.13	0.13
Western meadowlark	0.00	0.00	0.00	0.00	0.00	0.00
Wetland-breeding birds:						
Virginia rail	0.51	0.33	0.00	0.00	0.25	0.16
Sora	1.01	0.41	0.13	0.13	1.01	0.49
American coot	0.25	0.16	0.00	0.00	0.63	0.32
Marsh wren	1.39	0.84	2.15	1.12	0.38	0.18
Swamp sparrow	1.01	0.41	2.53	0.95	0.63	0.32
Yellow-headed blackbird	8.34	4.08	0.25	0.25	8.72	3.94
Other breeding birds ^a :						
Killdeer	0.00	0.00	0.13	0.13	0.00	0.00
Horned lark	0.00	0.00	0.00	0.00	0.00	0.00
Common yellowthroat	1.26	0.38	2.65	1.04	2.53	0.85
Vesper sparrow	0.00	0.00	0.00	0.00	0.00	0.00
Song sparrow	1.01	0.76	0.25	0.16	0.38	0.26
Red-winged blackbird	11.63	2.78	12.76	2.49	12.13	2.02
Brown-headed cowbird	0.00	0.00	0.13	0.13	0.00	0.00
American goldfinch	0.00	0.00	0.38	0.26	0.13	0.13

^aIncludes species that tend to breed in > 1 land cover type or are non-obligate grassland/wetland breeders

APPENDIX.—Density estimates (mean birds/ha, standard error) for five land cover types used to estimate changes in common bird species with habitat restoration in the Eagle Lake Wetland Complex, Iowa, 1999-2001

Species	Hayland		Pasture		Restored				Rowcrop agriculture	
					Grassland		Wetland			
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Grassland-breeding birds:										
Sedge wren <i>(Cistothorus platensis)</i>	0.17	0.10	0.16	0.09	0.66	0.12	0.25	0.12	0.00	0.00
Savannah sparrow <i>(Passerculus sandwichensis)</i>	1.17	0.33	2.33	0.54	0.81	0.21	0.17	0.17	0.06	0.04
Grasshopper sparrow <i>(Ammodramus savannarum)</i>	0.08	0.07	0.61	0.20	0.52	0.26	0.13	0.09	0.01	0.01
Dickcissel <i>(Spiza americana)</i>	0.74	0.32	0.13	0.07	0.45	0.12	0.04	0.04	0.01	0.01
Bobolink <i>(Dolichonyx oryzivorus)</i>	1.02	0.37	1.23	0.48	2.15	0.20	0.17	0.17	0.02	0.02
Western meadowlark <i>(Sturnella neglecta)</i>	0.00	0.00	0.21	0.10	0.04	0.02	0.00	0.00	0.00	0.00
Wetland-breeding birds:										
Virginia rail <i>(Rallus limocola)</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.14	0.00	0.00
Sora <i>(Porzana carolina)</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.72	0.22	0.00	0.00

APPENDIX. (continued)

Species	Hayland		Pasture		Restored				Rowcrop agriculture	
					Grassland		Wetland			
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
American coot (<i>Fulica americana</i>)	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.13	0.00	0.00
Marsh wren (<i>Cistothorus palustris</i>)	0.00	0.00	0.00	0.00	0.00	0.00	1.31	0.65	0.00	0.00
Swamp sparrow (<i>Melospiza geogiana</i>)	0.00	0.00	0.04	0.03	0.13	0.05	1.39	0.47	0.00	0.00
Yellow-headed blackbird (<i>Xanthocephalus xanthocephalus</i>)	0.00	0.00	0.00	0.00	0.00	0.00	5.77	2.54	0.08	0.08
Other breeding birds ^a :										
Killdeer (<i>Charadrius vociferus</i>)	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.35	0.11
Horned lark (<i>Eremophila alpestris</i>)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.03
Common yellowthroat (<i>Geothlypis trichas</i>)	0.28	0.08	0.08	0.05	0.76	0.16	2.15	0.52	0.02	0.01
Vesper sparrow (<i>Pooecetes gramineus</i>)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.06
Song sparrow (<i>Melospiza melodia</i>)	0.02	0.02	0.03	0.02	0.17	0.07	0.55	0.34	0.02	0.02

APPENDIX. (continued)

Species	Hayland		Pasture		Restored				Rowcrop agriculture	
					Grassland		Wetland			
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Red-winged blackbird <i>(Agelaius phoeniceus)</i>	1.78	0.49	1.57	0.71	1.63	0.25	12.17	1.37	0.27	0.13
Brown-headed cowbird <i>(Molothrus ater)</i>	0.00	0.00	0.19	0.12	0.09	0.05	0.04	0.04	0.06	0.03
American goldfinch <i>(Carduelis tristis)</i>	0.00	0.00	0.09	0.08	0.07	0.03	0.17	0.09	0.00	0.00

^aIncludes species that tend to breed in > 1 land cover type or are non-obligate grassland/wetland breeders

CHAPTER 6. CONSEQUENCES OF CLIMATE VARIATION ON DENSITY AND REPRODUCTION IN WETLAND SONGBIRDS

A paper to be submitted to *Oecologia*

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Abstract Annual variability in abiotic factors can be pronounced, especially in systems relying on precipitation, such as arid regions and prairie potholes. We report how annual variation in precipitation between 1999-2002 in the Prairie Pothole Region of Iowa affected both density and reproduction of two interspecific competitors: yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) and red-winged blackbirds (*Agelaius phoeniceus*). During dry years yellow-headed blackbirds, an obligate wetland-breeding species, showed a marked reduction in density and a complete reproductive failure, in which none of nests we monitored fledged young. This reproductive failure was attributed primarily to predation, which was negatively correlated with water levels in wetlands. Conversely, red-winged blackbirds, a facultative wetland-breeding species, showed little variation in density and nest success. Both species exhibited similar patterns of reduced clutch size and later nest initiation dates in dry years, measures often tied to bottom-up effects of food availability and/or age of individuals. Yet top-down effects of nest predation had stronger population implications, because lower clutch size did not result in fewer young fledged per successful nest. Ultimately, these effects could be exacerbated with either directional trajectories of decreased precipitation or increased variability in precipitation, owing to global climate change.

Key words Climate variation, precipitation variation, Prairie Pothole, top-down effects, wetland birds

Introduction

The relative importance of abiotic and biotic processes in regulating populations and structuring communities has been a long-standing debate in ecology (e.g., Davidson and

Andrewartha 1948, MacArthur 1958). In particular, the role of climate and climate variation has gained renewed interest in light of global climate change (e.g., Root et al. 2003). Recent evidence suggests that climate variation can have both direct and indirect impacts on primary productivity (Knapp and Smith 2001), behavior (Post et al. 1999), species distribution (Warren et al. 2001), population dynamics (Sæther et al. 2000, Sillett et al. 2000), species interactions (Spiller and Schoener 1995, Post et al. 1999), and natural selection (Grant and Grant 2002). Climate variation is thought to play a pivotal role in population and community dynamics in arid regions (Polis et al. 1997, Grant et al. 2000, Morrison and Bolger 2002), wetlands (Johnson et al. 1989, Weller 1999), and other systems constrained by either precipitation or temperature (e.g., Inouye et al. 2000, Sæther et al. 2000). Identifying the direct and indirect effects of climate variation on biotic processes will be critical for understanding population and community dynamics, especially for estimating population and community trajectories with global climate change (Martin 2001, Root et al. 2003).

Interannual variability in precipitation affects wetland conditions by altering both water levels and habitat structure (e.g., Weller 1999). This, in turn, can affect both habitat selection and fecundity of wetland-nesting birds. Some species, such as yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), may not settle to breed in areas of poor wetland condition that occur due to low precipitation (Weller and Fredrickson 1974). Furthermore, fecundity may be compromised for at least two reasons: 1) variation in life-history parameters, in which certain parameters tied to fecundity, such as clutch size, are negatively affected by shallow water levels, and 2) variation in nest success, in which nest predation is positively affected by shallow water levels (Picman et al. 1993). Variation in reproductive life-history parameters has been correlated with “bottom-up” effects of food availability for many songbirds (Arcese and Smith 1988, Rodenhouse and Holmes 1992, Turner and McCarty 1998; but see Arnold 1992), and food availability has been linked to variable water levels in wetlands (Voigts 1976, Turner and McCarty 1998, Murkin et al. 2000). However, “top-down” effects of predation are generally thought to be the primary factor responsible for nesting success and fecundity in songbirds (Ricklefs 1969), and predation rates can vary relative to water depth and wetland conditions (Robertson 1972, Johnson et al. 1989, Picman et al. 1993). Understanding the relative role of these potential

forces with climate variation will be critical for interpreting the long-term viability of wetland populations constrained by climate.

We compared how interannual variation in precipitation in the Prairie Pothole Region of Iowa affected both density and reproduction of two wetland-breeding species, the yellow-headed blackbird, an obligate wetland breeder, and the red-winged blackbird (*Agelaius phoeniceus*), a facultative wetland breeder. These species are related members of the family Icteridae (Lanyon and Omland 1999) that exhibit strong interspecific competition (Orians and Willson 1964), thought to be related to their vast overlap in food resources and preferences for similar nesting substrates (Orians and Willson 1964, Voigts 1973). Both species have recently declined in the Midwest, but yellow-headed blackbirds have declined at a faster rate than red-winged blackbirds (Fletcher and Koford 2003). In addition, we also untangled the importance of wetland conditions on various constraints of breeding birds by addressing diverse measures of reproductive output closely tied to predation and food limitation.

Methods

Study area

Our study area was located in Hancock and Winnebago counties, north-central Iowa (43°N 94°W), as part of a larger study on the effects of habitat restoration on bird populations (Fletcher and Koford 2002, 2003). The study area encompassed approximately 162 km² and contained a complex of federal waterfowl production areas (WPAs) and state wildlife management areas (WMAs) in an agricultural landscape. We focused on all WPAs and WMAs within the area that contained wetland potholes, totaling 10 restored wetland complexes, all of which also contained restored grassland surrounding wetland habitat. We defined wetland complexes as the total number of seasonal, semipermanent, and permanent wetlands (as defined in Cowardin et al. 1979) within a WPA or WMA (sensu Fairbairn and Dinsmore 2001). See Fletcher and Koford (2003) for detailed descriptions of restoration techniques for grassland and wetland habitat. Dominant wetland vegetation included cattails (*Typha* spp.), bulrush (*Scirpus* spp.), and reed canary grass (*Phalaris arundinacea*).

Bird surveys

From 1999-2002, we surveyed wetland birds using a standard protocol (cf. Delphey and Dinsmore 1993, Naugle et al. 1999). Each restored wetland complex was surveyed three times during the breeding season: 15 May-5 June, 6-22 June, and 23 June-5 July. We conducted wetland bird surveys using 8-min, 20-m fixed-radius point counts. Point count locations were ≥ 75 m apart. We played taped calls to detect secretive species (*Rallus limocola*, *Porzana carolina*, *Ixobrychus exilis*, *Botaurus lentiginosus*) during minutes 3-5 of each survey. Surveys were conducted between sunrise and 4 hours after sunrise and were not conducted during high wind velocities (≥ 20 km/hr) or during precipitation. During surveys, observers recorded all birds seen or heard, including how individuals were detected (song, visual, or call), sex of individuals, and distances of birds from the center point. We did not include birds flying over points in our analyses. Distances (m) to birds seen were estimated using a rangefinder. Here, we report on red-winged and yellow-headed blackbird densities, but see Appendix for density estimates of other species.

Wetland boundaries were delineated using aerial photographs taken in 1999 and count locations were selected using a geographic information system. We considered wetland complexes within WPAs and WMAs as independent units, so we combined the perimeters of each wetland in a complex into one overall length, split the length into three equal segments, and selected one random point along each segment, totaling three point-count locations for each complex ($n = 8$ complexes; two complexes were not surveyed due to small size but were used for monitoring breeding biology; see below). Based on 1999 photographs, points were centered in the emergent vegetation zone, or at the water's edge when no emergent vegetation was present (Delphey and Dinsmore 1993). We repeated surveys at each point-count location during each time period ($n = 72$ points/y). Although wetland conditions varied among years (see Results), the same count locations were repeated each year. Therefore, a count location could be along the water's edge in one year but not in another year if water levels changed between years.

Breeding biology

In 1999, we systematically searched five of the wetland complexes for wetland bird nests; in 2000-2002, we systematically searched all wetland complexes ($n = 10$). Once nests were found, we placed a wire flag or flagging tape 4 m away from the nest in a cardinal direction. We visited nests every 2-4 d to determine their fate. To minimize problems of assigning uncertain nest fates (Manolis et al. 2000), we considered nests successful if at least one host nestling remained in the nest at day 7-8 (approximately one day before the earliest known fledging date for these species; Twedt and Crawford 1995, Yasukawa and Searcy 1995). We defined the number of fledglings/successful nest as the number of host nestlings that remained in the nest on the final visit (day 7-8). We defined the clutch size as the maximum number of host eggs observed in nests during the incubation stage. We initially analyzed clutch size for all nests; however, we also analyzed non-parasitized nests only to determine if patterns were consistent because parasitism events could reduce clutch sizes of parasitized nests. Because we often found nests after the onset of incubation, we estimated the nest initiation date, defined as the first day of incubation, for each nest by estimating the age of eggs (using candlers; Lokemoen and Koford 1996) or nestlings (using descriptive accounts from known-aged nests). We did not include nests that were abandoned due to observer activity in any analyses ($n = 11$ for red-winged blackbirds; $n = 8$ for yellow-headed blackbirds). We considered nests abandoned due to observers if the nest was abandoned on the first nest-monitoring visit after the nest was found.

Climate variation

We compared the effects of precipitation at different scales. To examine density and reproduction at the scale of the wetland, we measured water depth (cm) at point-count locations after each survey at 4 locations within the point-count area: 1 at the center of the point, and at 3 locations 0° , 120° , and 240° from the center, at distances of 10 m. To examine breeding success at local scales within wetlands, we measured water depth directly beneath nest sites when nests were initially found and when nests were terminated (2000-2002 only). Since these measures were highly correlated ($r = 0.98$), for analyses we only use water depth at the time of nest termination.

At a larger temporal scale, we compared precipitation for each year during our study to long-term precipitation patterns gathered from 1932-2002 at a standard National Oceanic and Atmospheric Administration (NOAA) weather observation station located 7.5-23 km from study sites (<http://lwf.ncdc.noaa.gov/oa/climate/stationlocator.html>). For analyses, we defined a "bioyear" as the total precipitation occurring from August of the preceding year to July of the current year (*sensu* Rotenberry and Wiens 1991, Morrison and Bolger 2002). To better interpret settlement patterns, we compared the amount of precipitation occurring from August of the preceding year to April of the current year, just prior to the onset of breeding in these species (i.e., prebreeding season precipitation; *sensu* Morrison and Bolger 2002).

Statistical analyses

We calculated bird density (number of males or females/ha) for common species using the program DISTANCE (Buckland et al. 1993). DISTANCE uses distances from the center point to individuals for calculating detection functions and subsequently corrects for detectability when estimating density. Density was estimated for each site in each year using a global detection function across years (see Fletcher and Koford 2002 for more details). Using these density estimates, we then tested for among-year differences in male and female density (birds/ha) using a mixed-model analysis, with site as the repeated measure (Littell et al. 1996). This repeated measure was modeled by specifying four potential covariance structures: variance components, autoregressive order one, compound symmetric (exchangeable), and unstructured covariance (Littell et al. 1996:93-102). We then selected the most parsimonious covariance structure using Akaike's Information Criterion, adjusted for small sample sizes (AICc; Littell et al. 1996:93-102, Burnham and Anderson 1998). Density was log transformed ($\ln(x+1)$) to improve normality and homogeneity of variance. We tested for among-year differences in water depth measured at point count locations using a similar repeated measures framework.

To untangle the influence of abiotic effects on reproduction, we tested two reproductive measures tied to top-down forces and four measures independent of top-down forces that are more closely tied to bottom-up effects due to food availability. Top-down parameters included nest parasitism from brown-headed cowbirds (*Molothrus ater*) and nest

predation, both of which can have severe impacts on fecundity (e.g., Pease and Grzybowski 1995). Other parameters included nest initiation date, clutch size, nestling survival rate within nests, and the number of fledglings/successful nest. These parameters, particularly clutch size and nest initiation date, are commonly tied to food availability (reviewed in Arcese and Smith 1988). We considered nestling survival to be influenced by habitat quality based on food availability, rather than predation pressure (see also Rodenhouse and Holmes 1992, Morrison and Bolger 2002). Although it is possible that a predator could remove individual nestlings without removing the entire brood, this is unlikely (Knight et al. 1985, Rodenhouse and Holmes 1992, Pietz and Granfors 2000). Clutch size and nestling survival, in turn, directly affect the number of fledglings/successful nest.

We estimated daily predation rates (DPR) for nests using the Mayfield method (Mayfield 1975, Johnson 1979). We used the midpoint assumption for estimating failure dates between nest visits (Johnson 1979). We focused on DPR instead of daily survival rates (Johnson 1979) to isolate effects of predation, because some nests failed for reasons other than predation (e.g., weather; see Results). We used program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989) to test for differences in DPR among years for the incubation and nestling stage, and for the entire nesting cycle. To further evaluate nest predation, we developed models to explain the probability of nest predation for each species using generalized linear mixed models with a logit link function (Littell et al. 1996). Site was considered a repeated measure (as above) and explanatory variables included year, water depth beneath nests, and mean wetland water depth (derived from measurements taken at point counts). All possible combinations (not including interactions) were compared with an intercept only model ($n = 8$ models), because we expected each of these variables to potentially explain predation pressure. The most parsimonious model was selected using AICc (Burnham and Anderson 1998). Because brown-headed cowbirds only parasitized 4 nests with > 1 egg, we also tested for differences in the probability of brood parasitism among years using generalized linear mixed models with a logit link function, similar in structure to the mixed models listed above.

We tested for differences in clutch size and the number of fledglings/successful nest using a mixed model analysis, similar to that for surveys. For clutch size, we also included

nest initiation date (Julian date) as a covariate in models, because clutch size can decline over time within breeding seasons (Arnold 1992). We tested for year effects on nest initiation dates using Kruskal-Wallis nonparametric tests (Rodenhouse and Holmes 1992). We tested for year effects on partial brood loss by estimating individual nestling survival rates within nests using a modified Mayfield model that accounts for a lack of independence among nestlings within a nest by considering each nest as a clustered sampling unit (Flint et al. 1995). We right-censored data when nests terminated, either from fledging or failing, to focus on nestling mortality in the absence of predation pressure. As with DPR, we tested for year effects using program CONTRAST (Hines and Sauer 1989; Flint et al. 1995).

Prior to all analyses, we identified three orthogonal contrasts to interpret year effects on density, water depth, and reproduction: 1) contrasts between wet years (1999 v. 2001; see Fig. 1), 2) contrasts between dry years (2000 v. 2002), and 3) contrasts between the average of wet and dry years. We expected precipitation to govern any year effects and thus expected no evidence for differences within wet years and within dry years (contrast 1 and 2), but we expected evidence for differences between the average of wet and dry years (contrast 3).

Results

Climate conditions

Water depth at point count locations varied among years ($F_{3,21} = 25.64$, $P < 0.001$), with water depth being shallower in 2000 and 2002 (Fig. 1a). Based on contrasts, 1999 and 2001 did not differ ($F_{1,21} = 1.26$, $P = 0.275$), and 2000 and 2002 did not differ ($F_{1,21} = 1.18$, $P = 0.289$); however, water depth differed between wet years and dry years ($F_{1,21} = 67.68$, $P < 0.0001$). From NOAA data, total precipitation estimates in 2000 and 2002 were lower than the 71-year average for bioyear (August-July) and prebreeding season precipitation (August-April), whereas 1999 and 2001 were above the 71-year average (Fig. 1a). In each case, annual precipitation estimates were > 2 standard errors above or below the long-term average. Total precipitation for the prebreeding season and for the bioyear was highest in 1999, compared with the other three years (Fig. 1a). In 2000, conditions were very dry prior to breeding (Fig. 1b), but rainfall increased in June, increasing water levels within wetlands. In 2001, precipitation was extremely high in May and then dropped off in June and July (Fig.

1b). In 2002, precipitation was low during the entire year, causing total bioyear precipitation to be the lowest over the four years (Fig. 1a, b). Water depth measured in wetlands was more closely correlated with bioyear precipitation ($r = 0.88$) than prebreeding season precipitation ($r = 0.83$).

Density

Red-winged blackbirds were more commonly observed during point counts ($n = 385$ observations) than yellow-headed blackbirds ($n = 136$ observations). There was no evidence for red-winged blackbird density differing among years ($F_{3,21} < 0.68$, $P > 0.57$; Fig. 2a). However, both male and female yellow-headed blackbird density varied among years ($F_{3,21} > 3.43$, $P < 0.036$); densities were much lower during 2000 and 2002 (Fig. 2b). Based on contrasts, yellow-headed blackbird density did not differ between 1999 and 2001 ($F_{1,21} < 1.97$, $P > 0.17$), or 2000 and 2002 ($F_{1,21} < 0.07$, $P > 0.80$), although density differed between wet years and dry years ($F_{1,21} > 8.30$, $P < 0.009$). For each sex of each species, a uniform model function with no adjustments was best at explaining detectability, indicating that detectability was high within our entire fixed radius (see also Fletcher and Koford 2002). Although point locations were selected during a wet year (1999), which could potentially produce a negative bias for density estimates during dry years, we found very few nests of yellow-headed blackbirds (see below) and had few detections outside of count circles during dry years (2000: $n = 10$, 2002: $n = 4$), exemplifying that yellow-headed blackbird density was indeed substantially lower during dry years.

Reproduction

Between 1999-2002, we monitored 228 red-winged and 104 yellow-headed blackbird nests (Table 1). Red-winged blackbirds bred at all 10 sites, whereas yellow-headed blackbirds bred at only 4 sites. In red-winged blackbirds, predation and abandonment accounted for 95.1% and 2.8% of nest failure, respectively. In yellow-headed blackbirds, predation and abandonment accounted for 74.1% and 24.1% of nest failure, respectively. DPR for red-winged blackbirds did not differ among years for the entire nesting cycle ($\chi^2 = 2.011$, $df = 3$, $P = 0.570$) or for either the incubation or the nestling stages ($\chi^2 < 5.58$, $df = 3$, $P > 0.13$). In

2000 and 2002, yellow-headed blackbirds experienced a complete reproductive failure, in which all of the nests we monitored failed (Table 1). In these dry years, predation accounted for 93% of nest failure. DPR for yellow-headed blackbirds differed among years for the entire nesting cycle (2000 not included because only one nest found: $\chi^2 = 11.86$, $df = 2$, $P = 0.003$) and for the incubation and nestling stages ($\chi^2 > 6.14$, $df = 2$, $P < 0.047$). For each stage and for the entire cycle, DPR for yellow-headed blackbirds did not differ between wet years ($\chi^2 < 0.72$, $df = 1$, $P > 0.42$), but was much higher in dry years than in wet years ($\chi^2 > 6.14$, $df = 1$, $P < 0.014$). Daily survival rates, which included all sources of nest failure, showed similar patterns (Table 1).

The best model to explain the probability of predation for red-winged blackbirds included water depth beneath nests and wetland water depth ($\text{logit}(y) = 0.42 - 0.03(\text{nest}) + 0.02(\text{wetland})$; nest: $F_{1,152} = 2.64$, $P = 0.10$; wetland: $F_{1,152} = 0.87$, $P = 0.35$), but precision for parameter estimates in this model was low (Fig. 3a, b). The best model to explain the probability of predation for yellow-headed blackbirds included only the water depth beneath nests ($\text{logit}(y) = 2.76 - 0.06(\text{nest})$; nest: $F_{1,69} = 8.09$, $P = 0.006$; Fig. 3c). Throughout the study, yellow-headed blackbirds tended to nest over deeper water ($\bar{x} = 49.5 \pm 21.2$ cm, SD) than red-winged blackbirds ($\bar{x} = 7.0 \pm 15.0$ cm, SD). There was no evidence for parasitism rates differing among years for red-winged blackbirds (Fig. 4a; $F_{3,19} = 1.46$, $P = 0.256$). However, contrasts revealed weak evidence for higher parasitism rates in dry years than in wet years ($F_{1,19} = 3.31$, $P = 0.084$), but not differing between 1999 and 2001 ($F_{1,19} = 0.87$, $P = 0.361$), or 2000 and 2002 ($F_{1,19} = 0.59$, $P = 0.452$). None of the 104 yellow-headed blackbird nests were parasitized by brown-headed cowbirds.

When controlling for clutch variation as a function of Julian date, clutch size varied among years for red-winged blackbirds ($F_{3,19} = 3.60$, $P = 0.033$), with size being lower in dry years than in wet years ($F_{1,19} = 7.24$, $P = 0.015$; Fig. 4b); however, size did not differ between wet years ($F_{1,19} = 1.09$, $P = 0.310$) or between dry years ($F_{1,19} = 0.04$, $P = 0.843$), based on contrasts. This relationship remained consistent when only analyzing non-parasitized nests ($F_{3,19} = 3.21$, $P = 0.046$). Yellow-headed blackbirds showed similar patterns in clutch size estimates (Fig. 4b), but patterns were not significant and were based on few sites, so inference is limited ($F_{3,1} = 2.30$, $P = 0.443$). Clutch size declined with Julian

date in red-winged blackbirds ($F_{1,161} = 8.52, P = 0.004$), but showed no substantial decline in yellow-headed blackbirds ($F_{1,82} = 2.72, P = 0.103$).

The number of nestlings fledged/successful nest did not differ among years for red-winged blackbirds ($F_{3,16} = 1.94, P = 0.163$; Fig. 4c). For yellow-headed blackbirds, the number of nestlings fledged/successful nest tended to be lower in 2001 than 1999, but inference is limited because patterns were based on few sites (Fig. 4c). Partial brood loss from nestling mortality did not differ among years for red-winged blackbirds ($\chi^2 = 3.14, df = 3, P = 0.37$), but mortality differed for yellow-headed blackbirds ($\chi^2 = 59.03, df = 2, P < 0.001$; Table 2). For yellow-headed blackbirds, survival rates were lower in 2001 than in 1999 ($\chi^2 = 8.45, df = 1, P = 0.0037$) and rates differed between wet and dry years ($\chi^2 = 36.16, df = 1, P < 0.001$), although this contrast is limited because of the small sample size in dry years (5 nests, each of which was depredated after the first monitoring visit during the nestling stage).

Nest initiation dates varied among years for both red-winged blackbirds ($\chi^2 = 25.50, df = 3, P < 0.0001$) and yellow-headed blackbirds ($\chi^2 = 39.27, df = 3, P < 0.0001$; Fig. 5). Nest initiation dates for red-winged blackbirds tended to be later in 2002 than in other years (Fig. 5). For yellow-headed blackbirds, nest initiation dates were later in both dry years, but only one nest was found in 2000, limiting inference for that year. However, in 2002 there was a dramatic shift in initiation dates, in which the peak initiation occurred approximately 3 weeks later than peak initiation dates in wet years (Fig. 5).

Discussion

Abiotic variation among years had pronounced effects on both density and reproduction for blackbirds breeding in restored wetland potholes of northern Iowa. Although effects on density and reproduction were stronger for yellow-headed blackbirds, red-winged blackbirds also exhibited variation in some reproductive measures. Why were effects more severe for yellow-headed blackbirds? Both species prefer similar nesting areas in wetlands (Orians and Willson 1964, Miller 1968), exhibit marked overlap in foraging preferences (Orians and Willson 1964, Voigts 1973), and are closely related phylogenetically (Lanyon and Omland 1999). However, yellow-headed blackbirds are considered obligate wetland-breeders, being

closely tied with distinct wetland conditions that require emergent vegetation over deep water (Miller 1968), whereas red-winged blackbirds are more opportunistic, breeding in a variety of habitats (e.g., Miller 1968, Yasukawa and Searcy 1995). The relative plasticity in these preferences between species may help explain differences in both density and reproduction (see below), because water levels are closely tied to both nest-site availability (e.g., Lederer et al. 1975) and predation pressure (Robertson 1972, Picman et al. 1993).

Density and climate variation

Interannual variation in precipitation affected habitat selection in yellow-headed blackbirds, which tended not to settle in the study area during dry years. Yellow-headed blackbirds tend to settle for breeding in areas of high emergence rates of odonates, a primary prey item for feeding nestlings (Orians and Wittenberger 1991). Odonate and other aquatic insect emergence and abundance is closely tied with water levels in wetlands (Voigts 1976, Turner and McCarty 1998, Murkin et al. 2000), providing a link between annual abiotic variation and food supply in wetlands. However, yellow-headed blackbirds also prefer relatively high emergent vegetation density when selecting nest sites (Miller 1968, Orians and Wittenberger 1991), which can also vary with interannual annual variability in precipitation (Weller and Spatcher 1965, Lederer et al. 1975). Although it is unclear if the settlement patterns we observed were tied to insect emergence rates or habitat structure, it is clear that this pattern was closely linked with annual variation in precipitation.

Life-history parameters and climate variation

Two life-history parameters independent of predation pressure changed among years with climate variation: clutch size and nest initiation date. Red-winged blackbirds had lower clutch sizes during dry years and yellow-headed blackbirds showed similar patterns, although sample size was low in dry years because of their reduced density. Nest initiation dates for each species also varied among years; initiation dates were later in 2002 (a dry year) than during other years (Fig. 5). Arcese and Smith (1988) reviewed food supplementation experiments on birds and found that the life-history parameters most often influenced by food were nest initiation dates and clutch size. Yet in some migratory species, evidence

suggests that clutch size and nest initiation dates can also be influenced by the age of female, in which older females initiate nests earlier and lay larger clutches than younger individuals (Crawford 1977).

Although variation in annual precipitation influenced clutch size and nest initiation dates, the net effect on populations was limited because reduced clutch size did not result in a reduced number of fledglings per successful nest, a measure ultimately tied to seasonal fecundity (Pease and Grzybowski 1995). In part, this was due to higher nestling mortality during 2001, which was considered a relatively wet year. Yet precipitation during June and July of that year was much lower than other years (except for 2002; Fig. 2a), which may explain this phenomenon. This underscores the need to understand how the variability and timing of precipitation within years ultimately affects reproductive output in birds (Rotenberry and Wiens 1991, Patten and Rotenberry 1999). The net effect of nest initiation variability with precipitation might not be critical for red-winged and yellow-headed blackbird populations because these species rarely raise two broods per season (Willson 1966, Twedt and Crawford 1995, Yasukawa and Searcy 1995).

Top-down effects and climate variation

Annual variation in precipitation influenced top-down forces, especially for yellow-headed blackbirds. Predation rates were generally high for red-winged blackbirds during all years of the study. Predation rates on yellow-headed blackbirds were particularly high during dry years, causing a complete reproductive failure in the nests we monitored. For both species, predation rates were negatively correlated with water levels beneath nests (Fig. 3; see also Robertson 1972, Shipley 1979). Differences in predation pressure between these species might be explained based on the plasticity in nest-site selection relative to spatial and temporal predation pressure, if we assume a modal relationship of predation pressure increasing as water depth decreases, peaking at the water's edge, and decreasing slightly into adjacent uplands (see Shipley 1979). Yellow-headed blackbirds tend to displace red-winged blackbirds from preferred habitat (Orians and Willson 1964), such that in wet years when yellow-headed blackbirds were abundant, red-winged blackbirds nested on the peripheries of wetlands where water levels were lower and predation risk was higher, leading to relatively

high predation rates on red-winged blackbirds. During dry years, yellow-headed blackbirds were less common and tend to be concentrated only in the wettest areas (although these areas were still relatively dry compared to wet years) that were much smaller in area than in wet years, thus allowing red-winged blackbirds to settle throughout most of the wetlands. However, dry conditions potentially alter the severity and shape of the predation pressure gradient, in which pressure remains high along the water's edge (where yellow-headed blackbirds are concentrated) but is comparatively lower in the remainder of the wetland. Because red-winged blackbirds may to nest throughout the wetland, spatial variation in nest-site selection may increase and potentially reduce total predation pressure relative to yellow-headed blackbirds. Investigating variation in spatial patterns of nest-site selection with interannual precipitation and its subsequent consequences on predation risk might provide insight on the differences between species and mechanisms for factors influencing nest predation. Other possible factors to explain differences between species include differences in microhabitat structure near nests (Twedt and Crawford 1995, Yasukawa and Searcy 1995, Schafer 1996), and adult aggressive behavior at nest sites, in which red-winged blackbirds tend to be more aggressive than yellow-headed blackbirds in defending their nests (R. Fletcher, *personal observation*). Regardless, effects of high predation rates on fecundity could be mitigated with individuals renesting after failure or if individuals preferentially select areas with higher water levels (Miller 1968).

Parasitism rates by brown-headed cowbirds differed between species, and for red-winged blackbirds, differed slightly between wet and dry years, with rates being higher in dry years. Yellow-headed blackbirds were not parasitized in any year. In Colorado, Ortega and Cruz (1991) found that yellow-headed blackbirds will accept cowbird eggs (see also Twedt and Crawford 1995), but that the breeding season phenology was earlier than with red-winged blackbirds, and abandonment was more frequent later in the season, thus deterring cowbird parasitism. In our system, nest initiation dates between species were similar (Fig. 5). The reasons for differences in parasitism rates between these two species remain elusive (Twedt and Crawford 1995).

Variation in precipitation is often thought to have bottom-up effects on populations by reducing food availability (e.g., Meserve et al. 2001). Numerous studies have

documented strong correlations between precipitation, food availability, and measures of reproductive output tied to food availability (e.g., Rotenberry and Wiens 1991, Turner and McCarty 1998, Grant et al. 2000, Morrison and Bolger 2002). However, top-down effects of nest predation swamped any potential bottom-up effects in our system. These top-down effects can arise from either changes in the predator community (Picman et al. 1993) or from changes in predator behavior (Post et al. 1999). In wetlands, water levels can directly affect the predator community. Picman et al. (1993) found that as water depth increased in wetlands in Ontario, the diversity of the nest predator community declined to essentially one species, the marsh wren (*Cistothorus palustris*). Although wetlands are disparate from other systems constrained by climate in this respect, Morrison and Bolger (2002) also found evidence for top-down effects of predation governing fecundity dynamics with rainfall variation in certain years for populations of rufous-crowned sparrows (*Aimophila ruficeps*) in arid, coastal sage scrub habitat of California.

Temporal dynamics and population stability

The variability in wetland conditions and its implications on reproduction and habitat selection illustrate the dynamic nature of wetland communities. In the short term, these areas may have detrimental impacts on populations when conditions are poor, but these effects might be dissipated in the long term, in terms of individual lifetime reproduction and population growth, particularly if habitat selection is adaptive (Orians 1980, Beletsky and Orians 1994, Clark and Shutler 1999). Indeed, Beletsky and Orians (1994) argued that yellow-headed blackbirds have likely adapted to highly unstable interannual wetland conditions based on variable precipitation. Ultimately, the relative consistency and periodicity of climate variability across years in the long term will be critical in determining the stability of these populations. However, this variability might become less predictable and more severe with global climate change (Timmermann et al. 1999). If precipitation declines or becomes more variable in the future causing decreases in the number of wetlands and wetland quality (Poiani and Johnson 1993, Larson 1995), some species, such as yellow-headed blackbirds, could potentially decline or suffer local extinctions due to increased variation in population fluctuations (Lande 1993).

Our results documented some short-term consequences of abiotic variation on habitat selection and reproduction in wetland birds, yet investigating longer-term and larger spatial-scale dynamics will be fruitful. For example, the wetlands we considered were primarily seasonal and semipermanent wetlands, yet permanent wetlands (as defined by Cowardin et al. 1979), or wetlands that continue to hold water even during dry conditions, may be less variable in dynamics than wetlands we considered. If so, these areas could be acting as a consistent source of recruits to populations (*sensu* Pulliam 1988). Thus, to understand the ramifications of climate variation on population dynamics of wetland birds, future research needs to incorporate not only long time scales, but also large spatial scales that include diverse wetlands that may be operating in a metapopulation context (*sensu* Hanski 1998).

Conservation implications

Because much of the historical wetland habitat in the Prairie Pothole Region of the United States has declined in the past two centuries (Dahl 1990), conservationists have responded by restoring wetlands throughout the United States (e.g., Bishop et al. 1998). Recently, spatial and landscape scales have been emphasized for conserving wetland bird populations (Naugle et al. 1999, 2000, Fairbairn and Dinsmore 2001). However, at local scales managers can actively alter water levels in restored potholes using a variety of techniques (Bishop et al. 1998, Weller 1999). Although we found positive correlations with water depth and breeding biology of these species, these effects are probably nonlinear. Years of extremely high precipitation and water depth likely lead to a lower emergent vegetation/open water ratio, thus reducing the density of potential breeding sites (Weller and Spatcher 1965, Lederer et al. 1975). Therefore, managers should strive for a balance between water depth and emergent vegetation for breeding. Yet, actively managing wetland conditions is constrained by the total amount of water available for diverting into and out of wetlands. In the face of global climate change, possible options for mitigating precipitation effects on wetland birds may be limited.

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Table 1. Daily survival rates (DSR; mean, [SE]) and daily predation rates (DPR; mean, [SE]) for red-winged blackbird and yellow-headed blackbird nests in restored wetlands, northern Iowa, 1999-2002.

Year	N	Suc	Incubation			Nestling			Entire Cycle		
			DSR	DPR	Exposure days	DSR	DPR	Exposure days	DSR	DPR	Exposure days
Red-winged blackbird											
1999	35	13	0.956 (0.013)	0.044 (0.013)	248.0	0.917 (0.025)	0.074 (0.024)	121.0	0.942 (0.012)	0.055 (0.012)	381.0
2000	72	21	0.936 (0.012)	0.062 (0.012)	436.0	0.910 (0.020)	0.090 (0.020)	200.0	0.922 (0.011)	0.074 (0.010)	650.5
2001	54	24	0.918 (0.016)	0.078 (0.016)	294.0	0.964 (0.014)	0.036 (0.014)	168.0	0.937 (0.011)	0.061 (0.011)	479.0
2002	67	27	0.928 (0.014)	0.065 (0.014)	321.5	0.936 (0.017)	0.064 (0.017)	202.0	0.926 (0.011)	0.071 (0.011)	538.5
Total	228	85	0.934 (0.007)	0.063 (0.007)	1299.5	0.932 (0.010)	0.067 (0.009)	691.0	0.930 (0.006)	0.066 (0.005)	2049.0
Yellow-headed blackbird											
1999	17	10	0.991 (0.009)	0.009 (0.009)	111.5	0.933 (0.026)	0.056 (0.024)	89.5	0.966 (0.013)	0.029 (0.012)	208.0
2000	1	0	*		1.5	*		0.0	*		1.5
2001	72	40	0.980 (0.006)	0.011 (0.004)	649.0	0.952 (0.011)	0.034 (0.010)	352.0	0.969 (0.005)	0.019 (0.004)	1027.0
2002	14	0	0.895 (0.038)	0.105 (0.038)	66.5	0.583 (0.142)	0.417 (0.142)	12.0	0.841 (0.039)	0.148 (0.038)	88.0
Total	104	50	0.973 (0.006)	0.020 (0.005)	828.5	0.938 (0.011)	0.046 (0.010)	453.5	0.959 (0.005)	0.030 (0.005)	1324.5

*Not estimable: 1 nest found, which was depredated after 1.5 exposure days

Table 2. Daily nestling survival rates within nests (DSR; mean, standard error [SE]) for red-winged blackbird and yellow-headed blackbird nests in restored wetlands, northern Iowa, 1999-2002. Nests were right-censored for nest termination (failure or success) to isolate partial brood loss. Modified Mayfield estimates based on considering nestlings within a nest as a clustered sampling unit (Flint et al. 1995).

Year	Number of				Modified Mayfield estimates	
	Nests	Nestlings	Nestling mortalities	Exposure days	DSR	SE
Red-winged blackbird						
1999	23	71	2	338	0.994	0.006
2000	36	115	7	524	0.987	0.005
2001	30	92	11	495	0.978	0.008
2002	36	95	8	449	0.982	0.007
Total	125	373	28	1806	0.984	0.003
Yellow-headed blackbird						
1999	17	36	5	215	0.977	0.012
2000	0	0	0	0	*	*
2001	72	161	52	777	0.933	0.009
2002	5	11	0	14	1.000**	0.000
Total	104	208	57	1006	0.943	0.007

*Not estimable: 1 nest found, which was depredated during incubation

**All five nests were depredated after the first nestling visit, so inference is limited

Figure 1. A) Among-year variation in total precipitation and wetland water depth (\bar{x} , SE), and B) within-year variation in total precipitation in northern Iowa, 1999-2002, compared to the long-term precipitation average for northern Iowa (1932-2002). Wetland water depth was measured at point count locations, May-July, 1999-2002. Total precipitation was measured at a standard National Oceanic and Atmospheric Administration (NOAA) weather observation station located near the study area, northern Iowa. Total precipitation from NOAA was split into "bioyear" (the total precipitation occurring from August of the preceding year to July of the current year) and "prebreeding season precipitation" (the total precipitation occurring from August of the preceding year to April of the current year) to better understand settlement patterns (Morrison and Bolger 2002).

Figure 2. Density estimates (birds/ha; $\bar{x} + SE$) each year for male and female A) red-winged and B) yellow-headed blackbirds in restored wetlands, northern Iowa, 1999-2002.

Figure 3. Partial regression relationships (estimates and 95% confidence intervals) of the best logistic models (based on Akaike's Information Criterion, adjusted for small sample sizes) to explain the probability of predation on red-winged and yellow-headed blackbird nests, northern Iowa, 1999-2002. For red-winged blackbirds, the best model included A) the wetland water depth (based on measurements taken at point counts), and B) the water depth directly under nests ($\text{logit}(y) = 0.42 + 0.02(\text{wetland}) - 0.03(\text{nest})$). For yellow-headed blackbirds, the best model included only C) the water depth directly under nests ($\text{logit}(y) = 2.76 - 0.06(\text{nest})$).

Figure 4. Estimates of A) brood parasitism rate (probability of parasitism), B) clutch size, and C) number of fledglings/successful nest each year ($\bar{x} + SE$) for red-winged and yellow-headed blackbirds in restored wetlands, northern Iowa, 1999-2002.

Figure 5. Distribution of nest initiation dates (i.e., first day of incubation) each year for A) red-winged and B) yellow-headed blackbirds in restored wetlands, northern Iowa, 1999-2002.

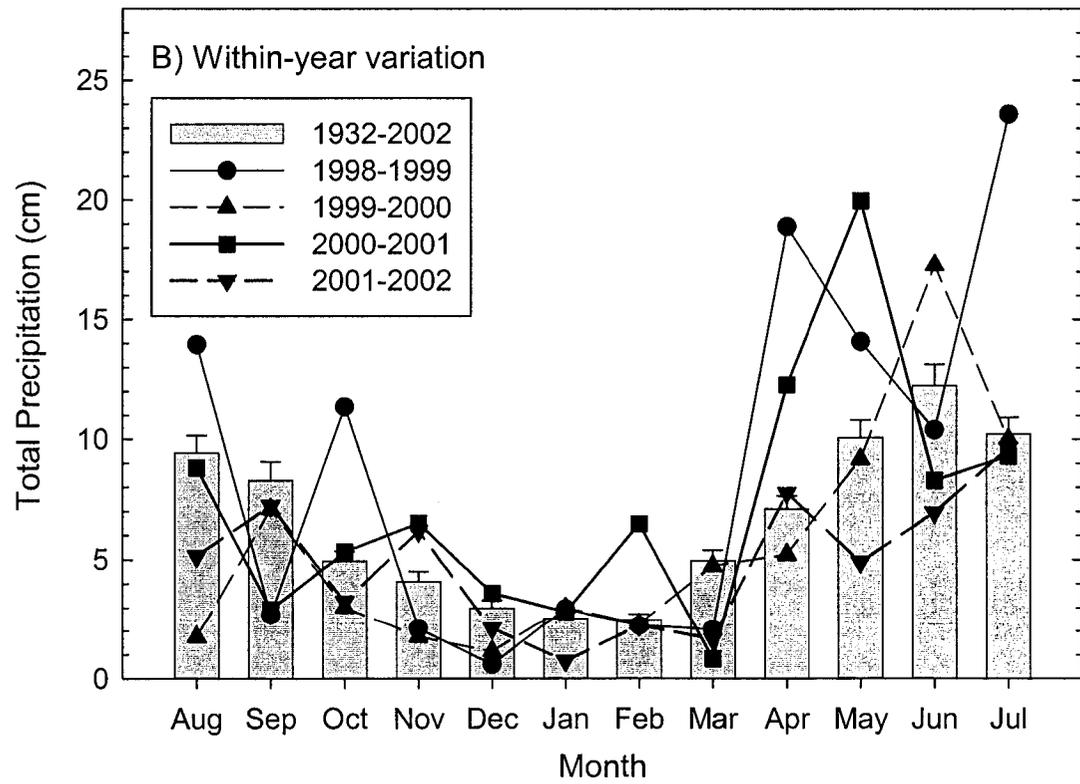
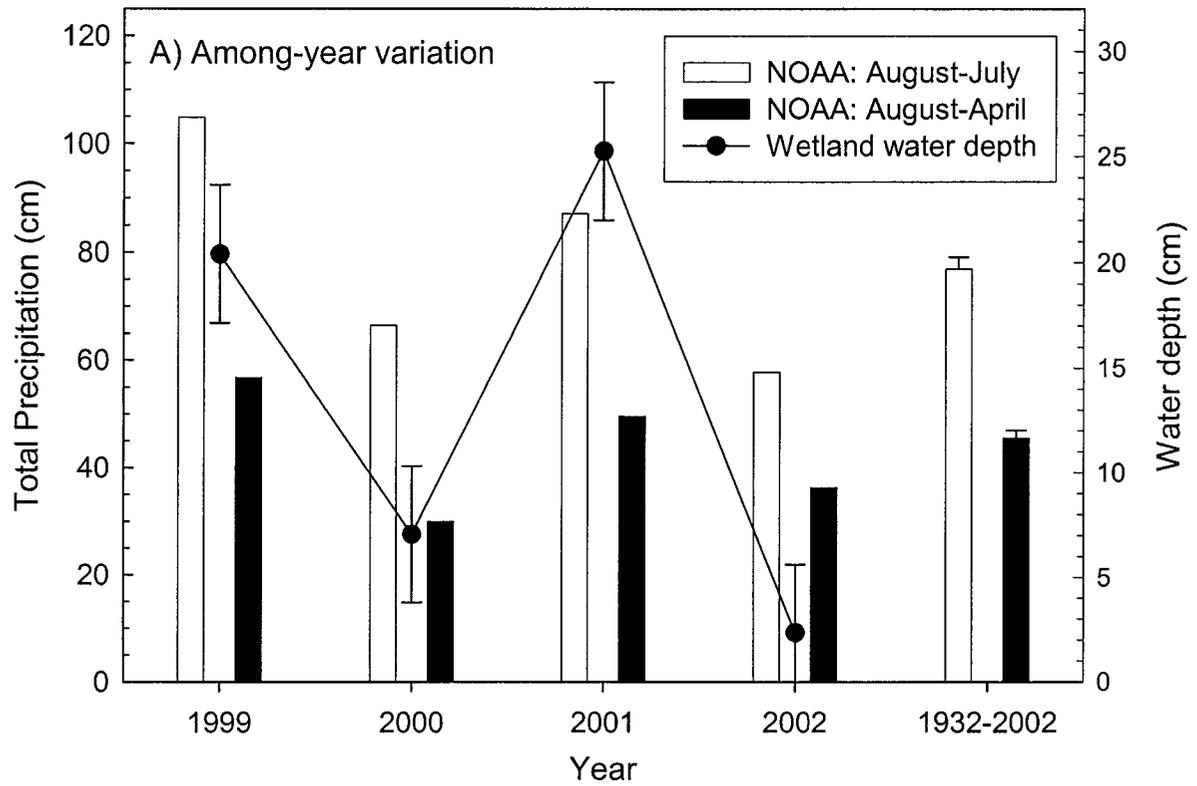


Figure 1

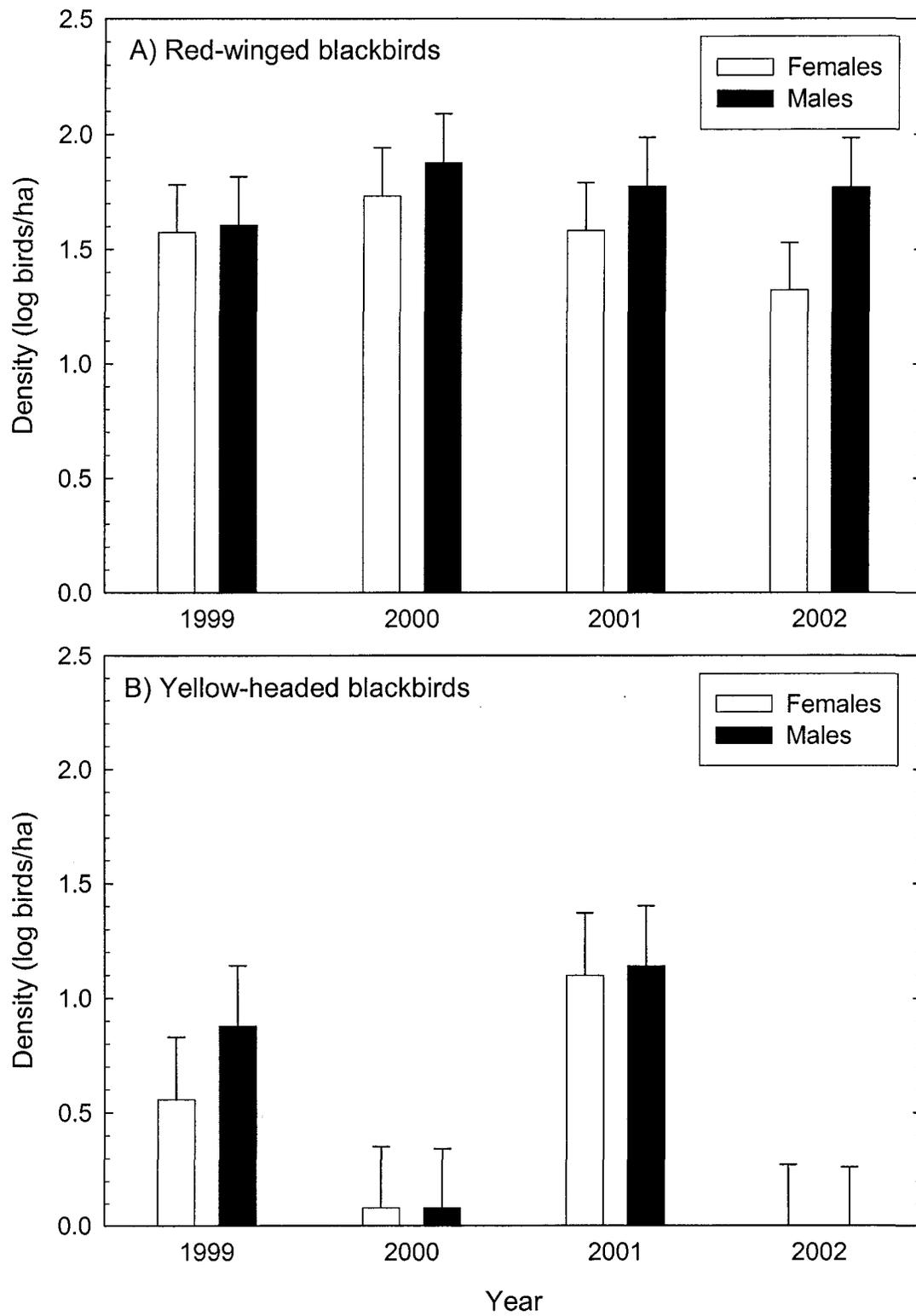


Figure 2

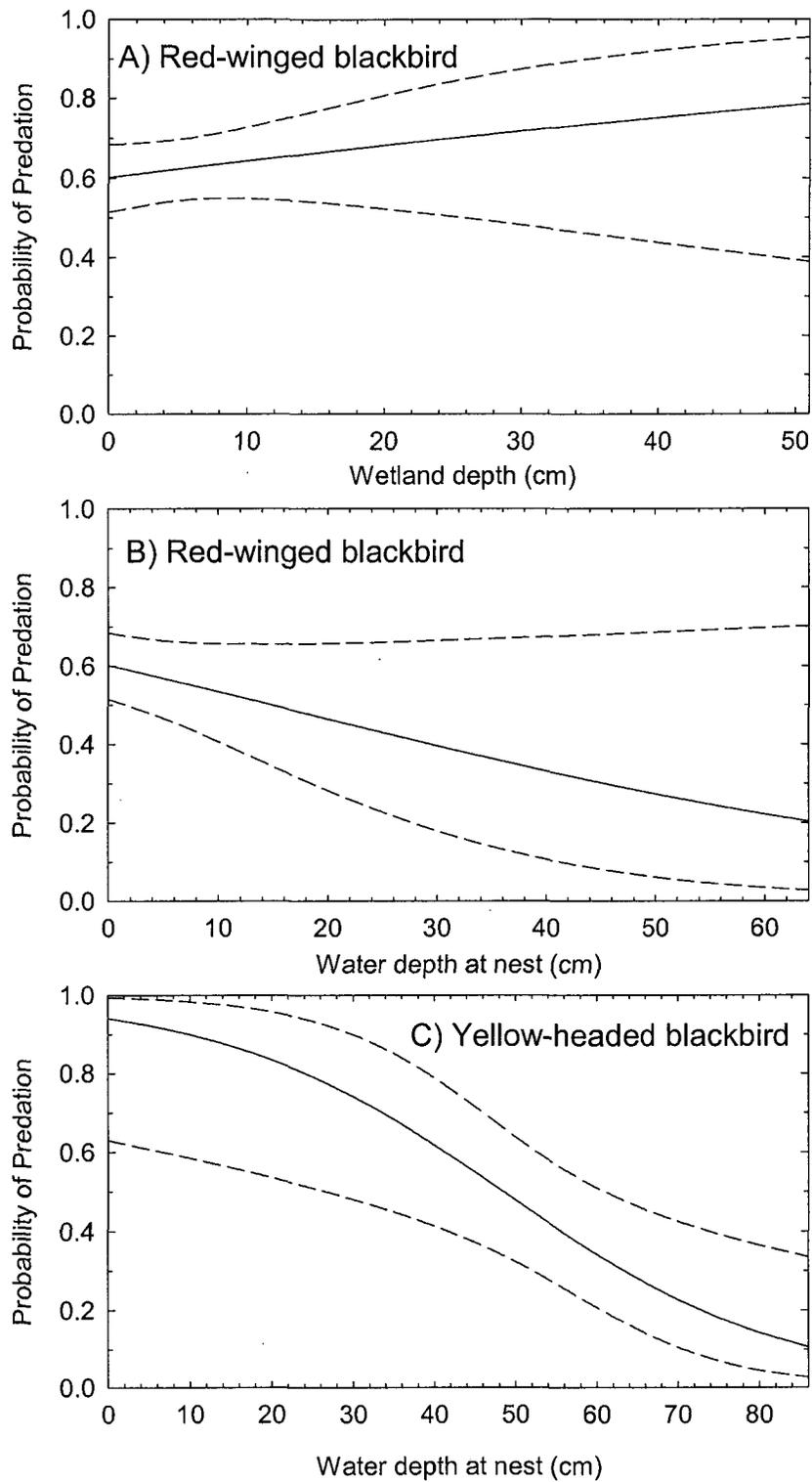


Figure 3

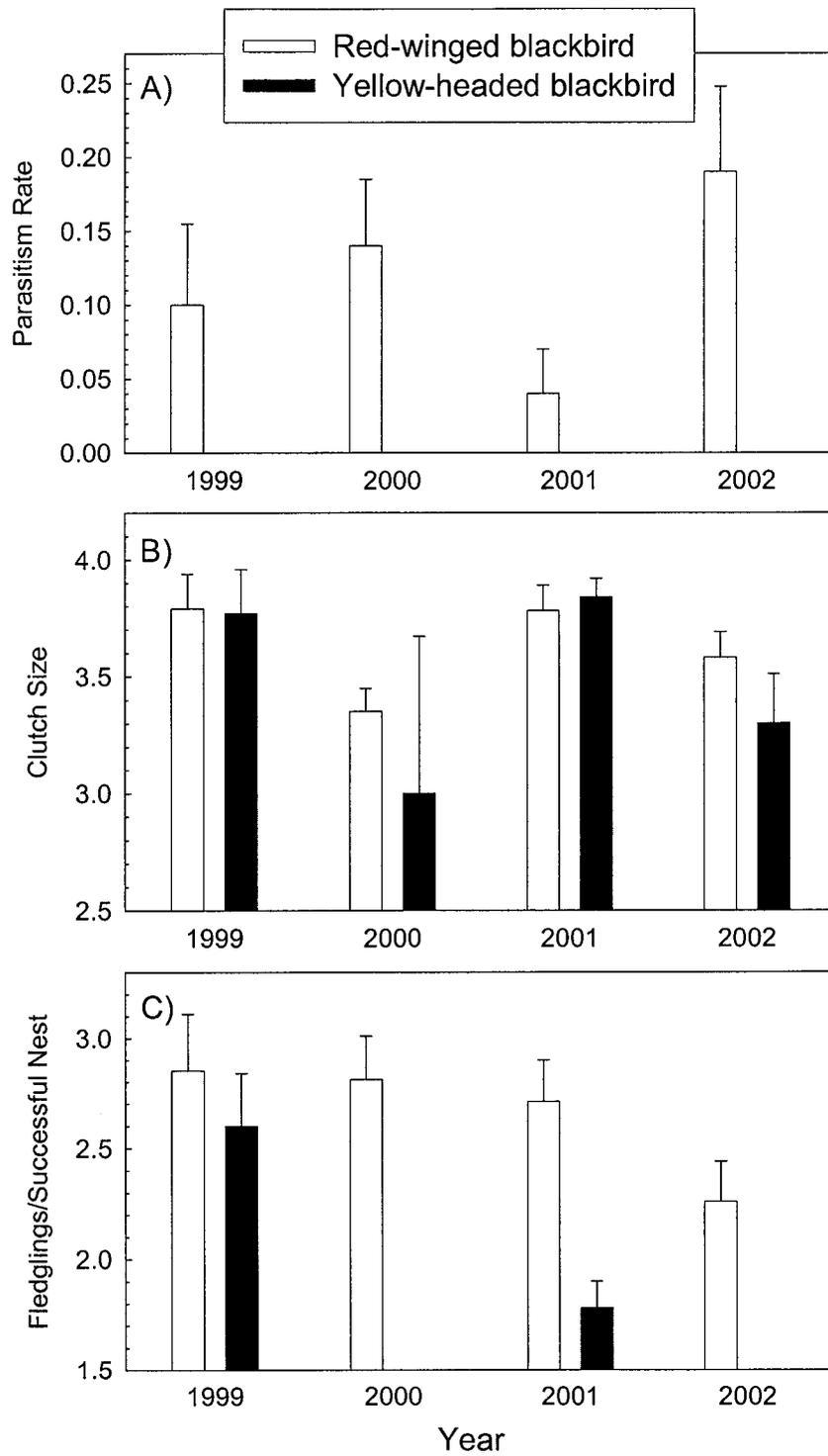


Figure 4

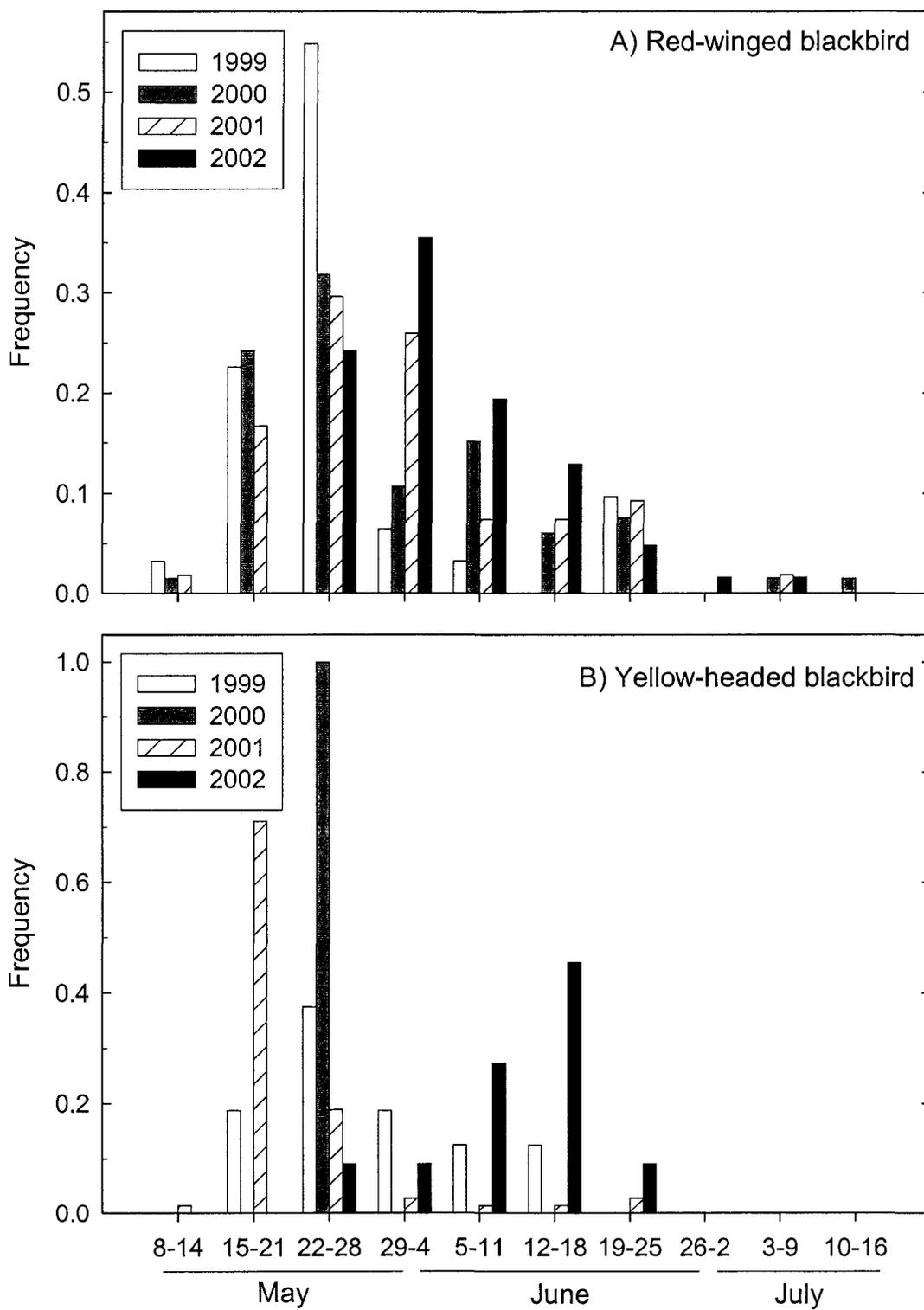


Figure 5

CHAPTER 7. DOES RESTORATION ACTUALLY RESTORE? MODELING THE CONTRIBUTION OF DEMOGRAPHIC PARAMETERS TO SONGBIRD POPULATION GROWTH RATES IN RESTORED GRASSLANDS

A paper to be submitted to *Conservation Biology*

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Abstract: *Tallgrass prairie has declined throughout the mid-continental United States during the past two centuries, and migratory birds breeding in these habitats have also experienced precipitous population declines. To conserve these communities, state and federal agencies have responded by restoring and reconstructing grassland habitats. We evaluated restoration practices in northern Iowa by combining intensive field data (nest monitoring, color marking, and radio telemetry) collected over four breeding seasons (1999-2002) with population projection models to estimate population growth rates of two declining songbirds that vary in life-history strategies and nest-site selection, Dickcissels (*Spiza americana*) and Bobolinks (*Dolichonyx oryzivorus*). Moreover, we estimated the relative contribution of nest predation, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and annual survival to population growth using elasticity analysis to determine what parameters are critical for conservation of these species. For Dickcissels, the population growth rate was not high enough to be sustainable without immigration into the area ($\lambda < 1$). For Bobolinks, restored areas harbored populations that were more sustainable than Dickcissel populations, yet populations were exhibiting weak evidence of declines. Population growth rates were most sensitive to adult survival across a wide range of parameter estimates, whereas sensitivity to brood parasitism was consistently low. Elasticities associated with nest predation were highly variable and dependent on survival estimates. These results underscore the need for reliable adult survival estimates and conservation strategies focused on the non-breeding season. In addition, our modeling approach provides a seamless and efficient framework for investigating the importance of demographic parameters to population growth rates of songbirds that are influenced by nest predation, brood parasitism, and renesting rates. Although habitat restoration is one of the*

few alternatives for conserving communities in threatened landscapes, restoration strategies will need to have positive contributions to population dynamics for species of concern, which has not yet been observed in our system.

Introduction

Habitat loss has occurred at devastating rates in many ecosystems throughout the world. Indeed, over 99% of native tallgrass prairie in the mid-continental United States has declined in the past two centuries (Samson and Knopf 1994). Many migratory grassland bird species using these habitats have also experienced consistent widespread declines throughout the United States (Peterjohn and Sauer 1999). To conserve avian communities, habitat restoration must occur and provide adequate resources needed by communities. Restoration can have diverse consequences, however, which complicates evaluating restoration and improving restoration efforts.

Although restoration has been documented to provide habitat for breeding birds (Fletcher and Koford 2002, 2003), arguably a more prudent measure to interpret the efficacy of restoration is to estimate population growth rates (Marzluff and Ewing 2001), because bird abundance or density may be uncorrelated with fitness (Vickery et al. 1992, Hughes et al. 1999, Winter and Faaborg 1999). Yet simply documenting growth rates is not enough for prescribing sound conservation strategies. Instead, biologists need to identify what demographic factors contribute most to population growth rates and subsequently implement strategies that have positive impacts on these parameters (Sæther et al. 1996), assuming that these factors are not constrained and can be actively managed (Benton and Grant 1999, Mills et al. 1999). For example, demographic analyses on populations of Loggerhead Sea Turtles (*Caretta caretta*) revealed that management strategies were focused on the life-history stage that contributed the least to the population growth rate (Crouse et al. 1987).

Similar issues could be occurring with some migratory songbirds, based on various direct and indirect attempts to manage for the detrimental effects of predation on nests (Reitsma et al. 1994, Heske et al. 2001) and/or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Smith et al. 2000, Smith et al. 2002). Although nest predation and brood parasitism both have negative consequences on seasonal fecundity (i.e., the number of

fledglings produced/female/year; Pease and Grzybowski 1995), these parameters operate in disparate ways. Nest predation results in complete failure, yet individuals can potentially re-nest following failure. Brood parasitism does not usually cause complete failure, but instead individuals can continue to raise cowbird young and a diminished number of host young. Furthermore, conservation strategies may ultimately differ for ameliorating detrimental effects of nest predators and brood parasites. Although some attempts have been made to determine the relative importance of nest predation and brood parasitism on seasonal fecundity (e.g., Pease and Grzybowski 1995, Schmidt and Whelan 1999, Grzybowski and Pease 2000), only Woodworth (1999) attempted to determine the importance of these parameters on population growth rates.

We combined intensive data on life-history strategies and demographic parameters of two declining migratory songbirds breeding in restored grasslands (Peterjohn and Sauer 1999), Dickcissels (*Spiza americana*) and Bobolinks (*Dolichonyx oryzivorus*), with population projection models to: 1) estimate population growth rates (i.e., the asymptotic finite rate of increase, λ ; Caswell 2001), and 2) estimate the relative contribution of nest predation, brood parasitism, and annual survival to the population growth rates of these species. In light of these results, we discuss potential options for future monitoring and conservation strategies of declining grassland birds.

Methods

Study Area and Focal Species

We collected demographic data on all restored grasslands greater than 10 ha within the Eagle Lake Wetland Complex ($n = 10$), located in Hancock and Winnebago counties, north-central Iowa (43°N 94°W; Fig. 1). The Eagle Lake Wetland Complex encompasses approximately 162 km², and contains a complex of waterfowl production areas (WPAs) and wildlife management areas (WMAs) situated in an agricultural landscape. Most restoration occurred in the past 15 years and is ongoing in the area. Grasslands were restored primarily from rowcrop agricultural areas, using several restoration techniques and both warm-season and cool-season grass plantings (see Fletcher and Koford 2002, 2003 for more details). 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 grass/alfalfa (*Medicago sativa*) mixtures.

We focused on two declining, single-brooded neotropical migrants that breed in temperate grasslands of the United States: the Dickcissel and the Bobolink. We chose these species for three primary reasons: 1) both have exhibited severe population declines throughout the continental United States (Peterjohn and Sauer 1999), 2) both species are large enough to attach radio-transmitters that can last for most of the breeding season, which facilitates estimating seasonal fecundity, and 3) both are common in the study area (Fletcher and Koford 2002). In addition, life-history strategies and nest-site selection vary between these species (Harmeson 1974, Martin and Gavin 1995, Winter 1999), enabling comparative analyses of parameters affecting population dynamics.

Estimating Seasonal Fecundity

We collected field data on all parameters required to estimate seasonal fecundity (sensu Schmidt and Whelan 1999) between 1999-2002. All parameters except for information on renesting were estimated using standard nest finding and monitoring methods (Martin and Geupel 1993, Winter 1999); renesting information was estimated using radio telemetry (see below). We used a combination of systematic searching and observing female behavior to find nests (Martin and Geupel 1993, Winter 1999). Systematic searching included using both rope-dragging procedures and observers systematically walking fields while using poles to disturb vegetation (Winter 1999, Pietz and Granfors 2000). We visited nests every 2-4 d to determine the fate of each nest. To minimize problems of assigning uncertain nest fates (Manolis et al. 2000), we considered nests successful and stopped counting nest exposure days if at least one host nestling remained in the nest at day 7-8 (approximately one day before the earliest known fledging date for these species; Ehrlich et al. 1988, Martin and Gavin 1995). To partition the components of nest success, we estimated daily predation rates and daily failure rates (from sources other than predation) using the Mayfield method (Johnson 1979, Heisey and Fuller 1985), using the midpoint assumption for estimating failure dates between nest visits (Johnson 1979). We subsequently exponentiated these daily estimates to the number of days in the nesting cycle (laying, incubation, and nestling stages) to estimate predation and failure rate (Dickcissels: 24 days; Zimmerman 1982; Bobolinks: 26

days; Martin and Gavin 1995). To incorporate site and year variability into our estimates of precision, we considered sites as a repeated measure among years. We then determined estimates and associated standard errors with a mixed model analysis (Littell et al. 1996), using the number of nest exposure days per site as a weighting factor (Koford 1999).

To estimate renesting probabilities, in 2000 we radio-marked adult female Dickcissels and Bobolinks in each of the study sites. We attached radios ($\bar{x} = 0.94 \pm 0.16$ g, SD; range: 0.63 - 1.10 g) using a modified leg-loop harness (Rappole and Tipton 1991). This method has been successfully used on breeding passerines (e.g., Powell et al. 2000 [wood thrush, *Hylocichla mustelina*]). We attempted to radio-mark females prior to or during their first breeding attempt. Once between 22 May-8 June, and again between 14-28 June, we opened four mist net lines (4 nets each) scattered across each site, passively catching and banding birds from approximately 0510-0800. Nets were distributed during the first visit to target Bobolinks and were distributed during the second visit to target Dickcissels. We supplemented this approach by trapping females at known nest sites. All individuals were banded with a unique combination of 3 plastic color leg bands and 1 U.S. Fish and Wildlife Service aluminum band. We only attached radios to females with brood patches or if the female was known to be nesting. We stratified our effort in radio-marking females in sites based on the size of the site and the density of each species estimated from the previous year of sampling (Fletcher and Koford 2002), resulting in 1-6 radios for each species per site. Females were monitored daily using hand-held and vehicle-mounted telemetry systems until battery failure or emigration from the study area. However, nests were only approached every 2-4 d, similar to nests of unmarked females. In addition, we tracked lost birds from a plane weekly, flying transects across the study area. The area searched for lost birds included > 8 km surrounding each site (Fig. 1).

Using these data, seasonal fecundity was estimated following the analytical single-brooded model developed by Schmidt and Whelan (1999), modified to incorporate sources of failure other than predation and parasitism (see Appendix 1). We chose this model in lieu of other analytical models (Ricklefs and Bloom 1977, May and Robinson 1985, Noon and Sauer 1992, Sæther and Bakke 2000, Sandercock and Beissinger 2002) because this approach partitions effects of nest predation and brood parasitism. We chose this approach in lieu of

other simulation models (e.g., Pease and Gryzbowski 1995, Powell et al. 1999) because it provides an analytical solution that can be incorporated directly into a population projection matrix, which allows for analytical estimates (sensitivities and elasticities) of the contribution of lower-level parameters (e.g., brood parasitism) to population growth rates (Caswell 2001; see below and Appendix 2). The Schmidt and Whelan (1999) model requires determining the total number of potential nesting attempts possible prior to the analysis (see also Donovan et al. 1995, McCoy et al. 1999). For each species we ran the models based on the maximum number of observed nesting attempts by females within each season, based on marked birds in the study area (Bobolinks: 2, see also Bollinger and Gavin 1989; Dickcissels: 3, see also McCoy et al. 1999). For example, to estimate seasonal fecundity, m , of Bobolinks, the analytical (unreduced) expression is:

$$m = E [(1 - P - F) (1 - N)][1 + \alpha P + \alpha F + a_p \gamma N] \\ + (E - R)[(1 - P - F)(1 - a_p)N][1 + \alpha P + \alpha F + a_p \gamma N]$$

where E is the number of host fledglings/successful unparasitized nest, P is the probability of predation, F is the probability of failure other than predation (not considered in Schmidt and Whelan 1999), N is the probability of brood parasitism, α is the probability of reneesting after failure, a_p is the probability of abandonment after brood parasitism, γ is the probability of reneesting after abandonment from brood parasitism (assumed one in Schmidt and Whelan 1999), and R is the reduction in number of host fledglings/successful nest due to parasitism (i.e., $E - R$ is the number of host fledglings/successful parasitized nest). Thus, the first part of the equation estimates the number of host fledglings produced from unparasitized nests, whereas the second portion of the equation estimates the number of host fledglings produced from parasitized nests (see Appendix 1). To estimate E and R , we separately ran analyses for parasitized and unparasitized nests. For both species, no individuals abandoned after brood parasitism, thus we assumed $a_p = 0$. We estimated the sensitivity of seasonal fecundity to each parameter (i.e., proportional change in seasonal fecundity from a proportional change in a parameter) by perturbing the model with small changes (5%) in a single parameter, x , while holding other parameters constant (Pulliam et al. 1992, Jørgensen 1994; cf. Morris and Doak 2002:330-332). In this framework, the sensitivity of seasonal fecundity, s_x , to parameter x is:

$$s_x = (x/m) \times (\Delta m / \Delta x).$$

Estimating Annual Survival

Between 1999-2002, we estimated apparent annual survival of adult Dickcissels and Bobolinks using mark-recapture-resighting techniques (Pollock et al. 1990, Lebreton et al. 1992). In 1999, we opportunistically marked individuals primarily using playback tapes to lure males into nets and by catching males and females at known nest sites. From 2000-2002, we distributed nets across sites in the same locations each year, as described above for radio telemetry, and we supplemented this technique by using playback tapes and catching individuals at nest sites. We resighted color-marked birds opportunistically during visits to sites and also used a spotting-scope to systematically resight birds approximately once every two weeks at each site during the breeding season.

Adult survival rates were estimated with Cormack-Jolly-Seber methods (Pollock et al. 1990, Lebreton et al. 1992) using program MARK (White and Burnham 1999). Apparent survival rates (ϕ) estimated in this framework represent a minimum estimate of survival, because these estimates do not distinguish permanent emigration from mortality (Pollock et al. 1990, Powell et al. 2000). We compared a series of candidate models that differed in complexity to explain survival. We expected that survival (ϕ) and resighting (p) probabilities could differ between sexes (i.e., $\phi(g)$ and $p(g)$), based on previous studies that estimated return rates of Dickcissels and Bobolinks (Bollinger and Gavin 1989, Zimmerman and Finck 1989). In addition, we expected that year could influence both parameters if nesting success differed among years (i.e., $\phi(t)$ and $p(t)$), because site fidelity can vary depending on nest success (Bollinger and Gavin 1989). Thus, we compared our global model ($\phi(g \times t)p(g \times t)$) to reduced models using Akaike's Information Criterion, adjusted for small sample sizes and overdispersion (QAICc), and Akaike weights (Burnham and Anderson 1998). Goodness-of-fit of global models and overdispersion (based on estimating the variance inflation factor, \hat{c}) were assessed using the bootstrap procedure implemented in MARK ($n = 1000$ replications; White and Burnham 1999).

Juvenile survival rates are notoriously difficult to estimate in migratory songbirds, because juveniles generally do not exhibit natal philopatry (Greenwood and Harvey 1982). Only Wittenberger (1978) reported information regarding return rates of juvenile Bobolinks

over two years; 41% (7/17) of juveniles returned, whereas 95% of adults (38/40) returned between years. No information has been reported on juvenile survival in Dickcissels. Attempts have been made to estimate juvenile survival by using count data to independently estimate λ (i.e., $\lambda = N_{t+1}/N_t$; Noon and Sauer 1992, Murphy 2001) or by assuming populations are stable ($\lambda = 1$; Pulliam et al. 1992) and combining this estimate with estimates of fecundity and adult survival. From these approaches, juvenile survival has been estimated as approximately half of the adult survival rate for some species (Ricklefs 1973, Greenberg 1980, Noon and Sauer 1992, Murphy 2001). We used this fraction as a first approximation (see also Temple and Cary 1988, Donovan et al. 1995, Brawn and Robinson 1996, McCoy et al. 1999), but we varied juvenile survival estimates across a wide range of parameter space to determine how our inference might change using different estimates (see *model variations*).

Estimating Population Growth Rates

We used a stage-structured, population projection modeling framework to estimate the asymptotic finite rate of increase (λ) for Dickcissels and Bobolinks breeding in restored grasslands of northern Iowa (Noon and Sauer 1992, Caswell 2001). This approach allows for a key issue to be addressed in the modeling process that is less attainable with other approaches—estimating the relative contribution of demographic parameters to λ using proportional sensitivity, or elasticity, analysis. Estimating the contribution of demographic parameters to λ helps to interpret estimates of λ and is useful for prescribing conservation and management strategies focused on increasing population growth rates (Benton and Grant 1999).

Our stage-structured model followed a post-breeding birth pulse model (Noon and Sauer 1992):

$$\begin{pmatrix} S_j \times 0.5m & S_a \times 0.5m \\ S_j & S_a \end{pmatrix}$$

Where S_j is the juvenile survival, S_a is the adult survival (approximated by apparent survival, ϕ), and m is the seasonal fecundity (Appendix 1). Seasonal fecundity is multiplied by the proportion of females fledged, 0.5, to focus exclusively on females in the model, assuming a 1:1 sex ratio of fledged young (see also Woodworth 1999, Sandercock and Beissenger 2002). We assumed that seasonal fecundity of second-year birds and after-second-year birds were

equal (see also Woodworth 1999). Using this framework, we estimated λ using the characteristic equation (Caswell 2001:73) and we approximated its standard error using the Delta method (following Lande 1988, Caswell 2001: 300-304) by assuming parameters were independent (no covariance; see also Lande 1988). We estimated variance for juvenile survival and dickcissel adult survival by using the coefficient of variation of adult bobolink survival. We quantified the contribution of demographic parameters to λ using elasticity analyses on both the matrix elements and on lower-level vital rates (e.g., nest predation rate, P), but we focus on elasticities of λ to vital rates (see Appendix 2). These elasticities should be interpreted as the proportional change in λ resulting from a proportional change in a parameter, x . Elasticities can be positive (e.g., adult survival) or negative (e.g., nest predation), depending on whether the parameter has a positive or negative influence on λ . In addition, we estimated the necessary change in vital rates to achieve stable populations ($\lambda = 1$) using the following equation (Caswell 2001: 607):

$$\delta_x = \frac{1}{e_x} \left(\frac{\lambda' - \lambda}{\lambda} \right)$$

where δ_x is the proportional change in vital rate, x , required to change λ to λ' (i.e., $\lambda' = 1$), and e_x is the elasticity of λ to the vital rate. We also estimated the necessary change in vital rates to population changes estimated independently from both Breeding Bird Survey (BBS) data (Peterjohn and Sauer 1999, Fletcher and Koford 2003) and density estimates derived from point counts conducted in the study area each year (see Fletcher and Koford 2002 for details on methods; the same count locations and methods were used each year).

Model variations

Because sensitivities and elasticities are local estimates (i.e., changing a demographic rate will change the elasticity and the potential rank of elasticities among demographic parameters; Mills et al. 1999) and we had little to no information on some parameters (e.g., juvenile survival, S_j), we ran a series of model variations to interpret how our conclusions might change given different parameter estimates. For seasonal fecundity, we ran three different model types: one that assumed two possible nesting attempts (one reneating attempt), one that assumed three possible nesting attempts, and one that assumed four possible nesting attempts (Appendix 1; equations 4, 5, and 6 respectively). We also varied

the renesting probability, α , because most other approaches assume renesting will occur if a nest fails before the end of the breeding season (Pease and Gryzbowski 1995, Powell et al. 1999). In addition, renesting probabilities estimated from radio telemetry could also be biased low if radios had negative impacts on the likelihood of renesting. For population projection models, we varied both adult and juvenile survival estimates to determine how these estimates affected estimates of population growth and elasticities. There have been no other studies estimating apparent survival in these species to our knowledge. However, return rates have been estimated for both species. For Dickcissels, Zimmerman and Finck (1989) reported 49% of males returned in at least one year, whereas females did not return. For Bobolinks, male return rates have ranged from 44-96%, whereas female return rates have ranged from 25-92% (Martin 1974, Wittenberger 1978, Bollinger and Gavin 1989), although the upper range of these estimates were based on a relatively small sample (Wittenberger 1978). Given these estimates, we varied juvenile survival between 20-50%, and adult survival between 40-90%.

Results

Seasonal Fecundity

Over the four years, we found a total of 216 Dickcissel and 259 Bobolink nests. We excluded from analyses any nests that failed due to mowing (Dickcissel: $n = 14$; Bobolink: $n = 1$) and human-caused desertion (Dickcissel: $n = 2$; Bobolink: $n = 21$), which was assumed if the nest was abandoned on the first nest-monitoring visit after the nest was found. We included 200 Dickcissel and 237 Bobolink nests in further analyses, of which 77 Dickcissel and 114 Bobolink nests were successful (See Appendix 3 for nest information of other common species). For all nesting components, there was no evidence for year effects for either species ($P > 0.22$), except for the number of young fledged/successful unparasitized nest (E) for Dickcissels (minimum, 1999: 2.4 ± 0.2 ; maximum, 2001: 3.6 ± 0.2 ; $F_{3,6} = 5.72$, $P = 0.034$). Therefore, we focused further analyses on mean estimates across years (Table 1), yet we investigated how variability in E for Dickcissels affected seasonal fecundity and population growth rates.

In 2000, we radio tracked 38 female Bobolinks and 25 female Dickcissels. There were no confirmed mortalities of radio-marked females during the breeding season. Only 2

female Bobolinks and 3 female Dickcissels renested after nest failure (Table 1), none of which renested more than once. However, in 2001 we observed a color-marked female Dickcissel renest twice after nest failures. There was no evidence of nest success differing among radio-marked and non-radiomarked females in 2000 (Dickcissels: $\chi^2 = 0.26$, $df = 1$, $P = 0.610$; Bobolinks: $\chi^2 = 0.04$, $df = 1$, $P = 0.837$). Renesting (onset of egg laying) occurred within 6-10 days of nest failure. Of those females that renested, distances between successive nesting attempts ranged from 35-125 m for Dickcissels and 430-8600 m for Bobolinks. In addition, nest initiation dates (based on all nests monitored) of Bobolinks were highly synchronous (Fig. 2; see also Wittenberger 1978), suggesting that this species probably does not renest frequently. However, Dickcissel nest initiation dates were less synchronous (see also Winter 1999), which could be a result of more frequent renesting or from staggered settlement in the study area (Fig. 2).

Estimates of seasonal fecundity were higher for Bobolinks than for Dickcissels (Table 1). Surprisingly, estimates were similar among the different models assuming 2-4 potential nesting attempts, probably because of our low estimates of renesting probability and high nest predation rates. Likewise, sensitivities of seasonal fecundity to renesting probability were low but did increase with the number of possible nest attempts allowed by the model (Table 2). Sensitivities of seasonal fecundity were highest for nest predation rate (Table 2). Because there was evidence for year effects on E (number fledged/successful unparasitized nest) for Dickcissels, we estimated fecundity using low and high annual estimates of E ; overall, m changed approximately 0.133 fledglings/female (0.013 SD) from mean estimates. Increasing renesting probability resulted in small increases in seasonal fecundity, but as the number of nesting attempts increased, increasing α had a stronger influence (Fig. 3).

Annual Survival

Between 1999-2002, we banded 102 Dickcissels (38 females and 64 males) and 268 Bobolinks (156 females and 112 males). Annual return rates were relatively high for male Bobolinks (48.2% returned in \geq one year). Of those individuals that returned in \geq one year, 34.1% dispersed to different sites within the study area. Dickcissels and female Bobolinks, however, exhibited very low return rates (female Bobolinks: 4.6%, $n = 5$; female Dickcissels: 2.9% $n = 1$; male Dickcissels: 10.0% $n = 4$), limiting our ability to estimate apparent survival

in Dickcissels and for female Bobolinks. Because Dickcissels exhibited such low return rates, for further analyses we approximated $S_a = 0.49$, based on return rates observed in Zimmerman and Finck (1989).

Overall, the global model for Bobolinks fit the data relatively well (bootstrap goodness-of-fit: $P = 0.315$). The best model describing survival was a constant apparent survival rate with a sex-specific resighting probability ($(\phi(.))p(g)$; Table 3); however, resighting rates were very low for females ($p = 0.044 \pm 0.017$; males: $p = 0.573 \pm 0.108$). We were interested in whether similar survival rates between sexes were reasonable, so we reanalyzed data from Bollinger and Gavin (1989) from their Moore Road site in New York (data collected from 1984-1986), to determine if survival was similar between sexes in their system. The best model describing survival at Moore Road was a constant apparent survival and resighting rate ($(\phi(.))p(.)$; Table 3), although survival estimates from their site were lower than estimates from Iowa ($\phi = 0.501 \pm 0.041$; $p = 0.912 \pm 0.057$). Murphy (2001) used survival rates of male Eastern Kingbirds (*Tyrannus tyrannus*) to approximate female survival rates, because females can be more difficult to detect than males (as indicated in our study by the low recapture probability estimate). A male only model from the Iowa data set provided a similar estimate ($\phi = 0.702 \pm 0.095$) to the two-sex model (Table 1), so for projection modeling we used estimates from the two-sex model as an approximation S_a .

Population Growth Rates

For both species, point estimates of growth rates were estimated to be less than one (Table 1). There was evidence for Dickcissel growth rate to be significantly lower than one (three-attempt model: $z = 6.191$, $P < 0.001$), but only weak evidence for Bobolink growth rate to be significantly lower than one (two-attempt model: $z = 1.306$, $P = 0.096$). When survival estimates were varied across a wide parameter space to account for uncertainty in these estimates, it is apparent that these areas are not self-sustaining for Dickcissels and are only sustainable for Bobolinks if juvenile survival is relatively high (> 0.4 ; Fig. 4). Each model type (2-4 nesting attempts) showed similar results (mean difference in λ between models < 0.002 ; Fig. 3). Varying renesting probabilities tended to have small effects on population growth rates of both species (Fig. 3). For both species, elasticity of λ was greatest for adult survival (Table 4). Elasticity associated with nest predation was strong but highly dependent

on survival estimates (Table 4, Fig. 5). Elasticity of λ to brood parasitism and renesting were weak (Figs. 3, 5), while elasticity associated with juvenile survival was also relatively weak compared with adult survival and nest predation (Table 4, Fig. 5). In addition, even if brood parasitism was reduced to zero, population growth rates would not be stable for either species (in the absence of changes of other parameters; Table 4).

Based on density estimates, D , derived from point counts (see Fletcher and Koford 2002; Fig. 6), the estimated population growth rates, defined as $\lambda = D_{t+1}/D_t$ (Powell et al. 2000), for Dickcissels and Bobolinks were 1.02 (\pm 0.49 SD) and 1.18 (\pm 0.17 SD), respectively. For Dickcissels, λ declined for two of three years, whereas λ was stable or increasing for Bobolinks each year. Regional BBS trends (U.S. Fish and Wildlife Service Region 3, from 1983-1999; Fletcher and Koford 2003) were -1.9% and -3.3% per year for Dickcissels and Bobolinks, respectively. Continental BBS trends (1966-1996; Peterjohn and Sauer 1999) for both species were -1.6% per year. For Dickcissels, only increasing adult survival to approximately 90% could result in stable population growth or growth estimates based on density and BBS trends, in the absence of changes in other parameters (Table 4). For Bobolinks, both lowering nest predation and increasing survival could result in stable population growth or growth estimates based on density and BBS trends (Table 4).

Discussion

Habitat restoration and avian population growth rates

Restoring grasslands can provide habitat for breeding grassland birds, because breeding birds, including Dickcissels and Bobolinks, can occur in high densities in restored habitats relative to other habitats (Fletcher and Koford 2002, 2003). However, there is growing evidence that density is not necessarily correlated with nesting success in grassland birds (Hughes et al. 1999, Winter and Faaborg 1999), and nesting success can be quite low for many grassland birds (e.g., Hughes et al. 1999, Koford 1999). Indeed, we found that in these areas fecundity cannot offset mortality in Dickcissels, in which the populations are not sustainable without immigration. McCoy et al. (1999) also found that Dickcissel populations breeding in Conservation Reserve Program fields in Missouri were apparently not self-sustaining, yet overall 4 of 7 species breeding in the area appeared to be self-sustaining. For

Bobolinks, restored areas are supporting populations that are more sustainable than Dickcissels, yet populations are exhibiting weak evidence of declines.

Estimates of population growth based on demographic data for both species did not match observed estimates of growth based on count data. There are two possible explanations for this incongruence: 1) estimates of demographic data were biased low, and 2) immigration into the area is counteracting demographic performance. The primary demographic parameters that could be biased low include renesting probabilities and survival. Although we might have underestimated renesting probabilities using radio telemetry, increasing these probabilities had a relatively small effect on population growth. Survival was based on return rates for Dickcissels (Zimmerman and Finck 1989) and mark-recapture methods for Bobolinks, both of which provide minimum estimates of survival. Yet for both species, increasing survival still could not produce growth estimates similar to estimates based on count data, except at extremely high (and perhaps unrealistic) levels. Immigration into the area is thus a likely factor influencing annual population numbers. This suggests that grassland bird population dynamics could be operating at very large scales and warrants investigation to determine where immigrants are originating.

Is habitat restoration ultimately bad for breeding grassland birds? Restoration could be increasing the amount of habitat in landscapes that function as ecological traps (Schlaepfer et al. 2002), in which individuals prefer settling in habitat that results in lower fitness relative to other, less-preferred habitats. Although nest success was relatively low in our study area, we did not estimate nest success in other potentially suitable habitats (e.g., hayland). However, nest success of grassland birds in many other midwestern grassland habitats tends to be as low or lower than what we have documented (Patterson and Best 1996, Hughes et al. 1999, Koford 1999, Temple et al. 1999). Furthermore, areas with low population growth rates could ultimately have positive impacts on population size if movement occurs between these areas and areas with high growth rates (Pulliam and Danielson 1991).

Contribution of demographic parameters to avian population growth rates

For both species, relative changes in adult survival consistently had the strongest relative effect on the population growth rate. Using a spatially-explicit modeling approach, Pulliam

et al. (1992) estimated that both adult and juvenile survival were the primary parameters influencing growth rates in Bachman's sparrows (*Aimophila aestivalis*). Murphy (2001) found that population growth rates in Eastern Kingbirds were most sensitive to adult survival, whereas sensitivities to juvenile survival and fecundity were similar and less than half of sensitivities to adult survival. Moreover, a recent review also suggested that adult survival is generally the predominant parameter influencing growth rates across a wide diversity of birds (Sæther and Bakke 2000) and that the contribution of fecundity to population growth rates increased with decreasing adult survival, similar to patterns of covariation in nest predation and adult survival elasticities we observed (Fig. 5). These results highlight the need for good estimates of adult survival, not only for understanding the contribution of survival to population growth but also for interpreting the importance of nest predation to population dynamics.

Perhaps more surprising was the small effect of brood parasitism and relatively small effect of juvenile survival on growth rates of both species. Parasitism rates in our system were moderate compared to other grassland systems (Zimmerman 1966, Martin and Gavin 1995, Winter 1999, Herkert et al. 2003), yet rates were much lower than what songbirds experience in many forested systems (e.g., Robinson et al. 1995). However, even when parasitism rates are high, high nest predation rates can swamp out detrimental effects of parasitism (e.g., Rogers et al. 1997, Schmidt and Whelan 1999). Indeed, Woodworth (1999) concluded that removing brood parasites would not be sufficient for positive growth in an island population of vireos (*Vireo latimeri*). Although brood parasitism rates had relatively small effects on population growth, our modeling approach and other similar approaches do not incorporate the positive feedback of cowbirds fledging from host nests. Modeling the interactions of hosts and parasites could provide a different picture in understanding population dynamics, but in our system low growth rates of hosts likely had negative effects on parasite dynamics, which in turn could further reduce detrimental parasite influence on host growth rates. Recently, attempts have been made to estimate post-fledging survival in some migratory songbirds (e.g., Anders et al. 1997, Powell et al. 2000). While these data have provided useful information on habitat use and survival during the post-fledging time

period, our results suggest that the importance of this period may be less than for other factors influencing population dynamics of grassland songbirds.

Model advantages and disadvantages relative to other models

Our modeling approach provided a seamless and efficient framework to interpret the contribution of demographic parameters to population growth rates in songbirds. The framework was seamless in that the seasonal fecundity model we used (modified from Schmidt and Whelan 1999) was incorporated directly into the population projection model. The framework was efficient in that the seasonal fecundity model allowed for analytical sensitivity and elasticity estimates of vital rates.

Other approaches for estimating seasonal fecundity either use simple measures that do not partition nest predation and brood parasitism (e.g., Noon and Sauer 1992, Donovan et al. 1995, McCoy et al. 1999) or use a simulation framework, in which individuals are tracked within the course of the breeding season (e.g., Pease and Grzybowski 1995, Powell et al. 1999). Simulation approaches tend to assume that if a nest fails, the female will subsequently reneest (but see the complex model of Pease and Grzybowski 1995 for a relaxation of this assumption). Thus, the number of nesting attempts is allowed to vary over the breeding season. Our data suggest, however, that for some species individuals might not reneest after failure (see also Zimmerman 1982). When using simulation approaches, reneesting probability is generally not estimated (e.g., Dececco et al. 2000, Whitehead et al. 2000), but estimating the length of the breeding season is required (Pease and Grzybowski 1995, Powell et al. 1999). Other parameters required among models are similar. Although estimating breeding season length might be easier than estimating reneesting probability, elasticity analyses for Dickcissels and Bobolinks in our study suggest that reneesting probability impacts seasonal fecundity and population growth rates less than many other demographic parameters. Functionally, both the Pease and Grzybowski (1995) model and the Schmidt and Whelan (1999) model can provide similar estimates of fecundity, and these estimates tend to be consistent with observed fecundity of marked populations (e.g., Prairie Warblers, *Dendroica discolor*, Nolan 1978; Schmidt and Whelan 1999).

Other approaches for estimating population growth rates in songbirds have typically used simple difference equations for linking seasonal fecundity, juvenile survival, and adult

survival (*sensu* Pulliam 1988; e.g., May and Robinson 1985, Brawn and Robinson 1996, Trine 1998, McCoy et al. 1999, Porneluzi and Faaborg 1999). While these approaches are similar in form to a two-stage population projection model (Noon and Sauer 1992), they do not allow analytical sensitivity and elasticity estimates. Our matrix model framework was relatively simple—it was deterministic, density independent, and only considered two stages (see also Noon and Sauer 1992, Woodworth 1999, Sandercock and Beissinger 2002).

However, matrix model theory has been developed thoroughly, in which many assumptions can be relaxed and increasing complexity can be incorporated (see Caswell 2001, Morris and Doak 2002). Therefore, a matrix model approach allows for flexibility and inference not attainable with other simple analytical approaches. In particular, expanding this modeling approach to include stochastic variation in parameters might improve interpretation of the relative importance of different parameters on population growth rates (Mills et al. 1999).

Conservation Implications

Population growth rates were consistently most sensitive to changes in adult survival. If we assume that survival rates are relatively constant throughout the annual cycle, conservation strategies during the non-breeding season might be more fruitful than strategies focused during the breeding season. Indeed, Dickcissels are considered agricultural pests on much of their wintering grounds, which includes parts of Venezuela and Ecuador, and mortality in these areas can be high (Basili and Temple 1999a, b). Less is known about Bobolink demography on their wintering grounds in South America (which includes Bolivia, Brazil, Paraguay, and Argentina; Martin and Gavin 1995), but this species is also thought to be an agricultural pest (Pettingill 1983, Martin and Gavin 1995). Furthermore, Sherry and Holmes (1995, 1996) provided evidence that winter habitat availability and quality can be limiting for many neotropical migrants. Yet we caution that when applying elasticity analyses for conservation, one must consider what demographic factors are not constrained and are amenable to management (Benton and Grant 1999, Mills et al. 1999).

On the breeding grounds, conservation strategies need to focus on ameliorating the detrimental effects of nest predation more than any other demographic factor for these grassland birds (and other migrant birds with similar demographic rates and life-history strategies). The predator community affecting grassland birds can be diverse (Pietz and

Granfors 2000), however, making cookbook prescriptions difficult and limited. One approach that could reduce the overall intensity of nest predation is increasing patch size and the amount of habitat in the landscape (Robinson et al. 1995, Winter and Faaborg 1999, Heske et al. 2001, Herkert et al. 2003). Yet, Herkert et al. (2003) recently found that only in extremely large patches (>1000 ha) did nest predation consistently decrease for many grassland birds. Nest predation can also increase near edges in grasslands, particularly near woodland edges (Johnson and Temple 1990), and edge effects have been documented to influence population growth rates (Flaspolher et al. 2001, With and King 2001). Clearly, understanding, and perhaps directly managing, the predator community will be critical for sound conservation strategies aimed at reducing nest predation in songbird populations (Heske et al. 2001, Chalfoun et al. 2002).

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Table 1. Baseline parameter estimates, estimated seasonal fecundity, and estimated population growth rates for Dickcissels and Bobolinks breeding in restored grasslands in northern Iowa, 1999-2002.

Parameter	Dickcissel		Bobolink	
	Mean	SE	Mean	SE
Nest predation rate, P	0.756	0.028	0.695	0.039
Nest failure rate ^a , F	0.015	0.002	0.011	0.001
Nest parasitism rate, N	0.187	0.063	0.178	0.028
Number fledged/successful unparasitized nest, E	2.984	0.125	3.990	0.144
Number fledged/successful parasitized nest, $E - R$	1.722	0.266	2.235	0.304
Probability of renesting, α	0.158	0.084	0.129	0.045
Seasonal fecundity ^b , m				
Two-attempt model:	0.707		1.180	
Three-attempt model:	0.716		1.189	
Four-attempt model:	0.717		1.190	
Juvenile survival ^c , S_j	0.245		0.360	
Adult survival ^d , S_a	0.490		0.721	0.097
Population growth rate ^e , λ				
Two-attempt model:	0.5766	0.0681	0.9334	0.0510
Three-attempt model:	0.5777	0.0682	0.9350	0.0513
Four-attempt model:	0.5779	0.0682	0.9352	0.0513

^aFailure from sources other than predation (e.g., weather-induced failure)

^bSee Appendix 1 for fecundity estimation

^cJuvenile survival was estimated as half of adult survival (see also Donovan et al. 1995, Murphy 2001)

^dFor Dickcissels, adult survival was taken from return rates observed in male Dickcissels in Kansas (Zimmerman and Finck 1989); for Bobolinks survival was based on mark-recapture data in Iowa estimated from a constant survival, sex-specific recapture probability (Table 3)

^eSee Appendix 2 for population growth rate estimation; standard error based on the Delta method (Caswell 2001: 300-304)

Table 2. Sensitivity^a of seasonal fecundity estimates to changes in parameters, based on three different models assuming 2-4 potential nesting attempts (Appendix 1).

Parameter	Dickcissel			Bobolink		
	Two-attempt	Three-attempt	Four-attempt	Two-attempt	Three-attempt	Four-attempt
Nest predation rate, P	-3.218	-3.190	-3.183	-2.287	-2.274	-2.275
Nest failure rate ^a , F	-0.071	-0.062	-0.058	-0.035	-0.035	-0.038
Nest parasitism rate, N	-0.096	-0.086	-0.083	-0.082	-0.083	-0.086
Number fledged/successful unparasitized nest, E	0.872	0.882	0.886	0.895	0.894	0.891
Reduction in number fledged/successful parasitized nest, R	-0.089	-0.086	-0.085	-0.084	-0.084	-0.085
Probability of renesting, α	0.098	0.133	0.142	0.086	0.100	0.099

^aSensitivity estimated by increasing one parameter (5%) while holding all other parameters in model constant (i.e., the sensitivity of fecundity to parameter x is: $s_x = (x/m) \times (\Delta m / \Delta x)$).

^bFailure from sources other than predation (e.g., weather-induced failure)

Table 3. Assessment of candidate models for estimating annual apparent survival of adult Bobolinks in northern Iowa, 1999-2002, and New York, 1984-1986.

Model ^b	Bobolinks: Iowa			Bobolinks: New York ^a		
	Np ^c	Δ QAICc ^d	QAICc weight	Np ^c	Δ QAICc ^d	QAICc weight
$\phi(.)p(.)$	2	24.98	0.00	2	0.00	0.33
$\phi(.)p(g)$	3	0.00	0.46	3	1.67	0.14
$\phi(g)p(.)$	3	5.30	0.03	3	1.38	0.17
$\phi(g)p(g)$	4	1.73	0.19	4	3.43	0.06
$\phi(g+t)p(g)$	5	3.26	0.09	5	3.91	0.05
$\phi(g)p(g+t)$	5	2.78	0.11	5	3.91	0.05
$\phi(g)p(t)$	5	8.39	0.01	6	6.01	0.02
$\phi(t)p(g)$	5	3.57	0.08	4	2.15	0.11
$\phi(g+t)p(g+t)$	7	6.87	0.01	6	6.01	0.02
$\phi(t)p(g+t)$	7	7.17	0.01	5	4.06	0.04
$\phi(g \times t)p(g \times t)$	10	12.86	0.00	6	6.01	0.02

^aData from E. K. Bollinger (as reported in Bollinger and Gavin 1989)

^bModel structure: ϕ = apparent survival, p = recapture probability, g = gender, t = time (year),
(.) = constant

^cNumber of estimable parameters

^dThe difference of the model with the lowest QAICc (Akaike's Information Criterion, adjusted for sample size and overdispersion) and each model

Table 4. Elasticities of population growth rates (λ) to demographic parameters and the change in parameters necessary to achieve a stable population ($\lambda = 1$), population growth based on density estimates in the area (density), Breeding Bird Survey trends for the region (BBS region, 1983-1999; Fletcher and Koford 2003), and BBS continental trends (BBS continent, 1966-1996; Peterjohn and Sauer 1999) for Dickcissels and Bobolinks breeding in northern Iowa, 1999-2002.

Species/Parameter	Elasticity ^a	Proportional change necessary for λ to equal:				Estimate necessary for λ to equal: ^b			
		1	Density	BBS region	BBS continent	1	Density	BBS region	BBS continent
Dickcissel									
Nest predation rate, P	-0.481	-1.52	-1.61	-1.46	-1.47	NP	NP	NP	NP
Nest failure rate ^b , F	-0.009	-79.46	-83.96	-76.23	-76.80	NP	NP	NP	NP
Nest parasitism rate, N	-0.013	-56.23	-59.42	-53.95	-54.35	NP	NP	NP	NP
Number fledged/successful unparasitized nest, E	0.165	4.43	4.68	4.25	4.28	NP	NP	NP	NP
Reduction in number fledged/successful parasitized nest, R	-0.013	-56.23	-59.42	-53.95	-54.35	NP	NP	NP	NP
Probability of renesting, α	0.020	36.19	38.24	34.72	34.98	NP	NP	NP	NP
Juvenile survival, S_j	0.152	4.81	5.09	4.62	4.65	NP	NP	NP	NP
Adult survival, S_a	0.848	0.86	0.91	0.83	0.83	0.91	0.94	0.90	0.90
Bobolink									
Nest predation rate, P	-0.519	-0.13	-0.51	-0.07	-0.10	0.60	0.34	0.65	0.62
Nest failure rate ^b , F	-0.009	-8.39	-31.08	-4.23	-6.38	NP	NP	NP	NP
Nest parasitism rate, N	-0.019	-3.70	-13.69	-1.87	-2.81	NP	NP	NP	NP
Number fledged/successful unparasitized nest, E	0.247	0.29	1.07	0.15	0.22	5.14	NP	4.57	4.87
Reduction in number fledged/successful parasitized nest, R	-0.019	-3.70	-13.69	-1.87	-2.81	NP	NP	NP	NP
Probability of renesting, α	0.019	3.76	13.91	1.89	2.85	0.61	NP	0.37	0.50
Juvenile survival, S_j	0.228	0.31	1.16	0.16	0.24	0.47	0.78	0.42	0.45
Adult survival, S_a	0.772	0.09	0.34	0.05	0.07	0.79	0.97	0.75	0.77

^aElasticity estimated using methods described in Appendix 2, in which seasonal fecundity was held constant and based on the three nesting attempt model for Dickcissels and the two-nesting attempt model for Bobolinks (Table 1; Appendix 1).

^bEstimate necessary while holding all other parameters constant; NP = not possible, or beyond the possible range of parameter values

^cFailure from sources other than predation (e.g., weather-induced failure)

Appendix 1. A derivation for estimating seasonal fecundity of single-brooded songbirds.

Schmidt and Whelan (1999) developed an analytical model for estimating seasonal fecundity of single-brooded and double-brooded songbirds; here we focus on modifying the single-brooded model. The premise of this model relies on the assumption of four possible outcomes of a nesting event: 1) successful and unparasitized, 2) successful, but parasitized, 3) parasitized and subsequently abandoned, and 4) depredated. The distinction between successful parasitized and unparasitized nests was made because brood parasitism can reduce the number of host young fledged per successful nest (Pease and Grzybowski 1995). This model (and other models of seasonal fecundity; e.g., Pease and Grzybowski 1995) assumes that parameters operate independently of each other. Given these possible outcomes, the expected number of young fledged in one nesting attempt would be:

$$E(1-P^*)(1-N) + (E-R)(1-P^*)(1-a_p)N \quad (1)$$

Where E is the number of host young fledged per successful unparasitized nest, P^* is the probability of nest predation (and other sources of nest failure), N is the probability of brood parasitism, R is the reduction in host young fledged per successful nest due to brood parasitism, and a_p is the probability of abandonment following nest parasitism. For projection modeling, E and R are divided by 2 to focus exclusively on females in the model, assuming a 1:1 sex ratio of fledged young (see also Donovan et al. 1995, McCoy et al. 1999, Sandercock and Beissinger 2002).

For simplicity, Schmidt and Whelan (1999) considered predation, P^* , to be any source of nest failure other than abandonment from brood parasitism, but predation can be easily partitioned from other sources of failure (e.g., weather), if we assume predation operates independently of other sources of failure, by adjusting equation 1 to:

$$E(1-P-F)(1-N) + (E-R)(1-P-F)(1-a_p)N \quad (2)$$

Where P is exclusively the probability of nest predation and F is the probability of nest failure from sources other than predation. P and F can be estimated following Heisey and Fuller (1985).

This framework can then be extended to estimate seasonal fecundity, given assumptions about the total number of renesting attempts individuals can make. For two nesting attempts, an unreduced expression for seasonal fecundity, m , would be:

$$\begin{aligned}
 m = & E(1 - P - F)(1 - N) + (E - R)(1 - P - F)(1 - a_p)N + \\
 & E(\alpha P)(1 - P - F)(1 - N) + (E - R)(\alpha P)(1 - P - F)(1 - a_p)N + \\
 & E(\alpha F)(1 - P - F)(1 - N) + (E - R)(\alpha F)(1 - P - F)(1 - a_p)N + \\
 & E(\gamma a_p N)(1 - P - F)(1 - N) + (E - R)(\gamma a_p N)(1 - P - F)(1 - a_p)N
 \end{aligned} \quad (3)$$

Where α is the renesting probability after nest failure (either from predation or other sources), and γ is the probability of renesting after abandonment due to brood parasitism (assumed to equal 1 in Schmidt and Whelan [1999]).

Based on empirical data for Dickcissels and Bobolinks, we assumed $a_p = 0$ (but see Zimmerman 1966). Given this assumption, equation 3 can be simplified to:

$$m = (E - NR)(1 - P - F)(1 + \alpha P + \alpha F) \quad (4)$$

For three nesting attempts, the reduced solution is:

$$m = (E - NR)(1 - P - F)(1 + \alpha P + \alpha F + \alpha^2(P + F)^2) \quad (5)$$

And for four nesting attempts, the reduced solution is:

$$m = (E - NR)(1 - P - F)(1 + \alpha P + \alpha F + \alpha^2(P + F)^2 + \alpha^3(P + F)^3) \quad (6)$$

Other assumptions of this framework include: 1) second and third renesting attempts occur with the same probability, 2) renesting attempts have the same number of host young fledged and reduction of host young from parasitism per nest, and 3) predation, failure, and nest parasitism rates are the same for renests. Each of these assumptions can be relaxed by incorporating new parameters into the framework. However, we used equations 4, 5, and 6 for estimating seasonal fecundity when running stage-based, population projection models because we lacked data on variability among renesting attempts and these equations provide a parsimonious framework for interpreting the contribution of key parameters to seasonal fecundity.

Appendix 2. Elasticity analyses for a stage-structured, post-breeding birth pulse model.

We estimated the contribution of demographic parameters to the population growth rate using proportional sensitivity, or elasticity analyses (Caswell 2001). For matrix elements, we estimated the elasticity as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} \times \left(\frac{v_i \times w_i}{v \times w} \right)$$

(Caswell 2001: 209-226), where e_{ij} is the elasticity of λ (the asymptotic finite rate of increase) to matrix element a_{ij} , $\partial \lambda / \partial a_{ij}$ is the sensitivity of λ to matrix element a_{ij} , v is the right eigenvector of the matrix (the stable stage distribution), and w is the left eigenvector of the matrix (the stage-specific reproductive value). However, elasticities of λ to matrix elements do not isolate contributions of specific vital rates. To this end, we estimated the elasticities of lower-level parameters as:

$$\frac{x}{\lambda} \frac{\partial \lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}$$

(Caswell 2001: 232), where x is the vital rate (e.g., nest predation rate, P). Note that elasticities on lower-level vital rates do not sum to 1 (unlike elasticities of matrix elements; Caswell 2001). These elasticities should be interpreted as the proportional change in λ resulting from a proportional change in x . Elasticities can be positive (e.g., adult survival) or negative (e.g., nest predation), depending on whether the parameter has a positive or negative influence on λ . Note that for N and R , elasticities are the same because these factors cannot be separated in the fecundity model (see Appendix 1).

Appendix 3. Daily survival rates (mean, standard error [SE]), estimated nest success, and the number of host fledglings/successful nest for five common species breeding in restored grasslands, northern Iowa, 1999-2002.

Species/year	Number of		Daily survival rate			Mayfield		Number of	
	Nests	Suc- cesses	\bar{x}	SE	Exposure days	nest success \bar{x}	SE	fledglings/ successful nest \bar{x}	SE
Savannah Sparrow^a									
1999	11	4	0.888	0.051	57.0	0.058	0.165	3.50	0.46
2000	8	4	0.976	0.018	77.5	0.559	0.311	2.75	0.46
2001	6	4	0.981	0.018	39.0	0.635	0.349	3.25	0.46
2002	6	6	1.000	0.000	39.0	1.000	0.000	3.50	0.38
Total	31	18	0.970	0.015	212.5	0.485	0.218	3.28	0.21
Grasshopper Sparrow^b									
1999	9	6	0.968	0.020	64.5	0.446	0.292	3.67	0.54
2000	12	6	0.939	0.024	98.5	0.208	0.182	3.00	0.54
2001	12	7	0.948	0.023	93.5	0.262	0.209	3.43	0.50
2002	9	7	0.981	0.013	86.0	0.624	0.237	3.57	0.50
Total	42	26	0.959	0.011	342.5	0.355	0.111	3.42	0.25
Dickcissel^a									
1999	20	8	0.930	0.019	124.5	0.173	0.107	2.75	0.37
2000	73	23	0.926	0.010	591.0	0.157	0.047	2.71	0.22
2001	56	22	0.935	0.010	473.5	0.200	0.061	3.32	0.23
2002	51	24	0.946	0.010	426.0	0.261	0.077	2.12	0.21
Total	200	77	0.933	0.009	1615.0	0.188	0.047	2.70	0.13
Bobolink^c									
1999	33	12	0.925	0.019	257.5	0.134	0.090	4.00	0.43
2000	73	30	0.933	0.012	581.5	0.165	0.065	3.53	0.27
2001	57	32	0.951	0.011	469.5	0.267	0.097	4.00	0.27
2002	74	40	0.953	0.009	669.0	0.286	0.083	3.68	0.24
Total	237	114	0.943	0.006	1977.5	0.220	0.040	3.76	0.14

Appendix 3. (continued)

Species/year	Number of		Daily survival rate			Mayfield		Number of	
	Nests	Suc- cesses	\bar{x}	SE	Exposure days	nest success	SE	fledglings/ successful nest	SE
Red-winged Blackbird ^b									
1999	34	13	0.928	0.018	289.5	0.155	0.097	3.08	0.26
2000	74	26	0.944	0.010	799.0	0.236	0.071	2.92	0.18
2001	77	31	0.937	0.011	675.0	0.197	0.070	3.00	0.17
2002	63	22	0.922	0.015	503.0	0.131	0.063	2.82	0.20
Total	248	92	0.935	0.006	2266.5	0.187	0.034	2.95	0.10

^aNest cycle considered to be 24 d (Zimmerman 1982, Jackson et al. 1996)

^bNest cycle considered to be 25 d (Jackson et al. 1996)

^cNest cycle considered to be 26 d (Martin and Gavin 1995)

Figure 1. Locations of restored grasslands ($n = 10$) used for estimating seasonal fecundity and population growth rates of Dickcissels and Bobolinks in northern Iowa, 1999-2002. Bold box around study area signifies the area searched for radio-marked birds using vehicle-mounted and aerial telemetry systems.

Figure 2. Distribution of nest initiation dates (i.e., first day of incubation; $\bar{x} \pm SE$) for Dickcissels and Bobolinks breeding in restored grasslands, northern Iowa, 1999-2002.

Figure 3. Model variations of renesting probability and its effects on estimates of seasonal fecundity and population growth, and the elasticity of renesting on seasonal fecundity and population growth for Dickcissels and Bobolinks breeding in northern Iowa, 1999-2002.

Figure 4. Estimated population growth rates under adult and juvenile survival model variations for Dickcissels and Bobolinks breeding in northern Iowa, 1999-2002. Seasonal fecundity was held constant and based on the three nesting attempt model for Dickcissels and the two-nesting attempt model for Bobolinks (Table 1; Appendix 1).

Figure 5. Elasticities of nest predation, brood parasitism, juvenile survival, and adult survival across a wide range of juvenile and adult survival parameter space for Dickcissels and Bobolinks breeding in northern Iowa, 1999-2002. Seasonal fecundity was held constant and based on the three nesting attempt model for Dickcissels and the two-nesting attempt model for Bobolinks (Table 1; Appendix 1).

Figure 6. Densities (males/ha; $\bar{x} \pm SE$) of Dickcissels and Bobolinks breeding in restored grasslands in northern Iowa, 1999-2002. Densities were estimated using point counts as described by Fletcher and Koford (2002). For both species, a uniform key function with no adjustments was the most parsimonious model to explain detectability within point counts.

Eagle Lake Wetland Complex

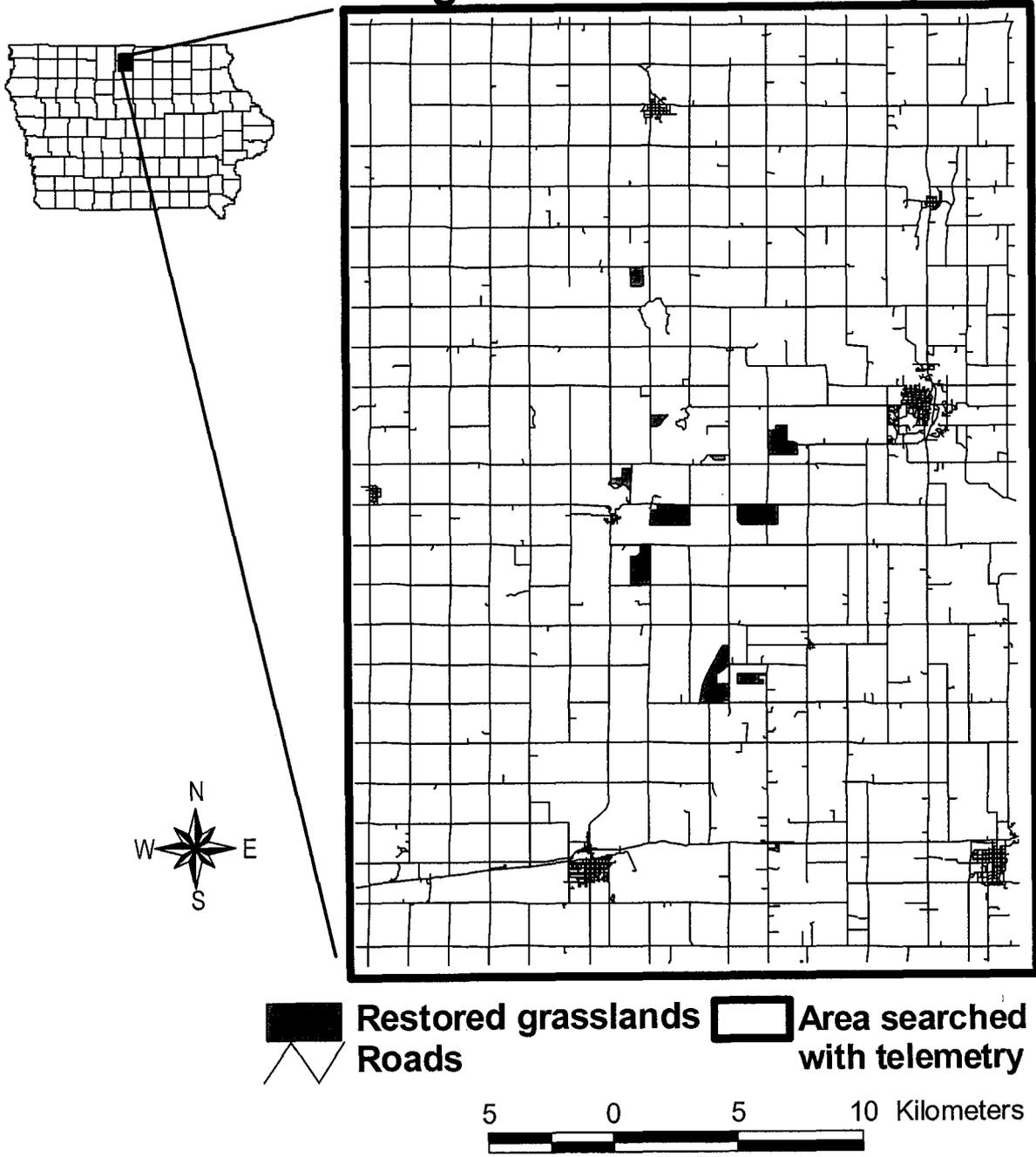


Figure 1

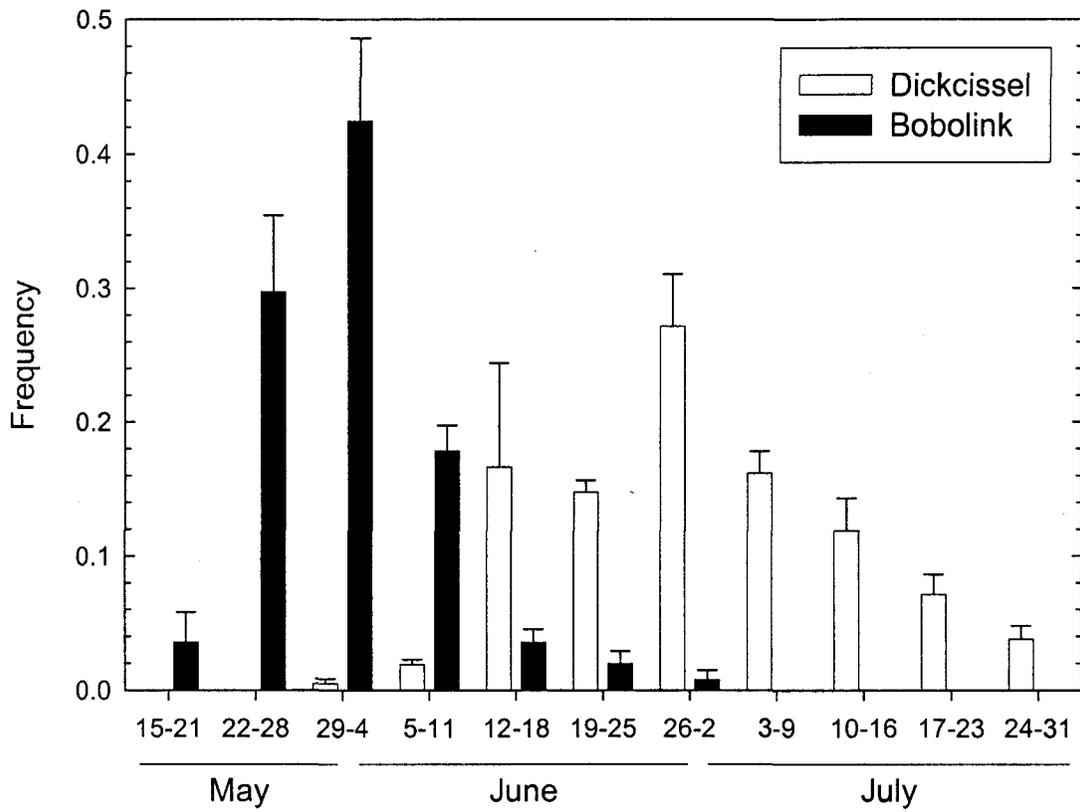


Figure 2

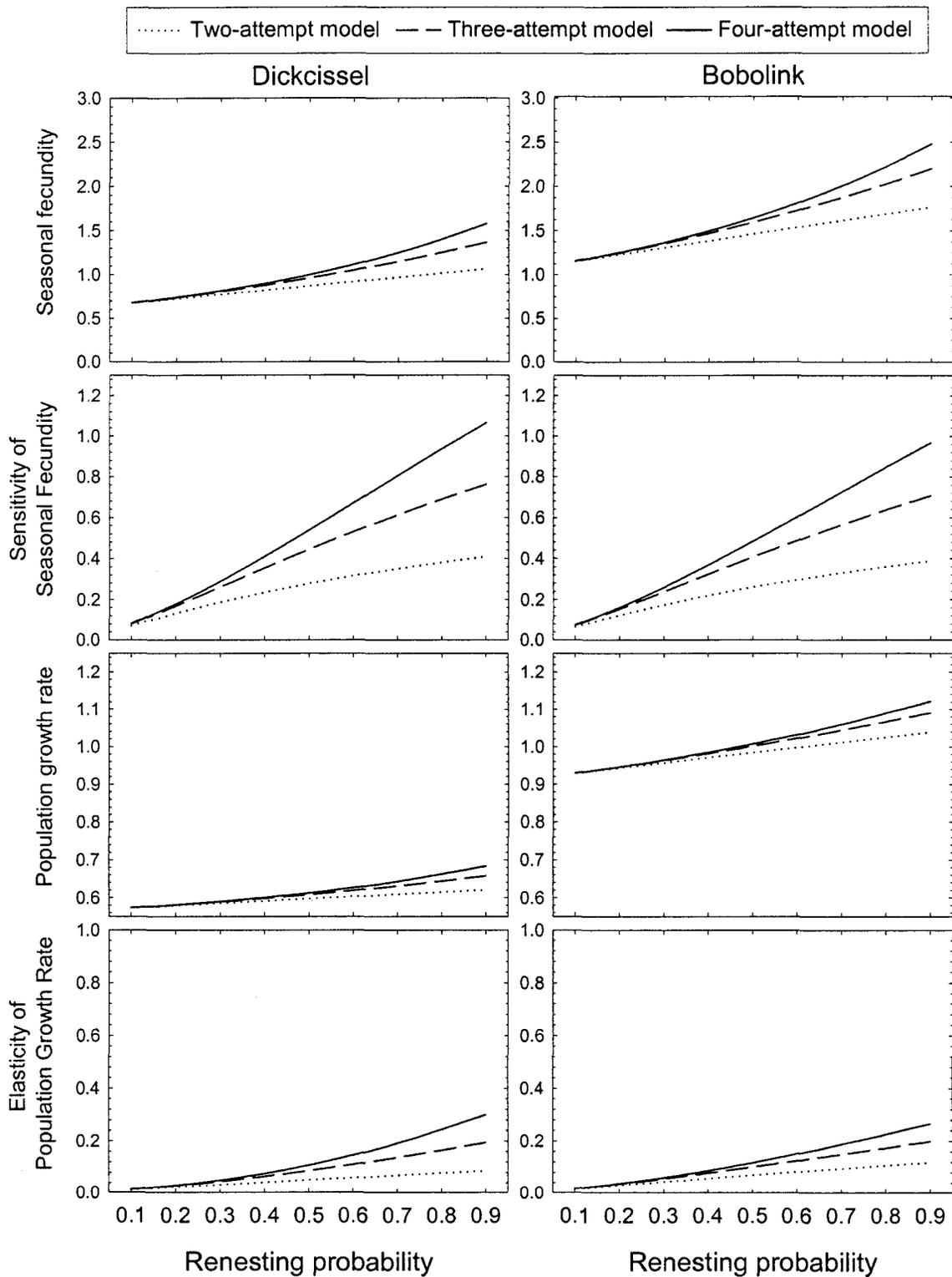


Figure 3

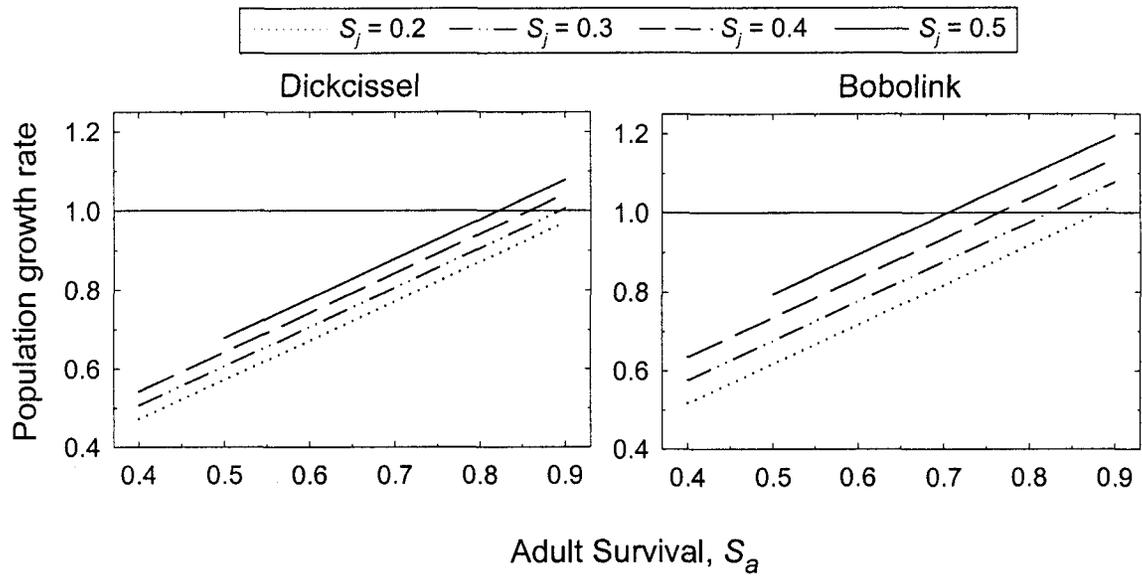


Figure 4

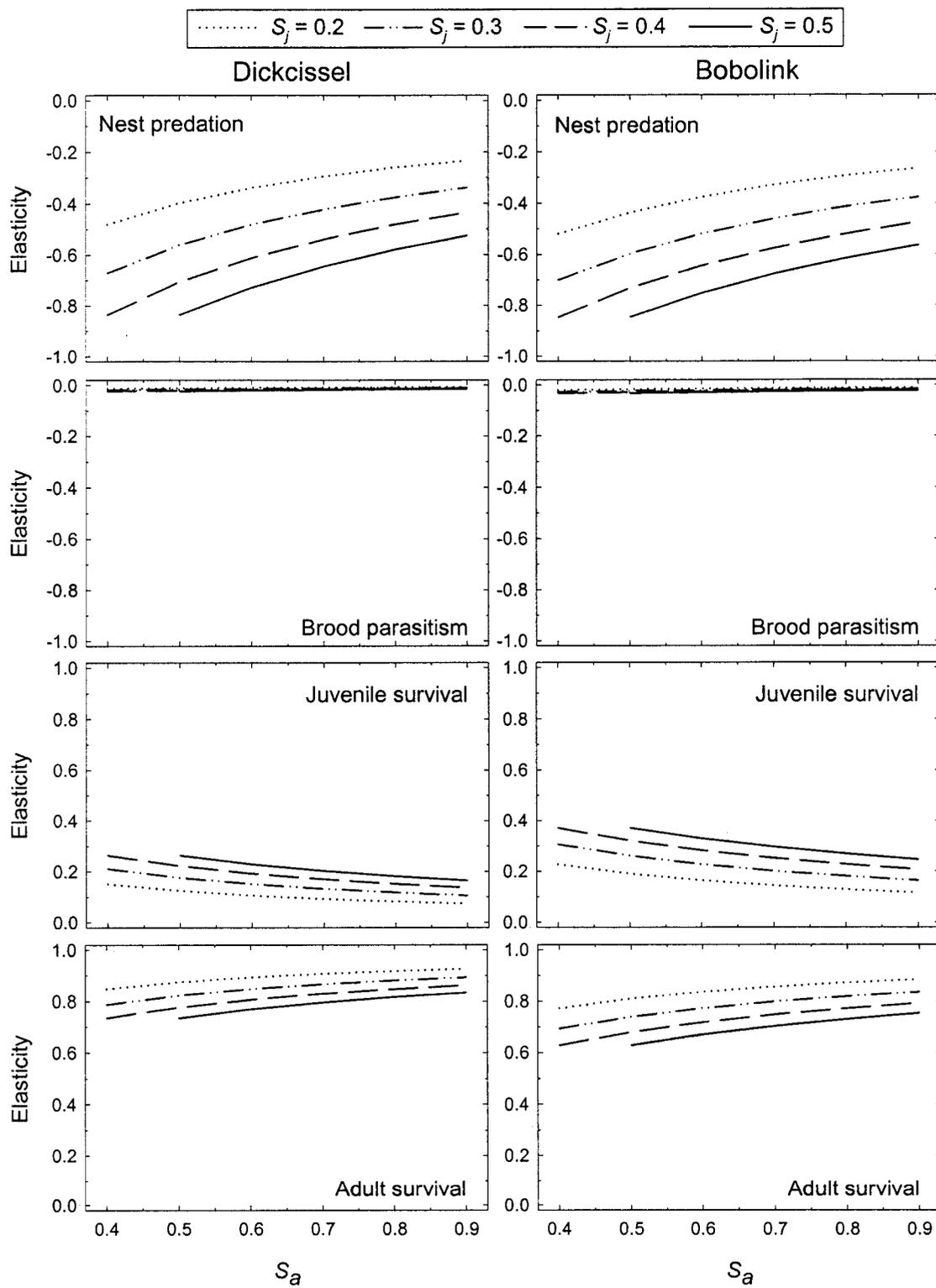


Figure 5

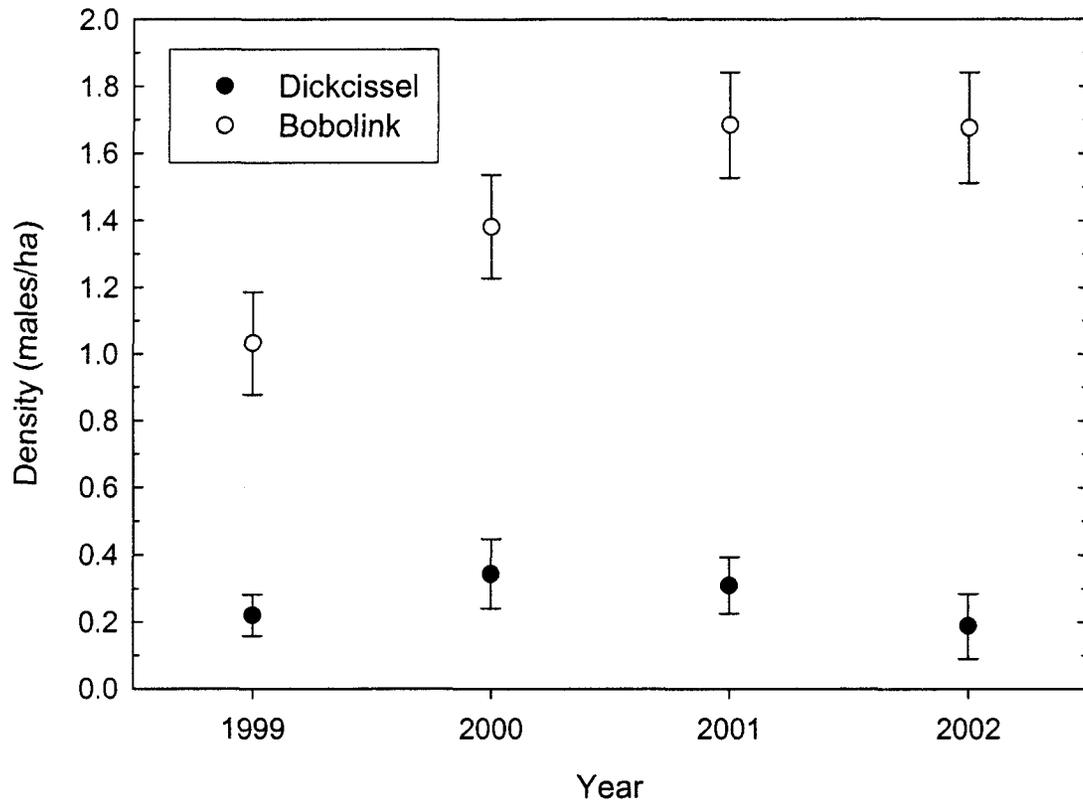


Figure 6

CHAPTER 8. GENERAL CONCLUSIONS

General Discussion

Edge avoidance and habitat fragmentation—Although habitat edges have been extensively studied (Murcia 1995, Risser 1995, Lidicker 1999), particularly in terms of how edges can influence nest success of songbirds (reviewed in Paton 1994, Andren 1995, Hartley and Hunter 1998, Lahti 2001), the potential role of edges influencing spatial patterns of distribution have remained poorly understood (but see Ortega and Capen 1999). Furthermore, factors mediating edge effects have remained unclear. In Iowa grasslands, there was a consistent signal of grassland birds avoiding edges, both at local and landscape scales. At local scales, grassland birds tended to exhibit stronger patterns of avoidance near woodland edges than near road or rowcrop agriculture edges. Other recent research suggests that woodland areas are adverse environments for grassland birds (e.g., Hughes et al. 1999, O’Leary and Nyberg 2000, Coppedge et al. 2001). Grassland birds have been documented to avoid woodland areas (Johnson and Temple 1986, Hughes et al. 1999), 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 both prevent woody encroachment within patches, as well as decrease the amount of woodland vegetation surrounding patches.

Processes underlying edge avoidance and other patterns of distribution in fragmented landscapes remain elusive. Yet in Iowa, similar patterns of edge avoidance by Bobolinks near different types of edges appeared to be the result of different mechanisms. Changes in habitat structure near edges, a hypothesis often considered potentially important in explaining bird distribution (Kroodsma 1984, Ortega and Capen 1999), could not explain patterns of edge avoidance. By estimating spatial components of territory dynamics in Bobolinks, it was apparent that males were actively avoiding grassland habitat near woodland edges, whereas edge avoidance near roads could primarily be explained based on territory size variation. While these results come one step closer in identifying processes underlying patterns of edge avoidance, we still do not ultimately understand the process of this interesting phenomenon.

In highly fragmented landscapes, multiple edges within fragments are often within close proximity to each other. Multiple edges in northern Iowa exacerbated edge effects on Bobolink distribution. The probability of occurrence of Bobolinks was lower in plots near two edges than in plots near only one edge, and within plots with two edges, both the nearest distance and the next-nearest distance from edges helped explain Bobolink occurrence. Furthermore, the distance of edge influence was greater near two edges than near one edge. If multiple edges generally intensify edge effects, this phenomenon needs to be incorporated into core-area models (Laurance and Yensen 1991) and other models on interpreting impacts of fragmentation (e.g., the Effective Area Model; Sisk et al. 1997).

Modeling revealed that local edge avoidance can potentially explain patch size effects and variation in landscape-level patterns and that multiple edges within fragments can further exacerbate this effect. Although edge avoidance has been suggested as a possible mechanism for area sensitivity (Burke and Nol 1998, Johnson and Igl 2001), there has been some debate on whether edge avoidance is a process that operates independently of area sensitivity (Villard 1998) and whether it can explain patch size effects (Bollinger and Switzer 2002). Results from this study suggest that local edge avoidance can indeed help explain larger scale patterns observed in fragmented landscapes. The next step is to validate these simulation models in real landscapes to determine if local patterns of edge avoidance can accurately predict bird distribution across fragmented landscapes.

Edge avoidance could ultimately have positive fitness consequences. If nest predation is indeed higher near edges in grasslands (e.g., Johnson and Temple 1990, Burger et al. 1994, Winter et al. 2000), then avoiding edges could result in higher nesting success of populations if individuals do reproduce in areas of higher habitat quality, leading to higher population growth rates, all else being equal. Using a modeling approach, With and King (2001) found that edge effects on reproduction had a greater effect on lifetime reproductive success than did area-sensitive distributions. This was due to direct effects of edges on reproduction. However, active edge avoidance by area-sensitive species could have strong indirect effects on lifetime reproductive success and population growth rates not considered in their model. Donovan and Lamberson (2001) also investigated effects of area sensitivity on population growth rates using a modeling approach and concluded that area sensitivity

could have positive impacts on population growth rates. Clearly, empirical data on this potential interaction are needed for understanding the link between habitat selection and demography of area-sensitive species in fragmented landscapes.

Habitat restoration and bird populations—Restoring grassland and wetland habitat provided breeding habitat for migratory songbirds in northern Iowa (see also Blankespoor 1980, Delphey and Dinsmore 1993). Densities of common grassland birds tended to be similar in both restored and native grasslands. For many species, these densities were correlated with characteristics of local habitat structure, which reflect their nesting requirements. Densities of common wetland birds were relatively high, although species richness tended to be lower in restored wetlands than richness observed in some natural wetlands in Iowa (Delphey and Dinsmore 1993). Based on land conversion that occurred with restoration practices, we also estimated that the temporal turnover in abundances of most species increased in the area, including many species of management concern. This is because restoration practices tended to convert rowcrop agriculture to grassland and wetland habitat, and densities of many species of birds in rowcrop agriculture are very low relative to other land use types (see also Best et al. 1997).

While these results on bird distributions were positive, demographic analyses provided a different picture. Dynamics of wetland birds breeding in these restored grasslands were highly variable and correlated with interannual climate variation and water levels within wetlands. During dry years, Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), an obligate wetland-breeding species, showed a marked reduction in density and a complete reproductive failure, in which none of the nests monitored fledged young. This reproductive failure was attributed primarily to nest predation, which was negatively correlated with water levels in wetlands. Conversely, Red-winged Blackbirds (*Agelaius phoeniceus*), a facultative wetland-breeding species, showed little variation in density and nest success. Both species exhibited similar patterns of reduced clutch size and later nest initiation dates in dry years, measures often tied to bottom-up effects of food availability and/or age of individuals. Yet top-down effects of nest predation had stronger population implications, because lower clutch size did not result in fewer young fledged per successful nest.

Nest success of many grassland birds in these areas tended to be very low (see also Hughes et al. 1999, Koford 1999, Winter and Faaborg 1999), such that populations of Dickcissels and Bobolinks, and perhaps other common grassland birds, are not sustainable at present without immigration into the area. McCoy et al. (1999) also found that Dickcissel populations breeding in Conservation Reserve Program fields in Missouri were apparently not self-sustaining, yet overall 4 of 7 species breeding in the area appeared to be self-sustaining. In northern Iowa, low nesting success was primarily attributed to the detrimental effects of nest predation. Although I did not identify nest predators in the study area, Pietz and Granfors (2000) identified nest predators on grassland songbird nests in North Dakota and found that the predator community was relatively diverse, in which at least 11 species depredated songbird nests. Identifying the contribution of different nest predators in fragmented grasslands will be key for implementing sound management strategies, yet the means to do so requires intensive monitoring techniques that might nonetheless be biased (Pietz and Granfors 2000).

Although nest predation was high in northern Iowa, elasticity analysis suggested that population growth in both Dickcissels and Bobolinks tended to be most sensitive to adult survival. Sæther and Bakke (2000) recently analyzed avian demography for many species and found that adult survival is generally the predominant parameter influencing growth rates across a wide diversity of birds. Moreover, the contribution of fecundity to population growth rates increased with decreasing adult survival, similar to patterns of covariation in nest predation and adult survival elasticities observed in this study. These patterns highlight the need for good estimates of adult survival, not only for understanding the contribution of survival to population growth but also for interpreting the importance of nest predation to population dynamics, a factor that is often assumed to be a driving force in avian population dynamics (Martin 1995, Robinson et al. 1995).

In this study, habitat restoration had both positive and negative effects on bird populations. Yet because population growth rates were low for some species, it appears that restoration might have more negative impacts than positive ones, if individuals would have settled in areas with higher breeding success in the absence of restored areas. Restoration is ongoing in the area, and planting techniques are continuing to improve. With increased

habitat in the landscape from restoration efforts, positive impacts might accumulate over time. Indeed, point estimates of nest success for many grassland birds in the area increased slightly each year (Chapter 7, Appendix 3), although this pattern was weak and not statistically significant. There have been calls for incorporating ecology theory, such as community assembly rules (Keddy 1999), into restoration practices. Including a landscape perspective and knowledge of habitat fragmentation should also improve restoration attempts at large scales, particularly if the processes occurring when adding habitat onto the landscape are functionally similar to processes observed with habitat loss and fragmentation.

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