Patch size and edge proximity are useful predictors of brood parasitism but not nest survival of grassland birds

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Abstract. Declines of migratory birds have led to increased focus on causative factors for these declines, including the potential adverse effects of habitat fragmentation on reproductive success. Although numerous studies have addressed how proximity to a habitat edge, patch size, or landscape context influence nest survival or brood parasitism, many have failed to find the purported effects. Furthermore, many have sought to generalize patterns across large geographic areas and habitats. Here, we examined evidence for effects of edge proximity, patch size, and landscape context on nest survival and brood parasitism of grassland birds, a group of conservation concern. The only consistent effect was a positive association between edge proximity and brood parasitism. We examined effects of patch size on nest survival (37 studies) and brood parasitism (30 studies) representing 170 and 97 different estimates, respectively, with a total sample size of >14,000 nests spanning eastern North America. Nest survival weakly increased with patch size in the Great Plains, but not in the Midwestern or Eastern United States, and brood parasitism was inversely related to patch size and consistently greater in the Great Plains. The consistency in brood parasitism relative to nest survival patterns is likely due to parasitism being caused by one species, while nest survival is driven by a diverse and variable suite of nest predators. Often, studies assume that predators responsible for nest predation, the main driver of nest success, either are the same or exhibit the same behaviors across large geographic areas. These results suggest that a better mechanistic understanding of nest predation is needed to provide meaningful conservation recommendations for improving grassland bird productivity, and that the use of general recommendations across large geographic areas should only be undertaken when sufficient data are available from all regions.

Key words: brood parasitism; Brown-headed Cowbird; edge proximity; grassland birds; landscape context; Molothrus ater; nest survival; patch size.

INTRODUCTION

Concern about the role of habitat fragmentation in the decline of migratory birds has led to considerable attention on the influences of edge proximity, patch size, and landscape context on avian reproductive success (e.g., Hoover et al. 1995, Robinson et al. 1995). Generally, nests close to edges, in smaller patches (i.e., with greater edge to area ratio), and in landscapes with greater amounts of non-suitable habitat are thought to be more susceptible to edge-dependent nest predators (Lahti 2001). Numerous studies have found evidence supporting adverse effects of fragmentation (Paton 1994), and effects may vary among spatial scales, geographic regions, and habitat types (Stephens et al. 2003, Batáry and Báldi 2004). Despite some support for an influence of fragmentation on reproductive success, most examinations have failed to find adverse effects (Lahti 2001), and conclusions are often based on artificial nests (62–73% of studies used in recent reviews; Stephens et al. 2003, Batáry and Báldi 2004), which give misleading results relative to natural nests (Thompson and Burhans 2004). Furthermore, many natural resource professionals have sought to generalize mechanisms across large geographic regions and multiple habitat types while making conservation and management decisions. These broad generalizations may not be warranted because of regional differences in the suite of nest predators, predator behavior, or the density of brood parasites. Indeed, the larger regional context has been shown to mediate effects of patch size and edge proximity on reproductive success (e.g., Thompson et al. 2002). Furthermore, many of the proposed predator-driven mechanisms remain untested, poorly supported, or may not apply to all habitats or regions (Chalfoun et al. 2002). Nonetheless, the same principles of minimizing edge, maximizing patch size, and minimizing “hostile” habitat in landscapes surrounding patches is generally
applied in an attempt to maximize reproductive success of conservation-priority birds (Winter et al. 2006).

Population declines of grassland birds have been more consistent and widespread than for any other bird group (Sauer et al. 2011). Due to these declines, grassland birds have received considerable research attention, with studies addressing effects of cover type, habitat structure, edge proximity, patch size, and landscape composition on habitat use or reproductive success (e.g., Herkert 1994, Winter et al. 2000, 2006, Fletcher and Koford 2002). Knowledge of habitat use is important for guiding management decisions, but demographic parameters, including reproductive success, ultimately determine population trajectories (McCoy et al. 1999, Fletcher et al. 2006). Largely based on studies focused on species diversity and abundance, large grassland patches in treeless landscapes are generally viewed as most favorable for grassland birds (Ribic et al. 2009). While there is evidence that reproductive success is greatest in such landscapes (Herkert et al. 2003), not all studies support this idea (Winter et al. 2006) and small patches can be relatively productive (Walk et al. 2010).

Understanding the demographic contributions of all grassland patches on the landscape is important given that most grasslands in some regions are relatively small patches on private land. Many of these patches are established through conservation programs, such as the Conservation Reserve Program, and understanding how the size and landscape context of these patches affects their conservation value for grassland birds may have significant implications for how these and similar programs are implemented in the future. In addition, there has been a desire to seek widely generalizable patterns to inform management; however, studies from different geographic areas have not necessarily produced the same results (Johnson and Igl 2001). Across large geographic areas, different processes may be inhibiting reproductive success. Therefore, promoting a “one-size-fits-all” approach to grassland bird management may be at best inefficient, and at worst detrimental, for some species. To begin addressing these topics, we set out to synthesize available information on the effects of edge proximity, patch size, and landscape context on grassland bird reproductive success. Specifically, we focused on studies evaluating nest survival and brood parasitism by Brown-headed Cowbirds (Molothrus ater).

We hypothesized that, because nest failure is driven by a diverse suite of nest predators that vary geographically, there would not be generalizable predictions for how patch size, edge proximity and landscape context would influence nest success across eastern North America. However, we expected that patterns of brood parasitism, because it is caused by a single species, would be more readily generalizable. Furthermore, we also expected patterns of nest survival and brood parasitism to vary regionally as landscape context and the identity and abundance of nest predators and brood parasites is also likely to vary among regions.

METHODS

We searched for sources of demographic information about grassland birds using internet resources, citations within published papers, and communication with other researchers. We confined our search to studies in eastern North America, focusing specifically on studies from three different regions: the Great Plains (Saskatchewan, Canada; and North and South Dakota, Nebraska, Kansas, Oklahoma, USA), core Midwestern states (Minnesota, Wisconsin, Iowa, Missouri, Illinois, USA), and Eastern states (Indiana, Ohio, Tennessee, Kentucky, Pennsylvania, New York, Vermont, USA). We focused on studies that investigated nest success or brood parasitism. For nest success studies, we concentrated on studies that produced estimates based on daily survival rates (DSR) rather than apparent nest success because of biases associated with the latter approach (Mayfield 1961). We used DSR estimates presented in studies or, when necessary, used nest success estimates along with the number of exposure days used to produce those estimates to back-calculate DSR; in a small number of cases we used the complement of reported daily predation rates. We excluded estimates based on sample sizes of <10 nests or artificial nest studies, and only included studies of obligate or facultative grassland passerines (Vickery et al. 1999). Along with estimates of nest success and brood parasitism rates, we collected data on study location, the years in which the study was conducted, the bird species included, patch size, whether the study investigated effects of edge proximity, patch size, or landscape context and, if so, what edge types and landscape metrics were included, and the results from these tests. We focused on these factors because they are relatively consistently measured and reported, and are commonly used in making conservation and management decisions for grassland birds. In some cases, studies did not present patch size, but did present patch dimensions that we used to calculate patch size. For some studies that did not present patch size, we used estimates of patch size presented in companion studies that used the same study sites. We used the mean patch size when possible, but used the midpoint of ranges when only minimum and maximum values were included. When multiple studies presented results based on the same monitored nests, we only included estimates from one of these studies.

For studies that investigated effects of edge proximity, patch size, or landscape context, we recorded the results from each species included in a study as separate tests. For these studies, we present the number of instances in which a positive effect, negative effect, or no effect was reported. We used generalized linear mixed models with a multinomial distribution and generalized logit link function or binomial distribution with logit link function (Littell et al. 2006) to produce estimates of the proportion of tests finding a positive effect, negative effect, or no effect while accounting for the nonindependence of multiple tests within a given study.
Approaches that explicitly consider effect size are generally favored over vote-counting approaches because of the potential relationship between sample size and significance of tests (Gurevitch and Hedges 1993). However, studies examining effects of edges, patch size, and landscape context varied in their treatment of explanatory variables as categorical or continuous and most failed to report at least one element required to successfully consider effect sizes (e.g., means, measures of variance, sample size, regression coefficients; Gurevitch and Hedges 1993). Moreover, there was no difference in sample size among cases where a positive, negative, or lack of relationship was found between patch size and DSR ($P = 0.282$), and instances of negative relationships between edge proximity and DSR (the generally expected relationship) had smaller sample sizes than those where a positive or lack of effect was found ($P = 0.025$). This suggests that the reported effects in these studies are not merely artifacts of sample size.

Because patch size is commonly reported, we investigated the relationship between patch size and nest survival (DSR) and brood parasitism using general linear mixed models (Littell et al. 2006). In these analyses, we logit-transformed DSR and the proportion of nests parasitized prior to analyses, and we included candidate models for effects of patch size, region (core Midwest, East, or Great Plains), patch size × region, and no effects (intercept only); study was included as a random effect (because some studies report multiple estimates per species or results for multiple species). We initially included species as a random effect, but dropped this term from analyses because the covariance parameter estimate was zero for nest survival and inclusion did not affect results for either nest survival or parasitism. To give more influence to estimates based on large sample sizes, we weighted estimates by the sample size of nests used to produce them. Values of patch size were discontinuous because of the relatively few estimates from very large patches, so we log-transformed patch size values prior to analyses. We evaluated models using Akaike’s information criterion (AIC) adjusted for small sample sizes (Burnham and Anderson 2002).

**RESULTS**

**Nest survival**

We found >75 studies with information on reproductive success in grassland habitats, containing >400 estimates of nest success based on >40 000 nests. Of those that focused on real rather than artificial nests and included information for obligate or facultative grassland species, there were 12 studies that examined edge effects, 10 that examined patch size effects, and 5 that examined the effect of landscape context on nest survival, presenting 27, 29, and 9 statistical tests of these effects, respectively (Appendix A). Three studies reported negative effects of edge proximity on nest survival, three reported positive effects, and six reported no effect. Two studies reported both positive and no effect of edge proximity for different species, and one study reported a negative relationship for one species, and no effect for another. Overall, 7 of 27 tests indicated a negative relationship, 4 of 27 a positive relationship, and 16 of 27 no effect (Fig. 1A). Accounting for the nonindependence of multiple tests per study, 16.1% ± 9.2% (mean ± SE) of tests indicated a negative relationship, 15.3% ± 12.1% indicated a positive relationship, and 68.6% ± 13.0% indicated no relationship between edge proximity and nest survival.

For patch size effects, five studies reported positive effects of patch size on nest survival, two reported negative effects, and seven reported no effect. This included two studies that reported both positive effects and no effect for different species, and one study that reported positive, negative, and no effect. Overall, 11 of 29 tests indicated a positive relationship, 4 of 29 a negative relationship, and 14 of 29 no relationship between patch size and nest survival (Fig. 1A). Based on the mixed model accounting for nonindependence of multiple tests per study, this corresponds to 32.8% ± 15.6% positive effects, 10.9% ± 8.3% negative effects, and 56.4% ± 14.8% no effects of patch size. Only a
survival rate estimates representing 16 species and 16,233 nests. Data are from 37 different studies, including 170 daily survival rate (mean ± SE) for grassland bird nests in each region. We generated model-averaged values while holding other variables at their mean values. Data are from 37 different studies, including 170 daily survival rate estimates representing 16 species and 16,233 nests.

FIG. 2. (A) Model-averaged relationship (with 95% confidence limits) between log-transformed patch size (originally measured in hectares) and daily survival rate for nests of grassland bird species, and (B) daily survival rate (mean ± SE) for grassland bird nests in each region. We generated model-averaged estimates while holding other variables at their mean values. Data are from 37 different studies, including 170 daily survival rate estimates representing 16 species and 16,233 nests.

single study reported evidence for effects of landscape context on grassland bird nest survival, corresponding to 1 of 9 tests finding an effect (11.1% ± 14.6%; Fig. 1A).

We collected data from 37 studies that reported estimates of nest survival and patch size, resulting in 170 DSR estimates representing from 10 to 918 nests (mean = 95, total = 16,233 nests; Appendix B). There were seven obligate or facultative grassland species with data from >1000 nests, including 4089 Dickcissel (Spiza americana; see Plate 1), 2197 Savannah Sparrow (Passerellus sandwichensis), 1966 Red-winged Blackbird (Agelaius phoeniceus), 1686 Grasshopper Sparrow (Ammodramus savannarum), 1629 Eastern Meadowlark (Sturnella magna), 1580 Clay-colored Sparrow (Spizella pallida), and 1208 Bobolink (Dolichonyx oryzivorus) nests. Studies spanned from 1965 to 2009, and covered from 2 to 15 years (mean = 3.4). Patch sizes ranged from 0.2 to 20,750 ha (mean = 1345.6 ha). This included 21 studies from the core Midwest, presenting 87 DSR estimates based on 2353 nests and patch sizes ranging from 7.5 to 3700 ha (mean = 797.49 ha), and 13 studies from the Great Plains (including Saskatchewan) presenting 55 DSR estimates based on 6182 nests and patch sizes ranging from 12.9 to 20,750 ha (mean = 3465.4 ha).

The best supported model for DSR incorporated an interaction between patch size and region (w1 = 0.43), although the constant (intercept only, w1 = 0.33) and patch size models (w1 = 0.17) also received support (Appendix C). Model-averaged estimates based on these top three models indicated no overall relationship between patch size and DSR (Fig. 2A), and little variation in DSR among regions (Fig. 2B). The top-ranked model indicated a weakly positive relationship between patch size and DSR in the Great Plains (β = 0.063, 95% CI = 0.02–0.11), and essentially no relationship in the core Midwest (β = −0.015, 95% CI = −0.064 to 0.035; Fig. 3A) or the East (β = −0.080, 95% CI = −0.220 to 0.061; Fig. 3C). However, the support for this model was only marginally greater than for the model with no patch size effect and, consequently, the model-averaged estimates reflected a weaker relationship in the Great Plains (model-averaged β = 0.032; Fig. 3B).

Brown-headed Cowbird parasitism

Six studies examined relationships between edge proximity and probability of cowbird parasitism, two studies examined patch size effects, and two studies examined effects of landscape context (Appendix D). Of the studies examining edge effects, five found evidence of a positive relationship between edge proximity and parasitism, four found evidence for no effect on at least one species, and no studies reported negative relationships; three studies reported both positive effects and no effect for different species. Of 15 tests for edge-proximity effects, 9 indicated a positive relationship and 6 indicated no relationship (Fig. 1B); based on the mixed model, the estimated proportion of cases finding a positive relationship was 58.3% ± 18.6%. Neither study examining effects of patch size found an effect despite 10 different tests, and one of two studies found an effect of landscape context with four of five tests finding a relationship (Fig. 1B).

We found at least 30 studies including data on cowbird parasitism, and were able to collect 97 parasitism-rate estimates from 27 of these (Appendix E). Study duration ranged from 2 to 15 years, spanning 1965 to 2009, and the total number of nests represented by these data was 14,909 (10–918 per study, mean = 154). Patch sizes ranged from 0.2 to 20,750 ha (mean = 1813.2 ha), and parasitism rates ranged from 0% to 85% (mean = 18.4%). These studies included 15 from the core Midwest, 3 from the East, and 10 from the Great Plains, presenting 42, 17, and 38 estimates from 6794, 1965, and 6150 nests, respectively. Patch sizes ranged from 0.2 to 1715 ha (mean = 291.4 ha), 21.1 to 302 ha (mean = 92.5 ha), and 34.6 to 20,750 ha (mean = 4401 ha) for the core Midwest, East, and Great Plains, respectively. Average
parasitism rates were 16.7% for the core Midwest, <1% for the East, and 28% for the Great Plains. Because of the general lack of cowbird parasitism in the East, we dropped estimates from this region in further analyses.

The best-supported model for brood parasitism included an additive effect of patch size and region ($w_i = 0.72$), and the only other well-supported model included an interactive effect of these variables ($w_i = 0.26, \Delta AIC_c = 2.07$; Appendix C). However, this second-ranked model was only supported because it included the parameters included in the top model, whereas the additional parameter for the interaction between patch size and region was uninformative. Parasitism rates were greater in the Great Plains than in the core Midwest, and decreased with increasing patch size in both regions (Fig. 4).

**DISCUSSION**

Evidence for effects of edge proximity and patch size on nest survival was equivocal. Although there are examples that support the widely held belief that edges and small patch size have negative demographic consequences for grassland birds (e.g., Johnson and Temple 1990, Winter and Faaborg 1999, Winter et al. 2000, Herkert et al. 2003), other examples suggest that this pattern is not widely generalizable (e.g., Davis et al. 2006, Grant et al. 2006, Walk et al. 2010, Hovick et al. 2012, Ribic et al. 2012). Indeed, our synthesis of results from studies investigating these factors suggests that one is most likely to find no effect of edge proximity on nest survival, and perhaps equally likely to find positive or negative edge effects. Although we combined results from woody and nonwoody edges, the same conclusions hold when focusing on either edge type (Appendix A). Moreover, even though positive relationships between patch size and nest survival are more frequently found than negative relationships, studies more often find no relationship, a result that is corroborated by our analysis that included 170 estimates from 37 different studies. In this analysis, we did find that patch size was positively related to nest survival in the Great Plains, but not in the core Midwestern states or Eastern states (Fig. 3). Nonetheless, there was considerable variation surrounding the predicted relationship for the Great Plains, suggesting that, in some circumstances, small patches may have good nest survival and large patches may have poor survival (Fig. 3B).

In contrast to the nest survival results, past studies showed a more convincing effect of edge proximity on brood parasitism rates. Furthermore, even though past studies did not indicate an effect of patch size on parasitism rates, our analysis combining estimates from numerous studies indicated consistent effects of patch size on the proportion of nests parasitized by Brown-headed Cowbirds (Fig. 4). Greater parasitism in smaller patches may be related to cowbirds disproportionately using habitat edges (Howell et al. 2007). There was also a large difference in the proportion of nests parasitized by cowbirds between studies conducted in the core Midwestern states vs. those in the Great Plains. This is consistent with the observation that, even within the Great Plains, parasitism intensity varies widely depending on the abundance of cowbirds (Jensen and Cully 2005). Even though cowbirds are relatively abundant in the Midwest, abundance is greater in the Great Plains (Sauer et al. 2011), and there are fewer cowbirds in the eastern areas where cowbird parasitism of grassland passerines appears to be negligible (Fig. 4).
Effects of landscape context were not consistent for nest survival or brood parasitism studies. However, it is notable that not many studies evaluated the effects of landscape context beyond potential effects of patch size or edge proximity, and these studies were exclusively in the Great Plains (Appendices A, D). Despite having relatively few examples to draw from, there was some evidence that grassland bird nests in Great Plains landscapes with more tree cover are less likely to be parasitized by cowbirds, presumably because cowbirds focus more attention on parasitizing nests of forest species (Pietz et al. 2009).

Overall, brood parasitism was more generalizable across space and time than nest survival. One reason for this difference is that brood parasitism results from the abundance and behavior of one species, whereas nest survival is a function of numerous factors. The primary cause of nest failure in passerines is nest predation (Ricklefs 1969), and nest survival is therefore dependent on the abundance and behavior of multiple potential predators, each of which has unique factors affecting the probability it will depredate a nest. For this reason, grouping predators when forming mechanistic explanations of what landscape or habitat factors influence nest predation often fail to reveal patterns. Fortunately, continual improvements in video technology and decreases in equipment cost have made studying nest predation logistically feasible (Cox et al. 2012). Indeed, considering the identity of nest predators may help identify habitat or landscape factors associated with nest predation that are obscured when predator identity is not known (Benson et al. 2010). Activity patterns of important nest predators have been found to be associated with temporal patterns of nest failure (Sperry et al. 2008, Weatherhead et al. 2010), and regional patterns in the identity of primary nest predators may have implications for conservation and management strategies (Thompson and Ribic 2012).

In grasslands, nests are susceptible to a diverse predator community and important nest predators appear to vary regionally (Pietz et al. 2012). Small mammals have been documented as important nest predators in northern areas of both the Great Plains and core Midwest (Pietz et al. 2012, Ribic et al. 2012), mesocarnivores have been documented as important in Wisconsin pastures (Renfrew and Ribic 2003, Ribic et al. 2012), and snakes have been identified as primary predators in some southern grasslands (Klug et al. 2010a, b). Importantly, nest–camera studies have begun to help us understand the mechanisms that make some nests vulnerable to predation. For example, higher nest survival near wooded edges in both North Dakota and Wisconsin appear to be caused by greater nest predation by thirteen-lined ground squirrels (Ictidomys tridecemlineatus) near the interior of grasslands (Grant et al. 2006, Ribic et al. 2012), and snake predation in Kansas is associated with shrubs (Klug et al. 2010a). Ultimately, these types of studies will allow us to both understand

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**PLATE 1.** Male Dickcissel (*Spiza americana*) in Vermilion County, Illinois, USA. Photo credit: M. P. Ward.
what causes larger scale patterns of nest failure and implement management actions that account for these patterns.

The results of our synthesis suggest that a one-size-fits-all strategy based on patch size or edge proximity will not produce the desired results of increasing grassland bird productivity. While this is true for nest survival, patch size and edge proximity seemed to be reliable factors for predicting parasitism by Brown-headed Cowbirds (Figs. 1B, 4). However, few nests fail to produce young solely due to cowbirds, and predation is generally a much larger source of reproductive failure. Therefore, it is not clear what role cowbird parasitism has in reducing seasonal fecundity of most grassland passerines or the costs and benefits of managing against cowbird parasitism relative to other potential actions that may improve nest survival.

Beyond taking a more predator-centric view of understanding landscape-level predictors of nest survival, a better understanding of links between management actions and nest predation is needed. Studies have increasingly focused on the effects of management on nest survival or brood parasitism (Murray and Best 2003, Patten et al. 2006, Churchwell et al. 2008, Kerns et al. 2010, Hovick et al. 2012, Ribic et al. 2012), although these studies are still relatively uncommon, and differences among studies make generalization impractical at this point. A better understanding of how management affects predator or cowbird abundance and behavior, and how this knowledge can be used to increase grassland bird productivity, remains a promising avenue for further research. Nonetheless, in some cases even reducing predation by a dominant group of nest predators may not lead to increased productivity (Ellis-Felege et al. 2012).

Although factors such as patch size, edge proximity, and landscape context influence occurrence or abundance of some grassland bird species (Ribic et al. 2009), and may affect nest survival and brood parasitism in some cases (Figs. 1, 3, 4), large and relatively unaltered grassland patches are rare in contemporary landscapes. Most grassland exists as relatively small patches in heavily agricultural landscapes, but even these patches can be productive for some grassland species. Taking a more mechanistic, rather than pattern-based, approach may help elucidate factors influencing demographic parameters as well as management approaches for affecting populations. These mechanisms likely vary regionally, so management may need to be tailored to region-specific drivers of demographic processes.

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Fig. 4. Relationship between log-transformed patch size and the proportion of nests parasitized by Brown-headed Cowbirds for nests of grassland bird species from the states and province in the core Midwest (6794 nests; shown in green), Great Plains (6150 nests; shown in blue), and East (1965 nests; shown in red). The solid and dashed lines represent predicted values and 95% confidence limits, respectively.
LITERATURE CITED


SUPPLEMENTAL MATERIAL

Appendix A
Summary of studies investigating relationships between grassland bird nest survival and edge proximity, patch size, or landscape composition (Ecological Archives A023-045-A1).

Appendix B
Summary of studies used in investigation of the relationship between patch size and nest survival of grassland birds (Ecological Archives A023-045-A2).

Appendix C
Model-selection results for candidate models predicting daily survival rate and brood parasitism of grassland passerines as a function of patch size, region, and additive and interactive combinations of these variables (Ecological Archives A023-045-A3).

Appendix D
Summary of studies investigating relationships between the proportion of grassland bird nests parasitized by Brown-headed Cowbirds and edge proximity, patch size, or landscape composition (Ecological Archives A023-045-A4).

Appendix E
Summary of studies used in investigation of the relationship between patch size and brood parasitism of grassland birds (Ecological Archives A023-045-A5).