7-2013

Minor Fitness Benefits For Edge Avoidance In Nesting Grassland Birds In The Northeastern United States

David G. Perkins
University of New England

Noah G. Perlut
University of New England, nperlut@une.edu

Allan M. Strong

The Auk 130(3):512–519, 2013

MINOR FITNESS BENEFITS FOR EDGE AVOIDANCE IN NESTING GRASSLAND BIRDS IN THE NORTHEASTERN UNITED STATES

David G. Perkins,[1] Noah G. Perlut,[1,3] and Allan M. Strong[2]

[1]*University of New England, Department of Environmental Studies, 11 Hills Beach Road, Biddeford, Maine 04074, USA; and*
[2]*University of Vermont, The Rubenstein School of Environment and Natural Resources, 347 Aiken Center, Burlington, Vermont 05405, USA*

Abstract.—Grassland birds are often affected negatively by habitat fragmentation. Outcomes include greater nest predation and brood parasitism, decreased colonization rates of small, isolated patches, and greater nest density in remnant core habitats. These effects have been well documented in the Midwest, but little is known about fragmentation and edge effects on grassland birds in the fragmented agricultural fields within the forested landscapes of the northeastern United States. From 2002 to 2010, we assessed how edges and edge types affected nest-site location and daily nest survival (DNS) of Savannah Sparrows (*Passerculus sandwichensis*) and Bobolinks (*Dolichonyx oryzivorus*) breeding in 11 fields (range: 13.2–38.3 ha; mean = 21.1 ha) within a large agricultural region of Vermont. Mean (± SD) distance to edge was 80.3 ± 39.6 m for Savannah Sparrows (n = 995) and 94.5 ± 56.5 m for Bobolinks (n = 652). Both species nested significantly less than expected within 50 m of the edge. For Savannah Sparrows nesting within 50 m of the edge, DNS increased with increased distance from the edge. Birds initiating nests later in the season nested closer to edges, but renests were farther from edges than first nests. Distance to edge had no detectable consequence for Bobolink nest success. Both species used portions of fields near hedgerows less than expected but used wetland, forest, agricultural, road, and developed edges in proportion to availability. For both species, DNS did not vary among edge types. Although edges were used less than expected, nesting near edges had only minor consequences for nest success. *Received 1 September 2012, accepted 20 February 2013.*

Key words: Bobolink, daily nest survival, *Dolichonyx oryzivorus*, edge effects, fitness, grassland management, *Passerculus sandwichensis*, Savannah Sparrow, Vermont.

Evitar los Bordes Acarrea Beneficios Menores en la Aptitud de Aves que Anidan en Praderas del Nororiente de Estados Unidos

Resumen.—Las aves de pradera son frecuentemente afectadas negativamente por la fragmentación del hábitat. Las consecuencias incluyen mayor depredación y parasitismo de los nidos, la disminución en la tasa de colonización de parches pequeños y aislados, y una mayor densidad de nidos en el núcleo del hábitat remanente. Estos efectos han sido bien documentados en el medio oeste de los Estados Unidos, pero se sabe poco sobre la fragmentación y los efectos de borde en las aves de pradera de campos agrícolas fragmentados dentro de los paisajes boscosos del nororiente del país. Entre 2002 y 2010, evaluamos cómo los bordes y los tipos de borde afectan la ubicación del sitios de anidación y la supervivencia diaria de los nidos de dos especies (*Passerculus sandwichensis* y *Dolichonyx oryzivorus*) que se reprodujeron en 11 campos (rango: 13.2–38.3 ha; promedio = 21.1 ha) en una región agrícola grande en Vermont. La distancia promedio (±DW) al borde fue de 80.3 ± 39.6 m para *P. sandwichensis* (n = 995) y 94.5 ± 56.5 m para *D. oryzivorus.* Ambas especies anidaron significativamente menos de los esperado a menos de 50 m del borde. Para los individuos de *P. sandwichensis* que anidaron a menos de 50 m del borde, la supervivencia diaria de los nidos aumentó con la distancia al borde. Las aves que iniciaron sus nidos tarde en la temporada anidaron más cerca de los bordes, pero en los casos en que hubo anidación repetida, los nidos posteriores se localizaron más lejos del borde que los nidos iniciales. La distancia al borde no tuvo consecuencias detectables para el éxito de los nidos de *D. oryzivorus.* Ambas especies usaron porciones de los campos cercanas a cercas vivas en un grado menor al esperado, pero usaron los bordes de humedales, bosques, áreas agrícolas, caminos y áreas desarrolladas en proporción a su disponibilidad. Para ambas especies, la supervivencia diaria de los nidos no fue diferente entre distintos tipos de borde. Aunque los bordes fueron usados menos de lo esperado, anidar cerca de los bordes solo tuvo consecuencias menores sobre el éxito de los nidos.

Habitat fragmentation can decrease bird populations by dividing core habitat into smaller, isolated patches of low-quality habitat (Johnson and Temple 1990, Winter et al. 2000, Herkert et al. 2003). Nesting in close proximity to the edge can have direct and indirect fitness effects (Gates and Gysel 1978), including decreased pairing success (Gibbs and Faaborg 1990, Van Horn et al. 1995, Hagan et al. 1996, Villard 1998), decreased nesting success (Bollinger 1995), increased interspecific competition (Whitcomb et al.

[3]Address correspondence to this author. E-mail: nperlut@une.edu

The Auk, Vol. 130, Number 3, pages 512–519. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2013.12163

1981, Ambuel and Temple 1983), and lower abundance of insect prey (Whitcomb et al. 1981, Burke and Nol 1998).

In the northeastern United States, the effects of habitat fragmentation and edge sensitivity have been studied extensively for both shrubland (Anderson et al. 1977, Askins et al. 2007, Chandler et al. 2009) and forest birds (Sargent et al. 1998, Ortega and Capen 1999, Stephens et al. 2003, Deng and Gao 2005), but little is known about edge effects on grassland birds in this region. This is a particularly important gap in knowledge because although significant grassland habitat remains, it is situated within a forested landscape. Nearly everything known about edge effects on grassland birds comes from North American midwestern grasslands, and there, wooded edges are consistently avoided (Fletcher and Koford 2003, Jensen and Finck 2004). In the Northeast, where grassland patches are smaller and more isolated, avoidance of wooded edges may eliminate a substantial proportion of otherwise suitable habitat.

We explored the effects of edges on nesting success of two grassland species breeding in Vermont's Champlain Valley, a region that includes 146,000 ha of managed grasslands (National Agricultural Statistics Service 2010). We used a long-term data set (2002–2010) for nesting Bobolinks (*Dolichonyx oryzivorus*) and Savannah Sparrows (*Passerculus sandwichensis*) and tested seven predictions from the hypothesis that there are both causes and consequences of nesting close to edges in northeastern grassland habitats. Our study area was composed of a mosaic of grassland types where the timing and frequency of hay harvest and/or grazing affect both ecological (Perlut et al. 2008c) and evolutionary (Perlut et al. 2008a) processes in these species. Birds breeding in more intensively managed fields (earlier and more frequent hay harvests) have lower reproductive success and apparent annual survival than those in less intensively managed fields (Perlut et al. 2006, 2008b). Therefore, we included predictions that explored the effects of edges across a gradient of management regimes. Each of these predictions is based on results from previous studies of edge effects on songbirds throughout North America. First, birds will select nest sites nonrandomly, such that portions of fields near edges will be used less than expected given their availability. Second, daily nest survival (DNS) will increase with increasing distance from edge (Batary and Baldi 2004, Bollinger and Gavin 2004, Renfrew et al. 2005). This prediction assumes that the density of nest predators is greater along edges than in patch interiors. Third, on fields mowed or grazed during the breeding season, nests at all distances from the edge are equally likely to fail (Renfrew et al. 2005) because management practices override potential edge effects. Importantly, data to test this prediction did not include nests that failed because of direct management practices. The implication is that management influences the predator community, and this influence has the potential to increase edge effects. Fourth, renests (clutches that follow a failure) will be farther from the edge than first clutches (Bollinger and Gavin 2004); however, second clutches (after success) will not be farther from the edge. Birds may react to nest failure by associating edges with predators and move away from the edge to decrease the likelihood of predation. Fifth, nestling mass will increase as distance to edge increases (Huhta et al. 1999). Adults with territories closer to the edge will have fewer resources with which to feed nestlings, thereby producing relatively smaller young (Huhta et al. 1999). Sixth, birds will avoid nesting near edge types they perceive as threats to nest survival (e.g., roads, Bollinger and Gavin 2004; wooded edges, Fletcher and Koford 2003); and as a corollary, our seventh prediction was that daily nest survival will be lower for nests located near edge types that are avoided (Bollinger and Gavin 2004).

METHODS

Study area and experimental design.—From 2002 to 2010, we studied songbirds breeding in the four most common grassland types in the Champlain Valley (Perlut et al. 2008c). Early-hayed fields (n = 3) were harvested between 27 May and 11 June and generally again in early to mid-July. Middle-hayed fields (n = 3) were harvested between 21 June and 10 July. Late-hayed fields (n = 3) were harvested after reproductive activity ended. Rotationally grazed pastures (n = 2) were fields in which cows were rotated through a matrix of paddocks and moved after all of the grass in a paddock was grazed to a farm-specific height. Each paddock was thereby given a multiple-week "rest" between grazing events (for more specific details on grazing management and the representative nature of these study fields to the region, see Perlut and Strong 2011). Fields were composed of a mixture of cool-season grasses and forbs. Early- and middle-hayed fields had a greater proportion of forbs than late-hayed fields or pastures, which were grass dominated. However, late-hayed fields generally had significant "oldfield" communities, including sedge (*Carex* spp.), vetch (*Vicia* sp.), bedstraw (*Galium* sp.), and native forbs (for further details on vegetation, see Perlut et al. 2006). Each study field was a minimum of 13.2 ha (range: 13.2–38.3 ha; mean = 21.1 ha; Fig. 1). The average (± SD) ratio of area (ha) to perimeter (total edge length, m) was

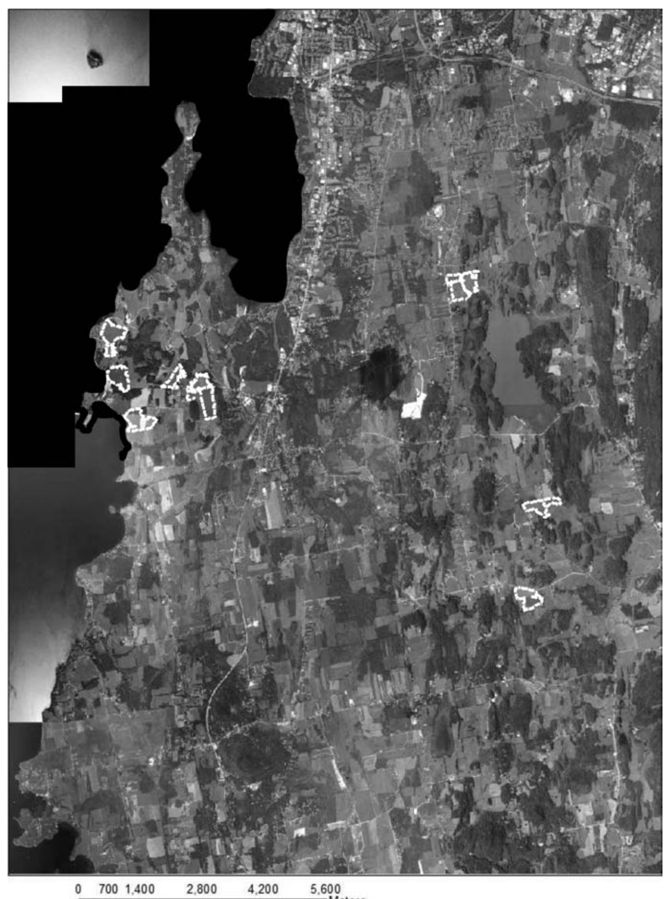

FIG. 1. Study fields (n = 11) in white hatched outline were located in Chittenden County, Vermont.

0.007 ± 0.002 (range: 0.003–0.009). Edge types included agriculture (management-defined boundary between pasture or hay field), forest, hedgerow, human development, road, and wetland. Edge types and lengths were consistent for the duration of the study.

Field methods.—Beginning in mid-May, we used mist nets to attempt to capture and band every adult breeding on every study field with a unique combination of three colored leg bands and one federal band. We also attempted to find the nests of every female using behavioral observations and by flushing incubating birds off nests. Once a nest was found, we immediately identified the adults associated with it; if they were not already banded, we attempted to capture the parents and band them as described above. Nest contents were monitored every 1 to 2 days until fledging or failure. Nestlings were weighed to the nearest 0.1 g and were banded around day 6. Although 85% were banded between days 5 and 7, because of the timing of when the nest was found, or to minimize disturbance at the nest site, some nestlings were weighed as early as day 3 (<1% of nests) or as late as day 10 (<1% of nests). When fields were hayed during the breeding season, >99% of all nests active at the time of haying failed because of management (Perlut et al. 2006). On early- and middle-hayed fields, haying caused 44.6% and 38.8% of all nests to fail, respectively. Therefore, to minimize potential bias associated with haying-induced failure, on early- and middle-hayed fields we removed any nest from the analysis that failed as a result of haying and limited our analyses to successful nests and nests that failed because of predation, weather, infertility, or abandonment. Nest locations were recorded with a hand-held GPS unit.

Analysis methods.—We plotted all nests using ARCGIS, version 9.2. To differentiate edge types, we used the polyline function to trace each field's corresponding habitat edges. An edge was classified as agricultural, forest, hedgerow, human development, road, or wetland as determined from ground truthing. To investigate the relationship between habitat edge and various measures of nest success, we calculated the distance to the closest edge corresponding to each nest and our six edge types. We calculated total edge length for each edge type making up the perimeter of each field.

We used a modified Mayfield method for calculating nest success (Mayfield 1975, Aebischer 1999). This method gives daily nest survival values for each nest based on nest fate and the number of days observed. With SAS, version 9.2 (SAS Institute, Cary, North Carolina), we then created generalized linear models to test our seven predictions for nest survival and productivity derived from the edge avoidance hypothesis. Because fields varied in both area and configuration (Fig. 1), we included field as a random effect. We tested for differences between edge use and availability using a chi-square test. Because this data set included six edge types, we tested whether edge type influenced DNS with a one-way analysis of variance and Bonferroni correction to control for multiple simultaneous comparisons.

Results

We found 1,647 nests (995 Savannah Sparrow, 652 Bobolink). Mean (± SD) distance to edge was 80.3 ± 39.6 m for Savannah Sparrows and 94.5 ± 56.5 m for Bobolinks (Fig. 2). Causes of nest failure included predation (68%), trampling by cows (12%), abandonment (11.8%), weather (flooding–heavy rains: 7.3%), infertility (0.6%), and adult mortality (0.3%).

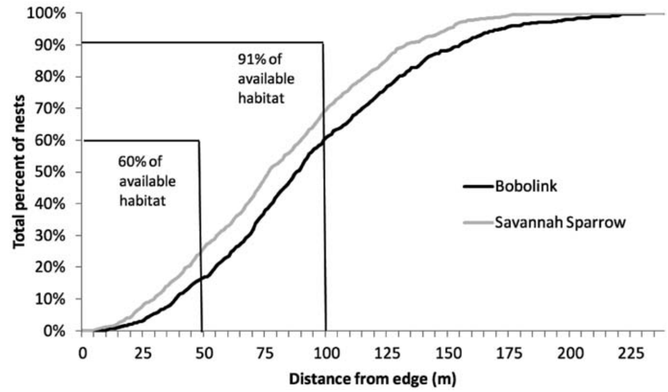

Fig. 2. Nest placement in relation to habitat availability for Savannah Sparrow and Bobolink nests in the Champlain Valley of Vermont, 2002–2010.

Both species used areas within 50 m of the edge significantly less than expected (Fig. 2). Although 60% of available habitat was found within 50 m of the edge, only 17.0% and 26.6% of Bobolink and Savannah Sparrow nests, respectively, were found in that area. By contrast, although only 31% of the available habitat was located between 50 and 100 m of the edge, this area contained 45.5% and 43.9% of Bobolink and Savannah Sparrow nests, respectively. Distance to edge did not vary significantly among years ($F < 2.18$, df = 8 and 559–812, $P > 0.09$).

Table 1 summarizes our predictions of the edge avoidance hypothesis and the test statistic for each prediction. Our tests of prediction 2 showed that across all fields and both species, DNS was unrelated to distance to edge (Table 1 and Fig. 3). However, there were significant differences among study fields when comparing all nests and nests <100 m from the edge for both species ($F > 2.69$, df = 1 and 2–427, $P < 0.001$). These site effects suggest that edge effects were generally influenced by site size and configuration. There were no site effects for Savannah Sparrows nesting within 50 m of the edge because DNS increased with increasing distance from edge on all fields (Table 1). Our tests of prediction 3 showed that on managed fields there was no effect of distance to edge on DNS for Bobolinks or Savannah Sparrows (Table 1 and Fig. 4); within each treatment, these effects varied among fields for Savannah Sparrows ($F > 2.00$, df = 2–4 and 50–345, $P < 0.04$) but did not vary among fields for Bobolinks (all $F < 2.00$, df = 2–4 and 94–107, $P > 0.14$). Early-nesting (prior to June 11) Savannah Sparrows nested 4.3 m farther from the edge than later-nesting birds ($F = 2.71$, df = 1 and 753, $P = 0.04$); distance to edge did not vary with timing of nest initiation for Bobolinks ($F = 1.48$, df = 1 and 510, $P = 0.22$). Prediction 4, that birds would respond to failure by moving farther from the edge, showed that for Savannah Sparrows, within-year renests (after failure, $n = 204$) were 9.6 m farther from the edge, on average, than first clutches. However, second nests (after success, $n = 89$) were not farther from the edge (Table 1). Although they rarely renested ($n = 32$), Bobolinks did not move farther from the edge between nesting attempts. More subtle negative consequences of nesting near edges were predicted to be manifested as reduced nestling mass (prediction 5). However, in neither species did the mean nestling mass per nest decline with increasing proximity to edge (Table 1 and Fig. 5).

TABLE 1. A summary of results from tests of the prediction that nesting in proximity to habitat edges has negative influences on daily nest survival (DNS) and growth of nestlings. Data are from studies conducted on Savannah Sparrows and Bobolinks in the Champlain Valley, Vermont, 2002–2010. Statistically significant results are in bold.

Prediction	Fields	Savannah Sparrow	Bobolink
(2) Daily nest survival will increase with increasing distance to edge (Batary and Baldi 2004, Bollinger and Gavin 2004, Renfrew et al. 2005).	All fields	*F* = 0.10, df = 12 and 815, P = 0.75	*F* = 0.03, df = 12 and 559, P = 0.86
Nests <50 m from edges		***F* = 3.84, df = 12 and 214, *P* = 0.05**	*F* = 0.44, df = 11 and 94, *P* = 0.51
Nests <100 m from edges		*F* = 1.35, df = 12 and 574, *P* = 0.25	*F* = 2.78, df = 12 and 348, *P* = 0.10
(3) On likely managed fields, nests at all distances from the edge will be equally to fail (Renfrew et al. 2005).	Early-hayed fields	***F* = 2.31, df = 5 and 345, *P* = 0.04**	*F* = 1.44, df = 3 and 94, *P* = 0.24
	Middle-hayed fields	*F* = 2.48, df = 4 and 50, *P* = 0.06	*F* = 0.22, df = 5 and 107, *P* = 0.95
	Rotationally grazed pastures	***F* = 2.83, df = 3 and 229, *P* = 0.04**	*F* = 0.21, df = 3 and 96, *P* = 0.89
(4) Second clutches (after failure) will be farther from the edge than second clutches (after success) (Bollinger and Gavin 2004).	All fields	***F* = 3.94, df = 1 and 289, *P* = 0.05**	*F* = 0.22, df = 1 and 28, *P* = 0.64
(5) Nestling mass will increase as distance to edge increases (Huhta et al. 1999).	All fields	*F* = 0.88, df = 1 and 245, *P* = 0.87	*F* = 1.06, df = 1 and 259, *P* = 0.31

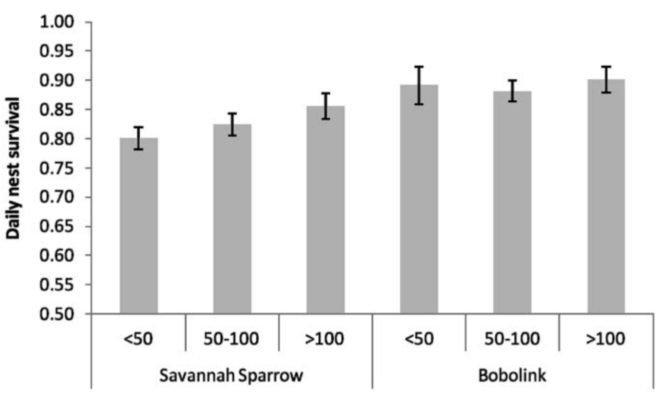

FIG. 3. Daily nest survival rates (mean ± SE) in relation to increasing distance to edge for Savannah Sparrow and Bobolink nests in the Champlain Valley of Vermont, 2002–2010.

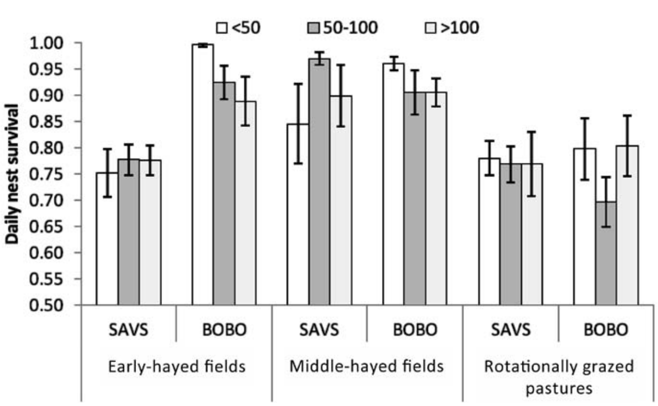

FIG. 4. When controlling for the study field, daily nest survival (mean ± SE) was not affected by distance to edge within any grassland management type in the Champlain Valley of Vermont, 2002–2010 (SAVS = Savannah Sparrow, and BOBO = Bobolink). Nests that failed directly as a result of field management were not included in this analysis.

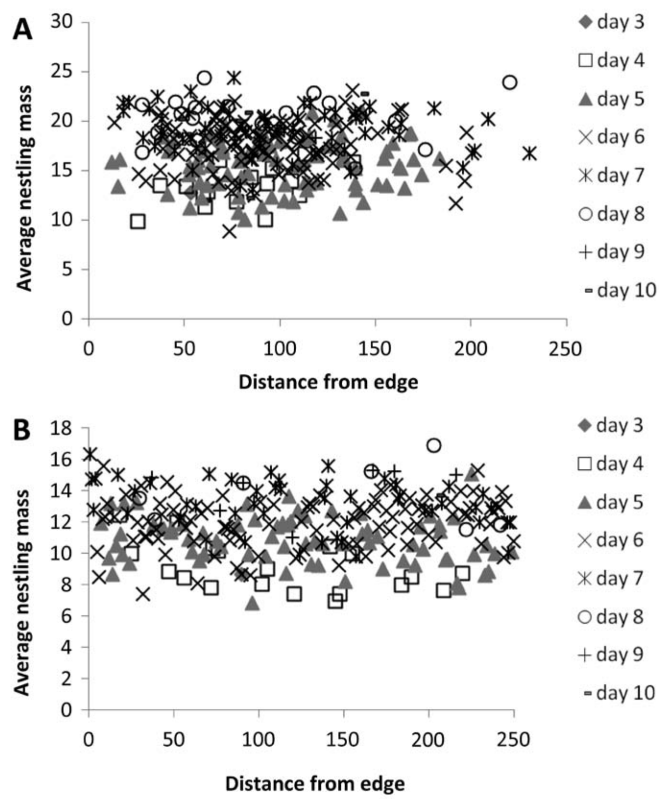

FIG. 5. Nestling mass (mean nestling mass per nest) in relation to distance from the edge for (A) Bobolinks and (B) Savannah Sparrows in the Champlain Valley of Vermont, 2002–2010. Nestlings in this population show initial rapid growth in their first few days, leading to substantial overlap in mass as illustrated here. Nonetheless, the data clumping illustrates the lack of correlation between nestling mass and distance from edge. Days indicate the number of days posthatching for each nestling.

Table 2. Two predictions of the edge avoidance hypothesis are that birds will avoid nesting near edge types they perceive as threats to nest survival (prediction 6) and that daily nest survival (DNS) will be lower for nests located near edge types that are avoided (prediction 7). Bold indicates where proportional use of an edge type was significantly different from availability ($\chi^2 < 0.001$).

		Percentage of nests nearest this edge type		
Edge type	Percent edge	All	Savannah Sparrow	Bobolink
Wetland	14	19	16%	24%
Road	18	20	19%	21%
Human development	5	4	4%	3%
Hedgerow	16	**1**	**<1%**	**1%**
Forest	35	48	52%	42%
Agricultural	13	10	10%	9%

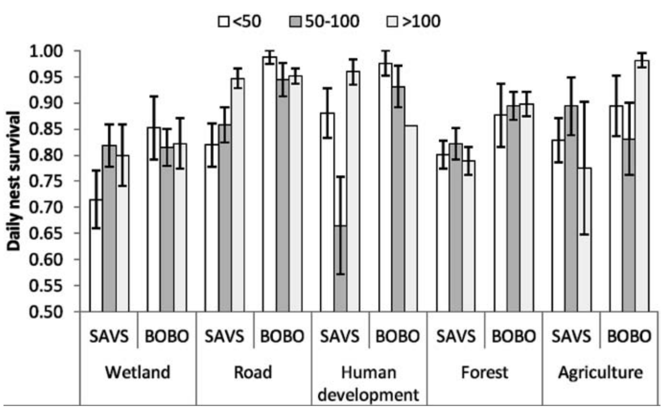

Fig. 6. When controlling for the study field, daily nest survival (mean ± SE) was not affected by distance to edge within any edge type (SAVS = Savannah Sparrow, and BOBO = Bobolink).

Our tests of avoidance of specific edge types (prediction 6) found that both species most frequently nested closest to a forest edge (Table 2); Savannah Sparrow nests were marginally closer to forested edges than expected given availability (35% of available edge, 52% of nests; $\chi^2 = 3.2$, df = 1, $P = 0.07$). However, both species used portions of fields near hedgerows less than expected ($\chi^2 = 12.1$–15.3, df = 1, $P < 0.001$; Table 2). As noted above, DNS varied among fields; after accounting statistically for this effect, we found that DNS did not vary with edge type for either species (prediction 7; $F < 1.38$, df = 8 and 2–412, $P > 0.09$; Fig. 6).

Discussion

Both Bobolinks and Savannah Sparrows used portions of fields near edges significantly less than expected given the habitat area. However, although they nested farther than expected from field edges, we could not detect any negative effect on Bobolinks' reproductive success. Across all fields, Savannah Sparrows' nesting success was lower when they nested within 50 m of an edge. Decreased nest survival rates were no longer apparent at 100 m from the edge, which suggests a distance threshold effect on predation. Although the absolute distance moved was <10 m, Savannah Sparrows renested significantly farther from the edge after nest failure, which suggests that nest-site selection decisions may be influenced by perceived predation risk. Finally, Savannah Sparrows that initiated nests after early June nested closer to field edges than those that initiated nests earlier in the breeding season. This result suggests that despotic interactions may play a role during settlement. Dominant or older birds may force subordinate or younger birds into areas (closer to the edge) that have a greater perceived risk of predation.

These results agree with those of others who have found that edge avoidance was similar across species within a given study system (Herkert 1994, Vickery et al. 1994, Helzer and Jelinski 1999). However, given similar patterns of nest placement with respect to distance to edge, the variation between species in effects of distance to edge on reproductive success in this system is intriguing. Given the strong negative response to edges in both species, we conclude that there must be a perceived fitness consequence for nesting near edges. We doubt that medium- to large-size mammalian predators caused most nest failures because depredated nests were rarely disturbed and we could not detect paths or tracks to nests. Although circumstantial, this suggests that a large percentage of predation events were the result of small mammals (*Microtus pennsylvanicus*, *Peromyscus* spp., and *Zapus hudsonius*) that are resident within our grassland study sites. *Peromyscus* and *Zapus* have been documented as grassland nest predators (Pietz and Granfors 2000). Given that female Bobolinks are ~50% heavier than Savannah Sparrows (Martin and Gavin 1995, Wheelwright and Rising 2008), Bobolinks may be better able to actively defend their nests from potential nest predators, although behavioral responses to predators (nest defense, incubation, and brooding behavior) may also play a role in the probability of nest predation (Murphy et al. 1997, Weidinger 2002). A complete understanding of the causal relationships surrounding both nest placement and the subsequent consequences requires more information on the distribution of nest predators. Our predictions are based on the premise that forest- or edge-based predators are primarily responsible for nest depredation events (Wilcove 1985, Andrén and Anglestam 1988). But small mammals could be evenly dispersed throughout grassland patches or could even exhibit edge avoidance as seen in these two bird species. As such, the distribution and identity of predators and their activity patterns within grasslands are likely better predictors of nest success.

Ribic et al. (2009) reviewed the literature describing area sensitivity of grassland birds and found that the correlation between distance to edge and probability of occurrence as well as distance to edge and density was variable for both Bobolinks and Savannah Sparrows. Bobolinks showed a positive relationship between distance to edge and probability of occurrence in some studies (Herkert 1994, Vickery et al. 1994, Johnson and Igl 2001), but DeJong et al. (2004) found a negative relationship. Because foraging and nest sites are disjunct spatially for both species (N. G. Perlut and A. M. Strong pers. obs), nest-site location and population density may be decoupled. Others have found a positive relationship between Bobolink nest density and distance to edge (Bollinger

1995, Johnson and Igl 2001, Renfrew 2002, Renfrew and Ribic 2002, Skinner 2004), but Davis et al. (2006) found the relationship to be variable. For Savannah Sparrows, some have found a positive relationship between distance to edge (Herkert 1994) or patch size (Vickery et al. 1994) and probability of occurrence, but Bakker et al. (2002) found the relationship to vary and Johnson and Igl (2001) found no area sensitivity. Again, many studies found a positive relationship between distance to edge and nest density for the Savannah Sparrow (e.g., Bollinger 1995, Johnson and Igl 2001, Renfrew and Ribic 2002), whereas Davis et al. (2006) found the relationship to be variable. Variation in results across these studies underscores the potential for landscape-level factors to confound simple tests of the influence of edge effects. Additional research that we have conducted in the Champlain Valley suggests that, for Bobolinks, abundance is more strongly related to landscape-level factors (open habitats within 2,500 m of the grassland patch) than to attributes of the particular field. By contrast, Savannah Sparrow abundance was more strongly related to patch-level attributes (Shustack et al. 2010). Because nest-site selection is embedded in a series of settlement decisions (regional, landscape, patch, microhabitat), the relationship between landscape composition and configuration can influence conclusions about edge avoidance if patch-level analyses are confounded by regional-level patterns.

Our results, coupled with those of other researchers, lead to the question: Why are edges used rarely in proportion to their availability when fitness consequences are seemingly minimal? One possible explanation is that edge avoidance is an innate trait of grassland birds, such that habitats that are perceived to be of lower quality are avoided. This response could be magnified through conspecific attraction (Nocera et al. 2006), such that early colonizers settle in sites farthest from edges and settlement patterns then move from the center to the edge of the patch. As noted above, this is supported by results for Savannah Sparrows where distance to edge decreased over the course of the breeding season. By contrast, this could be a learned behavior that has fitness benefits only when grassland patches are larger. We found differences among fields, which suggests that size and shape were important factors in assessing the influence of distance to edge on DNS. Compared to midwestern grasslands, our study sites are small and embedded in a forested matrix. Average (± SD) patch size of all grasslands in the Vermont side of the Champlain Valley is 3.9 ± 4.5 ha; however, only 13.8% of fields (<1.7% of area) in the Champlain Valley are <0.78 ha (A. M. Strong unpubl. data). Fields of this size would likely be avoided entirely by grassland birds because (if circular in shape) the entire patch is ≤50 m from an edge.

Our results are similar to those of Renfrew et al. (2005), who found no relationship between nest success and distance to edge. They concluded that their system in Wisconsin may support a high percentage of resident grassland predators and that pastures may provide little resistance to movement for predators typically associated with wooded or edge habitats. In our system, there was no support for any differential effect of management activities on the relationship between distance to edge and daily nest success. This result indicates that although agricultural management significantly affects the vegetative structure, these changes do not alter the predator community in ways that increase edge effects. Again, because of the small size of northeastern grasslands, differential effects of management activities on nest predation may be minimal, compared with field size, in terms of serving to deter predators. Further, in our study system, ~65% of all grassland habitat is managed during the breeding season (18% early-hayed, 25% middle-hayed, 22% grazed; Perlut et al. 2008c), providing another pathway whereby the benefits of edge avoidance are diluted. Of interest, however, is that over the 9 years of data collection, we did not document a single case of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*), despite the commonness of this species in the Champlain Valley.

In summary, our results show strong edge avoidance by Bobolinks and Savannah Sparrows but differences in fitness consequences between species. Irrespective of the fitness consequences, edge avoidance likely plays a role in decreasing the carrying capacity for grassland birds in the northeastern United States. In the Champlain Valley, where the majority of available patches are small and embedded in a forested matrix, the ability of this landscape to support populations of grassland birds has decreased through forest regeneration. As the agricultural industry has declined and the proportion of forested habitat has increased, abundances of grassland birds have decreased (Sauer et al. 2011). Given that this trend is likely to continue, efforts to increase habitat quality on the remaining suitable patches (Perlut et al. 2011) should be pursued.

Acknowledgments

This project was supported by the Initiative for Future Agricultural and Food Systems and the National Research Initiative of the U.S. Department of Agriculture Cooperative State Research, Education and Extension Service, grant nos. 2001-52103-11351 and 03-35101-13817, respectively. Additional funding was provided by the Natural Resource Conservation Service's Wildlife Habitat Management Institute. We thank Shelburne Farms and the Galipeau, Ross, Thibeau, Maile, and Stern families for generous access to their land. We thank the Galipeau family for additional financial support. Thanks to D. H. Johnson and two anonymous reviewers for helpful comments on the manuscript.

Literature Cited

Aebischer, N. J. 1999. Multi-way comparisons and generalized linear models of nest success: Extensions of the Mayfield method. Bird Study 46 (Supplement):S22–S31.

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057–1068.

Anderson, S. H., K. Mann, and H. H. Shugart. 1977. The effect of transmission-line corridors on bird populations. American Midland Naturalist 79:216–221.

Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. Ecology 69:544–547.

Askins, R. A., B. Zuckerberg, and L. Novak. 2007. Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland songbirds in southern New England? Forest Ecology and Management 250:137–147.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. Conservation Biology 16:1638–1646.

Batary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology 18:389–400.

Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. Auk 112:720–730.

Bollinger, E. K., and T. A. Gavin. 2004. Responses of nesting Bobolinks (*Dolichonyx oryzivorus*) to habitat edges. Auk 121: 767–776.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. Auk 115:96–104.

Chandler, R. B., D. I. King, and S. DeStefano. 2009. Scrub-shrub bird habitat associations at multiple spatial scales in beaver meadows in Massachusetts. Auk 126:186–197.

Davis, S. K., R. M. Brigham, T. L. Shaffer, and P. C. James. 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. Auk 123:807–821.

DeJong, J. R., D. E. Naugle, K. K. Bakker, F. R. Quamen, and K. F. Higgins. 2004. Impacts of agricultural tillage on grassland birds in western South Dakota. Pages 76–80 *in* Proceedings of the 19th North American Prairie Conference (D. Egan and J. A. Harrington, Eds.). University of Wisconsin, Madison.

Deng, W.-H., and W. Gao. 2005. Edge effects on nesting success of cavity-nesting birds in fragmented forests. Biological Conservation 126:363–370.

Fletcher, R. J., Jr., and R. R. Koford. 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. Auk 120:799–810.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology 59:871–883.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conservation Biology 4:193–196.

Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188–202.

Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4:461–471.

Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, and others. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conservation Biology 17:587–594.

Huhta, E., J. Jokimaki, and P. Rahko. 1999. Breeding success of Pied Flycatchers in artificial forest edges: The effect of a suboptimally shaped foraging area. Auk 116:528–535.

Jensen, W. E., and E. J. Finck. 2004. Edge effects on nesting Dickcissels (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. American Midland Naturalist 151:192–199.

Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: A regional perspective. Auk 118:24–34.

Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. Journal of Wildlife Management 54:106–111.

Martin, S. G., and T. A. Gavin. 1995. Bobolink (*Dolichonyx oryzivorus*). *In* The Birds of North America, no. 176 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Murphy, M. T., C. L. Cummings, and M. A. Palmer. 1997. A comparative analysis of habitat selection, nest site and nest success by Cedar Waxwings and Eastern Kingbirds. American Midland Naturalist 138:344–356.

National Agricultural Statistics Service. 2010. The Census of Agriculture. United States Department of Agriculture. [Online.] Available at www.agcensus.usda.gov/.

Nocera, J. J., G. J. Forbes, and L.-A. Giraldeau. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. Proceedings of the Royal Society of London, Series B 273:349–355.

Ortega, Y. K., and D. E. Capen. 1999. Effects of forest roads on habitat quality for Ovenbirds in a forested landscape. Auk 116:937–946.

Perlut, N. G., C. R. Freeman-Gallant, A. M. Strong, T. M. Donovan, C. W. Kilpatrick, and N. J. Zalik. 2008a. Agricultural management affects evolutionary processes in a migratory songbird. Molecular Ecology 17:1248–1255.

Perlut, N. G., and A. M. Strong. 2011. Grassland birds and rotational-grazing in the Northeast: Breeding ecology, survival and management opportunities. Journal of Wildlife Management 75:715–720.

Perlut, N. G., A. M. Strong, and T. J. Alexander. 2011. A model for integrating wildlife science and agri-environmental policy in the conservation of declining species. Journal of Wildlife Management 75:1657–1663.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: Behavioral responses and management strategies. Ecological Applications 16:2235–2247.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2008b. Grassland songbird survival and recruitment in agricultural landscapes: Implications for source–sink demography. Ecology 89:1941–1952.

Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2008c. Regional population viability of grassland songbirds: Effects of agricultural management. Biological Conservation 141:3139–3151.

Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. Journal of Wildlife Management 64:71–87.

Renfrew, R. B. 2002. The influence of patch and landscape characteristics on grassland passerine density, nest success, and predators in southwestern Wisconsin pastures. Ph.D. dissertation, University of Wisconsin, Madison.

Renfrew, R. B., and C. A. Ribic. 2002. Influence of topography on density of grassland passerines in pastures. American Midland Naturalist 147:315–325.

Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: A futile strategy in a fragmented landscape. Auk 122:618–636.

Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugle, K. K. Bakker, D. W. Sample, and

R. B. Renfrew. 2009. Area sensitivity in North American grassland birds: Patterns and processes. Auk 126:233–244.

Sargent, R. A., J. C. Kilgo, B. R. Chapman, and K. V. Miller. 1998. Predation of artificial nests in hardwood fragments enclosed by pine and agricultural habitats. Journal of Wildlife Management 62:1438–1442.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2011. The North American Breeding Bird Survey, Results and Analysis 1966–2009. Version 3.23.2011. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.

Shustack, D. P., A. M. Strong, and T. M. Donovan. 2010. Habitat use patterns of Bobolinks and Savannah Sparrows in the northeastern United States. Avian Ecology and Conservation 5:11.

Skinner, S. P. 2004. Linking decision support systems for ducks with relative abundance of other grassland bird species. M.S. thesis, University of Saskatchewan, Saskatoon.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nesting success: A review of the evidence at multiple spatial scales. Biological Conservation 115:101–110.

Van Horn, M. A., R. M. Gentry, and J. Faaborg. 1995. Patterns of Ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. Auk 112:98–106.

Vickery, P. D., M. L. Hunter, Jr., and S. M. Melvin. 1994. Effects of habitat area on the distribution of grassland birds in Maine. Conservation Biology 8:1087–1097.

Villard, M. A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk 115:801–805.

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424–437.

Wheelwright, N. T., and J. D. Rising. 1993. Savannah Sparrow (*Passerculus sandwichensis*). *In* The Birds of North America, no. 45 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest (Maryland Piedmont). Pages 125–205 *in* Forest Island Dynamics in Man-Dominated Landscapes (R. L. Burgess and D. M. Sharpe, Eds.). Springer, New York.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214.

Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

Associate Editor: M. T. Murphy