EDGE EFFECTS AND ECOLOGICAL TRAPS: EFFECTS ON SHRUBLAND BIRDS IN MISSOURI

APRIL A. WOODWARD,[1,2] Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA
ALIX D. FINK, Department of Fisheries and Wildlife Sciences, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA
FRANK R. THOMPSON, III, U.S. Forest Service, North Central Research Station, 202 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA

Abstract: The effect of habitat edge on avian nesting success has been the focus of considerable debate. We studied relationships between habitat edges, locations of nests, and predation. We tested the ecological trap hypothesis for 5 shrubland bird species in the Missouri Ozarks. We compared habitat selection and daily nest predation rates among 3 distance-to-edge categories. Edge effects were species specific. Indigo bunting (*Passerina cyanea*) and northern cardinal (*Cardinalis cardinalis*) preferred nest sites that were close (≤20 m) to habitat edges. Yellow-breasted chat (*Icteria virens*) and prairie warbler (*Dendroica discolor*) preferred nest sites >20 m from the edge. Field sparrow (*Spizella pusilla*) used habitat in proportion to availability. Daily nest predation varied by as much as 200–300% among distance-to-edge categories but did not decrease monotonically with distance from edge. The nest predation models without distance-to-edge categories were ranked the best models based on Akaike's Information Criterion; however, Akaike weights indicated some support for alternative models with distance-to-edge categories. Edges did not act as ecological traps for shrubland birds in this study because habitat preference was not positively correlated with nest predation across the 3 distance-to-edge categories. Researchers and land managers should not assume that shrubland birds respond to edges in the same way that forest species respond to edges. Furthermore, species with similar nesting ecology do not necessarily have similar nest-site preferences or nest predation rates in relation to distance to habitat edges.

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Habitat edge is the boundary or ecotone between adjacent habitats. Avian species richness and abundance often are elevated at or near habitat edges (Strelke and Dickson 1980, Chasko and Gates 1982, Morgan and Gates 1982, Hansson 1983). Nest predation and brood parasitism, however, also may be greater near edges (Gates and Gysel 1978, Temple and Cary 1988, Johnson and Temple 1990). Birds may be more vulnerable to nest predation and brood parasitism in edges than in the interior of a habitat because predators and brood parasites (such as brown-headed cowbirds; *Molothrus ater*) may be more abundant or active in the adjacent habitat and edge or because nests are more detectable near edges (Paton 1994, Andrén 1995).

This paradox of high bird abundance and richness but low nesting success near edges was termed an ecological trap by Gates and Gysel (1978). Ecological traps require (1) that an animal exhibits habitat preferences; (2) that fitness varies among habitats; and (3) that trap habitat is preferred and the animal has lower fitness there (Donovan and Thompson 2001). Few tests of the ecological trap hypothesis apply to edges and songbirds (Ratti and Reese 1988); however, habitat selection has been inferred by comparing bird abundances in edge and interior (Strelke and Dickson 1980, Morgan and Gates 1982, Noss 1991), and numerous studies have compared reproductive success in habitat edge and interior (reviewed by Paton 1994, Andrén 1995). Van Horne (1983) and Vickery et al. (1992) cautioned that high densities might not always be associated with quality habitat or breeding success. The conservation implications of ecological traps depend on population and landscape conditions. If the trap habitat is abundant across a landscape, numerous individuals select it, and reproductive success (or survival) is low, traps can act as a population sink that drains source populations and threatens viability (Donovan et al. 1995, Donovan and Thompson 2001).

Natural selection should favor individuals that accurately assess the relative quality of habitats and prefer high-quality habitat (Lanyon and

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[1] E-mail: awoodward@gf.state.az.us

[2] Present address: Arizona Game and Fish Department, Nongame and Endangered Wildlife Program, 2221 West Greenway Road, Phoenix, AZ 85023, USA.

Thompson 1986). Birds largely select habitats based on vegetative structure; this relationship is partially genetic but also modified by experience (James 1971). Birds depend not only on factors directly related to survival (ultimate factors) but also on landscape and vegetation cues (proximate factors; Hildén 1965). Breeding territories often are occupied long before factors that affect breeding success are observable. Therefore, cues may be misleading. As a result, several circumstances might result in ecological traps. For example, the mechanisms that evolved to guide birds to suitable habitat may no longer work because of changes in the environment. Dramatic landscape changes may occur too quickly for birds to adapt, and the type of terrain that induced individuals to settle may no longer provide the best nest sites (Hildén 1965). Some of the best examples of ecological traps for songbirds may be in agricultural habitats affected by intensive grazing, mowing, or tillage (Best 1986, Bollinger and Gavin 1992, Purcell and Verner 1998)—conditions only recently faced by songbirds.

Most research on edge effects has been on forest-interior species and examined differences in nest success between the edge and interior of forested habitats. These studies often classify shrubland birds as edge species because in this context they are limited to forest edges. Some species—such as the indigo bunting—select edges and are successful there (Suarez et al. 1997), but others—such as the prairie warbler and yellow-breasted chat—require larger shrubland patches (Annand and Thompson 1997). Little research has addressed the influences of edges on shrubland birds or whether edge effects occur between the edge and interior of shrubland habitats. Shrubland birds have some of the same characteristics (open-cup nests near the ground) that make forest-nesting species vulnerable to nest predation; however, shrubland habitat may support very different predator assemblages (Thompson et al. 1999). Although many shrubland birds are abundant, most are declining, and some regional or global populations are of conservation concern (Askins 2000, Pashley et al. 2000).

We conducted a comprehensive study of spatial, temporal, and habitat-specific factors that affect avian reproductive success. Our goal was to identify potential factors that limit shrubland bird populations. The objective of this component of the study was to determine whether shrubland birds suffer from edge effects and whether edges act as ecological traps. We addressed the 3 conditions for an ecological trap by determining whether (1) birds exhibited nest-site preferences among 3 distance-to-edge categories; (2) daily nest predation varied among distance-to-edge categories; and (3) nest predation was positively correlated with nest site preferences across the 3 distance-to-edge categories.

METHODS

Study Area

Our study was conducted from 1 May to 15 August 1997, 1998, and 1999 on 9 study sites on the Rolla-Houston Ranger District of the Mark Twain National Forest in Laclede and Pulaski counties in the Missouri Ozarks. The area is characterized by moderate to steep sloping hills. Approximately 56% of the landscape surrounding our study sites (10-km circles around the center point of each site) was oak (*Quercus* spp.)–hickory (*Carya* spp.) forest, 11% shortleaf pine (*Pinus echinata*) forest, 27% grassland, and 5% cropland (Woodward 2000).

We studied 3 types of shrubland habitat: regenerating forest, glades, and forest–pasture edge. These habitats are the dominant types of shrubland or early successional habitat in the Missouri Ozarks. They also are related to forest management issues concerning clearcutting and prescribed fire. We located 3 study sites, 2–13 ha in size, for each habitat. Each site was surrounded by forested habitats. Regenerating forest sites were clearcut in 1994 and had a thick understory of oak and hickory saplings and some residual trees and snags. Glades are fire-maintained habitats and were managed by prescribed burning; all sites were last burned in 1992. Glades were characterized by dolomite outcrops, a scattering of overstory trees and shrubs, and grassy areas. Dominant tree species were Eastern red cedar (*Juniperus virginiana*), white and red oaks, elms (*Ulmus* spp.), shortleaf pine, and hickories. Forest–pasture edge sites were the interface between a mature upland forest and a grazing allotment (see Woodward 2000 for detailed site descriptions). Site boundaries were mapped with a Trimball Pathfinder Pro (realtime mode) Global Positioning System (GPS) unit, which is accurate within approx. 1 m.

Nest Surveys and Monitoring

We located nests of 5 abundant, breeding bird species: indigo bunting, yellow-breasted chat, field sparrow, prairie warbler, and northern cardinal. We systematically searched for nests on an approx. 4-day rotation. We used behavioral cues and systematic searches of potential nest substrates to locate nests. Nest contents, species, approximate height of nest, and nest substrate were recorded when nests were found. Nest locations were marked at distances ≥5 m with plastic flagging and Universal Transverse Mercator coordinates were later determined with a GPS unit. We monitored nests every 3 to 4 days early in the nest period but every 1 to 2 days within approx. 4 days of the estimated fledging date. The date, time of visit, number of eggs, number of nestlings (with a description of development of young), presence of adults, brood parasitism, and predation events were recorded during each visit. We followed accepted conventions (Martin and Geupel 1993, Ralph et al. 1993, Martin et al. 1997) and considered nests successful (not depredated) if at least 1 young (host or cowbird) fledged. We assumed fledging occurred if there were no signs of predation and there was fledgling activity nearby, and we estimated fledging or predation date as the midpoint between the last 2 visits.

Data Analysis

We classified nests into 3 distance-to-edge categories: ≤20, 21–40, and >40 m. We determined nesting habitat preference and nest predation rates for each class. We selected these intervals to obtain an adequate distribution of habitat and nests across all intervals for statistical tests and because the strongest evidence for edge effects is for distances <50 m (Paton 1994). In all cases, the edge was the border between the shrubland-habitat patch and adjacent mature forest. We analyzed individual species and all species combined. Because our study focused on the effects of distance to edge, we pooled nests from the 3 types of shrubland habitats. In addition, not enough nests existed in all categories to test for interactions between habitat and distance-to-edge categories. We also pooled nests from all years because the proportion of nests in each distance-to-edge category did not differ among years for any species (χ^2, $P \geq 0.139$) and pooling increased sample sizes; we will focus on habitat and year effects in a forthcoming manuscript.

We determined whether each species and all species pooled preferred or avoided each distance-to-edge category by comparing the distribution of nests to habitat availability. We determined the number of nests in each of the 3 distance-to-edge categories by intersecting nest coordinates with distance-to-edge contour lines in a computer geographic information system. We calculated the expected number of nests in each edge category as the proportion of total area in a category times the total number of nests for a species. We used a maximum likelihood chi-squared statistic (G) with 2 df (3 edge categories – 1) to test the hypothesis that the distribution of nests among the distance-to-edge categories was in proportion to habitat availability (Alldredge and Ratti 1986, White and Garrott 1990). If we rejected this hypothesis, we used procedures by Neu et al. (1974) to determine which distance-to-edge categories were preferred or avoided ($P \leq 0.05$).

We calculated daily predation rates (DPR) by the Mayfield method (Mayfield 1961, 1975). We used program MICROMORT (Heisey and Fuller 1985) to calculate daily predation rates (DPR) and standard errors for each distance-to-edge category and likelihood values for models with and without distance-to-edge categories. We compared DPR (as opposed to nest success) to directly address the hypothesis that nest predation was related to distance to edge because additional factors affect nest success.

We compared model (1) with constant predation and no edge categories to 4 alternative models with predation rates for the following distance-to-edge categories: (2) ≤20 m and >20 m; (3) ≤40 m and >40 m; (3) 21–40 m and ≤20m + >40 m; and (4) ≤20 m, 21–40 m, and >40 m. We used an information-theoretic approach and calculated Akaike's Information Criterion, delta AIC, and Akaike weights (AIC, ΔAIC, and *w*, respectively; Burnham and Anderson 1998) to identify the best models. The model with the smallest AIC is the best approximating model for the data, and primary inference should be drawn from models with a ΔAIC of 1 or 2 to perhaps as many as 3 or 4 when models are nested and differ successively by 1 parameter; Akaike weights represent the likelihood of a given model (Burnham and Anderson 1998). We concluded there was an edge effect if strong evidence existed for a model with edge categories. We also compared the best model with edge categories (as determined above) to the reduced model with no edge categories with a likelihood ratio test (White 1983, Heisey and Fuller 1985).

We compared the results of the habitat preference and DPR analyses to evaluate the ecological trap hypothesis for each species and all species combined. We calculated the Spearman-rank correlation between habitat preference and DPR.

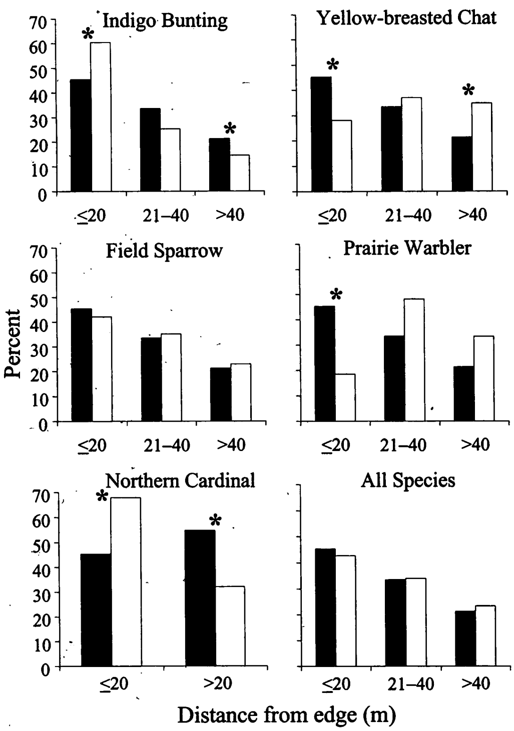

Fig. 1. Percent of habitat available (black bars) and percent of nests located (white bars) ≤20 m, 21–40 m, and >40 m from habitat edge for 5 species nesting in Missouri, 1997–1999. Asterisks denote significant differences between percent availability and percent use (χ^2, $P \leq 0.05$).

We used the difference between the percent of nests and percent of available habitat in each distance-to-edge category as a measure of preference (Alldredge and Ratti 1986). We concluded that an ecological trap existed if a significant positive correlation ($P \leq 0.05$) occurred, which indicated birds preferred to nest in categories with high DPR.

RESULTS

We found 339 nests of the 5 study species (93 in 1997, 128 in 1998, and 118 in 1999). We monitored 111, 89, 57, 54, and 28 indigo bunting, yellow-breasted chat, field sparrow, prairie warbler, and northern cardinal nests, respectively. Over all years and distance-to-edge categories, daily predation rate (± SE) of indigo bunting nests was 0.039 ± 0.0052 or 62% for a 24-day nest interval; yellow-breasted chat nests, 0.045 ± 0.0065 or 64% for a 22-day nest interval; field sparrow nests, 0.051 ± 0.0095 or 70% for a 23-day nest interval; prairie warbler nests, 0.032 ± 0.0069 or 51% for a 22-day nest interval; and northern cardinal nests, 0.033 ± 0.0117 or 55% for a 24-day nest interval.

Edge Preference

Nests ranged from 0.06 m to 122.76 m ($\bar{x}$ = 24.48) from the habitat edge. Neither preference nor avoidance existed of any distance-to-edge category by all species pooled ($\chi_2^2 = 1.80$, $P = 0.595$; Fig. 1). Habitat use by field sparrow was in proportion with habitat availability ($\chi_2^2 = 0.291$, $P = 0.865$). Habitat use by indigo bunting ($\chi_2^2 = 10.63$, $P = 0.005$), yellow-breasted chat ($\chi_2^2 = 13.14$, $P = 0.001$), prairie warbler ($\chi_2^2 = 19.34$, $P < 0.001$), and northern cardinal ($\chi_2^2 = 5.23$, $P = 0.022$) was not in proportion with available habitat. The indigo bunting preferred to nest in the ≤20-m distance-to-edge category and avoided the >40-m distance-to-edge category (Fig. 1). The yellow-breasted chat preferred to nest in the >40-m distance-to-edge category and avoided the ≤20-m distance-to-edge category (Fig. 1). The prairie warbler avoided nesting in the ≤20-m distance-to-edge category and moderately preferred ($P \leq 0.10$) the 21–40-m distance-to-edge category (Fig. 1). We used only 2 distance-to-edge categories (≤20 m and >20 m) for the northern cardinal because only 1 nest was >40 m from edge. The northern cardinal preferred to nest in the ≤20-m distance-to-edge category and avoided the >20-m distance-to-edge category (Fig. 1).

Edge Effects on Nest Predation

Daily predation rates varied among distance-to-edge categories by as much as 200–300%, and in different directions for some species (Table 1). The nest predation models with no edge categories were the best models for all species; however, supporting evidence existed for the alternative models (Table 2). Akaike weights ranged from 0.519–0.649 for the no edge category model, and all species had alternative models with AICs < 3, so not enough convincing evidence existed for any 1 model. The likelihood-ratio tests comparing models with distance-to-edge categories to models with all categories pooled were not significant for all species combined ($P \geq 0.317$), indigo bunting ($P \geq 0.317$), field sparrow ($P \geq 0.294$), or northern cardinal ($P \geq 0.584$). The likelihood-ratio tests for yellow-breasted chat and prairie warbler provided some support for edge effects. The models with edge categories ≤40 and >40, and 21–40, ≤20 + >40, were marginally different ($P = 0.078$ and $P = 0.074$, respectively) than the model with all categories pooled for

Table 1. Daily nest predation rates for nests ≤20 m, 21–40 m, and >40 m from edge and relationship to nest-site preference for 5 songbird species breeding in shrubland habitats in Missouri, USA, 1997–1999.

	≤20 m		21–40 m		>40 m		Rank correlation[a]	
Species	DPR	SE	DPR	SE	DPR	SE	*r*	*P*
Indigo bunting	0.035	0.006	0.048	0.011	0.042	0.014	−1.00	0.001
Yellow-breasted chat	0.046	0.012	0.032	0.008	0.063	0.014	0.50	0.667
Field sparrow	0.043	0.013	0.064	0.018	0.044	0.019	0.87	0.333
Prairie warbler	0.061	0.026	0.023	0.008	0.037	0.013	−1.00	0.001
Northern cardinal	0.048	0.015	0.036[b]	0.017				
All species	0.041	0.005	0.038	0.005	0.05	0.007	0.50	0.667

[a] Spearman-rank correlation of relationship between daily nest predation and nest-site preference (% use – % availability) for the 3 distance-to-edge categories.

[b] Includes 1 nest >40 m.

the yellow-breasted chat. The model with categories 21–40, ≤20 + >40, was marginally different ($P = 0.129$) from the model with all categories pooled for the prairie warbler.

Evaluation of the Ecological Trap Hypothesis

The only significant Spearman-rank correlations were for the indigo bunting and prairie warbler, and the correlations were in the opposite direction (negative) predicted by the ecological trap hypothesis (Table 1). Correlations for the other species were positive but not significant. Therefore, we found no evidence that the ecological trap hypothesis applied to the 5 species we studied in shrubland habitat patches.

DISCUSSION

We observed species-specific patterns in preferences for nest sites relative to distance to edge; some species preferred to nest near edges and others away from edges. Previous studies have reported a similar range of results. Territory density or bird abundance can be higher near edges (Strelke and Dickson 1980; Kroodsma 1982, 1987; Morgan and Gates 1982; Noss 1991); territories can be distributed equally among edge and interior (King et al. 1996); or pairing success can be lower near edges (Van Horn et al. 1995). Birds might have preferred or avoided distance-to-edge categories because of their proximity to the edge or because of differences in vegetation structure; however, we did not compare vegetation structure among distance-to-edge categories.

Nest predation levels were within the range of other studies of shrubland birds in central Missouri (Burhans and Thompson 1999), southern Missouri (Annand and Thompson 1997), and southern Illinois (Suarez et al. 1997); but lower than in some more fragmented landscapes in the Midwest (Robinson et al. 1995). We found some evidence that DPR varied in relation to distance to edge. Estimates of DPR varied greatly among distance-to-edge categories for some species (Table 1), and the magnitudes of Akaike weights for the models with no edge categories (Table 2) did not provide convincing evidence that they were the best models (Burham and Anderson 1998, Anderson et al. 2000).

We found some evidence of greater DPR closer to edges for the yellow-breasted chat and prairie warbler and edge effects were nonlinear. Nest predation was high closest to the edge, declined in the 21–40-m distance-to-edge category, and then increased >40 m from edge (Table 1). High nest predation near the edge likely is the result of activity patterns of nest predators in shrubland habitats. Thompson et al. (1999) used video cameras to determine that snakes (especially the black rat snake [*Elaphe obsolete*]) were the dominant predators of songbird nests in old-field habitats in central Missouri. Black rat snake activity and foraging may be clustered along field–forest ecotones during the songbird breeding season (Weatherhead and Charland 1985, Durner and Gates 1993). We can only speculate why nest predation was greater >40 m from edge; perhaps some shrubland predators avoid edges or nests are more visible at these locations. Evidence of edge effects from previous studies is mixed. The greatest proportion of studies reporting edge effects are for forest habitats adjacent to farmland; only a small proportion of studies have reported edge or area effects for birds in open habitats (reviewed by Andrén 1995).

Table 2. Nest predation models that differ by the number of distance-to-edge categories for 5 shrubland songbirds in Missouri, USA, 1997–1999. Models are ranked within each species in ascending order by Akaike's Information Criterion (AIC); models with lower AIC and ΔAIC and a greater Akaike weight (*w*) have more substantial support.

Model edge categories	$-2\mathrm{Log_e}$ x Likelihood	# model parameters	AIC	ΔAIC	*w*
Indigo bunting					
None	−456.0	1	−454.0	0.0	0.530
≤40, >40	−455.9	2	−451.9	2.1	0.185
21–40, ≤20 + >40	−455.1	2	−451.1	2.9	0.124
≤20, >20	−455.0	2	−451.0	3.0	0.118
≤20, 21–40, >40	−454.9	3	−448.9	5.1	0.041
Yellow-breasted chat					
None	−382.8	1	−380.8	0.0	0.649
≤20, >20	−382.8	2	−378.8	2.0	0.239
≤40, >40	−379.7	2	−375.7	5.1	0.050
21–40, ≤20 + >40	−379.6	2	−375.6	5.2	0.048
≤20, 21–40, >40	−378.8	3	−372.8	8.0	0.011
Field sparrow					
None	−213.8	1	−211.8	0.0	0.519
≤40, >40	−213.7	2	−209.7	2.1	0.181
≤20, >20	−213.3	2	−209.3	2.5	0.148
21–40, <20 + >40	−212.7	2	−208.7	3.1	0.110
≤20, 21–40, >40	−212.7	3	−206.7	5.1	0.040
Prairie warbler					
None	−185.4	1	−183.4	0.0	0.619
≤40, >40	−185.2	2	−181.2	2.2	0.206
≤20, >20	−183.4	2	−179.4	4.0	0.083
21–40, ≤20 + >40	−183.1	2	−179.1	4.3	0.072
≤20, 21–40, >40	−182.4	3	−176.4	7.0	0.018
Northern cardinal					
None	107.2	1	109.2	0.0	0.700
≤40, >40	106.9	2	110.9	1.7	0.299
All species					
None	−1,348.0	1	−1,346.0	0.0	0.536
≤20, >20	−1,348.0	2	−1,344.0	2.0	0.197
21–40, ≤20 + >40	−1,347.0	2	−1,343.0	3.0	0.119
≤40, >40	−1,347.0	2	−1,343.0	3.0	0.119
≤20, 21–40, >40	−1,346.0	3	−1,340.0	6.0	0.026

No significant evidence of ecological traps existed. The only significant relationships between nest predation and habitat preference were in the opposite direction predicted by the ecological trap hypothesis. Some species, however, preferred a single distance-to-edge category over another with a lower DPR; this resulted in positive (but nonsignificant) rank correlation between nest-site preference and predation (Table 1). While ecological traps were originally hypothesized for habitat edges (Gates and Gysel 1978), the best-documented examples for songbirds are agricultural habitats affected by grazing, mowing, or tillage (Best 1986, Bollinger and Gavin 1992, Purcell and Verner 1998).

No obvious explanation exists for the similarity or differences we observed in nest-site preference or DPR relative to distance to edge. For example, prairie warblers and yellow-breasted chats had the most similar patterns in DPR, yet were among the most different species in nest characteristics and nest placement. Prairie warbler nests are relatively small and usually placed in the top of saplings (Nolan 1976), while yellow-breasted chat nests are medium-sized and are usually located in a thick shrub or shrub patch (Petrides 1938).

MANAGEMENT IMPLICATIONS

We should not assume the generality of the traditional model of edge effects in which nest predation decreases monotonically with distance to edge or that patterns are similar among species. Landscape-, habitat-, and species-level factors affect nest success (Donovan et al. 1997, Thompson et al. 2002). Specifically, we cannot assume predators affect shrubland birds the same as forest birds. We need to better understand the predators and predation in shrubland habitats to accurately assess their impacts on nest success. Predator assemblages and activity patterns in these habitats may differ from those of forests and grasslands.

One focus of avian conservation efforts on the breeding grounds should be to manage areas for high-quality habitat where birds encounter low levels of nest predation. We suggest that this management goal would require multiple strategies to benefit the shrubland bird community. Indigo buntings select for and experience low levels of nest predation in edges of shrubland habitats. Indigo buntings were more abundant at the pasture-edge sites than yellow-breasted chats or prairie warblers (A. D. Fink, University of Missouri, unpublished data) and utilize small habitat patches (Annand and Thompson 1997). Thus, they can potentially benefit from edge and small and large habitat patches. Species such as the prairie warbler and yellow-breasted chat, however, may suffer high levels of nest predation in close proximity to edges. These species did not breed in the pasture-edge sites (A. D. Fink, University of Missouri, unpublished data) and do not use very small habitat patches (Annand and Thompson 1997). These species will benefit more from management that creates larger shrubland patches. Habitat patch size is affected by the choice of silvicultural methods, the use of prescribed fire, or by other methods used to manage shrubland habitat (Askins 1998, Thompson and DeGraaf 2001). These patterns also may explain why indigo buntings remain common across their range and prairie warblers and yellow-breasted chats are regional or national conservation priorities (Askins 2000, Pashley et al. 2000).

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