
Nesting Success of a Disturbance-Dependent Songbird on Different Kinds of Edges

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Abstract: We compared the nesting success of a disturbance-dependent species, the Indigo Bunting (*Passerina cyanea*), on different kinds of habitat edges in five sites (225 total nests) in southern Illinois from 1989 to 1993. Nest predation rates along agricultural and abrupt, permanent edges (e.g., wildlife openings, campgrounds) were nearly twice as high as rates along more gradual edges where plant succession was allowed to occur (e.g., treefalls, streamsides, gaps created by selective logging). Levels of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) varied significantly among sites and years, but not among edge types. Clutch sizes, however, were significantly smaller at agricultural edges where nest predation rates were also high, which suggests either decreased food availability or a population dominated by younger and/or lower-quality (poor condition) birds. The results of this study illustrate the need to reevaluate management practices (e.g., wildlife openings) that are designed to promote populations of disturbance-dependent wildlife.

Exito de Nidación de un Ave Paserina Dependiente de Disturbaciones en Diferentes Tipos de Bordes

Resumen: Comparamos el éxito de nidación de una especie dependiente de perturbaciones *Passerina cyanea*, en diferentes tipos de hábitat borde en cinco sitios (225 nidos en total) en el sur de Illinois de 1989 a 1993. La tasa de depredación de nidos a lo largo de bordes agrícolas y bordes abruptos permanentes (e.g., áreas silvestres abiertas y zonas de campamento) fueron dos veces más altas que aquellas en bordes más graduales donde la sucesión de plantas fue permitida (e.g., árboles caídos, bancos de arroyos y espacios abiertos creados por la tala selectiva). Niveles de parasitismo de nido por *Molothrus ater* variaron significativamente entre sitios y años, pero no entre tipos de borde. De cualquier manera, el tamaño de la nidada fue significativamente más pequeño en bordes agrícolas donde la tasa de depredación fue también alta, esto sugiere tanto una disminución en la viabilidad de alimentos, como una población dominada por aves jóvenes y/o de baja calidad (pobre condición). Los resultados de este estudio ilustran la necesidad de re-evaluar prácticas de manejo (e.g., áreas silvestres abiertas) que son diseñadas para promover poblaciones de vida silvestre dependientes de disturbaciones.

Introduction

In the extensive recent literature on the conservation of Neotropical migrant birds (Hagan & Johnston 1992; Finch & Stangel 1993; Martin & Finch 1995; Maurer & Villard 1996), relatively little attention has been paid to species that require disturbed habitat on breeding

grounds. Such species are generally assumed to benefit from habitat fragmentation because they depend on the edges or early successional habitats that are created by human activities (Whitcomb et al. 1981). Species inhabiting undisturbed forest interiors, however, have been shown to experience higher levels of nest predation and cowbird (*Molothrus* spp.) brood parasitism near habitat edges (reviewed in Yahner 1988; Wilcove & Robinson 1990; Paton 1994; Faaborg et al. 1995). Higher rates of nest predation near edges have been documented widely in both North America and Europe (reviewed in Paton 1994), indicating a possible general phenomenon.

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Predators may use edges as pathways or corridors between habitat types (Bider 1968), and nests may be more visible along edges, especially to avian predators (Angelstam 1986; Møller 1989; Andrén 1992). As a result of these findings, the habitat requirements and management needs of habitat-interior and edge species have been assumed to be in conflict (Wilcove et al. 1986; Yahner 1988). Edge species have been managed by promoting habitat heterogeneity, whereas management recommendations for habitat-interior species emphasize the creation and preservation of large, relatively homogeneous patches (Robbins 1979; Faaborg 1980; Harris 1984; Robinson 1988; 1992). Yet many species characteristic of edges and shrublands in disturbed areas are showing population declines comparable to or even exceeding those of many forest-interior species (Hagan 1993; Askins 1993, 1994).

In spite of widespread management to promote edge habitat, there have been few studies of the kinds of disturbances and management practices that create favorable habitat for edge species (Noss 1991). Ratti and Reese (1988) argue that abrupt edges may be ecological traps (Gates & Gysel 1978) for species that nest near them (but see Yahner et al. 1989). Such abrupt edges may provide the cues used by disturbance-dependent birds for habitat selection but may fail to provide safe nesting habitat because of high rates of nest predation and cowbird brood parasitism (Chasko & Gates 1982; Brittingham & Temple 1983; Temple & Cary 1988). These abrupt edges act as traps because they attract large populations that fail to produce enough young to compensate for adult mortality (possible population sinks; Pulliam 1988).

The adverse effects of certain kinds of edges have been discussed mostly in the context of forest-interior birds rather than those that live along the edges (Temple & Cary 1988). We adopt a different approach by comparing the nesting success of an edge-nesting species, the Indigo Bunting (*Passerina cyanea*), in different kinds of edges, including those created by natural disturbances (treefalls, stream floodplains, and other canopy gaps), agriculture, management of game animals (wildlife openings), and silviculture (selective logging). Our goals were to compare nesting success in natural disturbances, which we assume are the habitats historically occupied by Indigo Buntings, with success in managed habitats, which may or may not mimic such natural disturbances.

Specifically, we compared clutch sizes and levels of daily nest predation and cowbird brood parasitism among nests of Indigo Buntings in different kinds of edges. Based on our review of the literature on artificial nests, we predicted that nesting success would be lowest along abrupt agricultural edges (Wilcove 1985; Wilcove et al. 1986) and in abrupt or "hard" edges (Ratti & Reese 1988; Yahner et al. 1989; Paton 1994) and would be highest in natural edges along streams, treefalls, and

other canopy gaps in which natural succession creates more gradual edges. We predicted that levels of predation and parasitism would be low in selectively logged forests in which selective logging mimics natural gaps (Smith 1986; Thompson et al. 1993, 1995). If cowbirds favor edge habitats in which to search for nests (Brittingham & Temple 1983), we further predicted that cowbird parasitism levels would be lower in more shrubby, gradual edges where there are more places to hide nests (Ratti & Reese 1988).

Study Area and Methods

The study areas were located in extreme southern Illinois (U.S.A.; 37°25'–37°35'N, 89°19'–89°25'W) and included the Trail of Tears State Forest, three sites in the Shawnee National Forest (Pine Hills, Dutch Creek, and South Ripple Hollow), and two sites in the Cache River Bioreserve (Section Eleven Woods and Forman Tract). The Trail of Tears State Forest and the Shawnee National Forest are in the Illinois Ozarks region bordering the Mississippi River floodplain. The Illinois Ozarks are characterized by forested ravines and ridge tops surrounded by extensive row-crop agriculture. The vegetation of the Illinois Ozark region is primarily oak-hickory forest along slopes and ridges and mixed hardwood forest in the ravines (Iverson 1989). The Cache River Bioreserve consists of 20, 1800-ha fragments of floodplain forest embedded in an agricultural landscape.

Because we wanted to evaluate habitat quality based on the kind of disturbance associated with forest habitats, we used nests located only within a forest tract ("internal" nests) or on its immediate edge ("external" nests along agricultural openings). Nesting habitat was categorized according to the type of disturbance in which the nests were located (Table 1). The disturbance types included the following: treefall gaps (openings smaller than 0.2 ha in which shrubs and saplings are dense), stream beds in which erosion during floods creates canopy gaps with a dense understory, a 30-year-old sweetgum (*Liquidambar styraciflua*) plantation in which numerous canopy gaps were created by dying trees, wildlife openings (0.4–1.3 ha planted in grasses and legumes described in Overcash et al. [1989]), group selection cuts (2–6 years after cutting, 0.1–0.4 ha), edges of old fields (abandoned row crops and pastures), and abrupt agricultural edges (Table 1). All the nests we used were located in the shrubby vegetation of the edges themselves; nests in small gaps created by treefalls were considered to be along edges if they were within 10 m of the woody vegetation.

The composition of the shrub layer varied among edges. In agricultural edges, multiflora rose (*Rosa multiflora*) and various saplings dominated the shrub layer. In the sweetgum plantation, dense thickets of Japanese

Table 1. Edge types on which the nesting success of Indigo Buntings was measured in southern Illinois.

Edge type	Position	Edge contrast	Opening size
Treefall gaps	interior	gradual	small (<0.3 ha)
Stream beds	interior	gradual	long, narrow (<50 m wide), breaks in the canopy
Plantations	interior	gradual	small (<0.1 ha) gaps left by dying trees
Selective cuts	interior	gradual	(0.1-0.4 ha) with 2-6 years of shrubby regrowth
Wildlife openings	interior	abrupt	small (0.2-0.4 ha) openings planted in grasses and legumes (approximately 1.5 km sampled)
Old field edges	exterior	abrupt	large (>10 ha) openings along regenerating fields (1-2 years of regrowth)
Agricultural edges	exterior	abrupt	large (>100 ha) along row crops (approximately 2.5 km sampled)

honeysuckle (*Lonicera japonica*) and multiflora rose filled most of the treefall gaps. Treefall gaps and stream-side vegetation in older forest consisted of a mixture of shrubs, such as spicebush (*Lindera benzoin*) and wild hydrangea (*Hydrangea arborescens*) and saplings of canopy trees. The wildlife openings were bordered by dense multiflora rose, Japanese honeysuckle, and blackberry (*Rubus* spp.).

Following the initial comparisons among edge types, two contrasts were made: "abrupt" versus "gradual" edges and exterior versus interior edges (Table 1). We defined abrupt edges as permanent, anthropogenic edges characterized by a lack of shrubby vegetation. This category included forest-agriculture ecotones and wildlife openings maintained by mowing within a forest. All of these abrupt edges were characterized by ongoing mowing or harvesting that prevented natural succession in the disturbed (nonforested) area. In contrast, gradual edges included small-scale disturbances within continuous habitat such as natural treefall gaps, openings associated with creek beds, and selective cuts. Gradual edges were characterized by shrubby second growth (2-10 years old) in the disturbed area. To control for confounding effects of multiple edge types, interior edges were defined as those within the forest located at least 50 m from any agricultural edge (Paton 1994). The outer perimeter of a forest tract, which included the secondary growth separating the forest from agricultural fields, was defined as an exterior edge. Interior nests were further subdivided into abrupt (wildlife openings) and gradual (streamside edge, selective cuts, treefalls) categories to reveal differences between disturbance types within the forest. We could not find gradual edges in agricultural edges, so we were unable to control for edge type on exterior edges.

Nest searching was conducted throughout all sites and lasted from early May until the first week in August, 1989-1993. After nests were located, they were monitored every 2 or 3 days until the young fledged or the nest became inactive. Nests were considered depredated when all eggs or nestlings disappeared before the young were old enough to leave the nest. Flags were placed at least 5 m from the nest to mark its location and minimize the probability of attracting potential preda-

tors. Daily predation rates were calculated with the Mayfield Index (Mayfield 1975; Hensler & Nichols 1981), which measures daily predation rates during the period when nests were being observed. The measure was used in subsequent analyses. We defined levels of brood parasitism by the proportion of total nests that contained cowbird eggs during the incubation period. Field seasons included in the analysis are 1989-1993 for Dutch Creek, 1990-1993 for Trail of Tears and Pine Hills, 1989-1991 for South Ripple Hollow, and 1993 for Section Eleven Woods and Foreman Tract.

We compared daily nest predation rates, levels of brood parasitism, and average clutch sizes among the different kinds of edges from the study areas. When testing for differences among edge types, we used edge types available on each study site rather than individual nests because the experimental units and the study sites were used as a blocking factor. Nests within a given study plot area and edge type were not considered independent replicates.

Because the data were gathered from the same study areas over a series of years, repeated-measures analysis of variance was deemed the most appropriate analysis. There were some missing values in comparisons of nest fates (e.g., no nests were found along an edge type in a given site). For this reason we analyzed the effects of edge types on predation rates, parasitism levels, and average clutch size by means of a 5V program by BMDP Statistical Software which gives repeated measures analysis for an unbalanced design (Dixon 1992). For a given effect, we calculated Wald's χ^2 to test the null hypothesis that a given term could be left out of the model. A significant Wald's χ^2 indicates that the term accounts for a significant amount of variation in the data. Using the same methods, we also looked for effects of year-to-year variation and site effects on predation rates, parasitism levels, and average clutch size. All data on rates were arcsine transformed prior to analysis.

Results

We found 225 nests in various edge types when all study sites and years were combined (Table 2). Predation rates

Table 2. Summary of nest predation rates and levels of parasitism by disturbance type, all years and sites combined.*

Edge type	Daily percent predation (\pm SD) (exposure days)	Proportion of nests parasitized (n)
Treefall gap	2.1 \pm 1.0 (190.5)	0.36 (14)
Plantation	2.2 \pm 1.1 (178)	0.25 (12)
Stream bed	3.6 \pm 0.8 (473)	0.46 (28)
Selective cut	3.5 \pm 1.3 (200)	0.47 (17)
Wildlife opening	7.1 \pm 0.9 (564)	0.30 (53)
Old field	6.6 \pm 1.5 (272.5)	0.48 (25)
Agriculture	9.8 \pm 1.7 (317.5)	0.37 (30)

*Standard deviations (SD) calculated by the methods of Hensler and Nichols (1981).

on exterior edges were higher in all four sites in which both edge types were present; in three sites, daily predation rates were more than twice as high (Table 3). Overall, these differences in predation rates were highly significant (Table 4). When interior edges were separated into abrupt and gradual categories, abrupt interior edges had higher predation rates than gradual edges in four of the five sites (Table 3) and the difference was significant (Table 4). Predation rates did not vary significantly among years or study sites.

Parasitism levels, on the other hand, did not vary significantly among edge types (Table 4). There were marginally significant effects of sites (interior versus exterior edges: $\chi^2 = 14.29$, $df = 8$, $p = 0.075$; abrupt versus gradual: $\chi^2 = 13.58$, $df = 8$, $p = 0.093$) and years (interior versus exterior edges: $\chi^2 = 9.47$, $df = 4$, $p = 0.050$), and year-by-site effects (interior versus exterior edges: $\chi^2 = 9.87$, $df = 4$, $p = 0.043$).

Average clutch size was significantly higher on interior edges ($\bar{x} = 3.4 \pm 0.4$ [SD], $n = 156$) than on exterior edges ($\bar{x} = 2.8 \pm 0.4$ [SD], $n = 69$). No other differences between edge types were found (Table 4). Average clutch size, however, showed significant year-to-year variation in the comparisons of abrupt versus gradual edges and interior versus exterior edges (Wald's $\chi^2 = 15.628$, $df = 4$, $p = 0.004$ and Wald's $\chi^2 = 10.401$,

$df = 4$, $p = 0.034$, respectively). Average clutch size did not vary significantly with study area.

Discussion

These results supported our predictions about predation but not those about cowbird parasitism. Predation levels were higher on abrupt edges in the interior and on the exterior edges, a result consistent with that reported by Ratti and Reese (1988) but not those of Yahner et al. (1989) and Rudnicky and Hunter (1993). Parasitism levels showed no significant differences among edge types, perhaps because the annual and site-to-site variation gave our statistical tests low power. These results suggest that not all edges are equivalent: some edges may even be beneficial (Noss 1991), whereas others may be ecological traps (Ratti & Reese 1988). The daily predation rates on Indigo Bunting nests along gradual edges in the forest interior are by far the lowest recorded in an extensive sample of nests in other Illinois study sites (Robinson, unpublished data). Understanding why edges differ with respect to predation may enable managers to improve conditions for edge-nesting species.

Possible reasons for higher predation rates on exterior and abrupt edges include increased predator activity and nest visibility. Bider (1968) suggested that predators such as raccoons (*Procyon lotor*) and opossums (*Didelphis virginianus*) may use extensive edges as travel lanes and may be searching for food along permanent edges. Raccoons feed extensively in agricultural fields in Illinois during the summer (E. J. Heske, personal communication), and they may concentrate their activity along agricultural edges where nest predation levels are highest. Heske (1995) and Marini et al. (1995), however, found no evidence that mammalian nest predators were more abundant along agricultural edges than they were in the forest interior in some of the same sites used in this study. Marini et al. (1995) did find that Corvids such as Blue Jays (*Cyanocitta cristata*) and Crows (*Corvus* spp.) were more abundant along agricultural edges, as

Table 3. Daily percentage (mean \pm SD) of Indigo Bunting nests lost to predators by study area and edge type in southern Illinois.

Study area	Daily percent predation rate (exposure days)*			
	Exterior edges	Interior edges (abrupt and gradual) combined	Abrupt	Gradual
Dutch Creek	7.1 \pm 3.1 (70)	5.1 \pm 0.8 (809)	7.7 \pm 1.8 (207.5)	4.2 \pm 0.8 (601.5)
Trail of Tears	9.3 \pm 2.7 (118)	3.9 \pm 1.2 (281)	6.6 \pm 4.5 (30.5)	3.6 \pm 1.2 (250.5)
Pine Hills	11.6 \pm 3.4 (88)	3.0 \pm 1.1 (263)	8.1 \pm 4.5 (37)	2.2 \pm 1.0 (226)
Forman Tract	8.8 \pm 3.4 (69)	3.7 \pm 1.6 (134)	—	—
S. Ripple Hollow	—	—	2.5 \pm 2.5 (40)	3.6 \pm 2.0 (84)
Section II	—	—	18.2 \pm 15.8 (06)	4.3 \pm 3.0 (47)

*Daily predation rates translate to the following overall predation rates throughout the nest cycle: 2% = 38%; 3% = 52%; 4% = 62%; 5% = 71%; 6% = 77%; 7% = 82%; 8% = 86%; 10% = 92%; 12% = 94%.

Table 4. Repeated measures analysis of effects of edge type on nest predation rates, nest parasitism levels, and mean clutch size.

Comparison	Predation rates			Parasitism levels			Mean clutch size		
	Wald's χ^2	df	p	Wald's χ^2	df	p	Wald's χ^2	df	p
Interior versus exterior	8.52	1	0.004*	0.80	1	0.371	9.347	1	0.002*
Abrupt versus gradual	8.52	1	0.004*	1.421	1	0.233	2.445	1	0.118
Interior only, abrupt versus gradual	10.18	1	0.001*	2.27	1	0.130	0.148	1	0.701

*Significant effect of edge type.

has been reported by Angelstam (1986) and Andr en (1992). But the study by Marini et al. (1995) included only one field season and did not compare internal and external edge habitats, which limits the extent to which we can generalize their results to our study. Nor did Marini et al. (1995) measure snake predation, which may be the most important source of nest loss in southern Illinois (S. Robinson, unpublished data). The black rat snake (*Elaphe obsoleta*) shows a strong preference for traveling along external edges of woodlots (Durner & Gates 1993).

The dense regenerating shrub layer along gradual edges may provide numerous places where birds can hide their nests (Martin 1992) and may obstruct the visual field of a predator searching for nests from an opening. Conversely, a mammalian or avian predator moving along the edge of an agricultural field or a mowed old field may have an unobstructed view of the adjacent vegetation. Visually hunting predators such as corvids are especially likely to be affected by vegetation density. We did not measure nest concealment, however, so we cannot test this hypothesis.

Because all openings with gradual edges were small (<0.4 ha), we also cannot rule out the possibility that the size of an opening also influenced predation rates along edges. But abrupt edges around small wildlife openings (0.2–0.4 ha) also had high predation rates. Shrubby edges associated with relatively large openings along clearcuts have been found to have little effect on predation rates of artificial nests (Small & Hunter 1988; Rudnicki & Hunter 1993), which suggests that gradual edges along large openings do not necessarily have high predation rates. King et al. (1996), however, found predation rates on Ovenbird (*Seiurus aurocapillus*) nests to be almost twice as high near clearcuts as they were farther away. Experimental manipulations of shrubby cover along edges are needed to control for factors other than edge contrast that may also affect predation rates.

Our results provide some indications that low-volume selective logging might mimic the natural disturbances associated with low predation rates for Indigo Buntings. The regenerating saplings in the small (<1.0 ha) group-selection cuts may provide a vegetation layer sufficiently dense to impede predator searching. Similarly, the gaps left by tree mortality in tree plantations create the dense shrub and sapling layer required by Indigo Buntings

without either attracting additional predators or making nests more visible to predators. But nest predation rates on two other disturbance-dependent species that have similar nest sites, the White-eyed Vireo (*Vireo griseus*) and the Hooded Warbler (*Wilsonia citrina*), were nearly twice as high in selective cuts as they were in other kinds of disturbance (S. Robinson and W. D. Robinson, unpublished data). Similarly, ground-nesting Kentucky Warblers (*Oporornis formosus*) suffer higher predation rates in tree plantations than they do in forests that have undergone natural succession (L. Morse, unpublished data). Thus, the extent to which selective logging and plantation forestry mimic natural disturbances may vary among species.

But the abrupt edges associated with wildlife openings did not appear to mimic the conditions created by natural edges for Indigo Buntings. We hypothesize that the lack of regenerating shrubs, greater predator abundance, and increased nest visibility in permanent wildlife openings are responsible for high predation rates of Indigo Bunting nests found in wildlife openings. Many of the predators (e.g., raccoons and black rat snakes) that consume the eggs of Indigo Buntings are also likely predators of game species (e.g., Wild Turkey [*Meleagris gallopavo*] and Northern Bobwhite [*Colinus virginianus*]). Thus, our results suggest that wildlife openings with abrupt edges may not enhance the productivity of some of the game birds they were designed to promote (Overcash et al. 1989).

The very low predation rates in treefall gaps in older forest and in plantations suggest that short-lived, scattered gaps may provide the safest nest sites for Indigo Buntings (Table 2). Ephemeral, scattered edges may lack resident predator populations, may not be incorporated into predator travel lanes, and may not provide additional food sources that attract predators (e.g., waste grain). Natural treefall gaps also provide rich foraging habitat for many bird species (Noss 1991; Rotenberry et al. 1995). Viewed in this light, the smaller clutches of Indigo Buntings nesting on agricultural edges may result from younger age distributions and/or the lower quality of birds that are excluded from the best nesting habitats and forced to nest along agricultural edges (Payne & Payne 1993). Alternatively, abrupt edges may act as ecological traps that are more attractive than natural edges and lure birds away from more natural edges. Testing

this hypothesis would require data on the population age structure, population density, and season-long nesting success of Indigo Buntings nesting along different kinds of edges.

The smaller clutch sizes of birds nesting along agricultural edges might also reflect reduced food availability. We know little about how Indigo Buntings use the food resources available in agricultural fields. Detailed studies of the foraging ecology of birds along edges are needed to understand the extent to which food resources influence edge choice in Indigo Buntings.

Contrary to our predictions, we could detect no differences in levels of cowbird parasitism among edge types. These results are consistent with the conclusion that cowbirds have saturated the available habitat in the study areas (Robinson & Wilcove 1994; Thompson 1994; Robinson et al. 1995*b*; Thompson et al. in press). Levels of cowbird parasitism remain very high even 800 m from the nearest edge of any kind and 1.5 km from the nearest area where cowbirds forage (Thompson et al. 1997). Rather than responding to edge type or proximity to edge, cowbird abundance closely reflects host abundance and availability of nearby feeding areas (Thompson 1994; Thompson et al. in press). Annual variation in cowbird populations and the presence of alternative hosts may also affect levels of cowbird parasitism (Robinson et al. 1995*a*).

Our results also suggest that cowbird nest searching is unaffected by edge type. Perhaps by following host behavior rather than searching directly for host nests (Norman & Robertson 1975), cowbirds would be less affected by the availability of shrubby vegetation in which hosts can hide nests. Robinson et al. (1995*a*) found no consistent evidence that parasitism levels were lower in well-concealed nests.

Conclusions

Our results suggest that local land-use practices can have a profound influence on the nesting success of birds that depend upon disturbed habitats for nesting. Although many such species have clearly benefited from human activities (Whitcomb et al. 1981), many others have experienced major recent declines and are even endangered in some regions (Askins 1993; Hagan 1993; Peterjohn et al. 1995). Most of these declines likely reflect decreasing habitat availability resulting from landscape-level changes in agricultural practices (Hagan 1993; Warner 1994; Rodenhouse et al. 1995). Areas being managed for disturbance-dependent wildlife, most of which focus on game species, also have the potential to provide important habitat for these declining species. But many areas being managed to promote disturbance-dependent species may in fact be ecological traps not only for forest species but also for some of the species

they are designed to promote. We suggest that management practices designed to promote edge-breeding birds need the same kind of reevaluation currently underway for the management of forests and grasslands (Finch & Stangel 1993; Martin & Finch 1995).

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