

## THE EFFECTS OF PATCH SHAPE ON INDIGO BUNTINGS: EVIDENCE FOR AN ECOLOGICAL TRAP

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**Abstract.** Habitat loss and fragmentation have led to a widespread increase in the proportion of edge habitat in the landscape. Disturbance-dependent bird species are widely assumed to benefit from these edges. However, anthropogenic edges may concentrate nest predators while retaining habitat cues that birds use to select breeding habitat. This may lead birds to mistakenly select dangerous habitat—a phenomenon known as an “ecological trap.” We experimentally demonstrated how habitat shape, and thus amount of edge, can adversely affect nest site selection and reproductive success of a disturbance-dependent bird species, the Indigo Bunting (*Passerina cyanea*). We did so within a landscape-scale experiment composed of equal-area habitat patches that differed in their amount of edge. Indigo Buntings preferentially selected edgy patches, which contained 50% more edge than more compact rectangular patches. Further, buntings fledged significantly fewer young per pair in edgy patches than in rectangular patches. These results provide the first experimental evidence that edges can function as ecological traps.

**Key words:** disturbance-dependent birds; ecological trap; edge habitat; fragmentation; habitat selection; Indigo Bunting; nest success; *Passerina cyanea*; patch shape; reproductive success.

### INTRODUCTION

Habitat selection is an adaptive decision that should lead to increased fitness (Cody 1985). Birds presumably have evolved to associate environmental and structural cues with habitat quality (Jaenike and Holt 1991). However, in landscapes increasingly modified by humans, the relationships between habitat cues and quality may be altered. In drastically modified landscapes, traditional cues may become completely decoupled from true habitat quality, and may cause birds to make errors in habitat selection, a phenomenon known as an “ecological trap” (Gates and Gysel 1978, Schlaepfer et al. 2002, Kristan 2003). In recent years, many studies have addressed the ecological trap hypothesis both theoretically and empirically (reviewed in Battin [2004]). However, few studies have provided convincing support for the trap hypothesis (e.g., Boal and Mannan 1999), which may be a result of unreliable methods used to determine their existence. In this paper, we overcome prior limitations of assessing ecological traps by providing a comprehensive evaluation of nest site selection and reproductive success in a precisely controlled experimental system.

To fully satisfy the trap hypothesis, two fundamental requirements must be met: (1) organisms must preferentially select poor-quality habitat over available higher quality habitat, and (2) organisms must suffer reduced fitness in the preferred habitat (Donovan and

Thompson 2001). Satisfying both conditions requires knowledge of species-specific behaviors that influence habitat choice. However, habitat selection behavior is often difficult to measure in the field, forcing ecologists to rely on surrogate measurements of habitat preference. As a result, the first requirement of the ecological trap hypothesis is often violated. For example, many ecologists use breeding bird density as an indicator of habitat quality and, thus, of habitat choice. However, density can be a misleading indicator of habitat quality (Van Horne 1983, Vickery et al. 1992). Social interactions may allow dominant individuals to preempt preferred habitats, forcing subdominant individuals into less preferred habitats at higher densities (Holmes et al. 1996, Zanette 2001). Population density may thus denote either a habitat sink (Donovan et al. 1995) or an ecological trap, and may not accurately reflect habitat preferences.

To distinguish between habitat sinks and ecological traps requires knowledge of habitat preferences, and confusing the two may have serious consequences for understanding population viability (Kristan 2003). Unlike ecological traps, source–sink relationships involve adaptive decision making (Dias 1996), by which birds preferentially select high-quality habitat until that habitat becomes saturated with individuals (Donovan et al. 1995). Only after high-quality habitat becomes unavailable will birds select poorer quality habitat. Sources and sinks, therefore, generally achieve a stable population equilibrium (Pulliam 1988). Traps, on the other hand, may function similarly to an “ecological vacuum,” continuing to draw individuals from high-quality into poor-quality habitat (Kokko and Sutherland 2001,

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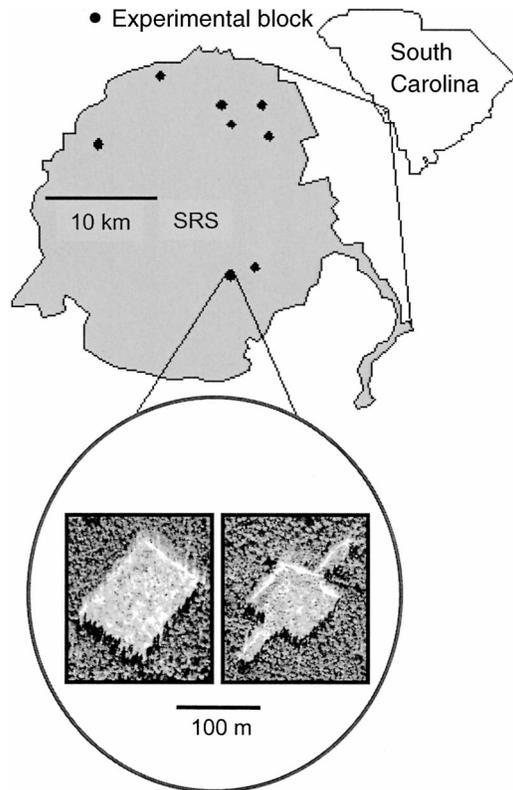


FIG. 1. The location of the Savannah River Site (SRS) and the eight experimental blocks within SRS. The inset shows infrared aerial photographs of the two different patch shapes within each block.

Kristan 2003). Thus, populations that are unable to adapt to trap habitats may be in danger of extirpation.

Although ecological traps can arise through a number of mechanisms (reviewed in Battin [2004]), the most commonly tested assumption is that anthropogenic edges function as traps for birds (Gates and Gysel 1978, Chasko and Gates 1982, Flaspohler et al. 2001). Species that nest along edges often require disturbed habitats that historically may have occurred within small and short-lived forest openings or larger expanses of fire-maintained successional habitat (Askins 1998, Hunter et al. 2001). Anthropogenic edges mimic natural disturbances by offering similar vegetative contrast between open and forested habitats, leading birds to preferentially nest along them. However, many studies have documented that edges tend to attract more predators and brood parasites than the natural habitats they mimic, creating a risky environment for birds nesting there (Brittingham and Temple 1983; reviewed in Paton 1994).

The habitat preferences of disturbance-dependent bird species may make them the avian group most susceptible to becoming trapped. Indeed, recent evidence indicates that many disturbance-dependent bird species are declining at rates comparable to, or even faster than,

high-profile forest species. Although many of these declines have been attributed to habitat loss (Askins 1993, Hunter et al. 2001, DeGraaf and Yamasaki 2003), additional influences, such as ecological traps, may further reduce the success of disturbance-dependent bird species.

We tested the ecological trap hypothesis within experimentally replicated landscapes of early-successional habitat patches. Each patch was equal in area but differed in shape, and thus, amount of edge. We used this system to determine if patch shape influences the habitat selection behavior and reproductive success of a species with strong edge preferences, the Indigo Bunting (*Passerina cyanea*).

## METHODS

### Study site

This study was conducted within eight experimentally replicated blocks separated by 3–30 km at the 80 000-ha<sup>2</sup> Savannah River Site, near Aiken, South Carolina, USA between May and August of 2002 and 2003 (Fig. 1). The experimental design is described in further detail in Tewksbury et al. (2002). Each block contained three early-successional patches created between October 1999 and April 2000 by clearing and burning timber from an area dominated by mature (40–50 year-old) loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine forest. All patches were equal in area (1.375 ha), but differed in shape between winged and rectangular forms. Winged patches contained 50% more edge than rectangular patches. Four of the experimental blocks were randomly assigned two winged patches and one rectangular patch, while the remaining four blocks were assigned two rectangular patches and one winged patch. Values from the duplicated patch type were averaged for all analyses to produce one treatment measure per block. The interpatch distances and the arrangement of patches with respect to each other within a block were standardized; however, the placement of individual treatments (shapes) within the arrangements was randomized. Vegetation structure was uniform within blocks and did not differ at the patch or nest level between treatments (Weldon 2004).

### Study species

Indigo Buntings (*Passerina cyanea*) are Neotropical migrant birds that show strong preferences for edges. Males are highly territorial and require numerous elevated perches for observation and territory defense (Payne 1992). Females build small, open-cup nests in saplings or shrubs ~1 m from the ground, and typically perform all nesting activities (Payne 1992). Indigo Buntings were the most common breeding bird in our experiment, with typical densities of 1–3 pairs/1.375-ha patch. Buntings have shown significant declines in many parts of the eastern United States over the past 37 years (Sauer et al. 2003).

### *Breeding bird abundance*

Male Indigo Buntings arrive on southeastern breeding grounds in late April to early May and immediately begin establishing territories (Taber and Johnston 1968). Between 5 May and 15 June 2002 and 2003, we identified the territories of all males occupying the patches by mapping the locations of singing individuals over six successive weeks. One block was visited each day, and the order in which individual patches were visited was randomized to avoid temporal bias in detectability. We plotted all movements onto gridded maps of each patch at a resolution of 12 m. Each patch was visited for 20 minutes, only in fair weather, starting shortly before sunrise and terminating before 08:30 hours. Only males that were seen or heard inside the patch were included in the counts. We then determined male abundance in each treatment by averaging individual counts across the six-week sampling period. Because nest detectability was high (>85% based on the total number of males) and territories were generally well defined, we used nest abundance to determine female abundance. The total number of unique females was determined by counting the maximum number of simultaneously active nests in each patch. We recognize possible limitations in our estimates of female abundance; however, we do not expect biases between treatments. Abundance estimates for males and females were tested for normality, and a paired *t* test was used to compare average abundance between treatments. Nest abundance data were checked for normality using a Shapiro-Wilk test and then were analyzed for treatment effects using PROC MIXED with block as a random effect and year as a repeated measure (SAS Institute 2000).

### *Age structure*

To simplify identification of current and returning male buntings, we captured and banded ~80% and 78% of known territory holders in 2002 and 2003, respectively. We used mist nets and a playback tape of Indigo Bunting song placed in known territories to attract and capture males. All captured individuals were uniquely banded with distinct color combinations and one U.S. Fish and Wildlife Service band.

Because age structure is considered an indicator of habitat quality (e.g., Holmes et al. 1996, Pärt 2001, Zanette 2001), all captured males in 2003 were classified as second-year (SY) and after-second-year (ASY) at the time of banding. Plumage characteristics or banded status were used to determine ages. Because the average number of males did not differ among treatments (see *Results*), we used the proportion of ASY individuals in each treatment as a measure of patch preference. We calculated this proportion from all "captured" birds, either through net captures or visual confirmation of bands or age status. Unbanded birds whose age could not be verified were excluded from



PLATE 1. Indigo Bunting nest. Photo credit: A. Weldon.

analyses, as were blocks that did not contain at least one bird of known age in each treatment. We arcsine-transformed proportions prior to analysis, and the proportion of ASY males in each treatment was compared with a paired *t* test. We analyzed the proportion of banded males from 2002 that returned to each treatment in 2003 using a chi-square test.

### *Reproductive success*

We systematically searched each patch for nests (see Plate 1) on a 4-day rotating cycle by walking transects between evenly spaced (25 m) rows of PVC markers for approximately one hour per patch. We used a combination of behavioral cues and systematic searches of potential nest substrates to locate nests, and active nests were monitored every 2–4 days to determine nest fate. A successful nest was defined as any nest that fledged at least one Indigo Bunting young. Predation was assumed if the contents of the nest disappeared before the estimated fledge date.

To examine temporal differences in nest survival, we distinguished "early" and "late" nesting periods, which corresponded closely to the first and second brood of the Indigo Bunting. We were able to track and determine brood status for 89% of nests, and used the timing of these nest attempts to assign brood status to unknown nests, such that nests initiated before 15 June belonged to brood one (early nests) and those initiated after this date to brood two (late nests).

We used the standard Mayfield (1975) method to calculate daily survival rates (DSR) by nesting period for each treatment within each block. One daily survival rate estimate was calculated per treatment by pooling nests from the duplicated treatment in each block. Daily survival rates did not differ between years for Indigo Buntings, so nests were pooled across years for analyses. Only total daily survivorship is reported, because no significant differences existed between the incubation and nestling stages for either treatment. We compared daily survival rates for each treatment and

nesting period within a block using the PROC MIXED analysis in SAS with block as a random effect (SAS Institute 2000). We chose this approach over recently developed model-based selection approaches (e.g., Shaffer 2004) because our unit of replication was a patch, not an individual nest. Furthermore, our replicated and randomized experimental design permitted determination of variance associated with treatment and block effects within a hypothesis-testing framework. We note that, although we considered our approach superior in this context, analysis using Shaffer's (2004) logistic exposure model produced qualitatively identical results. In each analysis, we weighted each treatment within a block by the number of representative nests to account for potential biases in estimates based on small sample sizes.

In each treatment within a block, we estimated total seasonal fecundity in winged and rectangular patches by dividing the total number of fledglings by the number of breeding females. We used PROC MIXED to test for between-treatment differences in seasonal fecundity and in the total clutch size and number of young fledged per successful nest (SAS Institute 2000). Years did not differ and were pooled for analyses.

#### *Nest placement*

The distance at which a nest is placed from the edge can impact its risk of predation, and this distance may vary with patch shape. For each Indigo Bunting nest known to have contained eggs, we measured and averaged the distance to the two closest edges and compared nest placement between treatments. To determine whether Indigo Buntings biased their nest location relative to the edge, we determined the proportion of nests in each of four distance categories from the edge (0–12.5 m, 12.6–25 m, 25.1–37.5 m, 37.6–50 m) and compared this to the proportion of habitat area available in each distance category in each treatment. To determine if survival rates varied with distance from the edge, we calculated Mayfield (1975) daily survival rates for nests in each distance category and then regressed these daily survival rates against distance to the edge.

#### *Food availability*

To test for treatment effects on food availability and nestling fitness, we obtained measures of relative food abundance in each treatment through video analysis of bunting nests in 2002. We determined provisioning rates for each nest on the third day after hatching over an 8-h period. We also measured nestling body mass at this time and continued to measure it in 2003. To ensure consistency in comparisons, all measurements of body mass were taken between 06:00 and 09:00 hours, and taping always began before 07:00. Camera systems consisted of hand-held camcorders (Sony CCD-TRV108 Hi8) erected on tripods ~3 m from the nest and camouflaged with a cryptic plastic casing and natural vegetation. Videotapes recorded all nest activ-

ities for 4 h and were then replaced. The second taping period always began between 11:00 and 12:30. We determined the average number of provisioning events, adjusted for the number of nestlings in each nest, across the 8-h period, as well as the average amount of time spent at the nest. For each provisioning visit, when possible, we recorded the size of the prey items as small (<1 bill-full), medium (~1–2 bill-fulls), or large (>2 bill-fulls). All provisioning rate, prey composition, and nestling fitness measures were compared using PROC MIXED as previously described (SAS Institute 2000).

## RESULTS

### *Patch preference*

The abundance of male and female Indigo Buntings did not differ between treatments. However, consistently higher proportions of ASY males were recorded in winged patches across all blocks. Nearly 83% of territories in winged patches (~1.4 males/patch), but only 53% of territories in rectangular patches (~0.9 males/patch), were held by ASY males ( $t = 3.95$ ,  $df = 5$ ,  $P < 0.01$ ). Furthermore, 53% of birds banded in winged patches ( $n = 19$  birds) returned to this treatment, but only 28% of birds banded in rectangular patches ( $n = 18$  birds) returned to rectangles, a marginally significant trend ( $\chi^2 = 3.42$ ,  $df = 1$ ,  $P = 0.067$ ). All birds returned to the patch in which they were banded, with the exception of one ASY male that moved from a rectangular to a winged patch.

### *Reproductive success*

In 2002 and 2003, we located 105 Indigo Bunting nests in winged and rectangular patches. Nest abundance did not differ between treatments. Predation was the primary cause of nest failure (83.6%), followed by abandonment (10.5%) and cowbird parasitism (5.5%). Abandoned nests ( $n = 6$ ) were not included in nest success analyses. Daily survival rates significantly declined from early to late nesting periods ( $F_{1,13} = 6.8$ ,  $P = 0.02$ ), and did not vary across treatments. The decline in daily survivorship was driven by a change from higher survivorship in rectangular patches in the early nesting period to lower survivorship in the late nesting period (Fig. 2A). This change is evident in the significant interaction between nesting period (per) and treatment (trt):  $F_{\text{per} \times \text{trt}} = 5.37$ ,  $P_{\text{per} \times \text{trt}} = 0.04$ . Despite the late-season increase in predation in rectangular patches, buntings in this treatment produced 52% more fledglings per female each year than did corresponding females in winged patches ( $F_{1,6} = 7.98$ ,  $P = 0.03$ , Fig. 2B). There were no differences in clutch size or the number of fledglings per successful nest between treatments, but both were lower in the late nesting period (for clutch size,  $F_{1,87} = 10.75$ ,  $P < 0.01$ ; for fledge,  $F_{1,38} = 9.26$ ,  $P < 0.01$ ).

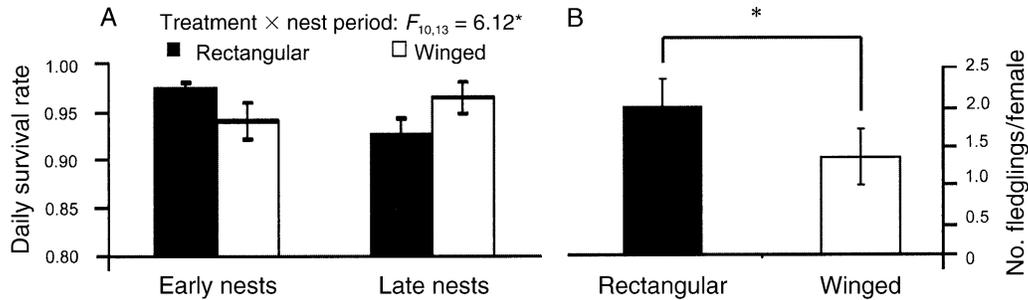


FIG. 2. (A) Daily survival rates for early and late nesting periods and (B) seasonal fecundity of Indigo Buntings in rectangular (black) and winged (white) patches. Values are mean  $\pm$  SE.

\*  $P < 0.05$ .

#### Nest placement

Indigo Buntings nested closer to the edge in winged than in rectangular patches ( $F_{1,124} = 12.84$ ,  $P < 0.001$ ). Based on the distribution of available habitat, the proportion of nests in each distance category in winged patches corresponded to expected proportions (Fig. 3B, D). Nest proportions in rectangular patches did not correspond as closely with expected patterns, particularly in the late nesting period where a greater proportion of birds nested near the edge (0–12.5 m) than expected (Fig. 3A, C).

Although daily survival rates did exhibit a generally positive relationship with distance from the edge (Fig. 3E, F), they were not significantly related to distance to the edge in either nesting period. However, the proportion of nests near the edge (0–12.5 m) was an important determinant of predation rates in each treatment. Across treatments and nesting periods, daily survival rates within 12.5 m from the edge were strongly and negatively related to the proportion of nests at that distance from the edge ( $R^2 = 0.98$ ,  $n = 4$ ,  $P < 0.01$ ). No relationship existed beyond 12.5 m from the edge, where the number of nests in each group began to converge. Female buntings showed a marginally significant trend in nesting at greater densities in the “wings” than in the more open areas of the winged patches ( $t = 2.11$ ,  $df = 7$ ,  $P = 0.07$ ).

#### Food availability

Video data from the 2002 breeding season revealed that Indigo Buntings spent an equal amount of time at the nest in winged and rectangular patches (Table 1). The number of trips to the nest and the total number of prey items brought to the nest per hour also did not differ between treatments. Females brought an equal number of small and large prey items to the nest in both treatments, but brought more medium-sized prey items to nests in rectangular patches. This result may account for the significantly higher nestling body mass in rectangular than in winged patches in 2002 (Table 1). Provisioning rate data were unavailable for the 2003 breeding season, but we continued to measure nestling mass and found no differences between treatments or

across years. However, mass was significantly higher in 2003 for both treatments (for rectangular,  $F_{1,10} = 6.73$ ,  $P = 0.03$ ; for winged,  $F_{1,17} = 6.53$ ,  $P = 0.02$ ), perhaps due to a greater abundance of preferred prey items associated with an unusually mild and wet summer.

#### DISCUSSION

This study demonstrates that patches with more complex shapes can function as ecological traps for at least one Neotropical migrant bird species. Indigo Buntings in winged patches experienced higher predation rates early in the season and lower seasonal fecundity than those in rectangular patches, where females produced >50% more fledglings, on average, than females in winged patches. Despite experiencing relatively low reproductive success in winged patches, Indigo Buntings preferentially selected these patches, providing evidence that winged patches are functioning as ecological traps.

#### Patch preference

More ASY male buntings established territories in, and a greater proportion of banded individuals returned to, winged patches. The mechanism leading to this preference remains unclear. Vegetation analysis indicated no consistent differences among treatments in patch-level vegetation or the suitability of nest microhabitats (Weldon 2004), nor was food availability a predictor of patch preferences. To the contrary, nestling body mass measurements were higher in rectangular than in winged patches in 2002, possibly due to an increase in the availability of medium-sized prey items, such as certain Orthopterans.

Because treatments do not obviously differ in any other way, buntings must be responding to something inherent in patch shape. Indigo Buntings are known to respond positively to edges, so the increased amount of edge in winged patches may simply send a stronger stimulus to males. In addition, our behavioral observations suggest that buntings are responding to specific features of patch shape. Unlike rectangular patches, winged patches contain two convex corners at the en-

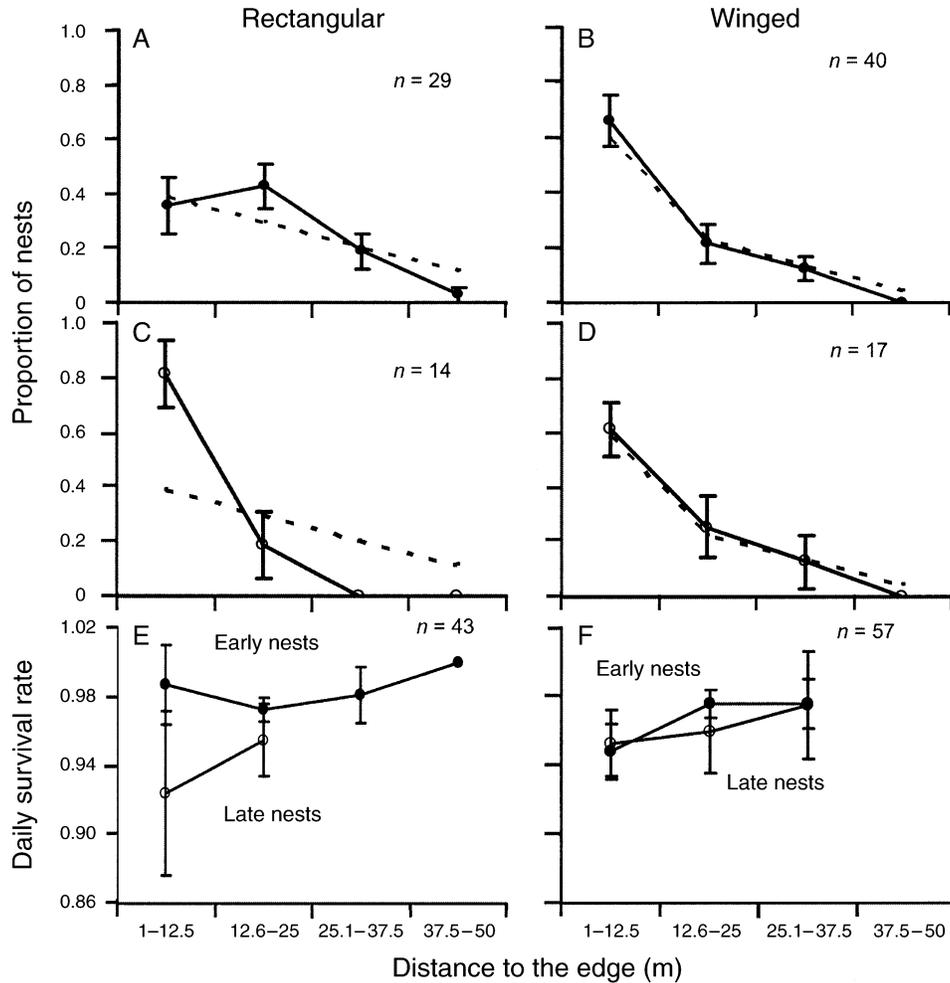


FIG. 3. The proportion of (A, B) early and (C, D) late Indigo Bunting nests and (E, F) associated daily survival rates of early and late nests combined, at increasing distances from the edge in rectangular and winged patches. All values are means  $\pm$  SE. The dashed lines in panels A–D represent the proportion of available habitat in each distance category.

trance to each wing. These corners may be attractive to male buntings as elevated and conspicuous song perches from which they can defend territories. Indeed, we frequently observed males using corner perches for singing and territory defense against intruding males,

an observation consistent with a study by Kroodsmma (1984), who concluded that the availability of song perches was an important determinant of territory selection for Indigo Buntings and other early-successional bird species. Female buntings also seemed to

TABLE 1. Provisioning rates, prey composition, and nestling body mass ( $\pm$ SE) for Indigo Buntings in rectangular and winged patches.

Measurement	Rectangular ( <i>n</i> = 17 nests)	Winged ( <i>n</i> = 26 nests)	<i>F</i>	df	<i>P</i>
Time (min) brooding or shading per hour	4.28 $\pm$ 0.98	5.11 $\pm$ 1.45	0.18	1,35	NS
Time (min) at nest per hour	9.15 $\pm$ 0.85	9.11 $\pm$ 1.45	0.00	1,35	NS
No. trips to nest per hour	5.93 $\pm$ 0.72	5.42 $\pm$ 0.42	1.03	1,35	NS
No. trips per nestling	2.23 $\pm$ 0.25	1.94 $\pm$ 0.13	1.32	1,35	NS
No. small pre per hour per nestling	0.47 $\pm$ 0.16	0.26 $\pm$ 0.05	2.20	1,35	NS
No. medium pre per hour per nestling	1.20 $\pm$ 0.15	0.68 $\pm$ 0.07	11.47	1,35	0.002
No. large pre per hour per nestling	0.32 $\pm$ 0.06	0.47 $\pm$ 0.07	1.95	1,35	NS
Total no. prey items per hour per nestling	2.28 $\pm$ 0.23	1.91 $\pm$ 0.13	2.54	1,35	NS
Nestling mass, 2002 (g)	5.99 $\pm$ 0.43	4.89 $\pm$ 0.26	6.40	1,10	0.03
Nestling mass, 2003 (g)	7.65 $\pm$ 0.49	7.08 $\pm$ 0.35	0.95	1,17	NS
Pooled nestling mass (g)	7.00 $\pm$ 0.32	6.16 $\pm$ 0.39	1.41	1,34	NS

prefer to place their nests within the wing areas, further supporting the shape hypothesis.

#### *Reproductive success*

Indigo Buntings experienced higher nest predation rates in winged patches during the first half of the breeding season, when birds nesting in rectangular patches initially experienced relatively low nest predation rates. However, predation pressure increased significantly in rectangular patches in the late nesting period. Temporal and spatial differences in predation rates were probably driven by physical and behavioral factors affected by patch shape. Our results indicate that patch shape influenced the proportion of nests near the edge and was the primary cause of differential predation rates between treatments. Indigo Buntings generally selected nest sites in response to available habitat, most noticeably in the early nesting period. Because winged patches inherently contained more edge habitat, they supported greater proportions of nests near the edge. Adult activity was most pronounced in the early nesting period and may have attracted predators to nests, particularly near (corner) song perches. In rectangular patches, the reduced availability of desired habitat, and possibly of conspicuous song perches, prevented such high proportions of birds from selecting areas along edges, and may have reduced detectability of nest areas. Thus, predators could concentrate their activities in winged patches close to the edge where the prey reward was highest (Martin 1988).

Similarly, the proportion of nests in edge habitat can also explain the differences in nest predation rates between nesting periods. Contrary to the expected distribution, a greater proportion of nests occurred near the edge in rectangular than in winged patches in the late nesting period. This increase may have been driven by successful nesters farther away from the edge not attempting additional nests, or by birds relocating to seemingly more attractive nest sites closer to the edge in the late nesting period. Regardless of the mechanism, birds nesting in rectangular patches experienced a significant increase in predation rate in the late nesting period.

Although we do not know the exact identity of the predator community, we observed corvids (Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*)), raptors (Red-shouldered Hawk (*Buteo lineatus*), American Kestrel (*Falco sparverius*)), and several snake species throughout our study. The condition of some depredated nests suggests that mesopredators such as raccoons (*Procyon lotor*) or opossums (*Didelphis virginiana*) were also present. However, most evidence indicates that snakes, primarily the black rat snake (*Elaphe obsoleta*), had a disproportionate influence on nesting success, consistent with other open-habitat studies (e.g., Thompson and Burhans 2003). We frequently observed snakes resting in small shrubs similar to those in which nests were lo-

cated. In addition, most nests were undisturbed, with the contents cleanly removed, characteristic of snake predation (Thompson et al. 1999). Snakes are particularly active predators of songbirds during the breeding season (Fitch 1963); previous work has indicated that snakes prefer edge habitats (Durner and Gates 1993, Blouin-Demers and Weatherhead 2001) and can respond to adult activity near nest sites when searching for prey (Mullin et al. 1998). These tendencies are consistent with the differential predation rates in winged and rectangular patches in this study.

#### *Ecological traps*

Indigo Buntings preferentially selected winged patches, but produced >50% more fledglings per female in rectangular than in winged patches. Low seasonal fecundity occurred in winged patches despite the late-season increase in predation rates in rectangular patches that could have countered early reproductive deficits in winged patches. This result suggests that the timing of predation pressure is important, and that early-season mortality has a greater biological impact than late-season mortality. Elevated predation pressure early in the season potentially can impact all members of the population, because most females should be breeding at this time. However, not all females initiate a second brood (~68% in this study). Even if predation pressure is relaxed later in the season, populations may not be able to compensate for nest losses, because fewer females are reneesting. Conversely, the impact of a late-season increase in predation, such as occurred in rectangular patches, may be less severe because most females (59% in this study) have already fledged nests successfully. Similarly, Morrison and Bolger (2002) demonstrated that an early-season suppression of snake predation allowed more Rufous-crowned Sparrows (*Aimophila ruficeps*) to successfully fledge multiple broods than in years when predation was high throughout the nesting season. In our study, female buntings in winged patches were apparently unable to ameliorate the effects of relatively high early-season predation rates, and subsequently suffered lower seasonal fecundity. Furthermore, a greater proportion of successful nests was produced in the second brood in winged than in rectangular patches. Typically, fewer dominant individuals are produced in later broods (Garnett 1981, Arcese and Smith 1985), and subdominance has been shown to reduce postfledging or winter survival (Kikkawa 1980, Baker et al. 1981). These conditions may lower annual survival rates for juveniles produced in winged patches.

If preferences were adaptive, Indigo Buntings should select rectangular patches, where the probability of reproducing successfully at least once is high and where nestling fitness may be higher. However, despite consistently poor early-season nest success in winged patches in both years of this study, males preferentially returned to them. Thus, the oldest and most experienced

individuals, who should fledge the most young (Holmes et al. 1996), were actually producing fewer offspring than the younger and less experienced individuals in this population.

The apparent maladaptive decision making of Indigo Buntings conflicts with previous work that documents the ability of birds to learn from past reproductive experiences (Pinkowski 1979, Herlugson 1981, Dow and Fredga 1983). Thus, it remains unclear why buntings did not respond to seemingly clear indicators of fitness. Payne and Payne (1993) found that neither older male nor female Indigo Buntings dispersed in response to previous nesting success. In addition, dispersing individuals did not achieve greater reproductive success than birds returning to previous territories. This suggests that buntings may be incapable of recognizing or responding to increases in predation pressure, possibly because it was often unnecessary to do so in historical breeding habitat. Prior to widespread anthropogenic influences, bunting habitat was frequently disturbed and may have supported relatively low predator populations (Suarez et al. 1997). Evolved responses to predation may have been less advantageous than responses to persistent and reliable habitat features, such as vegetation structure, for bird species occupying disturbed habitats. However, anthropogenic disturbances that mimic historical vegetation structure, but support large predator populations, have become increasingly common in modern fragmented landscapes, allowing evolved, adaptive behaviors to trick Indigo Buntings into mistakenly selecting poor-quality habitat.

We recognize that our interpretation of these results relies on some critical assumptions. For instance, we did not know the age structure of females in our study system, and cannot assure that females had similar dispersal responses as males. However, we do know that strong correlations between the ages of males and females within a pair exist for many species, including Indigo Buntings (Payne and Payne 1993, Holmes et al. 1996, Pärt 2001), and that female buntings have been shown to return more often to a familiar site and returning mate than to disperse in response to previous nesting success (Payne and Payne 1993). In addition, we did not have banded females, but instead relied on nest abundance and timing to determine female abundance and re-nesting rates. Although this method is not as accurate as counting banded females, the placement and timing of nests was generally predictable, such that we could confidently assign most nests to a female. And lastly, we do not know the impacts of patch shape on adult or juvenile fitness beyond the breeding season. Selecting winged patches may be an adaptive decision if adult or juvenile fitness is somehow elevated during the nonbreeding season, when they are not in these patches, by occupying this treatment during the breeding season. However, the fitness benefits to adults would have to outweigh the relatively low daily survival rates of eggs and nestlings, the consequent re-

duction in seasonal fecundity, as well as possibly poorer nestling and fledgling fitness in winged patches to overcome the effects of this ecological trap.

#### *Implications for management*

This study demonstrates the importance of incorporating landscape-level behavioral responses of birds into conservation and management plans. If behavioral components are excluded and habitat quality is determined solely through abundance estimates, traps may remain undetected, creating a potentially dangerous situation for some breeding bird populations. Small or threatened populations (Kristan 2003), species that exhibit strong site fidelity (Purcell and Verner 1998), or species that are unable to recognize or respond to predation threats (Indigo Buntings) may be particularly vulnerable to the harmful effects of ecological traps. For Indigo Buntings, traps could be avoided by creating patches with simple shapes that retain habitat quality, but do not contain attractive but risky features, such as convex corners, from which singing birds are most conspicuous. If not considered, traps may be created inadvertently as part of other strategies for habitat conservation. For example, the winged patches in this study were created to mimic the shape (but not connectivity) of corridors (Tewksbury et al. 2002). This study shows how the long, narrow shapes and convex corners created by corridors may have unintended negative consequences on avian nest success (Weldon 2004).

Brood parasitism may additionally increase the severity of traps for some populations of birds. This study was conducted within a primarily forested landscape, where predation pressure and parasitism rates are often lower than in agricultural landscapes (Brittingham and Temple 1983, Thompson et al. 2000). Birds occupying such landscapes, where parasitism is an additional source of mortality and where edge effects may be more severe, may be most at risk.

This study also reveals that the ability to double-brood may determine the severity of ecological traps, supporting results from a previous modeling study (Donovan and Thompson 2001). Had Indigo Buntings been incapable of producing a second brood, the difference between treatments would have been even more pronounced. Therefore, ecological traps may impose a significantly greater risk on single-brooded than on double-brooded species such as the Indigo Bunting. Future studies should incorporate season-long nest-monitoring programs to accurately assess the impact of habitat choice on seasonal reproductive output, particularly in habitats prone to producing traps. Perhaps most importantly, conservation biologists should work to identify behavioral mechanisms that might lead to ecological traps for a variety of species.

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