

ABSTRACT

Weldon, Aimee Jean. The effects of patch shape and connectivity on nest site selection and reproductive success of the Indigo Bunting. (Under the direction of Nick. M. Haddad)

Habitat fragmentation and its associated effects have been blamed for the recent population declines of many Neotropical migratory bird species. Increased predation and parasitism resulting from edge-related effects have been implicated for poor nesting success in many studies, mostly of forest interior species. However, little attention has been devoted to disturbance-dependent birds. In this study, I examine how patch shape and connectivity in fragmented landscapes affects the reproductive success of disturbance-dependent bird species, specifically the Indigo Bunting (*Passerina cyanea*). I conducted my study in a landscape-scale experimental system of similar-area habitat patches that differed in connectivity and in shape. Shapes differed between edgy and rectangular forms, where edgy patches contained 50% more edge than rectangular patches. I tested whether edgy patches function as ecological traps for species with strong edge preferences, by leading them to select dangerous habitats. Indigo Buntings preferentially selected edgy patches over rectangular patches, but experienced significantly lower reproductive success in edgy patches early in the season. Although predation pressure intensified in rectangular patches late in the season, seasonal fecundity was still significantly lower in edgy patches, providing the first empirical evidence that edges can function as ecological traps for Indigo Buntings.

A second objective of my study was to evaluate the efficacy of conservation corridors for disturbance-dependent bird species. Conservation corridors have become a popular strategy to preserve biodiversity and promote gene flow in fragmented landscapes, but corridors may also have negative consequences. I tested the hypothesis that corridors can

increase nest predation risk in connected patches relative to unconnected patches. Nest predation rates increased significantly in connected patches compared to unconnected rectangular patches, but were similar between connected patches and unconnected edge patches. This suggests that the increase in predator activity in connected patches is largely attributable to edge effects incurred through the addition of a corridor. This is the first landscape-scale study to experimentally demonstrate the potential negative effects of conservation corridors.

**THE EFFECTS OF PATCH SHAPE AND CONNECTIVITY ON NEST SITE
SELECTION AND REPRODUCTIVE SUCCESS OF THE INDIGO BUNTING**

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BIOGRAPHY

I, Aimee Weldon, was born on April 15, 1977 in Minneapolis, Minnesota. My older sister, Becky, and I grew up on a small hobby farm in rural Minnesota where we spent many hours exploring the woods and meadows near our home. Even as a child, the natural world fascinated me and I spent an inordinate amount of time studying and collecting everything from butterflies to plants. I attended college at the nearby College of St. Benedict where, strangely, I aspired to become a medical doctor someday. However, after taking a few ecology courses, I came back to my senses and realized that my true passion lay in understanding the fascinating intricacies of nature. This decision led to two years of field work across the country in almost every aspect of ecology. However, my favorite jobs always involved birds and my position studying raptor ecology with Hawkwatch International in Nevada set the course for my avian research interests. Ultimately, I found my way eastward again and was accepted into the Zoology department here at North Carolina State University. I feel very fortunate, as I was able to combine multiple interests - conservation, ecology, and avian behavior - into my Masters project. This work represents the final product of the last two and a half years of hard work, great people and continuous learning. I've enjoyed the journey immensely.

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CHAPTER 1:

**THE EFFECT OF PATCH SHAPE ON THE INDIGO BUNTING: EVIDENCE FOR
AN ECOLOGICAL TRAP**

ABSTRACT

Habitat fragmentation has 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 historical 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’. I 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*). I did so within a landscape-scale system 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. Other resident and migrant breeding bird species did not show evidence for ecological traps, although migrant species qualitatively demonstrated a similar pattern to the Indigo Bunting. These results provide the first experimental evidence that edges can function as ecological traps for at least one Neotropical migrant species.

INTRODUCTION

Habitat selection is an adaptive decision that leads to increased fitness and reproductive success (Cody 1985). Through natural selective processes, birds have presumably evolved to associate cues, such as environmental or structural characteristics, with habitat quality (Jaenike and Holt 1991). However, in landscapes increasingly modified by humans, the relationship 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 (Schlaepfer et al. 2002, Kristan et al. 2003). This phenomenon was first termed an ‘ecological trap’ when Gates and Gysel (1978) discovered that anthropogenic edges tended to concentrate breeding birds, leading to density-dependent predation. Since then, numerous studies have addressed the ecological trap hypothesis both theoretically and empirically (reviewed in Battin *in press*). However, few studies have provided convincing support for the trap hypothesis (e.g. Boal and Mannan 1999), possibly because the current methods used to determine the existence of ecological traps are unreliable. In addition, only recently was an appropriate theoretical framework in which to interpret traps developed (Donovan and Thompson 2001, Kristan 2003). In this paper, I overcome prior limitations of assessing ecological traps by providing an experimental and comprehensive evaluation of nest site selection and reproductive success.

Two fundamental requirements must be met in order to fully satisfy the trap hypothesis: 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 for habitat selection. 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 may be a misleading indicator of habitat quality (Van Horne 1983, Vickery 1992, Zquette 2001, Moorman et al. 2002), particularly for organisms that exhibit strong territorial behavior (Fretwell 1972). High

densities of birds may result from social interactions that allow dominant individuals to preempt territories in preferred habitats, forcing subdominant individuals into less preferred habitats (Holmes 1996, Zanette 2001). A greater density of birds may therefore denote a habitat sink (Donovan et al. 1995) or an ecological trap and may not accurately reflect habitat preferences.

The distinction 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 abilities (Dias 1996), where birds preferentially select high quality habitat until that habitat becomes saturated with individuals (Donovan et al. 1995). Only after quality habitat becomes unavailable will birds select poorer quality habitat. Sources and sinks, therefore, generally tend toward a stable population equilibrium (Pulliam 1988, Kristan 2003). Traps, on the other hand, may function similar to an ‘ecological vacuum’, continuing to draw individuals from high quality habitat into poor quality habitat (Koko and Sutherland 2001, 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 *in press*), the most common assumption is that anthropogenic edges function as traps for birds (Gates and Gysel 1978, Chasko and Gates 1982, Johnson and Temple 1990, Flaspohler et al. 2001). Species that nest along edges often require disturbed habitats and may have historically nested within small, naturally created, and short-lived forest openings or larger stretches 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, a number of authors 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).

Disturbance-dependent bird species, in particular, often select edge habitats and may thus be the most susceptible avian group to becoming trapped. These birds have been assumed to benefit from the artificial habitats created by human disturbance and as a result,

are often overlooked in conservation plans (DeGraaf and Yamasaki 2003). However, recent evidence has indicated that many disturbance-dependent bird species are declining at comparable or even faster rates than high-profile forest species (Askins 1993, Peterjohn 1994, Hunter et al. 2001). Although many of these declines have been attributed to habitat loss (Askins 1993, Hunter et al. 2001, DeGraff and Yamasaki 2003), additional influences, such as ecological traps, may further reduce the success of disturbance-dependent bird species.

In this study, I tested the ecological trap hypothesis within experimentally replicated landscapes of small early-successional patches. Each patch was equal in area but differed in shape, and thus, amount of edge. I used these patches to determine if patch shape influences the habitat selection behaviors and reproductive success of species with strong edge preferences, with a focus on responses by the Indigo Bunting (*Passerina cyanea*).

METHODS

Study Site

This study was conducted within 8 experimentally replicated landscapes at the Savannah River Site, near Aiken, SC, between May and August of 2002 and 2003 (Figure 1.1). Each landscape contained three early successional patches that were 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 percent more edge than rectangular patches. Four of the experimental landscapes, hereafter referred to as 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. Blocks were separated by 3 to 30 km across the 80,000 ha² Savannah River Site. The inter-patch 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. Patches were allowed to succeed naturally after clearing and were entering their third year of succession in the 2002 breeding season.

Study Species

I used the Indigo Bunting (*Passerina cyanea*) as my focal species. Buntings are Neotropical migrant birds known as a traditional ‘edge’ species, often occupying shrubby habitat along anthropogenic edges and forest canopy gaps (Payne 1992). Males require numerous singing and observation perches for territory defense and will aggressively defend their territories from intruding males (Payne 1992). Older males may replace younger males who preempt them on their breeding territories (Carey and Nolan 1979). Both males and females can begin breeding in their first breeding season and pairs are socially monogamous and multi-brooded (Payne 1989). Females build small open-cup nests in saplings or shrubs approximately 1 m from the ground and typically perform all incubation and brood activities (Payne 1992). Indigo buntings were the most common avian species in my experimental system and, during the breeding season, occupied sites at densities of 1-3 breeding pairs per 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), and their tendency to select edge habitat and build small open-cup nests makes them good models for other Neotropical migrant edge species that may be declining due to anthropogenic landscape alterations.

In addition to my focal species, I also tested how patch shape affected the reproductive success of other birds breeding in the system and if differences exist between the responses of resident and migrant groups. These species included the resident Brown Thrasher (*Toxostoma rufum*), Eastern Towhee (*Pipilo erythrophthalmus*) and Northern Cardinal (*Cardinalis cardinalis*), and the migrant Prairie Warbler (*Dendroica discolor*) and Blue Grosbeak (*Guiraca caerulea*). Both migrant species build open-cup nests similar in form and placement to those of the Indigo Bunting. All resident species generally build larger and more coarsely constructed nests most often placed near the center of dense shrubs (personal observation). I monitored nest success and collected indirect measurements of habitat selection (nest abundance, distance of nests from the nearest edge) for non-focal species but did not measure patch preference behavior or habitat characteristics (food, nest-level vegetation) for these species.

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 May 5 and June 15, 2002 and 2003, I identified the territories of all males occupying the study sites by mapping the locations of singing individuals in 20-minute intervals over the course of six successive weeks. I plotted all movements onto gridded maps of each patch at a resolution of 12 m. One block was visited each day and the order in which individual patches were visited was randomized to avoid temporal bias in detectability. Mapping was conducted only in fair weather starting shortly before sunrise and terminating before 0830. Only males that were seen or heard inside the patch were included in the counts. I determined male abundance in each treatment by averaging individual counts across the six-week sampling period. Because detectability was high (~85% based on the maximum number of males) and territories were generally well-defined, I 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. 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 (across nesting periods) were checked for normality using a Shapiro-Wilk test and then analyzed for treatment effects using ANOVA with year as a repeated measure.

I analyzed nest abundance between treatments for non-focal species using the same methods outlined above. Square root transformations were used when necessary to normalize the data. I divided all non-focal species into resident and migrant categories and conducted separate analyses for individual species and migratory groups.

Age Structure

To simplify identification of current and returning male buntings, I captured and banded approximately 80% and 78% of known territory holders in 2002 and 2003, respectively. I 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. Equal numbers of birds were captured in each treatment.

Since age structure is often an indicator of habitat quality (e.g. Holmes et al. 1996, Pärt 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 and the same observer aged all birds. ASY birds have uniformly blue plumage, while SY birds often have less saturated coloration and/or brown feathers intermixed on the upper body and greater primary coverts (Taber and Johnston 1968, Payne 1992). I used the percent of ASY individuals in each treatment as a measure of patch preference. I calculated this percent from all ‘captured’ birds, either through net captures or through visual confirmation of bands or age status. Unbanded birds whose age could not be verified were excluded from the analysis as were blocks that did not contain at least one bird of known age in each treatment. I arcsine transformed proportions prior to analysis, and the percent of ASY males in each treatment was compared with a paired t-test. I analyzed the proportion of banded males from 2002 that returned to each treatment in 2003 with a Chi Square test.

Reproductive Success

I systematically searched each patch for nests of all species on a 4-day rotating cycle by walking transects between evenly spaced (25 m apart) PVC markers. For Indigo Buntings, the maximum number of possible nests per patch was determined as the total number of singing males per patch. I used a combination of behavioral cues and systematic searches of potential nest substrates to locate nests. Each patch was searched for approximately one hour and I took care to alter my course to reduce the creation of trails that might be used by predators. All nests were marked by placing flagging tape at least 10 m from the nest, and active nests were monitored every 2 to 4 days to determine nest fate. The contents of each nest were recorded whenever possible during each visit. Successful nests were defined as any nest that fledged at least one host young. Predation was assumed if the contents of the nest disappeared any time before the estimated fledge date.

To examine temporal differences in nest survival for all species, I distinguished the ‘early’ from the ‘late’ nesting period, which corresponded closely to the first and second brood of the Indigo Bunting. I was able to track and determine brood status for 89% of Indigo Bunting nests, and used the timing of these nest attempts to assign brood status to any

unknown nests, such that nests initiated before June 15th belonged to brood one (early nests) and those initiated after this date to brood two (late nests). Because I was primarily interested in temporal patterns in nest predation, I used this definition for all other species as well, although it may not accurately describe nesting cycles.

I used the standard Mayfield method (1975) to calculate daily survival rates (DSR) for the early and late nesting period for each treatment within a block for all species. Daily survival rates did not differ between years for any species so all nests were pooled for analyses. Separate survival rates were calculated for the incubation and nestling periods to determine whether stage-specific factors influenced nesting success. However, stages did not differ significantly from each other, so I report only total daily survivorship. I compared daily survival rates using ANOVA. Analysis of variance calculates an error term from the variation among blocks rather than from variation within pooled samples. By controlling for block effects, I was better able to test for true differences in survival rates between treatments. In each analysis, I weighted each treatment within a block by the number of representative nests to adjust for estimates based on small sample sizes. Sample sizes were too small to compare daily survival rates of non-focal species independently, thus only migrant and resident groups are reported. I calculated total nest success (TNS) for each nesting period with the following equation:

$$\text{TNS} = \text{DSR}^n \quad (1)$$

where n equals the total length of the nesting period. For resident and migrant groups, I set n equal to the average nesting period length for all species within a group (residents: $n = 23$, migrants: $n = 21$).

I estimated total seasonal fecundity in winged and rectangular patches by calculating the total number of fledglings produced in each treatment within a block and dividing that number by the corresponding number of breeding females in each treatment within a block. I used a one-tailed ANOVA to test directional predictions of seasonal fecundity based on daily survival rates in each treatment. To determine if survival rates varied with distance from the edge, I calculated Mayfield daily survival rates for nests in four distance categories (0-12.5

m, 12.6-25 m, 25.1-37.5 m, 37.6-50 m) and then regressed these DSRs against distance to the edge. The total clutch size, proportion of eggs hatched, and number of young fledged per successful nest each year were compared using ANOVA.

Vegetation and Habitat Covariates

Nest Characteristics: The distance a nest is placed from the edge can impact its risk of predation and this distance may vary with patch shape. At small patch sizes, such as in this system, a greater proportion of habitat exists near the edge, which may allow more than one edge to influence nest success. To test this, I measured the distance to the two closest edges of all nests known to have contained eggs. I then averaged these distances to quantify the potential effect of edges on nests.

To determine whether birds selected nest sites closer to the edge in winged than in rectangular patches, we compared the average distance from each nest to the two closest edges between treatments using ANOVA. Separate analyses were conducted for each species group. In addition, since winged patches inherently contained more edge habitat than rectangular patches, I also determined whether nests were closer to the edge than would be expected based on habitat availability. I calculated the average distance of all grid cells in a patch to their nearest two edges and then compared this value to the observed placement of nests by analyzing overlap in 95% confidence intervals. Years did not differ for any species group so only pooled results are presented.

Food Availability: To test for treatment effects on food availability and nestling fitness, I obtained measures of relative food abundance in each treatment through video analysis of bunting nests in 2002. I determined provisioning rates for each nest on the third day after hatching over an 8 h period. I also measured nestling weights at this time and continued to measure them in 2003. To ensure consistency in comparisons, all weights were taken between 0600 and 0900 and taping always began before 0700. The camera system consisted of hand-held camcorders (Sony CCD-TRV108 Hi8) erected on tripods approximately 3 m from the nest and camouflaged with a cryptic plastic casing and natural vegetation. Videotapes recorded all nest activities for 4 h and were then replaced. The second taping period always began between 1100 and 1230. I 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, I recorded the size of the prey items as small (< 1 bill-full), medium (~1-2 bill-fulls) or large (>2 bill-fulls) when possible. Provisioning rates, the total time spent at the nest per hour and the total number of small, medium and large prey items brought to the nest per hour were compared using ANOVA.

Nest-site characteristics: For all Indigo Bunting nests in 2002 and all early nests in 2003, I assessed nest-level vegetation characteristics using an adaptation of the BBIRD Program protocol (Martin et al. 1997). Using each nest as the center point, I delineated a 5-m radius circle (.008 ha²) nested within an 11.3-m (.04 ha²) radius circle with a tape measure. Within each 5-m plot, I estimated the percent cover of grasses, forbs, shrubs, slash, bare ground, leaf cover and total green cover. I also counted the number of vertical stems for all woody species in three height classes (50 cm-1 m, 1-3 m, and >3 m). Woody species below 50 cm in height were not included in the stem counts and those with a diameter at breast height greater than 8 cm were classified as trees, which I recorded in the 11.3-m plot. This definition was set to distinguish suitable nesting substrates (shrubs) from unsuitable ones (trees) in which buntings were never observed to nest. Size classes of trees were not differentiated, as most trees were same-age Loblolly or Longleaf pines. To determine if patch shape affected the quality or abundance of preferred nest sites, I compared nest plots to unused random plots within each male's territory. Random plots were chosen through a random generation of numbers that corresponded to a 12.5 x 12.5 m grid cell and were equal in area to nest plots. I measured the same habitat variables in both nest and random plots and tested for treatment effects using ANOVA. All plots were measured between late June and mid-July in 2002 and 2003. A correlation analysis revealed that the total percent of green cover, leaf cover and slash were highly intercorrelated with other variables and were dropped from the analyses.

Patch-level vegetation: I compared patch-level vegetation between treatments in 2002 using existing 3x3 m vegetation plots from an unrelated project (Damschen, *unpublished methods*). Vegetation plots had a standardized distribution within patches with 22 located along edges (< 25 m from the edge) and 12 located within the patch interior (> 25 m from the edge). The total area surveyed equaled 23% of each patch. Similar to

measurements in nest plots, I recorded the number of woody stems in three height classes within each plot. However, I did not record percent cover information, as I was more concerned with gross habitat features than microhabitat features. All plots were measured within a 2-week period in mid-July, 2002 and vegetation variables were compared between treatments using ANOVA. I used a sequential Bonferroni correction to control for inflation of Type I error rates for all vegetation comparisons (Quinn and Keough 2002). All statistical analyses were performed using SAS version 8.1 (SAS Institute 2000).

RESULTS

Patch Preference

The abundance of male and female Indigo Buntings did not differ between treatments. However, a significantly greater proportion of ASY males established territories in winged than in rectangular patches ($t = 3.95$, $df = 5$, $P < 0.01$). This trend was consistent across all blocks. Furthermore, 53% ($n = 19$) of birds banded in winged patches returned to wings but only 28% ($n = 18$) of birds banded in rectangular patches 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 male that moved from a rectangular patch to a winged patch.

Reproductive Success

Indigo Buntings: I located 106 Indigo Bunting nests in winged and rectangular patches over the course of two years. 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. Nest abundance did not differ significantly between treatments but there was a significant block effect ($F_{9,14} = 6.40$, $P = 0.01$). Daily survival rates were significantly lower in winged than in rectangular patches ($F_{9,11} = 9.92$, $P < 0.01$) in the early nesting period but did not differ between treatments in the late nesting period (Table 1.1, Figure 1.2). Daily survival rates dropped significantly in the late nesting period for rectangular patches ($F_{7,4} = 8.76$, $P = 0.04$) but did not differ between nesting periods in winged patches. Overall, buntings in winged patches produced significantly fewer fledglings per female each season than corresponding females in

rectangular patches ($F_{9,13} = 3.73$, $P = 0.038$) (Table 1.1). There were no differences in clutch size, proportion of eggs hatched, or the number of fledglings per successful nest between treatments but all were lower in the late nesting period (Table 1.2).

Other Species: I included 83 resident nests (Brown Thrasher [$n=29$], Eastern Towhee [$n = 40$], Northern Cardinal [$n = 14$]), and 31 migrant nests (Blue Grosbeak [$n = 19$], Prairie Warbler [$n = 12$]) in nest success analyses. Nest abundance did not differ between treatments for any species. Daily survival rates did not differ between treatments or between early and late nests for either migrants or residents (Table 1.1, Figure 1.2). Migrants qualitatively exhibited a similar pattern as Indigo Buntings, with daily survival rates higher in rectangular patches in the early nesting period but lower in the late nesting period. Similarly, total seasonal fecundity for migrants was numerically higher in rectangular than in winged patches, but this difference was not significant (Table 1.1). Resident species showed no treatment effect but did experience generally lower overall daily survival rates than migrants and buntings in both treatments, although the difference between residents and buntings in rectangular patches in the early nesting period was the only significant difference ($F_{9,12} = 5.23$, $P = 0.04$) (Table 1.1, Figure 1.2).

Nest Placement

Indigo Buntings: Indigo Buntings nested significantly closer to the edge in winged than in rectangular patches, but not significantly closer than expected based on habitat availability (Table 1.3). Nest number was negatively correlated ($R^2 = 0.71$, $P < 0.01$) with distance from the edge in winged patches in both nesting periods, while rectangular patches showed no significant relationship in the early nesting period, a marginally significant relationship in the late nesting period and a significant negative relationship when nesting periods were combined ($R^2 = 0.68$, $P = 0.01$). The proportion of nests in each distance category corresponded to the expected proportions based on habitat availability in winged patches (Figure 1.3A,B). Nest proportions in rectangular patches did not correspond as closely with expected patterns, particularly in the late nesting period, where a significantly greater proportion of birds nested near the edge (0-12.5 m) than expected (Figure 1.3A,B).

The combined (across nesting periods) daily survival rates per treatment were significantly and positively related to distance from the edge in winged patches ($R^2 = 0.79$, P

= 0.02) but not in rectangular patches (Figure 1.3C). The importance of nest location on daily survival rates is demonstrated by the significant negative relationship across treatments and nesting periods between the proportion of total nests near (<12.5 m) the edge and the corresponding daily survival rates (Figure 1.4). No relationship existed beyond 12.5 m from the edge, where the number of nests in each group began to converge. In the early nesting period, winged patches supported a greater proportion of nests near the edge than did rectangular patches and experienced the lowest daily survival rate. Conversely, the greatest proportion of nests located near the edge in the late nesting period was found in rectangular patches, which experienced lower daily survival rates than winged patches. Regardless of treatment or nesting period, nests closest to the edge were subject to the highest predation rates.

Other Species: Migrant species (excluding Indigo Buntings) nested closer to the edge in winged than in rectangular patches and this distance was closer than expected (Table 1.3). Resident species exhibited a similar but insignificant trend and did not nest closer to the edge than expected in either treatment (Table 1.3).

Vegetation

Although center plots contained more total woody stems than edge plots in winged patches, the combined patch-level vegetation did not differ between winged and rectangular patches for any measure (Table 1.4). At the nest level, Indigo Buntings selected similar nest sites in winged and rectangular patches; nest plots did not differ between treatments for any vegetation measures. However, there were some year effects, which were likely a result of succession. Nest plots contained fewer small (0.5-1 m) woody stems and more tall woody stems in 2003 than in 2002 in both treatments and a greater percent shrub cover and lower percent bare cover in winged patches between years. In winged patches, Indigo Buntings chose nest sites with significantly more medium (1-3 m) stems than in corresponding random plots ($F_{9,86} = 8.99, P < 0.01$) but no differences existed in rectangular patches. Nest plots did not otherwise differ from random plots.

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 1.5). 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 to the nest in both treatments but brought significantly more medium-sized prey items to nests in rectangular patches. This result may account for the significantly higher nestling weights in rectangular than in winged patches in 2002. Provisioning rate data were unavailable for the 2003 breeding season, but I continued to measure nestling weights and found no differences between treatments or across years. However, weights were significantly higher in 2003 for both treatments (Rectangular: $F_{7,10} = 6.10$, $P = 0.03$; Winged: $F_{7,17} = 15.81$, $P = 0.001$), 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 experienced significantly higher predation rates in winged patches early in the season and significantly lower seasonal fecundity compared to rectangular patches, where females produced over 52% more fledglings on average than females in winged patches. Despite experiencing relatively low reproductive success in winged patches, Indigo Buntings still preferentially selected these patches, providing evidence that winged patches are functioning as ecological traps.

Conversely, winged patches did not function as ecological traps for resident species or the other migrant species in my system. Reproductive success in both treatments was nearly equal for resident species, while other migrants qualitatively exhibited similar patterns to Indigo Buntings in both daily survival rates and seasonal fecundity. However, I could not draw solid conclusions about migrant responses to patch shape due to small sample sizes and the lack of habitat selection information.

Patch Preference

More ASY male buntings established territories in, and a greater proportion of banded individuals returned to, winged patches. It remains unclear why buntings preferred winged patches, as vegetation analysis indicated no consistent differences among treatments

in patch-level vegetation or the suitability of nest microhabitats. Females in winged patches selected nest plots with more medium woody stems (1-3 m tall) than corresponding random plots, but nest plots did not differ from random plots in rectangular patches. This result may suggest that fewer nest substrates (medium stems) are available, overall, in winged patches, but this apparently did not negatively influence habitat choice. Food availability was also not a predictor of patch preference. Nestling weights were higher in rectangular than in winged patches in 2002, perhaps due to an increase in the availability of medium-sized prey items, such as certain Orthopterans. If food were a primary cue for buntings, I would expect more returning males to select rectangular patches, but this was not the case. The structure of winged patches may indicate a greater abundance of food for buntings, when in fact winged patches offer equal or less food than rectangular patches. Alternatively, food availability, may convey less information about fitness for Indigo Buntings than other habitat features, as several studies of other species have shown (e.g. Martin and Roper 1988, Orians and Wittenberger 1991, Steele 1993).

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, my behavioral observations suggest that buntings are responding to particular features of patch shape. Unlike rectangular patches, winged patches contain two convex corners at the entrance to each 'wing'. These corners may be attractive to male buntings as elevated and conspicuous song perches from which they can defend their territories. Indeed, I frequently observed males using these corner perches for singing and territory defense against intruding males. This observation is consistent with a study by Kroodsma (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.

Reproductive Success

Indigo Buntings experienced significantly higher predation rates in winged patches during the first half of the breeding season, while birds nesting in rectangular patches initially experienced relatively low predation rates. However, predation pressure increased

significantly in rectangular patches in the late nesting period. Temporal and spatial differences in predation rates were likely driven by physical and behavioral factors affected by patch shape. My results indicate that the proportion of nests near the edge was the primary cause of differential predation rates between treatments and that patch shape can drive nest location. 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 early in the breeding season. The reduced availability of edge habitat in rectangular patches prevented such high proportions of birds from selecting areas along edges. Thus, predators could concentrate their activities in winged patches where the prey reward close to the edge was highest and they could maximize efficiency (Martin 1988).

Similarly, the proportion of nests in edge habitat can also explain the observed trends in rectangular patches. Contrary to their expected distribution, a greater proportion of nests occurred near the edge in rectangular than in winged patches in the later nesting period. This increase may have been driven by successful nesters further away from the edge not attempting a second nest 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. These results are consistent with Gates and Gysel's (1978) conclusion that edges can concentrate birds and their predators.

By influencing adult behavior, patch shape may have further contributed to differential predation rates. In winged patches, male courtship activity early in the season around corner perches near the entrance to each 'wing' may have attracted more predators to nest areas. Although I do not know the exact identity of the predator community, I 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 my study. The condition of some depredated nests suggests that medium-sized mammals 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 (Thompson and Burhans 2003). I frequently observed snakes resting in small shrubs similar to those in which nests were located. In addition, most nests were undisturbed and the contents cleanly removed, characteristic of snake predation (Thompson et al. 1999). Snakes are particularly active songbird predators during the breeding season (Fitch 1963), and previous work has indicated that snakes prefer edge habitats (Durner and Gates 1993, Blouin-Demers 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 observed in winged and rectangular patches in this study.

Ecological Traps

To clearly identify an ecological trap and to distinguish traps from sinks, researchers must demonstrate that birds preferentially select poor quality habitats over available, higher quality habitats. In this study, Indigo Buntings showed a clear preference for winged patches, despite experiencing significantly lower reproductive success there. Thus, winged patches are likely functioning as ecological traps. To determine whether rectangular patches were functioning as population sources, I calculated a population growth rate using my fecundity estimates and adult survival estimates from the literature as detailed in Flaspohler et al. (2001). I computed juvenile survivorship to be one half of adult survivorship, consistent with studies for other Neotropical migrant landbirds (Temple and Cary 1988, Thompson 1993, Donovan et al. 1995). According to this estimate, both treatments are functioning as sinks. However, the only available estimates of adult survival for the Indigo Bunting in the literature ($\sim .56$) were based solely on band returns and did not incorporate dispersal probabilities (Payne 1989) likely leading to a negative bias. In addition, juvenile survival cannot necessarily be assumed to be equal in each treatment (Garnet 1981, Arcese and Smith 1985). If I assume a moderate adult survival rate of .66 and maintain equal fledgling survivorship in each treatment, rectangular patches become sources and winged patches remain traps. Studies that determine true adult and juvenile survivorship would be a valuable avenue of future research for understanding ecological traps.

Indigo Buntings in rectangular patches produced over 52% more fledglings per female than bunting pairs in winged patches. Low seasonal fecundity occurred in winged

patches despite the significant late-season increase in predation rates in rectangular patches that could have theoretically 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 can potentially impact all members of the population, since all females are theoretically breeding at this time. However, only a fraction of these females typically initiates a second brood. Even if predation pressure is relaxed later in the season, populations may not be able to compensate for nest losses because fewer females are reneating. 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 my 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 total successful nests were produced late in the season in winged than in rectangular patches. Fewer dominant individuals are typically produced in later broods (Garnet 1981, Arcese and Smith 1985) and subdominance has been shown to reduce post-fledging or winter survival (Kikkawa 1980, Baker et al. 1981, Garnet 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 nest success early in the season in both years of this study, males preferentially returned to winged patches. Thus, the oldest and most experienced individuals, who should be fledging the most young (Holmes et al. 1996), were actually producing fewer offspring than the younger and less experienced individuals in the 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 are 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 small 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 this type of habitat. However, anthropogenic edges that mimic historical vegetation structure but support large predator populations have become increasingly common in modern fragmented landscapes. Evolved, adaptive behaviors to historical habitats may now lead Indigo Buntings to mistakenly select poor quality habitat and then not recognize when dispersal is advantageous.

I recognize that my interpretation of these results relies on some critical assumptions. For instance, I did not know the age structure of females in this study system and cannot assure a similar response and age structure of females as males; however, 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, Nol and Smith 1987, Pärt 2001). In addition, I did not have banded females, but instead relied on nest abundance and timing to determine female abundance. Although this method is not as accurate as counting banded females, the placement and timing of most nests was generally predictable such that I could confidently assign most nests to a female. We also do not know the impacts of patch shape on adult fitness beyond the breeding season and have assumed the impacts on juvenile fitness. Selecting winged patches may be an adaptive decision if adult or juvenile fitness is somehow elevated by occupying this treatment. However, the fitness benefits to adults would have to outweigh the relatively low daily survival rates of eggs and nestlings, the consequent reduction in seasonal fecundity, as well as possibly poorer nestling 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, ecological 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. In addition, 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, Moorman et al. 2002). Brood parasites may exploit prominent perch points along edges to locate hosts (Brittingham and Temple 1983, Yahner 1987). Thus, in agricultural landscapes where parasitism is an additional source of mortality, and where edge-effects may be more severe, the effects of ecological traps may be amplified. This study also revealed 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 species than on double-brooded or relatively abundant species such as the Indigo Bunting. However, in years where low food supplies or other environmental factors prevent renesting for double-brooded species, trap effects may be equally severe. Future studies should incorporate season-long nest monitoring programs to accurately assess the impact of habitat choice on seasonal reproductive output. But perhaps most importantly, land managers and conservation biologists should work to understand and identify important behavioral mechanisms that might lead to ecological traps for a variety of species.

LITERATURE CITED

Arcese, P and J. N. M. Smith. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *Journal of Animal Ecology* **54**: 817-830.

Askins, R.A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology* **11**: 1-34.

Askins, R.A. 1998. Restoring forest disturbances to sustain populations of shrubland birds. *Restoration and Management Notes* **16**: 166-173.

Baker, M.C., C.S. Belcher, L.C. Deutsch, G.L. Sherman and D.B. Thompson. 1981. Foraging success in junco flocks and the effects of social hierarchy. *Animal Behaviour* **29**: 137-142.

Battin, James. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*. In press.

Blouin-Demers, G. and P.J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* **82**: 2882-2896.

Boal, C.W. and R.W. Mannan. 1999. Comparative breeding ecology of Cooper's hawks in urban and exurban areas of southeastern Arizona. *Journal of Wildlife Management* **63**: 77-84.

Brittingham, M.C. and S.A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* **33**: 31-35.

Carey, Michael and V. Nolan Jr. 1979. Population dynamics of indigo buntings and the evolution of avian polygyny. *Evolution*. **33**: 1180-1192.

Chasko, G.G. and E.J. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* **82**: 1-41.

Cody, M.L., editor. 1985. *Habitat selection in birds*. Academic Press, New York, New York, USA.

DeGraaf, R.D. and M. Yamasaki. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. *Forest Ecology and Management* **185**: 179-191.

Dias, P.C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* **11**: 326-330.

Donovan, T.M., F.R. Thompson III, and J. Faaborg. 1995. Reproductive success of

- migratory birds in habitat sources and sinks. *Conservation Biology* **9**: 1380-1395.
- Donovan, T.M. and F.R. Thompson III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications* **11**: 871-882.
- Dow, H. and S. Fredga. 1983. Breeding and natal dispersal of the goldeneye, *Bucephala clangula*. *Journal of Animal Ecology* **52**: 681-695.
- Durner, G.M. and J.E. Gates. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. *Journal of Wildlife Management* **57**: 812-826.
- Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, New York, New York, USA.
- Fitch, H.S. 1963. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia* **4**: 649-658.
- Flaspohler, D.J., S.A. Temple, and R.N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications* **11**: 32-46.
- Fretwell, S. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey, USA.
- Garnet, M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis* **123**: 31-41.
- Gates, J.E. and L.W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**: 871-883.
- Herlugson, C.J. 1981. Nest site selection in mountain bluebirds. *Condor* **83**: 252-255.
- Holmes, R.T., P.P. Marra, and T.W. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* **65**: 183-195.
- Hunter, W.C., D.A. Buehler, R.A. Canterbury, J.L. Confer, and P.B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* **29**: 440-455.
- Jaenike, J. and R.D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. *The American Naturalist* **137**: S67-S90.
- Johnson, R.G. and S.A. Temple. 1990. Nest predation and brood parasitism of tallgrass

- prairie birds. *Journal of Wildlife Management* **54**: 106-111.
- Kikkawa, J. 1980. Winter survival in relation to dominance classes among silvereyes *Zosterops lateralis chlorocephala* of Heron Island, Great Barrier Reef. *Ibis* **122**: 437-446.
- Kokko, H. and W.J. Sutherland. 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research* **3**: 537-551.
- Kristan, W.B. III. 2003. The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos* **103**: 457-468.
- Kroodsmas, R.L. 1984. Ecological factors associated with degree of edge effect in breeding birds. *Journal of Wildlife Management* **48**: 418-425.
- Martin, T.E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Proceedings of the National Academy of Science, USA* **85**: 2196-2199.
- Martin, T.E. and J.J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* **90**: 51-57.
- Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, D. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, Montana, USA.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**: 456-466.
- Moorman, C. E., D. C. Guynn Jr., and J. C. Kilgo. 2002. Hooded warbler nesting success adjacent to group-selection and clearcut edges in a southeastern bottomland forest. *Condor* **104**: 366-377.
- Morrison, S.A. and D.T. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia* **133**: 315-324.
- Mullin, S.J., R.J. Cooper, and W.H.N. Gutzke. 1998. The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*). III. Searching for different prey types in structurally varied habitats. *Canadian Journal of Zoology* **76**: 548-555.
- Nol, E. and J.N.M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology* **56**: 301-313.
- Orians, G.H. and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *The American Naturalist* **137**: S29-S49.

- Pärt, T. 2001. The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. *Animal Behaviour* **62**: 379-388.
- Paton, P.W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**: 17-26.
- Payne, R.B. 1989. Indigo Bunting. Pages 153-172 in I. Newton, editor. *Lifetime Reproduction in Birds*. Academic Press Inc, San Diego, USA.
- Payne, R. B. 1992. Indigo Bunting. No.4 in A. Poole, P. Stettenheim, F. Gill, editors. *The Birds of North America: Life Histories for the 21st Century*. Academy of Natural Sciences. Philadelphia, Pennsylvania, USA.
- Payne, R.B. and L.L. Payne. 1993. Breeding dispersal in indigo buntings: circumstances and consequences for breeding success and population structure. *Condor* **95**: 1-24.
- Peterjohn, B.G. 1994. The North American breeding bird survey. *Birding* **26**: 387-398.
- Pinkowski, B.C. 1979. Nest site selection in eastern bluebirds. *Condor* **81**: 435-436.
- Pulliam, R.H. 1988. Sources, sinks, and population regulation. *The American Naturalist* **132**: 652-661.
- Purcell, K.L. and J. Verner. 1998. Density and reproductive success of California towhees. *Conservation Biology* **12**: 442-450.
- Quinn, G.P. and M.J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- SAS Institute. 2000. *SAS user's guide*. Version 8.1. SAS Institute, Cary, North Carolina, USA.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2003. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2002*. Version 2003.1, USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schlaepfer, M.A., M.C. Runge, and P.W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* **17**: 474-480.
- Steele, B.B. 1993. Selection of foraging and nesting sites by black-throated blue warblers: their relative influence on habitat choice. *Condor* **95**: 568-579.
- Suarez, A.V., K.S. Pfennig, and S.K. Robinson. 1997. Nesting success of a disturbance-

dependent songbird on different kinds of edges. *Conservation Biology* **11**: 928-935.

Taber, W. and D.W. Johnston. 1968. *Passerina Cyanea*: Indigo Bunting. In O.L. Austin Jr.. Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. Smithsonian Institution Press, Washington, D.C. USA.

Temple, S.A. and J.R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* **2**: 340-347.

Thompson, F.R., III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. *Conservation Biology* **7**: 325-333.

Thompson, F.R., III. W. Dijk, and D.E. Burhans. 1999. Video identification of predators at songbird nests in old fields. *Auk* **116**: 259-264.

Thompson, F.R., III. S.K. Robinson, T.M. Donovan, J.R. Faaborg, and D.R. Whitehead and D.R. Larsen. 2000. Biogeographic, landscape, and local factors affecting cowbird abundance and host parasitism levels. Pages 271-279 in J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson and S.G. Sealy, editors. *Ecology and Management of Cowbirds and Their Hosts*. University of Texas Press, Austin TX.

Thompson, F.R. and D.E. Burhans. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *Journal of Wildlife Management* **67**: 408-416.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**: 893-901.

Vickery, P.D., M.L. Hunter, and J.V. Wells. 1992. Is density an indicator of breeding success? *Auk* **109**: 706-710.

Yahner, R.H. 1987. Use of even-aged stands by winter and spring bird communities. *Wilson Bulletin* **99**: 218-232.

Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. *Journal of Avian Biology* **32**: 38-46.

Table 1.1: Daily survival rates, total nest success and total seasonal fecundity (# fledglings produced/female/season) for breeding bird species in rectangular and winged patches. Daily survival rates and nest success are presented for both early and late nests.

Species/Group	Treatment	n	Daily Survival Rate	Total Nest	Daily Survival Rate	Total Nest	Seasonal Fecundity (SE)
			Early Nests (SE)	Success Early Nests ^b	Late Nests (SE)	Success Late Nests ^b	
Indigo Bunting	Rectangular	43	0.9763 (.006)	0.5898	0.9282 (.017)	0.1940	1.986 (.37)
	Winged	57	0.9415 (.018)	0.2653	0.9664 (.016)	0.4716	1.300 (.38)
Migrants ^a	Rectangular	18	0.9393 (.034)	0.2682	0.8867 (.064)	0.0801	2.860 (.93)
	Winged	13	0.9295 (.030)	0.2153	0.9197 (.049)	0.1721	2.000 (.79)
Residents	Rectangular	31	0.9173 (.013)	0.1372	0.9445 (.008)	0.2686	1.119 (.43)
	Winged	52	0.9178 (.036)	0.1390	0.9109 (.024)	0.1168	1.521 (.53)

a=Indigo Bunting not included

b=DSR based on nesting cycle of 22 days for Indigo Buntings, 21 days for migrants and 23 days for residents. Migrant and resident nesting durations were calculated as the average length of the included species nesting cycles obtained from Ehrlich et al. 1988

Table 1.2: Reproductive measures (\pm SE) for breeding bird species in winged and rectangular patches in the early and late nesting periods. No significant differences existed between treatments for any group or measure.

Species/Group	Treatment	Early Nesting Period				Late Nesting Period				Early vs. Late Nesting Periods	
		Clutch Size	n	# Fledge	n	Clutch Size	n	# Fledge	n	Clutch Size	Fledge
Indigo Bunting	Rectangular	3.31 \pm .12	21	2.90 \pm .24	20	2.60 \pm .19	15	1.33 \pm .33	3	F _{8,35} = 9.80; P < .01	F _{8,14} = 10.29; P < .01
	Winged	3.11 \pm .16	29	2.95 \pm .15	20	2.71 \pm .17	17	2.17 \pm .31	6	F _{9,44} = 4.25; P = .05	F _{7,18} = 5.91; P = .03
Migrants	Rectangular	3.50 \pm .19	12	3.00 \pm .27	8	3.50 \pm .29	4	4.00 \pm .	1	NS	NS
	Winged	3.67 \pm .17	9	3.00 \pm .71	4	2.75 \pm .25	4	2.00 \pm .	1	NS	NS
Residents	Rectangular	3.40 \pm .16	10	3.17 \pm .31	6	2.88 \pm .30	8	3.00 \pm .58	3	NS	NS
	Winged	3.33 \pm .15	27	3.08 \pm .21	13	2.81 \pm .13	21	1.88 \pm .30	8	F _{9,38} = 7.00; P = .01	F _{6,14} = 12.23; P < .01

Table 1.3: Mean (\pm SE) distance from the edge for breeding bird species in winged and rectangular patches compared to the expected distance from the edge.

	Winged	Rectangular	df	F	P
Indigo Buntings	20.1 \pm 1.13	26.4 \pm 1.46	9,124	10.87	0.001
Migrants	14.6 \pm 1.54	25.8 \pm 2.51	9,29	11.00	< 0.01
Residents	21.5 \pm 1.46	24.8 \pm 2.76	9,95	3.58	0.06
Expected Distance	19.3	28.6			

Table 1.4: Patch-level vegetation in edge and center plots for winged and rectangular patches. The first two P-values contrast edge and center plots within a treatment, while the final two P-values contrast edge plots and center plots between treatments. Italicized numbers were significant before Bonferroni correction. No significant differences exist when edge and center plots are combined.

Vegetation Variable	Winged			Rectangular			Winged vs. Rectangular	
	Edge (n=239)	Center (n=132)	P	Edge (n=277)	Center (n=146)	P	P (Edge[n=516])	P (Center[n=278])
Small Stems (<1m)	3.3 ± .27	4.1 ± .39	0.12	3.2 ± .21	3.9 ± .38	0.09	0.69	0.98
			<i>F_{7,363} = 2.58</i>			<i>F_{8,414} = 2.83</i>	<i>F_{8,507} = 0.16</i>	<i>F_{8,269} = 0.00</i>
Medium Stems (1.1-3m)	6.0 ± .47	7.4 ± .70	0.07	6.7 ± .65	6.8 ± .57	0.98	1.00	0.06
			<i>F_{7,363} = 3.36</i>			<i>F_{8,414} = 0.00</i>	<i>F_{8,507} = 0.00</i>	<i>F_{8,269} = 3.51</i>
Tall Stems (>3m)	0.15 ± .04	.04 ± .04	0.08	0.1 ± .03	0.2 ± .08	0.08	0.14	0.75
			<i>F_{7,363} = 3.00</i>			<i>F_{8,414} = 3.12</i>	<i>F_{8,507} = 2.22</i>	<i>F_{8,269} = 0.10</i>
Total Stems	9.5 ± .56	11.5 ± .84	0.03	10.0 ± .68	10.8 ± .67	0.48	0.81	0.11
			<i>F_{7,363} = 4.91</i>			<i>F_{8,414} = 0.51</i>	<i>F_{8,507} = 0.06</i>	<i>F_{8,269} = 2.64</i>

Table 1.5: The average amount of time spent at and type of food items brought to (\pm SE) the nest by female Indigo Buntings in winged and rectangular patches.

	Winged (n=26)	Rectangular (n=17)	F	df	P
Average time (min) brooding/shading/hour	5.11 \pm 1.45	4.28 \pm .98	0.69	9,33	0.41
Average time (min) at nest/hour	9.11 \pm 1.45	9.15 \pm .85	0.13	9,33	0.72
Average # trips to nest/hour	5.42 \pm .42	5.93 \pm .72	1.18	9,33	0.29
Average # trips/nestling	1.94 \pm .13	2.23 \pm .25	1.01	9,33	0.32
# small prey/hour/nestling	0.26 \pm .05	0.47 \pm .16	0.86	9,33	0.36
# medium prey/hour/nestling	0.68 \pm .07	1.20 \pm .15	14.15	9,33	0.001
# large prey/hour/nestling	0.47 \pm .07	0.32 \pm .06	2.00	9,33	0.17
Total # prey items/hour/nestling	1.91 \pm .13	2.28 \pm .23	1.67	9,33	0.21
Average Nestling Weights 2002	4.89 \pm .26	5.99 \pm .43	8.82	7,10	0.02
Average Nestling Weights 2003	7.08 \pm .35	7.65 \pm .49	0.19	8,30	0.66
Average Pooled Nestling Weights	6.16 \pm .39	7.00 \pm .32	0.82	9,33	0.82

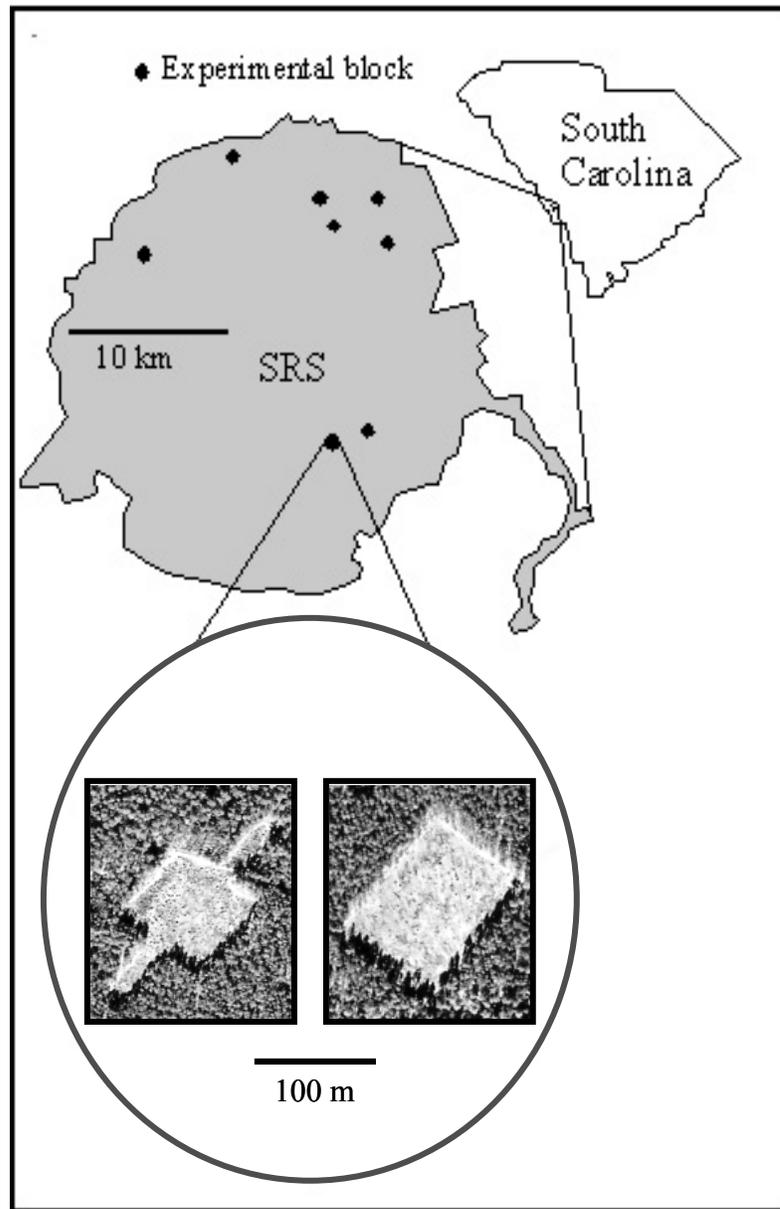


Figure 1.1: The location of the Savannah River Site (SRS) and the eight experimental blocks within SRS. The inset shows an infrared aerial photograph of the two different patch shapes within each block.

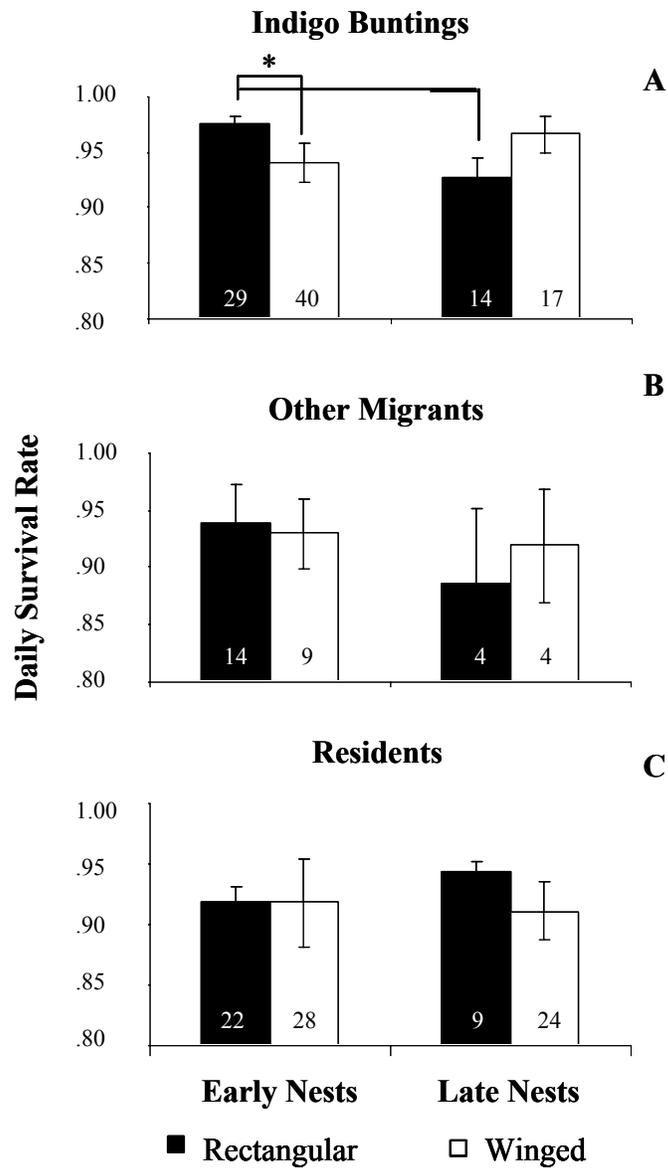


Figure 1.2: Daily survival rates for early and late A) Indigo Bunting, B) other migrant, and C) resident nests in rectangular and winged patches. Numbers at the base of each bar indicate sample sizes. * $P < 0.05$.

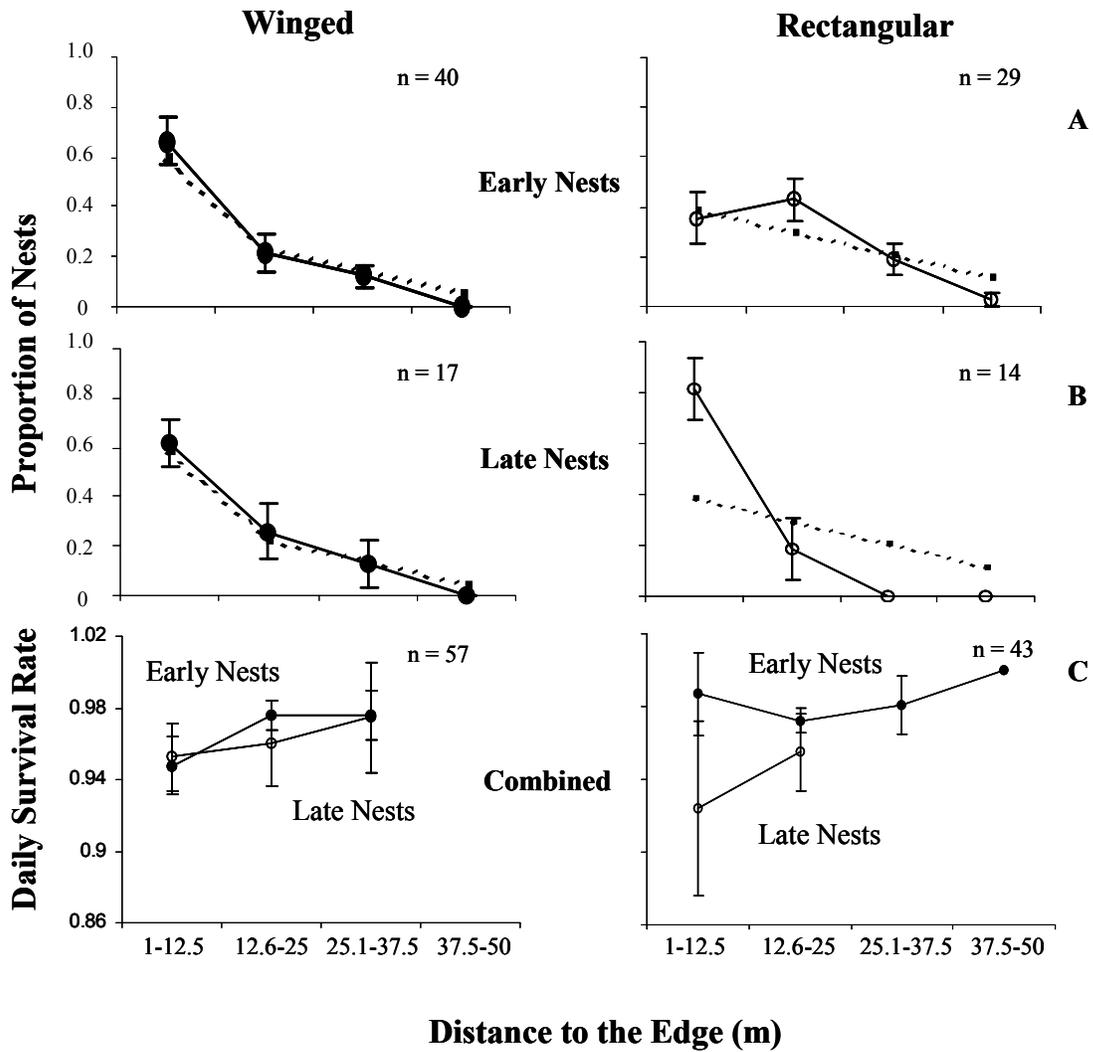


Figure 1.3: A,B) The proportion (\pm SE) of A) early and B) late Indigo Bunting nests and C) corresponding daily survival rates (\pm SE) at increasing distances from the edge. The dotted lines in A and B represent the proportion of available habitat in each distance category.

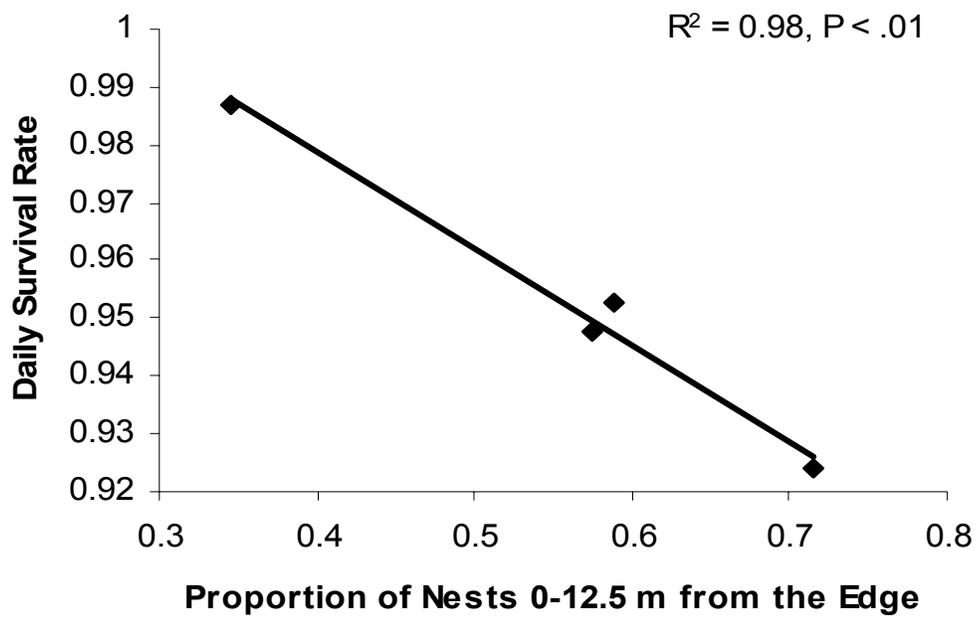


Figure 1.4: Daily survival rates as a function of the proportion of nests 0-12.5 meters from the edge across nesting periods and treatments. No relationship exists beyond 12.5 meters from the edge.

CHAPTER 2:

**THE EFFECTS OF CONSERVATION CORRIDORS ON THE REPRODUCTIVE
SUCCESS OF THE INDIGO BUNTING**

ABSTRACT

Conservation corridors have become a popular strategy to preserve biodiversity and promote gene flow in fragmented landscapes. Corridor effectiveness has been bolstered by the fact that no empirical field studies have shown negative effects on populations or communities. In this study, I tested the hypothesis that corridors increase nest predation in connected habitat fragments relative to unconnected fragments. I evaluated this hypothesis in a large-scale experimental system of small open-habitat fragments that varied in shape and connectivity. My results show that corridors increased nest predation rates relative to unconnected fragments with lower edge:area ratios. Nest predation rates were similar between connected patches and unconnected patches with higher edge:area ratios. This suggests that the increase in predator activity is largely attributable to edge effects incurred through the addition of a corridor. However, qualitative evidence suggests that corridors may further increase predator activity beyond the effects of edge by providing connectivity between suitable foraging habitats. This is the first field study to empirically demonstrate that corridors can negatively impact animal populations in connected fragments.

INTRODUCTION

Conservation corridors have been widely promoted as an effective way to preserve biological diversity and maintain population stability in fragmented landscapes (Rosenberg et al. 1997). Corridors achieve this goal by promoting immigration between otherwise isolated habitat fragments (Wilson and Willis 1975). Movement between isolated fragments can theoretically ‘rescue’ threatened populations from extinction risk (Brown and Kodric Brown 1977) by increasing gene flow, which reduces inbreeding and genetic drift. To date, empirical evidence for the usefulness of corridors is largely positive. Numerous studies have reported increased movement rates between, or abundance within, connected habitat fragments for a wide range of animal species (Fahrig and Merriam 1985, La Polla and Barrett 1993, Dunning et al. 1995, Haas 1995, Sutcliffe and Thomas 1996, Bier and Noss 1998, Haddad 1999, Haddad and Baum 1999, Tewksbury et al. 2002, Haddad et al. 2003). Others have demonstrated that corridors can maintain genetic exchange between connected habitat fragments (Aars and Ims 1999, Hale et al. 2001, Mech and Hallett 2001) and stabilize population structure (Mansergh and Scotts 1989, Gonzalez 1998). These results provide convincing evidence that corridors can promote the long-term viability of threatened populations.

Although evidence suggests that corridors generally promote stability among animal populations, corridors may also have unintended and harmful conservation consequences. For example, corridors may influence predator-prey interactions by facilitating the movement or efficiency of predators (Simberloff and Cox 1987). This idea is supported in microcosm experiments, in which predators more efficiently eradicated prey in connected than in isolated systems (Burkey 1997) and generally persisted longer in highly connected systems (Holyoak 2000). At the landscape level, Brinkerhoff et al. (*in review*) showed that corridors and simulated predators interactively influenced the foraging behavior of small mammals. Similarly, Orrock et al. (2003) found that corridors increased the foraging activity of mammalian seed predators, and thus, seed predation. Therefore, corridors can affect predator-prey dynamics and lead to negative effects on some species, but these effects and the mechanisms leading to them remain poorly understood.

In this study, I tested the effects of corridors on the reproductive success of breeding birds in an experimental system of small (~1.3 ha) early-successional habitat fragments that differed in shape and connectivity. Although corridors were unlikely to influence avian responses (dispersal, abundance) at this scale, they may influence predator responses, and thus the risk of nest predation through edge effects and predator movement patterns. Nest predation is the primary determinant of reproductive success for birds (Ricklefs 1969, Martin 1992) and some researchers have shown that corridors can influence the diversity or abundance of the predator community, which can increase nest predation rates (Ambuel and Temple 1983, Vander-Haegen and Degraaf 1996). Shifts in the predator community may be due to habitat edges that increase the abundance of generalist mammalian and avian predators or of edge-specialist reptiles, such as snakes (Blouin-Demers and Weatherhead 2001), associated with fragmented landscapes. Indeed, nest predation rates have been shown to increase with proximity to edges for many species (reviewed in Paton 1994). Corridors may magnify the effects of edges on predator abundance and efficiency by not only providing more suitable habitat for edge-specialist predators but also by providing connectivity between suitable foraging habitats. Consequently, this could have serious impacts on many breeding bird populations, particularly those that preferentially nest along edges.

Because of their influence on edges, corridors may also influence habitat selection behaviors of some bird species. Many disturbance-dependent bird species are attracted to the structural heterogeneity found near habitat edges because it mimics historical breeding habitat (Askins 1993, Hunter et al. 2001). These species, in particular, may be susceptible to the potentially adverse effects of corridors. However, no studies have directly tested the effects of corridors on the reproductive success of birds (but see Vander-Haegen and DeGraaf 1996). Behavioral studies have demonstrated that birds use corridors as conduits for dispersal and foraging (Haas 1995, Machtans et al. 1996, Schmiegelow et al. 1997, Tewksbury et al. 2002, Haddad et al. 2003) and that some corridors can serve as breeding habitat (Bentley and Catterall 1997, Hannon et al. 2002). Although demonstrating that corridors facilitate movement or provide habitat is critical to understanding the long-term effects of corridors, simply knowing that birds use corridors says little about the actual

suitability of connected fragments for reproduction. Measures of reproductive success are a more important metric for understanding the full impact of corridors on population growth and sustainability.

In this study, I evaluated the effects of corridors on the reproductive success of the Indigo Bunting (*Passerina cyanea*) and other disturbance-dependent bird species. I tested the hypothesis that corridors would increase predation rates in connected patches relative to similar-sized unconnected patches. This study expands on and incorporates data from a previous study conducted within this system that focused specifically on the effects of patch shape on the reproductive success of Indigo Buntings (Weldon and Haddad *in review*). I will use the results from this previous study to separate the relative influence of corridors from the influence of edge effects on avian reproductive success.

METHODS

Study Site

This study was conducted within 8 experimentally replicated landscapes, or blocks, at the Savannah River Site, near Aiken, SC, between May and August of 2002 and 2003 (Figure 2.1). The design and layout of experimental blocks are detailed in Weldon and Haddad (*in review*). Each block was composed of 3 same-sized (1.375 ha) unconnected early-successional patches that varied in shape between winged and rectangular forms and 2 connected patches that were joined by a 150 x 25 m corridor. Connected patches were slightly smaller in area than unconnected patches (1.188 ha) and consisted of a 1-ha square plus half the length of the corridor. Because all patches were of similar area but differed in shape, the amount of edge varied across treatments. Edge to area ratios increased from rectangular (.034), to connected (.044), to winged patches (.051), a 50% increase from the simplest to the most complex treatment. This unique design allowed me to separate the relative impacts of corridors from effects of edge on avian reproductive success.

Study Species

Indigo Buntings (*Passerina cyanea*) served as my focal species. Buntings are Neotropical migrant birds known as a traditional ‘edge’ species, often occupying shrub habitats along anthropogenic edges and forest canopy gaps. Females build small open-cup

nests in saplings or shrubs approximately 1 m from the ground and typically perform all incubation and brood activities (Payne 1992). Indigo buntings are the most common avian species in my experimental system during the breeding season and occupy sites at abundances from 1-3 breeding pairs per patch. Buntings have shown significant declines in many parts of the eastern United States over the past 37 years (Sauer et al. 2003) and their tendency to select edge habitat and build small open-cup nests makes them good models for other Neotropical migrant edge species that may be declining due to anthropogenic landscape alterations.

In addition to my focal species, I also tested how patch shape and connectivity affected the reproductive success of other breeding birds in this system and whether the responses of residents differed from those of migrant species. These species included the resident Brown Thrasher (*Toxostoma rufum*), Eastern Towhee (*Pipilo erythrophthalmus*) and Northern Cardinal (*Cardinalis cardinalis*), and the migrant Prairie Warbler (*Dendroica discolor*) and Blue Grosbeak (*Guiraca caerulea*). All resident species generally build larger and more coarsely constructed nests often placed near the center of dense shrubs (personal observation). Both migrant species build open-cup nests similar in form and placement to those of the Indigo Bunting.

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 May 5 and June 15, 2002 and 2003, I determined the abundance of territorial males occupying each treatment by mapping the territories of singing males in 20-minute intervals over the course of 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. Mapping was conducted only in fair weather starting shortly before sunrise and terminating before 0830. Only males that were seen or heard inside the patch were included in the counts. Because detectability of nests was high (>85% based on the number of males/patch) and the territories generally well-defined, the total number of breeding females was determined by counting the maximum number of simultaneously active nests in each patch. I did not obtain adult abundance estimates for non-focal bird species.

Average male and female abundance estimates were tested for normality and analysis of variance (ANOVA) was used to test for differences among treatments. I divided all non-focal species into resident and migrant categories and conducted separate analyses for each group. Square root transformations were used when necessary to normalize the data, which were then analyzed for treatment effects using ANOVA with year as a repeated measure.

Reproductive Success

I systematically searched each patch for nests of all species on a 4-d rotating cycle by walking transects between evenly spaced (25 m) PVC markers. Winged and rectangular patches were searched in both 2002 and 2003, while connected patches were only searched in 2003. For Indigo Buntings, the maximum number of possible nests per patch was determined as the total number of singing males per patch. I used a combination of behavioral cues and searches of potential nest substrates to locate nests. Each patch was searched for approximately one hour and care was taken to alter courses among visits to reduce the creation of trails that might be used by predators. All nests were marked with flagging tape at least 10 m from the nest and active nests were monitored every 2 - 4 days to determine nest fate. Successful nests were defined as any nest that fledged at least one host young. Predation was assumed if the contents of the nest disappeared before the estimated fledge date.

To examine temporal differences in nest survival for all species, I distinguished the ‘early’ from the ‘late’ nesting period, which corresponded closely to the first and second brood of the Indigo Bunting. I was able to track and determine brood status for 90% of Indigo Bunting nests, and used the timing of these nest attempts to assign brood status to any unknown nests, such that nests initiated before June 15th belonged to brood one (early nesting period) and those initiated after this date to brood two (late nesting period). For consistency and to adjust for temporal variation in predation pressure, I used this definition for all other species as well, although it may not accurately describe true nesting cycles.

I used the standard Mayfield method (1975) to calculate daily survival rates (DSR) by nesting period for each treatment within a block for Indigo Buntings and migrant and resident groups. Daily survival rates did not differ between years for Indigo Buntings so all nests were pooled for analyses. Migrant and resident species were pooled across years due to

sample size limitations. I used ANOVA to compare daily survival rates among treatments. Analysis of variance calculates an error term from the variation among blocks, unlike conventional Z-tests, which calculate error terms from variation within pooled samples. By controlling for block effects, I was better able to detect true differences in survival rates between treatments. In each analysis, I weighted each treatment within a block by the number of representative nests to adjust for estimates based on small sample sizes. I calculated total nest success (TNS) for each nesting period with the following equation:

$$\text{TNS} = \text{DSR}^n \quad (1)$$

where n equals the total length of the nesting period. For resident and migrant groups, I set n equal to the average nesting period length for all species within a group according to Ehrlich et al. (1988).

I estimated total seasonal fecundity in winged and rectangular patches by calculating the total number of fledglings produced in each treatment within a block and dividing that number by the corresponding number of breeding females in each treatment within a block. I tested for differences in fecundity between treatments using ANOVA. The total clutch size, proportion of eggs hatched and number of young fledged per successful nest were compared using ANOVA.

Vegetation and Habitat Covariates

The distance a nest is located from the edge can affect its risk of predation and this distance may vary with patch shape. To test this, I measured the distance to the two closest edges of all nests known to have contained eggs. I then averaged these distances to quantify the potential effect of edge on nests. The average was used rather than the distance to the first edge alone because the small size of each patch may allow more than one edge to influence nest success. I compared these averages among treatments for each species and migratory group using ANOVA. Because winged patches inherently contain more edge habitat than rectangular patches, I also determined whether nests were closer to the edge than would be expected by habitat availability. I calculated the average distance of all grid cells in a patch to their nearest two edges and then compared this value to the observed placement

of nests by analyzing overlap in 95% confidence intervals. Years did not differ for any species group so only pooled results are presented.

I compared vegetation among treatments in 2002 using existing 3x3 m vegetation plots from an unrelated project (Damschen, unpublished methods). Vegetation plots had a standardized distribution within patches with 22 plots located along edges (< 25 m from the edge) and 12 located within the patch interior (> 25 m from the edge). The total area surveyed equaled 23% of each patch. Within each plot I recorded the total number of woody stems in each of three height classes (50 cm-1 m, 1.1-3 m, >3 m). Woody stems below 50 cm in height were not included in the stem counts. All plots were measured within a 2-week period in mid-July, 2002. Vegetation variables were compared among treatments using ANOVA. All statistical analyses were performed using SAS version 8.1 (SAS Institute 2000).

RESULTS

Breeding Bird Abundance

The abundance of male and female Indigo Buntings did not differ among treatments. Similarly, total nest abundance did not differ among treatments for any species or for collective resident or migrant groups.

Reproductive Success

Indigo Buntings: I found 139 Indigo Bunting nests over the course of two years. Predation was the primary cause of nest failure (88.8%), followed by nest abandonment (7.4%) and cowbird parasitism (3.8%). Abandoned nests (n = 6) were not included in nest success analyses. Daily survival rates were significantly lower in connected patches than in rectangular patches in the early nesting period ($F_{9,11} = 12.23$, $P < 0.01$) but did not differ between connected and winged patches. Daily survival rates did not differ among treatments in the late nesting period (Table 2.1, Figure 2.2). Seasonal fecundity estimates were significantly higher in rectangular patches than in connected patches ($F_{9,13} = 6.98$, $P = 0.02$, Table 2.1) but did not differ between connected and winged patches. The average clutch size and proportion of eggs hatched did not differ among treatments (Table 2.2). Clutch size, and thus the number of fledglings produced per successful nest, dropped in the late nesting period for all treatments. Females in connected patches fledged significantly more young per

successful nest than females in winged ($F_{13,44} = 5.65$, $P = 0.02$) or rectangular ($F_{13,44} = 4.12$, $P = 0.049$) patches.

Other Species: I used 109 resident nests (Brown Thrasher [$n = 35$], Eastern Towhee [$n = 50$], Northern Cardinal [$n = 24$]), and 40 migrant nests (Blue Grosbeak [$n = 23$], Prairie Warbler [$n = 17$]) in nest success analyses. Daily survival rates did not differ among treatments for either group nor did they differ between nesting periods for migrant species in any treatment, although daily survival rates were always lowest in connected patches (Table 2.1, Figure 2.2). Resident species experienced a significant drop in nest success between the early and late nesting period in connected patches ($F_{7,4} = 8.76$, $P = 0.04$), but nest success did not differ between nesting periods in winged or rectangular patches.

Nest Placement

Indigo Buntings: Indigo Buntings nested closer to the edge in connected ($F_{9,124} = 4.89$, $P = 0.03$) than in rectangular patches, but not significantly closer than expected based on habitat availability (Table 2.3). Nest placement did not differ between connected and winged patches. Nest proportion near the edge was the primary determinant of nest success. In the first 12.5 m from the edge, daily survival rates exhibited a strong negative correlation with the proportion of nests across treatments and nesting periods within this zone (Figure 2.3). No relationship existed beyond 12.5 m from the edge.

Other Species: As a group, migrants (excluding Indigo Buntings) nested closer to the edge in winged than in connected patches ($F_{9,29} = 8.33$, $P < 0.01$) but did not differ in nest placement between rectangular and connected patches (Table 2.3). Residents collectively showed no differences in nest placement among treatments. Neither group nested closer to the edge than expected (Table 2.3).

Vegetation

Within winged patches, center vegetation plots contained more total woody stems than edge plots. Winged center plots also contained more medium (1-3 m) and total stems than center plots of connected patches. However, when edge and center plots were combined, patch level vegetation did not differ among treatments for any measure (Table 2.4).

DISCUSSION

The results of this study provide support for the hypothesis that corridors increase nest predation rates in connected patches relative to unconnected patches, but indicate that the magnitude of the difference may depend on the shape of the unconnected patches. Unconnected patches with higher edge:area ratios (winged patches) experienced similar seasonal fecundity as connected patches, but those with lower edge:area ratios (rectangular patches) experienced significantly higher seasonal fecundity. Therefore, high nest predation rates in connected patches were primarily attributable to a consequent increase in the relative amount of edge per unit area with the construction of a corridor.

Corridors, Edges and Nest Predation

For the purposes of this discussion, I focus only on the differences between connected patches and each of winged and rectangular patches and will not address specific differences between the two unconnected treatments. A full discussion that addresses the influences of patch shape, specifically, on nest success is contained in a previous study (Weldon and Haddad *in review*).

Corridors significantly influenced the nest success of Indigo Buntings in connected patches relative to unconnected patches. Buntings nesting in connected patches experienced higher predation rates and produced significantly fewer fledglings per female than buntings nesting in unconnected rectangular patches. This result is consistent with microcosm studies that demonstrated increased predator efficiency in connected systems relative to unconnected systems (Burkey 1997, Holyoak 2000, Holyoak and Lawler 1996). Conversely, nest success and total seasonal fecundity did not differ between connected and winged patches, likely because these treatments contained similar amounts of edge. The significantly lower nest success in edgy, winged patches compared to simple, rectangular patches early in the season also supports this assumption. These results demonstrate that corridors mainly facilitate predator activity through the addition of edges, which provide profitable foraging habitat for edge-specialist predators. Similar-sized patches that differ in shape also differ in the proportion of total habitat near the edge. More complicated shapes, such as winged and connected patches, have relatively high proportions of habitat near the edge and consequently contain more nests near the edge, which can negatively influence nest success (Weldon and

Haddad *in review*). Indeed, in this study, daily survival rates were significantly and negatively related to nest proportion near the edge across nesting periods and treatments. Together, these results support the idea that edge effects are the primary determinants of reproductive success for Indigo Buntings in this system, regardless of whether or not patches are connected by a corridor.

Although edges appear to be the primary influence on predation rates, corridors may also influence predation by increasing connectivity for foraging predators. Total seasonal fecundity in connected patches was 19% lower than in winged patches, despite the greater total area and higher edge:area ratio (16% greater) of winged patches. If predators were responding only to the amount of edge in each patch, predation rates should be higher in winged than in connected patches because the amount of suitable habitat for predators in winged patches was higher. Instead, connected patches supported the highest predation rates, suggesting that corridors may enhance predator abundance or efficiency beyond that of simple edge effects. Predator abundance may increase if predators use edges as habitat (e.g. snakes, Blouin-Demers and Weatherhead 2001) or if corridors function as ‘drift-fences’ in the landscape, intercepting dispersing predators and funneling them into connected patches (Haddad and Baum 1999). Likewise, predation efficiency may increase within connected patches because corridors provide convenient links between foraging habitats. In addition, both residents and other migrants generally experienced their lowest daily survival rates in connected patches across nesting periods, although small sample sizes prevented conclusive determination of corridor effects. These patterns suggest that corridors may magnify the effects of edge by facilitating predator activity in connected patches.

The Future of Corridors

This study provides the first landscape-scale empirical evidence that corridors can increase predator activity and disproportionately decrease the reproductive success of prey populations occupying connected habitat fragments. The previous lack of evidence for negative effects of corridors may largely be due to the single-species focus of most corridor studies. Focusing studies on selectively chosen target species may bias evidence toward largely positive results (Haddad et al. 2003), particularly if only movement or abundance data are collected and if studies are short-term. Moreover, ignoring the often complex

interactions among diverse suites of species may be dangerous, particularly if corridors disproportionately impact some species but not others (Orrock et al. 2003). For example, in this study, corridors did not influence avian abundance, but did alter the foraging efficiency of important nest predators, which may have a particularly severe impact on disturbance-dependent bird species. Historical habitat for these species may have consisted of short-lived and often scattered natural disturbances within forested habitats (Suarez et al. 1997). These birds may have depended on the ephemeral nature and isolation of natural disturbances as an escape from predators. Corridors may disrupt this balance by not only providing a permanent link between isolated habitats where predation risk is often lower, but also by mimicking historical cues that these birds use to select breeding habitat. Corridors may then function as ecological traps by attracting birds into riskier habitats (Gates and Gysel 1978, Weldon and Haddad *in review*), which could have serious implications for some avian populations.

This study indicates that corridor design is an important component of management plans for preserving target species, especially if corridors are used as habitat as well as dispersal. Land managers may diminish the harmful effects of corridors for disturbance-dependent species if transitions between habitat types are gradual rather than abrupt, as is characteristic of many forest management practices today. Gradual edges more closely mimic natural edges and may provide greater structural complexity that may increase nest concealment and reduce predator efficiency (Ratti and Reese 1988, Seitz and Zegers 1993, Suarez et al. 1997). Gradual edges may also decrease density-dependent predation by allowing birds to spread out within their preferred habitat. In addition, although this study dealt only with edge-nesting bird species, this design would also benefit habitat interior species. Harmful edge effects may extend well beyond the field-forest edge (Paton 1994) and could affect nest success for interior species as well, particularly if the majority of the corridor encompasses edge habitat. Land managers could avoid strong edge effects for interior bird species by providing gradual edges and constructing corridors that are wide enough to encompass less-risky interior habitat (Hannon et al. 2002).

Corridors show promising long-term conservation benefits if used appropriately (Beier and Noss 1998). Determining the true efficacy of corridors will require a more

complete understanding of how different types of corridors influence organisms from a community approach. To accomplish this, more studies are needed that not only measure movement or abundance for multiple species, but also investigate species interactions, survival, reproductive success, or habitat occupancy over the long-term, as some have already done (Bentley and Catterall 1997, Orrock et al. 2003, Brinkerhoff et al. *in review*). These studies will allow land managers to construct corridors that minimize negative consequences and maximize conservation benefits to entire communities.

LITERATURE CITED

- Aars, J. and R.A. Ims. 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology* **80**: 1648-1655.
- Ambuel, B. and S.A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**: 1057-1068.
- Askins, R.A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology*. Plenum Press, New York, pp. 1-34.
- Beier, P. and R.F. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* **12**: 1241-1252.
- Bentley, J.M. and C.P. Catterall. 1997. The use of bushland, corridors, and linear remnants by birds in southeastern Queensland, Australia. *Conservation Biology* **11**: 1173-1189.
- Blouin-Demers, G. and P.J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* **82**: 2882-2896.
- Brinkerhoff, R.J., N.M. Haddad, and J.L. Orrock. *in review*. Responses of prey to predator cues in a fragmented landscape with corridors.
- Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**: 445-449.
- Burkey, T.V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria and protozoa communities as model ecosystems. *The American Naturalist* **150**: 568-591.
- Dunning, J.B., R. Borgella Jr., K. Clements, and G.K. Meffe. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* **9**: 542-550.
- Ehrlich, P. R., D. S. Dobkin and D. Wheye. 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, New York, New York, USA.
- Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* **66**: 1762-1768.
- Gates, J.E. and L.W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* **59**: 871-883.

- Gonzalez, A., J.H. Lawton, F.S. Gilbert, T.M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* **281**: 2045-2047.
- Haas, C.A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology* **9**: 845-854.
- Haddad, N.M. 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* **9**: 612-622.
- Haddad, N.M. and K.A. Baum. 1999. An experimental test of corridor effects on butterfly densities. *Ecological Applications* **9**: 623-633.
- Haddad, N.M., D.R. Bowne, A. Cunningham, B.J. Danielson, D.J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* **84**: 609-615.
- Hale, M.L., P.W.W. Lurz, M.D.F. Shirley, S. Rushton, R.M. Fuller, and K. Wolff. 2001. Impact of landscape management on the genetic structure of red squirrel populations. *Science* **293**: 2246-2199.
- Hannon, S.J., C.A. Paszkowski, S. Boutin, J. DeGroot, S.E. Macdonald, M. Wheatley and B.R. Eaton. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. *Canadian Journal of Forest Research* **32**: 1784-1800.
- Holyoak, M. 2000. Habitat patch arrangement and metapopulation persistence of predators and prey. *The American Naturalist* **156**: 378-389.
- Holyoak, M. and S.P. Lawler. 1996. The role of dispersal in predator-prey metapopulation dynamics. *Journal of Animal Ecology* **65**: 640-652.
- Hunter, W.C., D.A. Buehler, R.A. Canterbury, J.L. Confer, and P.B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* **29**: 440-455.
- LaPolla, V.N. and G.W. Barrett. 1993. Effects of corridor width and presence on the population dynamics of the meadow vole. *Landscape Ecology* **8**: 25-37.
- Machtans, C.S., M. Villard, and S.J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* **10**: 1366-1379.
- Mansergh, I.M. and D.J. Scotts. 1989. Habitat continuity and social organization of mountain pygmy-possum restored by tunnel. *Journal of Wildlife Management* **53**: 701-707.

- Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 in J. M. Hagan & D. W. Johnston, editors. Ecology and conservation of neotropical migrants. Smithsonian Institution Press, Washington, D.C., USA.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**: 456-466.
- Mech, S.G. and J.G. Hallett. 2001. Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* **15**: 467-474.
- Orrock, J.L., B.J. Danielson, M.J. Burns, and D.J. Levey. 2003. Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. *Ecology* **84**: 2589-2599.
- Paton, P.W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* **8**: 17-26.
- Payne, R. B. 1992. Indigo Bunting. No.4 in A. Poole, P. Stettenheim, F. Gill, editors. *The Birds of North America: Life Histories for the 21st Century*. Academy of Natural Sciences. Philadelphia, Pennsylvania, USA.
- Ratti, J.T. and K.P. Reese. 1988. Preliminary test of the ecological trap hypothesis. *Journal of Wildlife Management* **52**: 484-491.
- Ricklefs, Robert E. 1969. An analysis of nesting mortality in birds. 1969. *Smithsonian Contributions to Zoology* **9**.
- Rosenberg, D.K., B.R. Noon, and E.C. Meslow. 1997. Biological corridors: form, function, and efficacy. *Bioscience* **47**: 677-687.
- SAS Institute. 2000. SAS user's guide. Version 8.1. SAS Institute, Cary, North Carolina, USA.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2003. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2002*. Version 2003.1, USGS Patuxent Wildlife Research Center, Laurel, MD.
- Schmiegelow, F.K.A., C.S. Machtans, and S.J. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology* **78**: 1914-1932.
- Seitz, L.C. and D.A. Zegers. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. *The Condor* **95**: 297-304.

Simberloff, D. and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* **1**: 63-71.

Suarez, A.V., K.S. Pfennig, and S.K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conservation Biology* **11**: 928-935.

Sutcliffe, O.L. and C.D. Thomas. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology* **10**: 1359-1365.

Taber, W. and D.W. Johnston. 1968. *Passerina Cyanea*: Indigo Bunting. In O.L. Austin Jr., Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. Smithsonian Institution Press, Washington, D.C. USA.

Tewksbury, J.J., D.J. Levey, N.M. Haddad, S. Sargent, J.L. Orrock, A. Weldon, B.J. Danielson, J. Brinkerhoff, E.I. Damschen and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings from the National Academy of Sciences* **99**: 12923-12926.

Vander Haegen, W.M. and R.M. DeGraaf. 1996. Predation on artificial nests in forested riparian buffer strips. *Journal of Wildlife Management* **60**: 542-550.

Weldon, A.J. and N.M. Haddad. The effects of patch shape on the indigo bunting: evidence for an ecological trap. In review.

Wilson, E.O. and E.O. Willis. 1975. Applied Biogeography. Pages 522-534 in M.L. Cody and J.M. Diamond, editors. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, USA.

Table 2.1. Daily survival rates, total nest success and total seasonal fecundity (# fledglings produced/female/season) for breeding bird species in rectangular, winged and connected patches. Daily survival rates are presented for early and late nesting periods.

Species/Group	Treatment	n	Daily Survival Rate		Total Nest		Seasonal Fecundity (SE)
			Early Nests (SE)	Success: Early Nests ^b	Late Nests (SE)	Success: Late Nests ^b	
Indigo Bunting	Rectangular	43	0.9763 (.006)	0.5898	0.9282 (.017)	0.1940	1.986 (.37)
	Winged	57	0.9415 (.018)	0.2653	0.9664 (.016)	0.4716	1.300 (.38)
	Connected	33	0.9451 (.011)	0.2887	0.8710 (.050)	0.0479	1.094 (.43)
Migrants^a	Rectangular	18	0.9393 (.034)	0.2682	0.8867 (.064)	0.0801	2.860 (.93)
	Winged	13	0.9295 (.030)	0.2153	0.9197 (.049)	0.1721	2.000 (.79)
	Connected	11	0.8804 (.067)	0.0690	0.8801 (.067)	0.0684	0.917 (.66)
Residents	Rectangular	31	0.9173 (.013)	0.1372	0.9445 (.008)	0.2686	1.119 (.43)
	Winged	52	0.9178 (.036)	0.1390	0.9109 (.024)	0.1168	1.521 (.53)
	Connected	26	0.9632 (.026)	0.4217	0.8266 (.064)	0.0125	1.686 (.80)

Table 2.2. Reproductive measures (\pm SE) for all species groups in rectangular, winged, and connected patches in the early and late nesting periods. No significant differences existed among treatments for any group or measure.

Species/Group	Treatment	Early Nesting Period			Late Nesting Period				
		Clutch Size	n	# Fledge	n	Clutch Size	n	# Fledge	n
Indigo Bunting	Rectangular	3.31 \pm .12	21	2.90 \pm .24	20	2.60 \pm .19	15	1.33 \pm .33	3
	Winged	3.11 \pm .16	29	2.95 \pm .15	20	2.71 \pm .17	17	2.17 \pm .31	6
	Connected	3.29 \pm .18	21	3.86 \pm .14	20	2.67 \pm .22	12	2.50 \pm .50	2
Migrants	Rectangular	3.50 \pm .19	12	3.00 \pm .27	8	3.50 \pm .29	4	4.00 \pm .	1
	Winged	3.67 \pm .17	9	3.00 \pm .71	4	2.75 \pm .25	4	2.00 \pm .	1
	Connected	3.67 \pm .21	6	3.25 \pm .48	4	3.00 \pm .58	3	.	0
Residents	Rectangular	3.40 \pm .16	10	3.17 \pm .31	6	2.88 \pm .30	8	3.00 \pm .58	3
	Winged	3.33 \pm .15	27	3.08 \pm .21	13	2.81 \pm .13	21	1.88 \pm .30	8
	Connected	3.40 \pm .16	10	2.80 \pm .58	5	3.15 \pm .15	13	3.20 \pm .37	5

Table 2.3. Mean (\pm SE) distance from the edge for breeding bird species in rectangular, winged and connected patches compared to the expected distance from the edge in each treatment.

	Winged	Rectangular	Connected
Indigo Buntings	20.1 \pm 1.13	26.4 \pm 1.46	23.8 \pm 1.98
Migrants	14.6 \pm 1.54	25.8 \pm 2.51	23.6 \pm 1.66
Residents	21.5 \pm 1.46	24.8 \pm 2.76	19.8 \pm 1.82
Expected Distance	19.3	28.6	21.4

Table 2.4. Mean (\pm SE) patch-level vegetation in winged, rectangular and connected patches. No differences were significant at the $\alpha = .05$ level among treatments for any variable.

Vegetation Variable	Rectangular (n=423)	Winged (n=371)	Connected (n=486)
Small Stems (<1m)	3.4 \pm .19	3.6 \pm .22	3.8 \pm .20
Medium Stems (1.1-3m)	6.8 \pm .47	6.5 \pm .39	5.9 \pm .31
Tall Stems (>3m)	.11 \pm .03	.1 \pm .03	.09 \pm .02
Total Stems	10.3 \pm .50	10.2 \pm .47	9.8 \pm .37

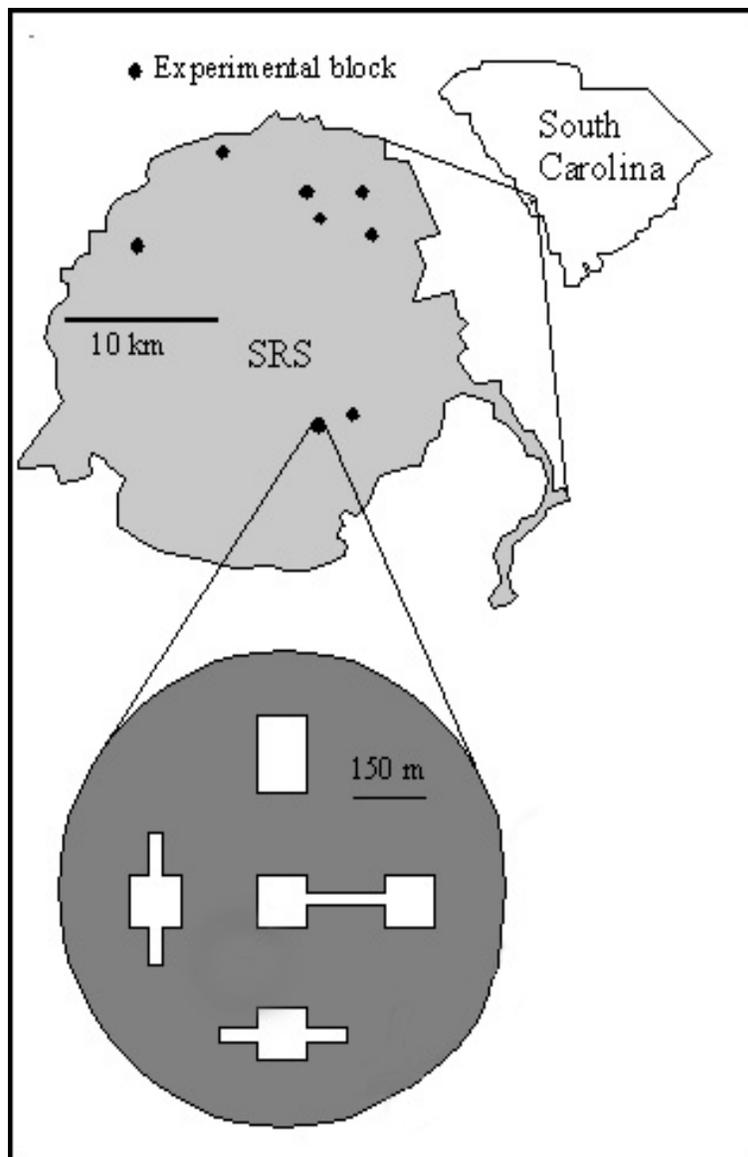


Figure 2.1. The location of the Savannah River Site (SRS) and the eight experimental blocks within SRS.

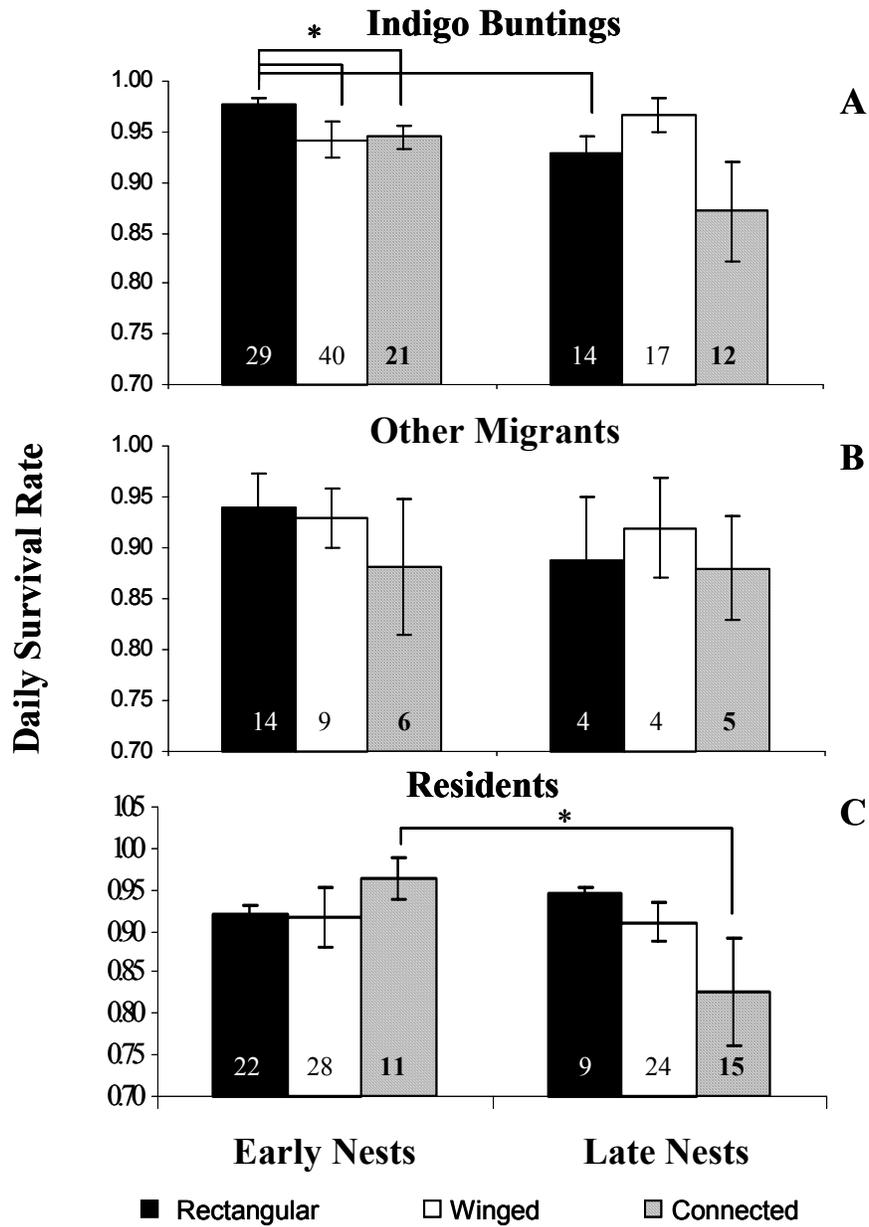


Figure 2.2. Daily survival rates (\pm SE) for early and late A) Indigo Bunting, B) other migrant and C) resident nests in rectangular, winged and connected patches. Numbers at the base of each bar indicate sample sizes. * $P < 0.05$.

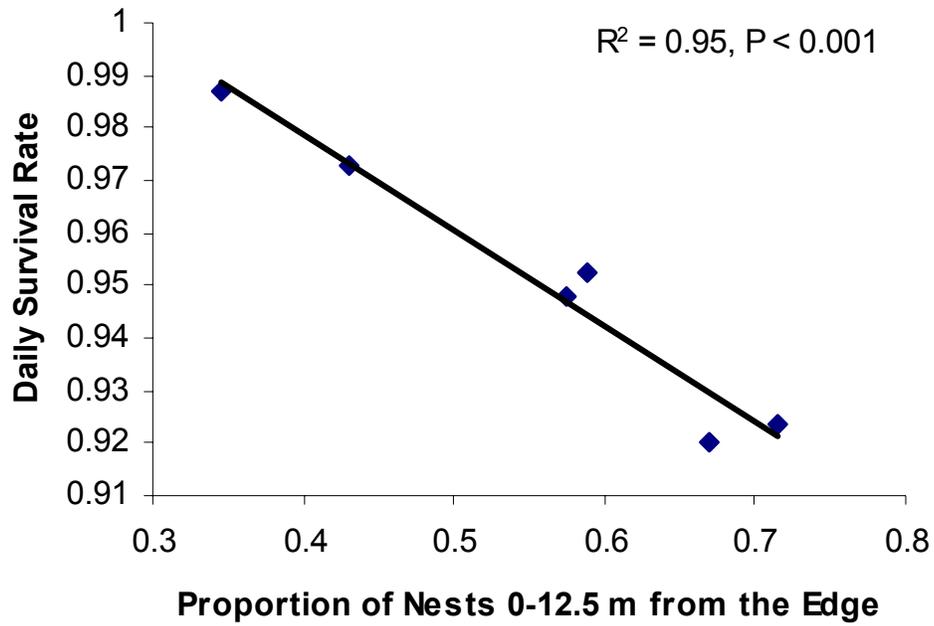


Figure 2.3. Daily survival rates as a function of the proportion of nests 0-12.5 meters from the edge across nestin periods and treatments. No relationship existed beyond 12.5 m from the edge.