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# How Corridors Reduce Indigo Bunting Nest Success

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**Abstract:** *Corridors are a popular strategy to conserve 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. 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 open-habitat fragments that varied in shape and connectivity. Corridors increased nest predation rates in connected fragments relative to unconnected fragments with lower edge:area ratios. Nest predation rates were similar between connected and unconnected fragments with higher edge:area ratios. These results suggest that the increase in predator activity is largely attributable to edge effects incurred through the addition of a corridor. This is the first field study to demonstrate that corridors can negatively impact animal populations occupying connected fragments.*

**Keywords:** connectivity, edge effects, habitat fragmentation

Los Corredores Reducen el Éxito de Anidación de *Passerina cyanea*

**Resumen:** *Los corredores son una estrategia popular para conservar la biodiversidad y promover el flujo de genes en paisajes fragmentados. La efectividad de los corredores se ha reforzado con el hecho de que no hay estudios de campo empíricos que muestren los efectos negativos sobre las poblaciones o comunidades. Probé la hipótesis de que los corredores incrementan la depredación de nidos en fragmentos de hábitat conectados en comparación con fragmentos no conectados. Evalué esta hipótesis en un sistema experimental de fragmentos de hábitat abierto que variaban en forma y conectividad. Los corredores incrementaron las tasas de depredación de nidos en fragmentos conectados en comparación con fragmentos no conectados con menores proporciones borde:área. Las tasas de depredación de nidos fueron similares en los fragmentos conectados y no conectados con mayores proporciones de borde:área. Estos resultados sugieren que el incremento en la actividad de depredadores es atribuible en buena medida a los efectos de borde resultantes de la adición de un corredor. Este es el primer estudio de campo que demuestra que los corredores pueden impactar negativamente a las poblaciones de animales que ocupan fragmentos conectados.*

**Palabras Clave:** conectividad, efectos de borde, fragmentación de hábitat

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## Introduction

Conservation corridors have been promoted widely as an effective way to preserve biodiversity and maintain population stability in fragmented landscapes (Rosenberg et al. 1997). Corridors achieve this goal by promoting immigration between otherwise isolated habitat fragments (Wilson & Willis 1975), which can rescue populations

from extinction (Brown & Kodric Brown 1977) by increasing colonization and gene flow. To date, empirical evidence for corridor usefulness is largely positive and in some cases neutral (e.g., Bowne et al. 1999; Hannon & Schmiegelow 2002). Results of numerous studies show increased movement rates between, or abundance within, connected habitat fragments for a wide range of animal species (e.g., Beier & Noss 1998; Tewksbury et al. 2002

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and references therein). Results of other studies demonstrate that corridors can maintain genetic exchange between connected habitat fragments (e.g., Aars & Ims 1999; Hale et al. 2001) and stabilize population structure (Mansergh & Scotts 1989; Dunning et al. 1995).

In addition to these beneficial effects, corridors may also have unintended and harmful conservation consequences (e.g., Simberloff & Cox 1987; Hess 1994, 1996). For example, corridors may influence predator-prey interactions by facilitating the movement or efficiency of predators. 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). Similarly, Orrock and Damschen (2005) found that corridors, through their creation of habitat edge, increased mammalian seed predation.

I tested the effects of corridors on the reproductive success of breeding birds in an experimental system of early successional habitat fragments ( $\sim 1.2$ – $1.4$  ha) that differed in shape and connectivity. Although corridors are 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. Edges associated with corridors may increase the abundance of generalist mammalian and avian predators (Ambuel & Temple 1983) or of edge-specialist reptiles such as snakes (Blouin-Demers & Weatherhead 2001). Indeed, many studies have documented higher nest predation rates with proximity to edges for many bird species (reviewed in Paton 1994). Additionally, corridors may magnify edge effects on predator abundance and efficiency by not only providing more suitable habitat for edge-specialist predators but also by providing connectivity between foraging habitats for predators that may “trapline” along them (Bider 1968). Consequently, many breeding bird populations may be seriously affected by increased predator pressure, particularly those that exhibit preferences for habitat edges.

As of yet, no studies have directly tested the effects of corridors on the reproductive success of birds. Behavioral studies have demonstrated that birds use corridors as conduits for dispersal and foraging (Haas 1995; Machtans et al. 1996; Tewksbury et al. 2002; Haddad et al. 2003; Levey et al. 2005) and that some corridors can serve as breeding habitat (Bentley & Catterall 1997; Hannon et al. 2002). However, simply knowing that birds use corridors says little about the suitability of connected patches for reproduction. Measures of reproductive success are critical for understanding the full impact of corridors on population growth and viability.

I evaluated the effects of corridors on the reproductive success of the Indigo Bunting (*Passerina cyanea*) by testing the hypothesis that corridors would increase predation rates in connected patches relative to similar-sized unconnected patches. This study expands on and incor-

porates data from a previous study conducted within this system that focused specifically on the effects of patch shape (but not connectivity) on the reproductive success of Indigo Buntings (Weldon & Haddad 2005).

## Methods

### Study Site and Species

This study was conducted within eight experimentally replicated landscapes, or blocks, at the Savannah River Site, near Aiken, South Carolina (U.S.A.), between May and August of 2002 and 2003 (Fig. 1). Each experimental block was composed of three equal-area (1,375 ha), unconnected, early successional patches that varied in shape between winged and rectangular forms, and two connected patches that were joined by a  $150 \times 25$  m corridor.

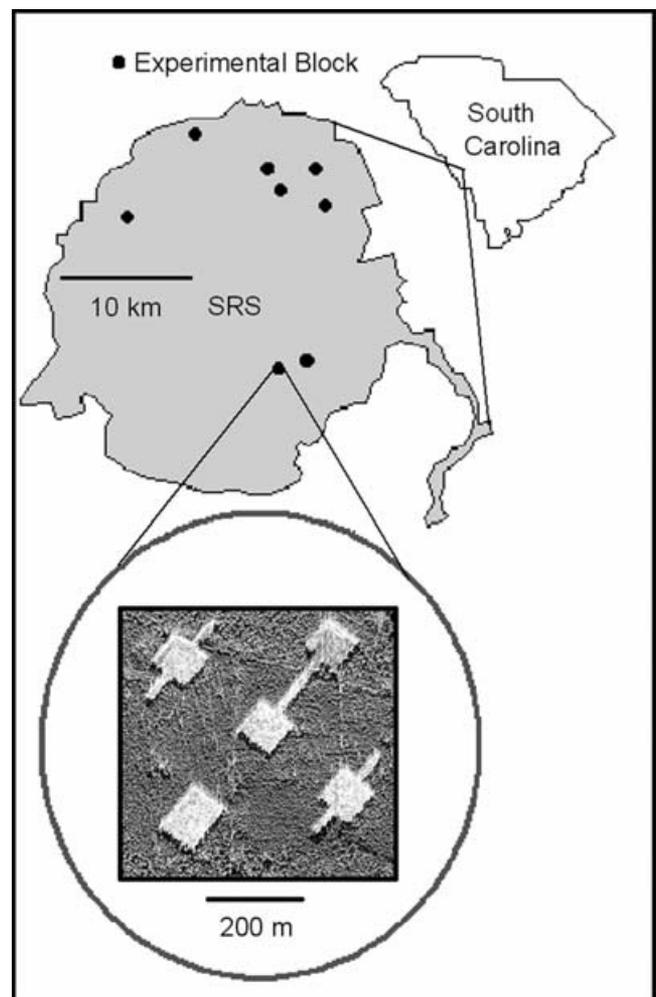


Figure 1. Location of the Savannah River Site (SRS) and the eight experimental blocks within SRS. The inset shows an infrared aerial photograph of one individual block.

All patches were embedded within a 30- to 40-year-old loblolly (*Pinus taeda* L.) and longleaf pine (*Pinus palustris* Miller) forest matrix. Connected patches were slightly smaller in area than unconnected patches (1.19 ha) and were defined as a 1-ha square plus half the length of the corridor (Fig. 1). This definition of a connected patch was supported by bunting behavior, as all but one territory that included a portion of the corridor also included a portion of the nearest patch. Vegetation structure was similar among all patch types (Weldon 2004).

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 (0.034), to connected (0.044), to winged patches (0.051), a 50% increase from the simplest to the most complex treatment. Because the edge-to-area ratio between connected and winged patches was similar but was nearly 30% greater in connected than in rectangular patches, I was able to separate the relative influence of corridors from the effects of edge on avian reproductive success.

The Indigo Bunting is a Neotropical migrant that has declined significantly in recent years in many parts of the eastern United States (Sauer et. al 2003). Justification for use of this focal species and additional details about the design of experimental blocks, methods, and analyses are detailed in Weldon and Haddad (2005).

### Breeding Bird Abundance

Soon after Indigo Buntings arrived, between 5 May and 15 June 2002 and 2003, I determined the abundance of territorial males through 20-minute point counts at the center of each patch as detailed in Weldon and Haddad (2005). Because nest detectability was high (>85% based on the total number of singing males), female abundance was determined as the maximum number of simultaneously active nests. Abundance estimates for all measures were tested for normality with a Shapiro-Wilk test and then analyzed for differences among treatments with the software package PROC MIXED with block as a random effect and year as a repeated measure (SAS Institute 2000).

### Reproductive Success

I located nests through systematic searches of each patch on a 4-day rotating cycle throughout the breeding season and then monitored nests on this schedule to determine their fate. I searched winged and rectangular patches for nests in 2002 and 2003 and connected patches only in 2003. For each nest, I determined reproductive measures such as clutch size, proportion of eggs hatched, and number of fledglings produced per successful nest. To test for temporal differences in nest success, I divided the breeding season into early and late nesting periods. Because there were no differences in daily survival rates between years (Weldon & Haddad 2005), I pooled nests for each patch before calculating Mayfield (1975) daily survival rates for each treatment and period. I calculated seasonal

fecundity by dividing the total number of fledglings produced by the total number of breeding females in each treatment. Finally, I tested for differences in reproductive measures, including clutch size, number of hatchlings, and number of fledglings per successful nest, across nesting periods (a repeated measure). For winged and rectangular patches that had estimates from both 2002 and 2003, fecundity, clutch size, number of hatchlings, and number of fledglings were averaged across years before analysis. All analyses were conducted using PROC MIXED (SAS Institute 2000), with treatment as a fixed effect and block as a random effect.

Because nest placement in relation to an edge can influence predation risk, and this distance may vary with patch shape, I compared nest placement among treatments by averaging the distance from each nest to its two closest edges. I then divided each treatment into four distance categories from the edge (0–12.5 m, 12.6–25 m, 25.1–37.5 m, 37.6–50 m) and determined the proportion of nests that fell into each category within a treatment for each nesting period. I then calculated the associated daily survival rates for each category. To determine whether daily survival rates were related to nest proportion, I regressed daily survival rates against nest proportion for each distance category across treatments.

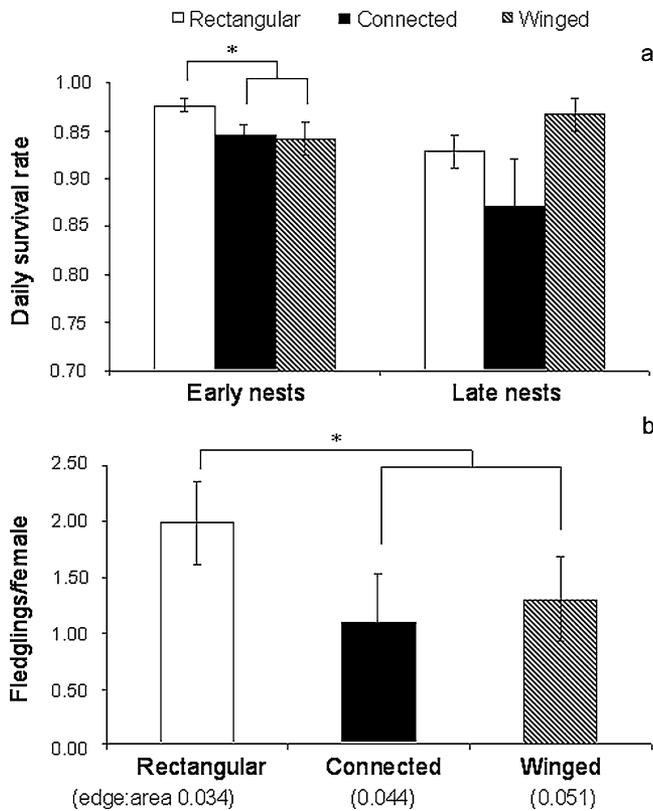
## Results

### Breeding Bird Abundance and Nest Success

Neither the abundance of male and female Indigo Buntings nor the abundance of nests differed among treatments. I found 138 bunting nests over the course of 2 years, 54% ( $n = 75$ ) of which failed. Predation was the primary cause of nest failure (88%), followed by nest abandonment (8%) and Brown-headed Cowbird (*Molothrus ater*) parasitism (4%). Abandoned nests ( $n = 6$ ) were not included in nest success analyses. Daily survival rates for early nests were significantly lower in connected patches than in rectangular patches (Fig. 2;  $F_{1,11} = 11.17$ ,  $p < 0.01$ ) but did not differ between connected and winged patches. Daily survival rates did not differ among treatments in the late nesting period (Fig. 2). Similarly, seasonal fecundity estimates were 45% lower in connected than in rectangular patches ( $F_{1,13} = 7.35$ ,  $p = 0.02$ , Fig. 2), but did not differ between connected and winged patches. The average clutch size and proportion of eggs hatched did not differ among treatments, but clutch size, and thus the number of eggs hatched and fledglings produced per successful nest, declined in the second brood for all treatments.

### Nest Placement

On average, Indigo Buntings nested closer to the edge in winged than in connected patches and closer in connected than in rectangular patches (mean distance to

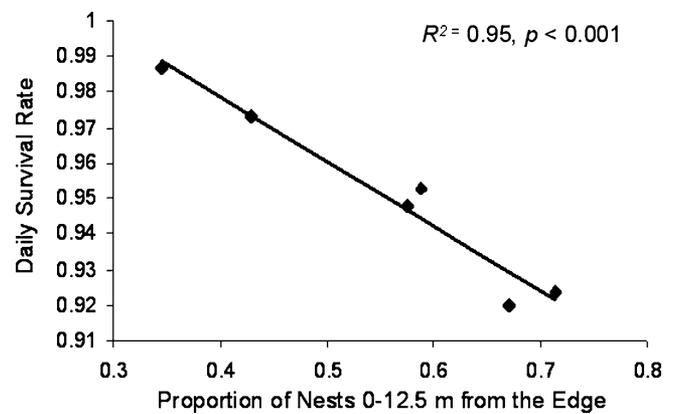


**Figure 2.** (a) Daily survival rates ( $\pm$ SE) by nesting period and (b) seasonal fecundity ( $\pm$ SE) for Indigo Buntings in connected patches compared with winged and rectangular patches (\* $p < 0.05$ ). The x-axis in (b) shows the increase in edge per unit area from rectangular to winged patches. Data for winged and rectangular treatments are taken from Weldon and Haddad (2005).

edge: winged, 20.1 m; connected, 23.8 m; rectangular, 26.4 m), as would be expected based on edge to area ratios. However, this difference was only significant between winged and connected patches ( $F_{1,124} = 3.86$ ,  $p = 0.05$ ). The proportion of nests 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 ( $R^2 = 0.95$ ,  $p < 0.001$ ) with the proportion of nests across treatments and nesting periods within this zone (Fig. 3). No relationship existed beyond 12.5 m from the edge.

## Discussion

My results supported the hypothesis that corridors increase nest predation rates in connected patches relative to unconnected patches but indicated that predation is increased by edge effects inherent in corridor design. Unconnected patches with higher edge:area ratios (winged patches) had seasonal fecundity similar to



**Figure 3.** Daily survival rates of Indigo Buntings as a function of the proportion of nests 0–12.5 m from the edge across nesting periods and treatments.

connected patches, but those with lower edge:area ratios (rectangular patches) had greater seasonal fecundity than connected patches. Therefore, high rates of nest predation in connected patches were primarily attributable to the increase in the relative amount of edge per unit area created by the corridor.

## Corridors, Edges, and Nest Predation

Buntings nesting in connected patches experienced higher predation rates and produced significantly fewer fledglings per female than buntings nesting in unconnected rectangular patches. Conversely, nest success and total seasonal fecundity did not differ between connected and winged patches, likely because these treatments contained similar amounts of edge. These results demonstrate that corridors mainly facilitated predator activity through the addition of edges, which provide profitable foraging habitat for edge-specialist predators. More complicated shapes, such as winged and connected patches, have relatively high proportions of habitat near the edge and consequently contain more nests per unit area near the edge than more simple shapes of similar size, which can negatively influence nest success (for a full discussion on the influences of patch shape on nest success, see Weldon and Haddad [2005]). In my 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 may be the dominant influence on predation rates, corridors may also influence predation by increasing connectivity for foraging predators. Though not significant, total seasonal fecundity in connected patches was 19% lower than in winged patches, a trend that ran counter to predictions based on the higher edge:area ratio

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 experienced the highest predation rates in both nesting periods, suggesting that corridors may magnify the effects of edge by facilitating predator movement or efficiency in connected patches beyond that of simple edge effects.

Although I did not determine the exact identity of the predators within this system, 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 the study. The condition of some nests suggested that mammalian predators such as raccoons (*Procyon lotor*) or opossums (*Didelphis virginiana*) were present in this system; however, the majority of evidence indicated that snakes, primarily the black rat snake (*Elaphe obsoleta*), were the dominant nest predator. I frequently observed snakes coiled in shrubs similar to those used by Indigo Buntings, and the majority of failed nests were cleanly removed and undisturbed, typical of snake predation (Thompson et al. 1999). Studies have shown that snakes prefer edge habitat (Blouin-Demers & Weatherhead 2001) and are active predators of songbird nests (Fitch 1963).

### Implications

This study provides the first landscape-scale evidence that corridors can increase predator activity and disproportionately decrease the reproductive success of prey populations occupying connected habitat fragments. Not surprisingly, these results seem to be driven by edge effects. The previous lack of evidence for negative effects of corridors may largely be due to the single-species focus of most corridor studies. Ignoring complex interactions, such as predator-prey interactions, among diverse suites of species may be dangerous. For example, in my study, corridors did not influence avian abundance but did influence nest predator abundance or foraging efficiency on a disturbance-dependent bird species. Historical habitat for such species may have consisted of short-lived and/or 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 providing a permanent link between once-isolated habitats that may increase edge predator abundance and by mimicking historical habitat cues that these birds use to select breeding habitat, such as structural heterogeneity, tall perches used for singing, and appropriate nesting substrates. Corridors may then function as ecological traps by attracting birds into riskier habitats (Gates & Gysel 1978; Battin 2004). Because I have shown

that winged patches in this study were traps (Weldon & Haddad 2005), there is a strong chance that connected patches were as well.

Corridor design is an important component of management plans for conserving target species. Land managers may diminish the harmful effects of corridors for disturbance-dependent species by creating gradual transitions between habitat types, rather than abrupt transitions characteristic of many forest management practices today. Gradual edges more closely mimic natural edges and provide greater structural complexity that may increase nest concealment and reduce predator efficiency (Ratti & Reese 1988; Suarez et al. 1997). Additionally, because harmful edge effects can extend well beyond the field-forest edge, this design would benefit habitat interior species as well. To maximize corridor benefits to multiple species, land managers should provide both gradual edges and corridors wide enough to encompass less-risky interior habitat (Hannon et al. 2002).

Corridors show promising long-term conservation benefits if used appropriately (Beier & Noss 1998). Determining the true efficacy of corridors will require a more complete understanding of how different types of corridors influence communities of organisms. To accomplish this, more studies are needed that not only measure movement or abundance for multiple species but also investigate species interactions (e.g., Orrock et al. 2003; Brinkerhoff et al. 2005), survival, reproductive success, or habitat occupancy over the long term. These studies will allow land managers to construct corridors that minimize negative consequences and maximize conservation benefits to entire communities.

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