

Indigo Bunting *Passerina cyanea*

Preferred breeding habitat: Forest edge habitats, particularly regenerating shrubland adjoining forest and within forest clearings, and a variety of brushy and weedy habitats in old fields, utility corridors, riparian areas, and swamps.

Nest placement: The open-cup nest is usually placed 0.3-1 m above ground, and incorporates several vertical or oblique stems of a branching herb or shrub as supports.

Mean clutch size and fledging brood size (\pm SD):

- Non-parasitized nests: clutch 3.39 ± 0.64 ; brood 2.83 ± 0.92
- Cowbird parasitized nests: clutch 2.72 ± 0.83 ; brood 1.26 ± 1.21

Number of broods per season: Two

Annual adult survival rates: Males 59%, females 49%

Requirements for population stability ($\lambda \geq 1$): Uncertain

Nest mortality and parasitism rates in relation to landscape context:

- Daily nest predation: 6.6-9.8% within forest edges bordering permanent, abrupt edges; 2.1-3.6% within interior forest edges with natural plant succession; 3.5-4.8% within regenerating shrubland adjoining forest
- Daily nest predation can increase as percent forest cover within a 10 km radius is reduced.
- Nest parasitism can be substantially higher within forest-edge habitat adjoining successional old fields than in the old fields themselves.
- Nest parasitism increases as percent forest cover within a 5-10 km radius is reduced.

The importance of spatial scale to the relationship between nesting success and landscape context:

- The parasitism rate experienced at any plot is influenced primarily by the degree of forest fragmentation at the local landscape scale (within 5-10 km radii), and only marginally by edge effects at the patch scale.
- The relative magnitude of patch-scale edge effects on nest predation is constrained by the degree of forest fragmentation (primarily edge density) at the local landscape scale (1-5 km radii).

General conclusions:

- Cowbird parasitism has a severe effect on Indigo Bunting breeding productivity, reducing the fledging success of parasitized individuals by up to 75%, and reducing the annual fecundity of females parasitized in at least one nest by approximately 50%.
- Both nest parasitism rate and nest predation rate generally increase as the degree of forest fragmentation at the local landscape scale (within 1-10 km radii) increases.
- Breeding productivity and λ decrease as the degree of forest fragmentation at the local landscape scale (within 1-10 km radii) increases.

Management guidelines:

- Maintain large areas of rank herbs and shrubs wherever possible e.g. within riparian zones, old fields, utility corridors, and along forest edges, roads and cultivated lands.
- Keep any buffer of rank, regenerating shrubland at a forest edge as broad as possible, given that predation rates may be higher within 50 m of the forest edge.
- Given the severe effect of cowbird parasitism on bunting breeding productivity, any management efforts that reduce cowbird abundance both locally and in the broader landscape (within up to a 15 km radius) will benefit bunting populations.

DETAILED and BACKGROUND INFORMATION

Distribution and habitat preference

A Neotropical migrant, the Indigo Bunting breeds in eastern North America and winters primarily in extreme southern Florida, Mexico, Central America and the Caribbean Islands (Payne 1992). The breeding distribution stretches from the Atlantic seaboard westward to the Great Plains, and from southeastern Saskatchewan, southern Manitoba, western and southern Ontario, southwestern Quebec, southern Maine, and southern New Brunswick south to Colorado, New Mexico, central and southeastern Texas, the Gulf Coast and central Florida. It also breeds locally in Utah, Arizona and California (Payne 1992).

The Indigo Bunting inhabits a variety of brushy and weedy habitats along the edges of cultivated lands, woods, roads and utility corridors, and also riparian habitats, shrubby clearings within deciduous and mixed forests, old fields and swamps. It is generally absent from closed-canopy forests, human residential areas, and intensively cultivated and grazed areas (Payne 1992).

As a disturbance-dependent species, the Indigo Bunting prefers forest-edge habitats, particularly regenerating shrubland adjoining forest (Woodward et al. 2001), and generally increases in abundance when disturbance to closed-canopy forest creates a more open canopy with a shrubby understory (Crawford et al. 1981). Following the creation of 0.02-0.4 ha gaps through group and single-tree selection logging within a 2,000 ha mature deciduous forest in southern Illinois, the relative abundance of Indigo Buntings started to increase in the second year after logging, from <0.5 detections/10-min point count in mature forest to a peak of around 6 detections/10-min point count in year 4, and declining thereafter to reach the low abundance levels typical of mature forest within 5-11 years (Robinson & Robinson 1999).

In a managed Missouri forest, Indigo Buntings were markedly more abundant in clearcut (1.6 detections/10-min point count), shelterwood (1.42 detections), and group selection (0.91 detections) logging treatment plots than in single-tree treatments (0.21 detections), or mature forest (0.19 detections: Annand & Thompson 1997). Similarly, Indigo Buntings were more abundant in Arkansas oak-hickory forest plots receiving a combination of heavy understory cutting and selective overstory harvest (0.63 detections/10-min point count) than either plots receiving only a heavy understory cutting (0.26 detections) or control (mature secondary) forest (0.1 detections: Rodewald & Smith 1998). Furthermore, Indigo Buntings were more abundant in mixed-oak and aspen forest

plots with 50-75% of their area constituting regenerating (2-10 years old) clear-cuts (2.3-3.2 individuals/10 ha) than uncut forest (0.0 individuals /10 ha) in Pennsylvania (Yahner 1993). In the Mississippi Alluvial Valley, Indigo Bunting breeding densities were substantially greater in harvested (single tree and group selection) bottomland hardwood stands (20.4 territories/40 ha) and intensively managed (6-9 years old) cottonwood plantations (25.2-27.1 territories/40 ha) than in mature (>30 years since last harvest) bottomland hardwood forest (3.4 territories/40 ha: Twedt et al. 1999). Management of Appalachian pine-oak forest involving the removal of mid-story shrubs and trees (2.5-17.5 cm dbh) and repeated prescribed burns increased the density of Indigo Buntings (Hines 1999).

There are no data to suggest that the habitat requirements of juveniles or post-breeding adults on the breeding range differ from those of breeding adults. Migrating birds frequent open grasslands, weedy fields and croplands (especially recently harvested sites), and low secondary growth (Payne 1992).

Locally, Indigo Bunting populations decrease with intensification of agriculture, frequent mowing of roadsides and farmland, reversion of old fields to forests, and increasing urbanization. Numbers increase with the growth of rank shrubs and herbs (Payne 1992). In general, Indigo Buntings have increased in range and breeding density within North America, particularly since the 1940's (Payne 1992). Density was estimated to have increased by 47% between 1909 and 1958 in southern Illinois (Graber & Graber 1963), and to have increased or remained approximately the same through 1965-1979 in eastern and central North America (Robbins et al. 1986). Local decreases and extinctions have occurred in areas of increasing forest regeneration in the northeast (Taber & Johnston 1968).

Breeding territory size averages 1.4 ha, but varies from 0.4-8.0 ha, being smallest in the shrubby edge of woods and old fields, and largest in shrubby swamps (Payne 1992). Breeding density estimates vary with region, habitat, and census method (Payne 1992). In linear transects, estimated adult density per 100 ha was 6.9, 3.2 and 1.6 in southern, central and northern Illinois respectively, with highest densities in edge and shrub habitats (Graber & Graber 1963). Using area sampling, densities averaged 38 singing males per 100 ha in West Virginia (Hall 1983) and 28 pairs/100 ha in North Dakota (Faanes & Andrew 1983). Densities in two colour-banded populations in southern Michigan averaged 35 pairs/100 ha and 15 pairs/100 ha (Payne et al. 1988). Estimates of density from all Breeding Bird Surveys (1966-1988) within 100 km of each of these latter two populations averaged 21.97 and 9.61 birds per route respectively, leading to density estimates of 6.7 and 2.89 pairs/100 ha respectively (Payne 1992).

Nest site characteristics

Indigo Buntings nest in fields and the edges of woods, roadsides and railways. They only occasionally nest in shrubs in closed-canopy forest when the tree canopy is late in leafing out or is defoliated by caterpillars (Payne 1992). In Missouri, Indigo Buntings display a marked preference for nesting in regenerating shrubland within 20 m of both interior (treefall gap and clearcut) and exterior (pasture or old field) forest edges than at distances >40 m from the forest edge (Burhans 1997, Woodward et al. 2001).

The open-cup nest is usually placed 0.3-1 m above ground, occasionally (<2%) 10 m or higher in trees, and incorporates several vertical or oblique stems of a branching herb or shrub as supports (Payne 1992). In Missouri, mean nest height was 0.47 m within forests and 0.65 m in adjoining old field habitat (Burhans 1997). Nests are generally hidden from above by leaves (within 10 cm of nest), but are often visible from the side (Payne 1992, Burhans 1997).

BREEDING PRODUCTIVITY

Laying seasons

BBIRD nest initiation data are derived largely from latitudes 30-40°N, where most nest initiation (92% of 449 records) occurs within the period 14 May to 24 June (range 2 May to 22 July) and the estimated laying season is 51 days long (Figure 1). In southern Michigan, the laying season starts approximately two weeks later, with nest initiation dates ranging from 14 May through 13 August (n = 2,492 nests over 9 years) and most laying occurring from early June to mid-July (Payne 1992). Similarly, nest initiation (n = 128 nests) occurred from 26 May to 15 August in Ontario (Peck and James 1987).

Assumptions in calculations of breeding productivity

Eggs are laid at daily intervals (Payne 1992). The mean clutch size of unparasitised nests is 3.2 (n = 261) in southern Michigan. BBIRD data indicate a mean clutch size in unparasitised nests of 3.39 (SD = 0.64, n = 265). Based on presumably large samples (no actual data presented), Dearborn (1999) cites a modal incubation period of 12 days and a modal nestling period of 10 days in Missouri. In an Arkansas study, a mean incubation period of 12.0 days (n = 14) and a mean nestling period of 8.7 days (n = 24) were recorded (Li 1994). BBIRD data indicate a mean incubation period of 11.3 days (n = 53) and a mean nestling period of 9.5 (range 9-11; n = 97). There is no published information on re-nesting interval after nest loss, but females may lay up to 7 clutches in a season and replacement nests are constructed in 2 days (Payne 1992). The length of the re-nesting interval following successful fledging depends on the degree of male parental care (Westneat 1988). When the male parent fed the fledglings, the female's re-nesting interval was 11.2 days (n = 5), whereas when males did not feed the fledglings, the female's re-nesting interval was 20.0 days (n = 7). The average re-nesting interval after successful fledging was 14.6 days (n = 16; Westneat 1988). In an average season in southern Michigan, 56.5% of females fledge one brood, 12.8% fledge two broods, and 0.1% fledge three broods (Payne 1992). To calculate breeding productivity, we used a 51-day laying season, 24-day nesting period (2-day laying; 12-day incubation; 10-day nestling), and re-nesting intervals of 5 days and 15 days after nest loss and successful fledging respectively.

Assumptions in calculations of finite rate of population increase (λ)

The most comprehensive analysis of Indigo Bunting adult survival rates is that of Payne and Payne (1990) at two study sites in southern Michigan. The mean annual survival rates of males banded as second-years (calendar year after hatching) were 51.9% (SE 2.1%; n = 260) and 58.6% (SE = 1.8%; n = 215) at the two sites respectively (for years 1979-1990), similar to the estimate of 57% (SE = 3.7%; n = 60) from Bird Banding Laboratory band-recovery data. The corresponding survival rates of females were 33.5% (SE = 3.6%) and 46.5% (SE = 2.3%) respectively. These estimates did not control for resighting probabilities, so probably underestimate survival slightly, although large study areas and study populations meant that the rate of unaccounted absences was only 0.2% for males, but 6% for females i.e. 6% of females in any season were missed but subsequently reappeared (Payne & Payne 1990). Adjusting the female survival estimates up by 6% yields estimates of 35.5% and 49.3% respectively. For both sexes, the lower estimates were from a site where the population declined by 50% over the study period, suggesting increased dispersal may have reduced the survival estimates. We therefore assumed adult survival rates of 59% for males and 49% for females in our calculations of λ . This Indigo Bunting female/male survival ratio of 0.84 is similar to that recorded for other Neotropical migrant passerines (Hann 1948; Holmes & Sherry 1992).

Effects of nest micro-habitat on probability of nest predation and parasitism

There are few data, but less well concealed nests were more likely to be parasitized (Burhans 1997), and higher nests were less likely to experience predation in old field habitats (Burhans et al. 2002).

Effects of Brown-headed Cowbird nest parasitism on host reproductive success

Indigo Buntings rarely abandon parasitized nests (Payne 1992), abandoning only 3.5% of 142 parasitized nests in one study (Burhans et al. 2000). Among BBIRD sites, the mean number of cowbird eggs laid per parasitized Indigo Bunting nest increased non-significantly ($F_3 = 1.75$; $P = 0.32$), and the mean number of host young fledged per successful nest decreased significantly ($F_5 = 7.26$; $P = 0.054$) as the site-specific parasitism rate increased (Figure 2). The average Indigo Bunting clutch size was 20% lower among parasitized nests (Mean = 2.72; SD = 0.83; N = 39), than non-parasitized nests (Mean = 3.39; SD = 0.64; N = 265). In southern Michigan, where mean parasitism levels of 20-27% were experienced, mean clutch size was 25% lower among parasitized nests (Mean = 2.4; n = 134) than unparasitized nests (Mean = 3.2; n = 261; Payne 1992). At BBIRD sites, the number of host young fledged per successful nest was 55% lower among parasitized nests (Mean = 1.26; SD = 1.21; N = 31) than non-parasitized nests (Mean = 2.83; SD = 0.92; N = 232). In southern Michigan, the number of host young fledged per successful nest was approximately 75% lower among parasitized nests (Mean = 0.37-0.4) than non-parasitized nests (1.54-1.62; Payne & Payne 1998).

Cowbird parasitism can also increase nest predation risk and reduce the survival of successfully fledged host young. In forest edge habitat adjoining old fields in Missouri, daily predation rate was 7.98 % (n = 1090 exposure days) for cowbird-parasitized nests and 5.77 % (n = 1578) for non-parasitized nests (Dearborn 1999). Similarly, in southern Michigan, unparasitized nests are nearly three times more likely to fledge a bunting than

parasitized nests (Payne & Payne 1998). Furthermore, the seasonal fecundity of unparasitized females (2.45-2.58 fledglings) was greater than the fecundity of females that were parasitized in at least one nest (1.25-1.77 bunting fledglings: Payne & Payne 1998). Bunting nestlings in parasitized nests receive less food and exhibit reduced rates of mass gain in comparison with buntings in non-parasitized nests (Dearborn et al. 1998). Buntings that fledged from nests where a cowbird also fledged were only 18% as likely to survive and return to their natal area in the next year as buntings from nests where a cowbird did not fledge (Payne & Payne 1998). Although adult Indigo Buntings provision nests at a higher rate at parasitized nests than non-parasitized nests (Dearborn et al. 1998), this increased effort does not appear to affect subsequent adult survival (Payne & Payne 1998).

Table 1. Summary of Indigo Bunting breeding productivity and estimated finite rate of population increase (λ) across BBIRD sites. See Figure 1b for site locations.

Site	No. of nests	Clutch size ¹	Parasitism rate (%) ²	Daily predation rate (%) ³	Nest success (%) ⁴	Fledglings/nest ⁵	Annual fecundity ⁶	Lambda
Mississippi R., MN/WI	31	3.60	54.84	3.04	33.75	2.33	1.72	0.75
Wayne Natl Forest, OH	21	3.50	19.05	5.73	15.60	3.00	1.33	0.69
Northern Ohio	6	3.67	16.67	3.49	42.65			
Hoosier Natl Forest, IN	114	3.57	12.28	4.29	33.60	2.70	1.99	0.79
Ouachita Natl Forest, AR	280	3.26	11.43	3.89	34.61	2.58	1.93	0.78
Ozark Natl Forest, AR	74	3.40	4.05	4.02	35.95	3.10	2.37	0.85
NW Monongahela Natl Forest, WV	39	3.40	0	2.58	48.36	3.08	2.80	0.91
Nicolet Natl Forest, WI	6	3.50	0	7.59	15.02			

¹Number of host eggs incubated in non-parasitized nests

²Percentage of nests that received 1 or more cowbird eggs

³Percentage of nests lost to predators per day

⁴Percentage of nests that produced at least 1 host fledgling or cowbird

⁵Number of host young fledged per successful nest

⁶Average number of host young fledged per female per year

Effects of landscape-level habitat variables on nest parasitism

The edge density of all forest within a 5 km radius was the best predictor of parasitism rate across all plots ($F = 9.43$, $P = 0.005$, $R^2 = 0.26$: Table 2). Edge density at this scale was significantly correlated with percent forest cover ($r = -0.57$, $P = 0.003$). At only Ouachita and Hoosier National Forests was there sufficient variation in percent forest cover among plots to examine within-site relationship between forest fragmentation and nest parasitism rate (Figure 3). Nest parasitism rate was positively related to percent developed land at the 1 km radius scale, and with edge density of forest at the 5 km radius scale across plots within Ouachita National Forest (Table 3). Nest parasitism rate was similarly positively related to edge density of forest ($F = 20.54$, $P = 0.02$, $R^2 = 0.83$) and negatively related to angular second moment ($F = 134$, $P = 0.001$, $R^2 = 0.97$) within a 5 km radius of plots at Hoosier National Forest (Table 3). Thus, the positive relationship between nest parasitism rate and degree of forest fragmentation appeared to be strongest at the 5 km radius scale.

Nest parasitism rate among BBIRD sites was significantly related with indices of fragmentation across all spatial scales, this relationship being most significant with percent grassland cover (a negative relationship) at the 10 km radius scale ($F = 27.14$, $P = 0.002$, $R^2 = 0.79$: Table 2, Figure 4). Percent grassland cover at this scale was significantly correlated with percent forest cover ($r = -0.94$, $P < 0.001$). Robinson et al. (1995) similarly found a significant negative correlation between nest parasitism rate and percent forest cover within a 10 km radius of nine sites across the Midwestern United States.

We were unable to detect a significant relationship between parasitism rate among plots and any patch-scale variable (e.g. distance to edge). This is likely due to a combination of potential error in our plot center locations, and patch-scale parasitism risk being constrained by factors operating at larger spatial scales, such as the 5-10 km radii landscape scales. Indeed, the site-level analysis strongly suggests that the average parasitism rate is strongly influenced by the degree of forest fragmentation at the 10 km radius scale. In summary, this suggests that the parasitism rate experienced at any plot is influenced primarily by the degree of forest fragmentation at the local landscape scale (within 1-10 km radii), and only marginally by edge effects at the patch scale.

In cowbird-saturated habitats in southern Illinois, where parasitism levels are high even 800 m from the nearest forest edge of any kind and 1.5 km from the nearest edge where cowbirds forage, there was no significant difference in parasitism levels of nests in small, interior forest edges (25-40% parasitism) than in exterior edges bordering old fields and agriculture (37-48%: Suarez et al. 1997), further suggesting that factors at the landscape scale overwhelm local edge effects. In central Missouri, parasitism was substantially higher among Indigo Bunting nests in forest adjoining successional old fields (73 % parasitism; mean distance from edge = 12 m) than in the old fields (51% parasitism; mean distance from forest edge = 22 m: Burhans 1997).

The Indigo Bunting is frequently heavily parasitized, with other reported parasitism rates: 24.2% (n = 165 nests) in Ontario (Peck & James 1987), 19.8% (n = 693) to 26.6% (n = 1,040) in Michigan (Young 1963; Payne & Payne 1998), 46% (n = 26) in Wisconsin (Young 1963), 20% (n = 30) in Quebec (Terrill 1961), 31-40% (n = 16,43) in Ohio (Hicks 1934; Trautman 1940), 35% (n = 63) in Indiana (Carey 1982), 39% (n = 41)

in Illinois (Twomey 1945), and 51-73 % in old-field and adjoining forest-edge habitats in Missouri (Burhans 1997). Parasitism rate decreased in frequency after early July at two sites in Michigan, from 23-41% in May, 26-49% in June, 9-11% in July and none in August (Payne & Payne 1998).

Table 2. Summary of the best predictor variables (fragmentation indices) for the relationship between each of nest parasitism rate, nest predation rate and lambda across plots (all plots with ≥ 5 nests) and sites (plot averages for scales of patch and 1-10 km radii) using multiple regression analysis. Spatial scales included: the patch of forest within which the study plot was embedded; 1-10 km radii of study plot centers; and 50-100 km radii of study site centers. Independent variables included: patch size; the distance between the plot center and nearest non-forest edge; edge density; percentage of core forest; percent developed land (grassland, cropland and other forms of development); percent grassland cover; and angular second moment. In all cases, single parameter models were most parsimonious. Non-significant results included for comparison across scales. * $P < 0.05$; ** $P < 0.01$.

Scale	Plots			Sites			
	Dependent variables	Independent variables	Adjusted R^2	Slope	Independent variables	Adjusted R^2	Slope
Patch	Parasitism	Patch size	0.08		% core	0.43*	-0.12
	Predation	Edge density	0.02		To edge	-0.12	
	Lambda	To cowbird edge	0.04		% core	-0.01	
1 km	Parasitism	% developed	0.21*	2.04	Patch size	0.46*	-0.21
	Predation	Angular 2 nd moment	0.24**	-0.12	% grass	-0.1	
	Lambda	Fractal dimension	-0.01		% grass	0.29	
5 km	Parasitism	Edge density	0.26**	1.26	% grass	0.71**	1.61
	Predation	Edge density	0.1		Patch size	-0.12	
	Lambda	Percent core	-0.02		% grass	0.45	
10 km	Parasitism	Edge density	0.07		% grass	0.79**	1.65
	Predation	Edge density	0.01		% grass	0.04	
	Lambda	Percent forest	0.01		% grass	0.37	
50 km	Parasitism				% grass	0.54*	1.21
	Predation				% grass	0.18	
	Lambda				% core	0.09	
100 km	Parasitism				Patch size	0.60*	-0.22
	Predation				% grass	0.3	
	Lambda				Patch size	0.12	

Table 3. Adjusted R^2 , slope (b) and significance (P) of the relationship between nest parasitism rate or nest predation rate and fragmentation index for either plot patch area or percent forest cover at each of three different radii from plot centers at two sites.

Site		Patch	1km	5km	10km	Patch	1km	5km	10km
		Nest parasitism				Nest predation			
Ouachita NF	R^2	0.03 ^a	0.28 ^b	0.31 ^c	-0.00 ^c	0.14 ^a	0.18 ^c	0.25 ^c	0.09 ^d
	b	-0.67	2.21	1.60	0.69	-0.088	0.11	0.13	-0.091
	P	0.23	0.02*	0.01*	0.34	0.07	0.04*	0.02*	0.12
Hoosier NF	R^2	0.66 ^a		0.97 ^e	0.65 ^f	0.59 ^c		0.46 ^g	-0.25 ^d
	b	-1.24		-3.01	2.08	-0.23		-0.20	-0.019
	P	0.06		0.001**	0.06	0.08		0.13	0.68

Independent variables: ^apatch core forest area; ^b percent developed land (grassland, cropland and other forms of development); ^cedge density of forest; ^dpercent core forest; ^eangular second moment; ^f Shannon-Weaver diversity index; ^gfractal dimension. * $P < 0.05$; ** $P < 0.01$.

Table 4. Correlations (r) between site means for fragmentation variables and each of nest parasitism rate, daily nest predation rate, and finite rate of population increase (lambda) among sites. Fragmentation variables include edge density of the forest patch within which plots are embedded, and percent cover of grassland (planted pasture/hay and semi-natural grassland/herbaceous), forest, and cropland (row crops, small grains, fallow and orchards/vineyards) at 1-100 km radii.

	Parasitism rate vs			Daily predation rate vs			Lambda
	Grass	Forest	Crop	Grass	Forest	Crop	Grass
	r	r	r	r	r	r	r
Patch edge density		0.61			0.04		
1 km	0.73*	-0.69	0.58	-0.05	0.18	-0.09	-0.65
5 km	0.86*	-0.81*	0.73*	0.04	0.12	-0.07	-0.75
10 km	0.91**	-0.81*	0.76*	0.03	0.11	-0.11	-0.71
50 km	0.78*	-0.76*	0.68	0.15	0.02	-0.05	-0.49
100 km	0.68	-0.78*	0.74*	0.13	-0.05	0.07	-0.32
150 km		-0.79*			-0.01		

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Effects of landscape-level habitat variables on nest predation rate

Multiple regression analysis using data from all plots with ≥ 5 nests revealed a single significant relationship between nest predation rate and index of fragmentation across all spatial scales from the plot patch to within 1-10 km radii – a negative relationship with angular second moment ($F = 8.36$, $P = 0.008$, $R^2 = 0.24$) was slightly stronger than a positive relationship with forest edge density within a 1 km radius ($F = 7.58$, $P = 0.011$, $R^2 = 0.22$) (Table 2, Figure 5). As forest fragmentation increases, the angular second moment fragmentation index decreases and edge density increases. This result suggests that as the degree of fragmentation in the landscape immediately surrounding plots (within a 1 km radius) increases, and the relative amount of forest edge increases, daily predation rate increases. At Ouachita National Forest, the relationship with edge density was stronger than that with angular second moment, and was slightly more significant at the 5 km radius scale than the 1 km radius scale (Table 3).

Among BBIRD sites, nest predation rate was not significantly correlated with any index of fragmentation at any spatial scale (Table 2). In contrast, Robinson et al. (1995) found a significant negative correlation between daily nest mortality rate and percent forest cover within a 10 km radius of nine sites across the Midwestern United States.

In forest edge habitat adjoining old fields in Missouri, the average daily predation rate was 6.67% (Dearborn 1999). In regenerating shrubland habitat adjoining interior (treefall and clearcut) and exterior (pasture) forest edges in Missouri, Woodward et al. (2001) noted daily predation rates of 3.5% within 20 m of the forest edge, 4.8% 21-40 m from the forest edge, and 4.2% in shrubland at distances greater than 40 m from the forest edge. In contrast, Burhans et al. (2002) found that nests in successional old fields adjoining forest in central Missouri were more likely to be predated the closer they were to the forest edge.

In southern Illinois, daily nest predation rates were nearly twice as high in edge habitats along permanent, abrupt edges such as those bordering agricultural row crops (9.8% daily predation), old fields (6.6%) and 0.2-0.4 ha wildlife openings within forests planted with grasses and legumes (7.1%) than along interior-forest edges with plant succession such as edge habitat associated with <0.3 ha treefall gaps (2.1%), <0.1 ha gaps left by dying trees, <50 m wide stream beds (3.6%) and 0.1-0.4 ha group-selection logging cuts with 2-4 years of shrubby regrowth (3.5%: Suarez et al. 1997).

In forest habitats >200 m from agricultural edges within the Mississippi Alluvial Valley, daily nest mortality rates (largely from predation) were slightly lower (6.3%) in bottomland forest (mature and subjected to single-tree and group-selection timber harvest), than in 6-year-old, intensively managed cottonwood plantations regenerated by either planted stem cuttings (7.2%) or coppicing (9.5%) following harvest (Twedt et al. 2001).

To summarise, there is some evidence of elevated nest predation risk in the immediate vicinity of abrupt forest edges with no natural plant succession, and in the immediate vicinity (both internally and externally) of forest edges bordering regenerating shrublands, such as old fields. It also appears as if the relative magnitude of the patch-scale edge effect is constrained by the degree of forest fragmentation (primarily edge density) at the local landscape scale (1-5 km radii).

Effects of landscape-level habitat variables on finite rate of population increase

Estimated annual productivity ranged from 1.3-2.8 bunting fledglings per female at six BBIRD sites with sufficient data on both nesting success and mean number of bunting fledglings per successful nest. The highest productivity value, from a site with no cowbird parasitism, is similar to the annual productivity of non-parasitized females in southern Michigan (2.45-2.58 fledglings: Payne & Payne 1998), suggesting our estimates of annual productivity are reasonable. Nonetheless, our estimates of lambda among sites (0.69-0.91) are all below unity, suggesting that the estimates of annual adult female and/or juvenile survival we use to calculate lambda are too low. The partial correlations between each of daily predation rate and nest parasitism rate and lambda are equivalent ($r_p = -0.94$ and -0.95 respectively), suggesting that nest predation and parasitism have equally important effects on lambda, through their effects on seasonal productivity. Given the strong relationship between nest parasitism rate and degree of forest fragmentation, one might expect an equally strong relationship with lambda. Among all plots, lambda was not at all related to any fragmentation index (Table 2). There was, however, a general increase in lambda with a reduction in the degree of forest fragmentation at any scale across sites (Table 2). This relationship was marginally non-significant for grassland cover within a 5 km radius (Figure 6).

Effects of silviculture on nest predation and nest parasitism

In southern Illinois, daily nest predation rates in forest bordering 0.1-0.4 ha group-selection logging cuts with 2-4 years of shrubby regrowth (3.5%) were not significantly higher than along other interior-forest edges with plant succession, such as edge habitat associated with <0.3 ha tree-fall gaps (2.1%), <0.1 ha gaps left by dying trees, and <50 m wide stream beds (3.6%: Suarez et al. 1997).

In forest habitats >200 m from agricultural edges within the Mississippi Alluvial Valley, daily nest mortality rates (largely from predation) were slightly lower (6.3%) in bottomland forest (mature and subjected to single-tree and group-selection timber harvest), than in 6-year-old, intensively managed cottonwood plantations regenerated by either planted stem cuttings (7.2%) or coppicing (9.5%) following harvest (Twedt et al. 2001).

Effects of burning on nest success

No data.

Effects of grazing on nest success

No data.

Overview of landscape-level habitat effects on breeding productivity and population growth rate

Cowbird parasitism has a severe effect on Indigo Bunting breeding productivity, reducing the fledging success of parasitized individuals by up to 75%, and reducing the annual fecundity of females parasitized in at least one nest by approximately 50%.

Consequently, nest parasitism rate and predation rate have equally severe effects on annual productivity, and thus on lambda. Among BBIRD sites, lambda decreased as the degree of forest fragmentation at landscape scales increased, largely as a result of the significant positive relationship between nest parasitism rate and percent grassland cover (Figure 6). Robertson et al. (1995) found firm evidence of increases in both nest parasitism rate and nest predation rate with reduced percent forest cover within a 10 km radius of study sites across the midwestern United States, further suggesting that lambda of local populations is strongly influenced by the degree of forest fragmentation at landscape scales. Based on the parameter estimates for adult female and juvenile survival, and productivity, our estimates of lambda suggest that the populations at all BBIRD sites with sufficient data were sinks ($\lambda < 1$). However, Indigo Bunting numbers have increased or remained the same through 1965-1979 in eastern and central North America (Robbins et al. 1986). Thus, our lambda estimates are likely biased low due to underestimation of adult female survival, juvenile survival and/or seasonal productivity. If we increase all of these parameter estimates by 20%, the range in lambda estimates across BBIRD sites increases from 0.69-0.91 to 0.88-1.19.

Mapping predicted source and sink habitat

Mapping predicted source and sink habitat is problematic due to uncertainty with our estimates of lambda, and insufficient resolution in the relationship between lambda and landscape metrics of forest fragmentation across BBIRD sites.

MANAGEMENT GUIDELINES

The Indigo Bunting is abundant in eastern North America, so it has been suggested that no special efforts are needed to ensure its survival on a continental scale (Payne 1992). At local scales, however, Indigo Bunting numbers decrease with intensive agriculture, frequent mowing of herbs along roadsides and farms, reversion of old fields to closed-canopy forests, and increasing urbanization, whereas numbers increase with local disturbance to closed-canopy forest and increased growth of rank shrubs and herbs (Payne 1992). Specific management guidelines include:

1. Maintain large areas of rank herbs and shrubs wherever possible e.g. within riparian zones, old fields, utility corridors, and along forest edges, roads and cultivated lands.
2. Keep any buffer of rank, regenerating shrubland at a forest edge as broad as possible, given that predation rates may be higher within 50 m of the forest edge.
3. Given the severe effect of cowbird parasitism on bunting breeding productivity, any management efforts that reduce cowbird abundance both locally and in the broader landscape (within up to a 15 km radius) will benefit bunting populations.

FILLING THE GAPS – FUTURE RESEARCH AND MONITORING NEEDS

We have provided strong evidence of a relationship between Indigo Bunting lambda and landscape characteristics associated with forest fragmentation (Figure 6). However, we are unable to detail the threshold for source/sink dynamics, due to uncertainty in

parameter estimates and small sample size in the test of the relationship between lambda and landscape structure.

Accurate estimates of lambda depend most critically on accurate estimates of annual adult female survival, and to a lesser extent on juvenile survival and breeding productivity. Our modeled estimates of lambda suggest that the current best estimate of annual adult female survival (49%), based on a single study in the north of the breeding range, is too low. A further estimate of female survival, using re-sighting data of a color-banded population, and preferably from a locality in the southern half of the breeding range would therefore be useful.

Our confidence in the modeled relationship between lambda and landscape characteristics could be substantially improved with an increased sample of breeding success data from more sites across the range of the Indigo Bunting. These data are not difficult to collect, requiring a sample of ideally at least 25 nests (to give a sample of at least 10 successful nests for a reliable estimate of mean number of host young fledged per successful nest) that are monitored frequently enough to accurately determine their fate, and collected from a plot, up to 50 ha in size, of homogenous habitat whose center can be geo-referenced with a precision of approximately 30 meters (to allow plot-specific landscape features to be characterized from a digital land cover map). If any nests are located within 100 m of a habitat edge, measurements of the distance between that nest and the nearest edge would be useful for investigating patch-scale edge effects.

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Figure 1. Indigo Bunting laying season (number of new nests initiated each week) in relation to latitude. Laying season length estimated using the MacArthur index (see text for details).

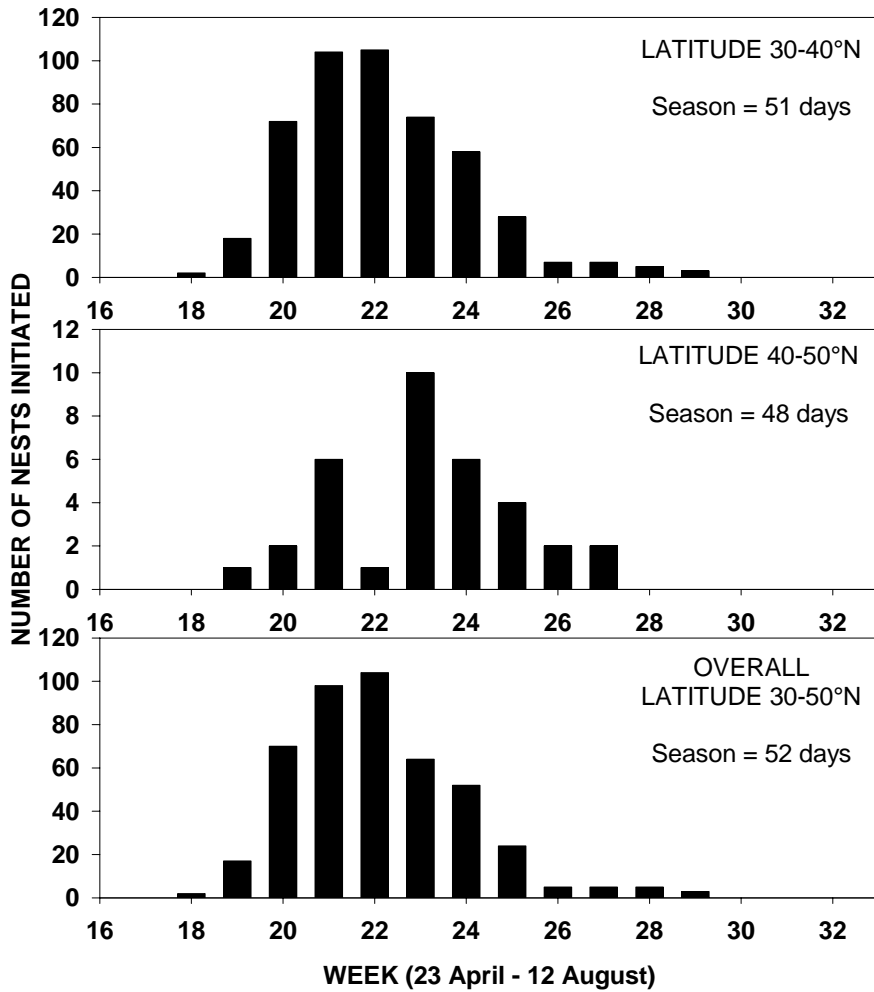


Figure 2. The mean number of Indigo Bunting young fledged per successful nest decreases as the site-specific parasitism rate increases ($F_5 = 7.26$; $P = 0.054$).

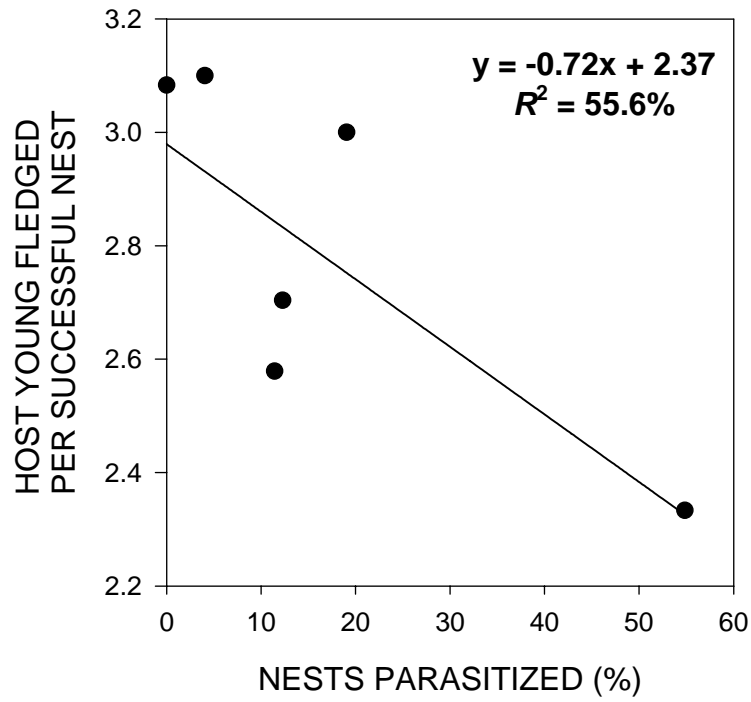


Figure 3. Relationship between Indigo Bunting nest parasitism rate (arcsine transformed) and: A) forest patch size (ln-transformed) at the patch scale; B) percent developed land cover within a 1 km radius; C) edge density of forest within a 5 km radius; and D) edge density of forest within a 10 km radius of plot centers (all arcsine transformed) at each of Hoosier National Forest and Ouachita National Forest.

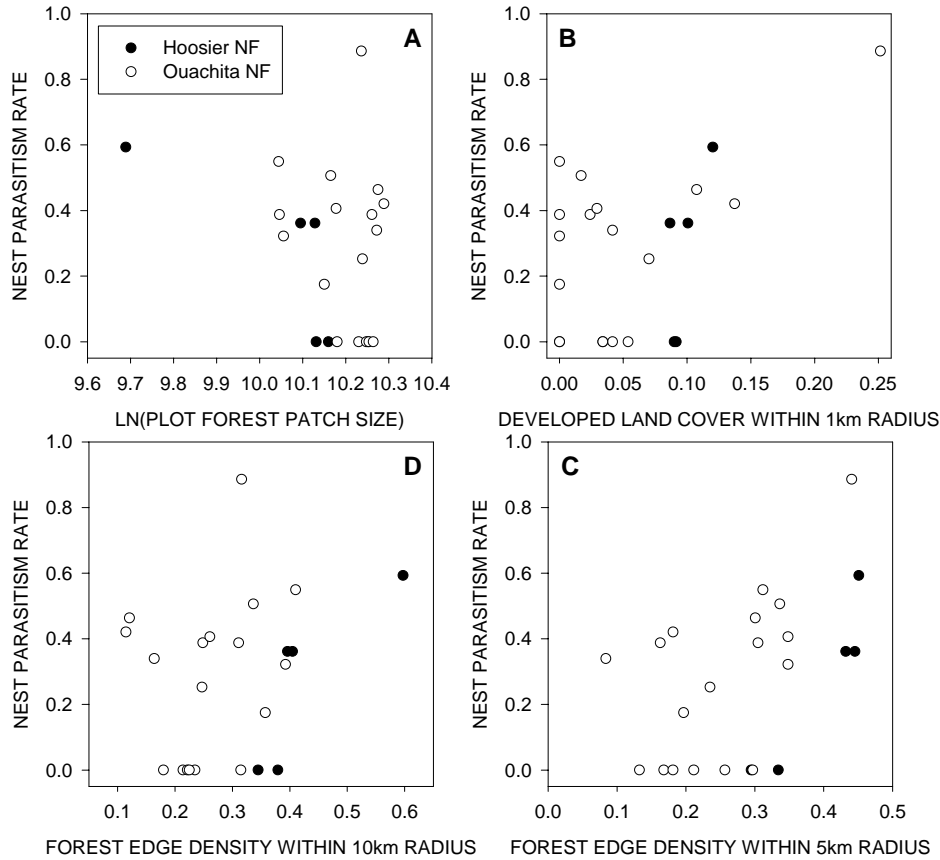


Figure 4. Relationship between nest parasitism rate (arcsine transformed) and forest fragmentation index (ln or arcsine transformed) at spatial scales of the plot patch and 1-10 km radii of plot centers (site averages), and 50-100 km radii of site centers. Relative percent forest cover at the 100 km radius scale is classified as low, medium, or high.

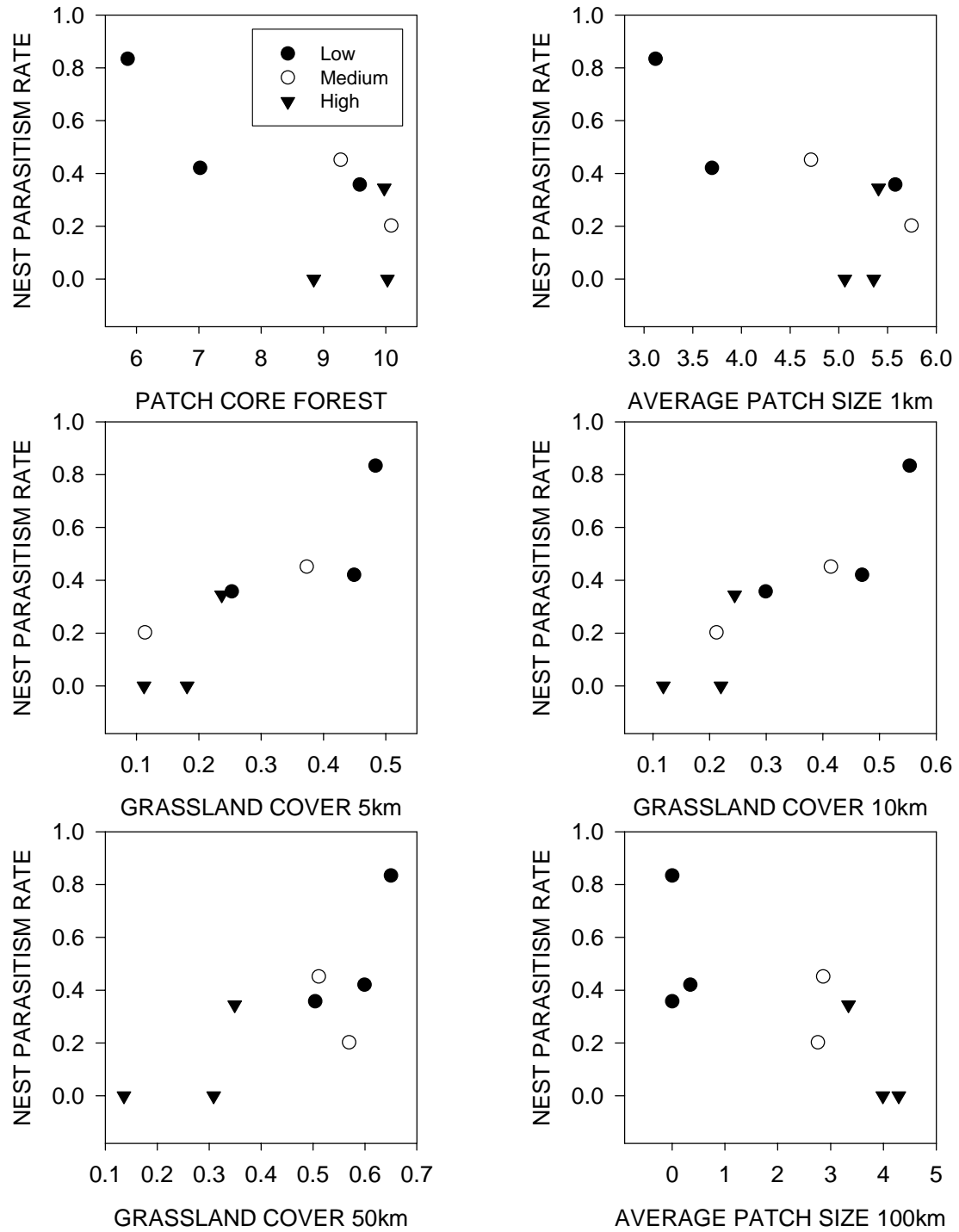


Figure 5. Relationship between nest predation rate and edge density of all forest within a 1 km radius of all plots with ≥ 5 nests.

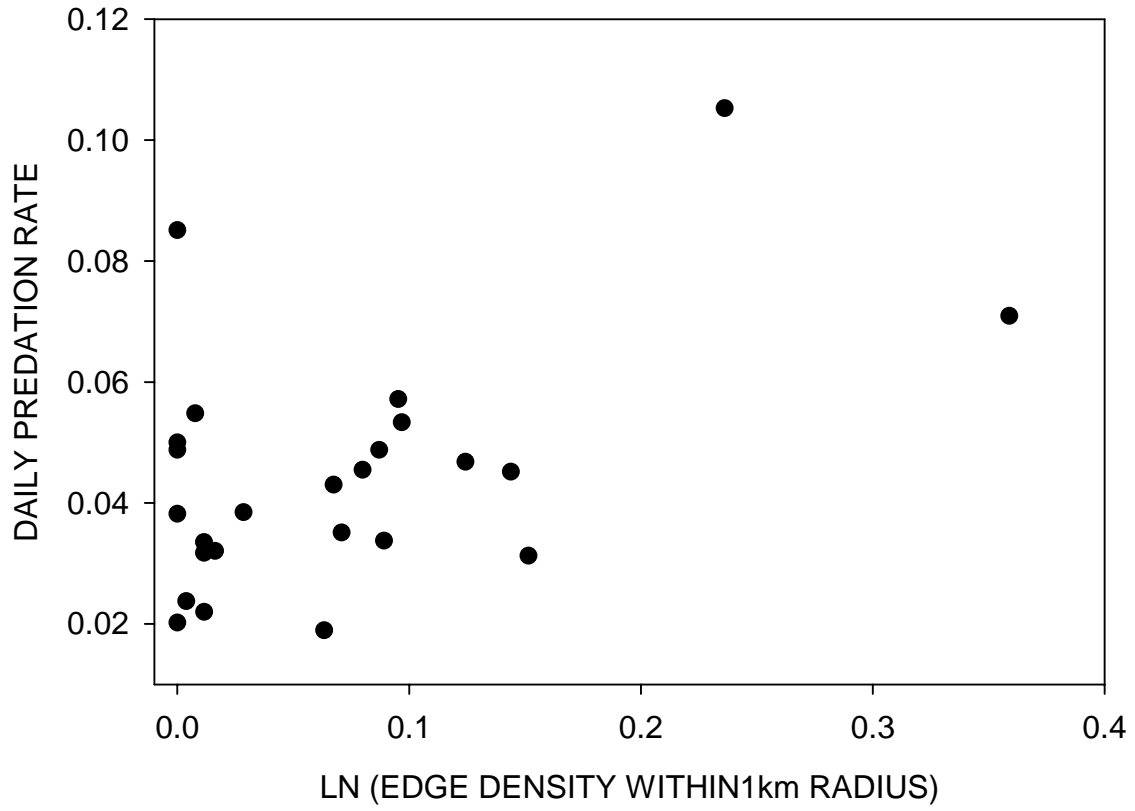


Figure 6. Relationship between Indigo Bunting finite rate of population increase (λ) and percent grassland cover (arcsine transformed) within a 5 km radius of plot centers (site averages). Regression $F = 5.07$, $P = 0.09$.

