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HABITAT AND MICROHABITAT FEATURES ASSOCIATED WITH COWBIRD PARASITISM IN TWO FOREST EDGE COWBIRD HOSTS[1]

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Abstract. I examined the relationship of habitat and nest microhabitat features of Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*) to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) in central Missouri. In old field habitats, Indigo Buntings were more frequently parasitized than Field Sparrows, but Indigo Buntings nesting in forested habitat were parasitized at higher frequencies than buntings in old fields. Logistic regression models showed that nest concealment best explained parasitism for all Indigo Buntings and field-nesting Indigo Buntings, with poorly concealed nests more likely to be parasitized. However, side concealment was not related to parasitism for heavily-parasitized Indigo Buntings in forested habitats. Microhabitat variables did not explain parasitism at Field Sparrow nests, but their nests were lower and better concealed than field-nesting Indigo Buntings. Results suggest that nest microhabitat features may influence probability of parasitism, but species and habitat characteristics may override microhabitat in explaining frequency of parasitism.

Key words: Brown-headed Cowbird, Molothrus ater, *Field Sparrow,* Spizella pusilla, *Indigo Bunting,* Passerina cyanea, *microhabitat, brood parasitism.*

INTRODUCTION

Brown-headed Cowbirds (*Molothrus ater*) are generalist avian brood parasites that parasitize the nests of many host species (Friedmann 1963, Lowther 1993). The mechanisms by which cowbirds choose hosts and select nests to parasitize are poorly understood. Whereas female cowbirds presumably focus on host behavior in searching for nests (Norman and Robertson 1975, Uyehara and Narins 1995), features of the immediate nest microhabitat potentially influence the probability that female cowbirds will find and parasitize a given nest. Levels of brood parasitism may decrease with increased canopy cover around the nest (Brittingham and Temple 1996) and increase with proximity of perches (Anderson and Storer 1976, Alvarez 1993, Romig and Crawford 1995). Other studies indicate relationships between nest height and frequency of parasitism (Briskie et al. 1990, Robinson 1992, Hahn and Hatfield 1995).

However, the habitat used by hosts or cowbirds also may influence frequency of parasitism (Zimmerman 1983, Hahn and Hatfield 1995), as may other characteristics of hosts themselves (Gochfeld 1979, Mason 1986). In this study, I address the importance of nest microhabitat and the extent to which habitat and species characteristics supersede microhabitat in explaining parasitism. The questions I asked were: (1) does the relationship between parasitism and nest microhabitat change across habitats for a single host species? and (2) does this relationship change across similar host species in a single habitat? My two study species, Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*), nest in apparently similar microhabitats, but are parasitized at different frequencies. Because Indigo Buntings nest in both old field and adjoining forest, I was able to compare the importance of microhabitat to habitat in explaining parasitism within the same species.

METHODS

My field assistants and I located bird nests in old fields and adjoining forest on the Thomas S. Baskett Wildlife Research and Education center (38°45′N, 92°12′W) near Ashland, Missouri (Boone County) from April through July, 1992–1994. Old fields were located in a matrix of forest in this 920 ha study area. Five upland old fields ranging from 2.4 to 15.4 ha and a lowland old field (16.3 ha) were searched daily for nests. In 1993 and 1994, we also searched a moder-

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ately grazed agricultural field (30.8 ha). Indigo Bunting nests also were found in forested habitat adjoining old field sites. Three sites had long fencerows composed of trees and shrubs. Shrubs at all sites included red cedar (*Juniperus virginiana*), blackberry (*Rubus allegheniensis*), coralberry (*Symphiocarpus orbiculatus*), and wild plum (*Prunus americana*). Trees at the upland sites included American elm (*Ulmus americana*) and oaks (*Quercus* spp.). The third and largest old field site was located in a flood plain and contained several riparian forests along streams and rivers, as well as cottonwood (*Populus deltoides*) and black walnut (*Juglans nigra*) plantations. Forested parts of this site were characterized by hackberry (*Celtis occidentalis*), sycamore (*Platanus occidentalis*), silver maple (*Acer saccarhinum*), and box elder (*Acer negundo*). Two fields were adjoined across roads and the agricultural site adjoined two others. Except where sites were bordered by roads or other sites, all fields were surrounded by mature forest.

Other songbirds nesting in the old fields and adjoining edges included Yellow-breasted Chat (*Icteria virens*), Northern Cardinal (*Cardinalis cardinalis*), Yellow-billed Cuckoo (*Coccyzus americanus*), Blue-winged Warbler (*Vermivora pinus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Gray Catbird (*Dumatella carolinensis*), White-eyed Vireo (*Vireo griseus*), Brown Thrasher (*Toxostoma rufum*), Orchard Oriole (*Icterus spurius*), Blue Grosbeak (*Guiraca caerulea*), Dickcissel (*Spiza americana*), Kentucky Warbler (*Oporonis formosus*), and Common Yellowthroat (*Geothlypis trichas*). Quantities of these species' nests were much smaller (range 1–62, 1992–1995) than those of Field Sparrows and Indigo Buntings. I focused the study on the latter two species because of their abundances and the comparability of their nest sites across and within habitat types.

I flagged nests from at least 3 m distance and monitored them daily during building and egg-laying stages and every 2–3 days thereafter until fledging approached, when they were again monitored daily. I classified nests into two-week initiation intervals starting from 16 April. Nests found after initiation were classified by back-dating from hatching or fledging dates using incubation and nestling periods (Payne 1991, Carey et al. 1994) for both species (Field Sparrows: incubation 11 days, nestling 8 days; Indigo Buntings incubation 12 days, nestling 9 days).

VEGETATION SAMPLING

After termination of nesting, I sampled vegetation in the manner of James and Shugart (1970) to characterize habitat and microhabitat in the vicinity of nests. I counted potential cowbird perches as the number of trees in three stem-diameter categories (10–20, 21–50, and > 50 cm dbh) in a circular 0.04 ha area centered around each nest. Nest height was measured in meters to the bottom of the nest cup, and side nest concealment was estimated as percent of the nest concealed when viewed from the side from each of the four cardinal directions (N, S, E, W) at a distance of 1 m. Top concealment was measured from above at a distance of 1 m. For analysis, side concealment was taken as a mean of the four side measures, and top concealment was considered a separate variable. Bunting nests found under closed forest canopy were classified as forest Indigo Bunting nests and nests in old fields were classified as nonforest Indigo Bunting nests. Nests directly under the forest "dripline" (distance to edge = 0 m) were classified as nonforest nests. Distance to the nearest edge, whether forest edge for nonforest birds or field edge for forest Indigo Buntings, was estimated by pacing (calibrated at 1 m pace^{-1}) to the place where canopy overhangs the field.

Female cowbirds may be attracted to snags (Robbins 1979, Gates and Giffen 1991, Brittingham and Temple 1996), and I often noticed them perched on dead trees, shrubs, fenceposts, and telephone poles. I used a point-quarter method (Noon 1980) to assess distance and height of dead wood perches. Quarter sections lined up in north, south, east, and west directions were determined around each nest. For each quarter, I measured snag distance as distance to the nearest dead tree or shrub ≥ 1 m high, including wooden fenceposts and telephone poles, and estimated the height of the snag (to the nearest m). Distances for some snags often were quite far (> 200 m) from the nest, so I categorized snag distance by intervals (1–10 m, 11–20 m, 21–30 m, 31–40 m, 41–50 m, and > 50 m). I gave each interval a score from 1 to 6 (e.g., 1 = 1–10 m; 6 = > 50 m) and calculated a mean of the distance scores for each nest. Height of the nearest snag was calculated for each nest as the mean height of the four snags (within 50 m) for each nest.

I measured vertical foliage density by dropping a 1-cm diameter rod in each quarter transect at 1 m distance from the nest and counting the number of vegetation touches along the rod below 1 m. Vertical foliage density was calculated as the mean number of touches over the four quarters for each nest.

Concealment and vertical foliage density measurements were not taken for nests where trampling by animals had occurred, or where flooding in 1993 disturbed vegetation. Concealment measurements could not be taken for nests pulled from vegetation by predators. All measurements were taken from 1992–1994, except for vertical foliage density, snag distance, and snag height, which were taken in 1993 and 1994 only.

DATA ANALYSIS

Different nesting biologies and behavior between host species may account for differing parasitism levels (Robertson and Norman 1977, Gochfeld 1979, Briskie et al. 1990), so Field Sparrow and Indigo Bunting nests were analyzed separately. I used logistic regression to analyze the relationship of the habitat and microhabitat variables to frequency of parasitism. For each nest, I analyzed ten variables: nest height, side concealment, top concealment, vertical foliage density, snag distance, snag height, distance to edge, stems 10–20, stems 20–50, and stems > 50 cm dbh. Univariate logistic regressions were run on each variable to determine its potential relationship to parasitism and were kept in a preliminary model if univariate *P* values were 0.25 or less (Hosmer and Lemeshow 1989). Variables were kept in the final model if the probability level for the entire model and each variable was below $\alpha = 0.05$.

Indigo Buntings nesting in forested habitats were much more heavily parasitized than buntings nesting in old fields (see Results). I ran models that included a dichotomous variable for habitat for Indigo Buntings from both habitats combined. If variables were significant, I evaluated interactions by habitat for the combined Indigo Bunting model. Forest and nonforest Indigo Buntings also were analyzed with separate logistic regression models. I performed Hosmer and Lemeshow (1989) goodness-of-fit tests on all models. Models should be considered descriptive in nature, and although suggestive of factors related to parasitism, may not reveal direct causes of parasitism (James and McCullogh 1990).

To elucidate differences in habitat and nest microhabitat between the two hosts, I compared each of 10 variables for combined parasitized and unparasitized nests with ANOVA using forest Indigo Bunting, nonforest Indigo Bunting, and Field Sparrow as the three factor levels. I used the Bonferroni adjustment for joint significance (10 tests; $\alpha = 0.005$) and performed Tukey-Kramer pairwise comparisons to identify significant differences ($P < 0.05$) between species within each variable. For variables that differed between Field Sparrows and nonforest buntings, I compared parasitism frequencies between species of nests above and below the Indigo Bunting median for the variable using chi-square tests. Within each season, all nests initiated prior to and including the day that the last cowbird egg was laid in a nest were considered for analysis. Results for statistical tests are indicated as mean ± SE.

RESULTS

PARASITISM FREQUENCIES

Indigo Bunting nests were parasitized at frequencies of 63.9% ($n = 36$), 52.3% ($n = 65$), and 62.1% ($n = 87$) for 1992, 1993, and 1994, respectively, while Field Sparrows were parasitized at frequencies of 11.7% ($n = 60$), 14.9% ($n = 87$), and 14.8% ($n = 81$), respectively for the same three years. There were no statistically significant differences in parasitism frequencies between years within each species (Field Sparrows $\chi^2_2 = 0.38$, $P > 0.8$; Indigo Buntings: $\chi^2_2 = 1.9$, $P > 0.3$), so all three year's data were combined in the analysis. For all three years combined, 14.0% of Field Sparrow nests ($n = 228$) and 59.0% of Indigo Bunting nests ($n = 188$) were parasitized (Fig. 1). Indigo Bunting nests were parasitized at significantly higher frequencies in forest habitat, with 73% of forest Indigo Bunting nests ($n = 68$) parasitized compared to 50.8% ($n = 120$) of nonforest nests (Fig. 1; $\chi^2_1 = 9.2$, $P < 0.01$). Nonforest Indigo Buntings were more frequently parasitized than Field Sparrows in the same habitat ($\chi^2_1 = 54.4$, $P < 0.001$).

LOGISTIC REGRESSION MODELS

Of 11 variables considered (including habitat) for all Indigo Bunting nests, only the side con-

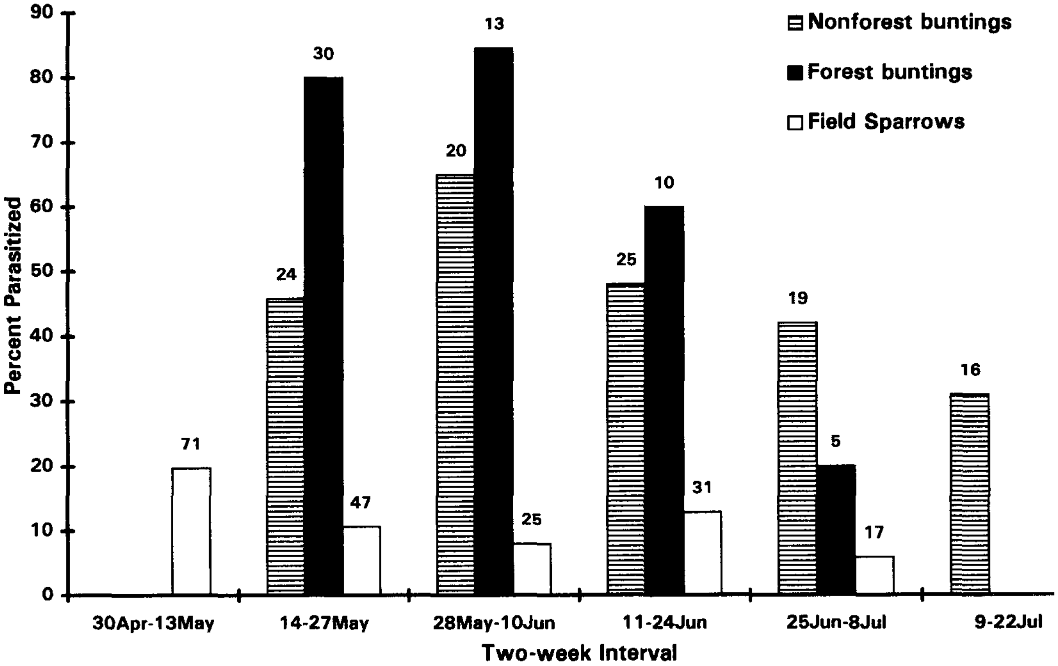

FIGURE 1. Percent of Indigo Bunting and Field Sparrow nests parasitized (*n*) by two-week interval of initiation from 1992–1994. Figure includes only those nests that could be placed into two-week intervals.

cealment variable explained parasitism at a statistically significant level (Table 1; Log-likelihood for model = 212.4, $\chi^2_1 = 4.8$, $P < 0.03$). Neither the habitat variable or a side concealment-by-habitat interaction were significant in explaining parasitism for bunting nests from both habitats combined. The model for nonforest buntings similarly contained side concealment only (Table 1; Log-likelihood for model = 136.4, $\chi^2_1 = 4.8$, $P < 0.03$). For both models, side concealment at parasitized nests was lower on average than at unparasitized nests (Table 1).

A univariate model including side concealment for forest Indigo Bunting nests was not statistically significant (Log-likelihood for model = 68.6., $\chi^2_1 = 0.4$, $P > 0.5$). No other variables significantly explained parasitism for forest Indigo Bunting nests; however, there was a tendency for parasitized nests to have more trees > 50 cm dbh (Wald $\chi^2 = 2.8$, $P = 0.09$) and fewer trees between 10–20 cm dbh (Wald $\chi^2_1 = 3.6$, $P = 0.06$).

None of the 10 variables in univariate logistic regression models explained parasitism for Field Sparrows, although unparasitized Field Sparrow nests tended to have higher mean nest conceal-

TABLE 1. Means of variables and parameter estimates for logistic regression model for all Indigo Bunting nests and nonforest Indigo Bunting nests. Means ± SE (*n*) are for parasitized nests (top row) and unparasitized nests (bottom row).

Model/Variable	Mean % ± SE (*n*) of observations	Parameter estimate ± SE	Wald χ^2	*P*
All Indigo Bunting nests				
side concealment	56.81 ± 2.71 (96) 66.25 ± 3.41 (65)	−0.01 ± 0.01	4.59	0.03
Nonforest Indigo Bunting nests				
side concealment	61.99 ± 3.60 (53) 72.95 ± 3.40 (49)	−0.02 ± 0.01	4.55	0.03

TABLE 2. Comparisons of means ± SE (n) for ten habitat and nest microhabitat variables for all Field Sparrow, nonforest Indigo Bunting, and forest Indigo Bunting nests.

Variable	Species	Mean ± SE (n)	F	$P <$
Nest height (m)	Field Sparrow	0.36 ± 0.02 (225)a	30.2	0.001
	Nonforest bunting	0.65 ± 0.03 (118)b		
	Forest bunting	0.47 ± 0.02 (65)c		
Top concealment (%)	Field Sparrow	77.68 ± 1.96 (195)a	5.9	0.003
	Nonforest bunting	81.33 ± 2.85 (94)a		
	Forest bunting	65.53 ± 4.08 (57)b		
Side concealment (%)	Field Sparrow	89.27 ± 1.07 (198)a	100.6	0.001
	Nonforest bunting	67.25 ± 2.53 (102)b		
	Forest bunting	49.15 ± 3.43 (59)c		
Vertical foliage 1 m	Field Sparrow	11.44 ± 0.38 (164)a	25.3	0.001
	Nonforest bunting	10.33 ± 0.48 (96)a		
	Forest bunting	6.11 ± 0.43 (49)b		
Snag distance (score)	Field Sparrow	2.48 ± 0.10 (168)a	11.9	0.001
	Nonforest bunting	2.74 ± 0.14 (99)a		
	Forest bunting	1.72 ± 0.10 (53)b		
Snag height (m)	Field Sparrow	2.75 ± 0.11 (167)a	11.9	0.001
	Nonforest bunting	2.96 ± 0.20 (92)a		
	Forest bunting	4.12 ± 0.34 (53)b		
Distance to edge (m)	Field Sparrow	20.67 ± 1.49 (226)a	4.5	0.01
	Nonforest bunting	22.81 ± 2.46 (119)a		
	Forest bunting	12.47 ± 2.06 (66)b		
Stems 10–20 cm dbh	Field Sparrow	0.99 ± 0.14 (227)a	123.8	0.001
	Nonforest bunting	1.48 ± 0.23 (120)a		
	Forest bunting	7.06 ± 0.58 (68)b		
Stems 20–50 cm dbh	Field Sparrow	0.68 ± 0.11 (227)a	175.6	0.001
	Nonforest bunting	0.75 ± 0.14 (120)a		
	Forest bunting	5.84 ± 0.43 (65)b		
Stems >50 cm dbh	Field Sparrow	0.03 ± 0.01 (227)a	80.8	0.001
	Nonforest bunting	0.03 ± 0.02 (120)a		
	Forest bunting	0.72 ± 0.11 (65)b		

Tests were calculated with ANOVAs using a Bonferroni adjustment of $\alpha = 0.005$ as the level of significance. Means with the same letter within each variable were not different (Tukey-Kramer multiple comparisons, $P > 0.05$).

ment than parasitized nests (Wald $\chi^2 = 3.3$, $P = 0.07$).

DIFFERENCES BETWEEN HOSTS AND HABITAT TYPES

Field Sparrow and nonforest Indigo Bunting nests differed only for the variables nest height and mean side nest concealment, with Field Sparrow nests significantly lower and better concealed than nonforest Indigo Bunting nests (Table 2). Parasitism frequency was lower both for Field Sparrows at or above the median nonforest Indigo Bunting nest height of 0.6 m (Field Sparrows 17.3%, $n = 23$ nests; Indigo Buntings 55.0%, $n = 60$ nests; $\chi^2_1 = 9.5$, $P = 0.002$) and below the median bunting nest height (Field Sparrows 13.9%, $n = 202$ nests; Indigo Buntings 46.6%, $n = 58$ nests; $\chi^2_1 = 28.9$, $P = 0.001$). Similarly, parasitism frequency was lower for Field Sparrow nests at or above the median nonforest Indigo Bunting side concealment of 70% (Field Sparrows 12.6% parasitized, $n = 182$ nests; Indigo Buntings 41.2% parasitized, $n = 51$ nests; $\chi^2_1 = 21.2$ $P = 0.001$) and below the median bunting nest concealment (Field Sparrows 18.8% parasitized, $n = 16$ nests; Indigo Buntings 62.8% parasitized, $n = 51$ nests; $\chi^2_1 = 9.4$ $P = 0.002$).

All forest Indigo Bunting variables differed significantly from both nonforest Indigo Bunting and Field Sparrow variables, except for distance to edge (Table 2). The overall difference for distance to edge did not meet the $P = 0.005$ criteria for significance, but Tukey tests indicated significant differences ($P = 0.05$) between Field

Sparrows versus forest buntings, and nonforest versus forest buntings.

DISCUSSION

The most prominent results from this study are differences in parasitism frequencies among Indigo Buntings nesting in different habitats and among Field Sparrows and nonforest Indigo Buntings nesting in the same habitat (Fig. 1). Side concealment explained parasitism for all Indigo Buntings and those in nonforest habitat, but not for Indigo Buntings in forests alone. Parasitism frequency increased sequentially from Field Sparrows, to nonforest buntings, to forest buntings, whereas side nest concealment decreased within this sequence (Table 2).

Lack of a relationship between concealment and parasitism within heavily-parasitized forest Indigo Buntings suggests that habitat may be more important in determining parasitism than nest concealment. Although forest Indigo Bunting nests were not as well concealed as nonforest bunting nests (Table 2), higher parasitism in forests may occur because of habitat preference by cowbirds rather than poor nest concealment. Although I did not measure cowbird abundance, previous radio-telemetry studies of cowbirds at the same sites (Thompson 1994) have shown that female cowbirds overwhelmingly favor forested habitats in the morning, which is the time when they are engaged in breeding activity (Rothstein et al. 1984, Thompson 1994). Hahn and Hatfield (1995) found higher parasitism frequencies in forest than old field songbird communities, and suggested that cowbird preference for forest hosts or habitats were the cause. For one host found in both habitats (Eastern Phoebe, *Sayornis phoebe*) they similarly found much higher parasitism frequencies in the forest. In the present study, forest Indigo Bunting nests were extremely susceptible to cowbird parasitism, with parasitism frequencies approaching 90% early in the breeding season (Fig. 1). If higher parasitism frequencies in forest are driven by cowbird habitat preference, it appears that forest bunting nests are so vulnerable to cowbirds that nest concealment makes no difference.

Differences in parasitism frequency between nonforest Indigo Buntings and Field Sparrows may be attributable to the latter having lower placement and better concealment, but even the highest and most poorly concealed Field Sparrow nests were parasitized less frequently than comparable bunting nests. Smith (1981) found no relationship between concealment and parasitism at the nests of Song Sparrows (*Melospiza melodia*). Briskie et al. (1990) found that despite having better concealment, Yellow Warbler (*Dendroica petechia*) nests were more heavily parasitized than nests of Least Flycatchers (*Empidonax minimus*). Studies have shown varying results on the importance of nest height, with some indicating higher parasitism at low nests (Briskie et al. 1990, Hahn and Hatfield 1995) and others indicating higher parasitism at high nests (Robinson 1992, Martin 1993). Other factors, such as host behaviors (Robertson and Norman 1977, Uyehara and Narins 1995, Burhans, in press), or host choice by cowbirds (Gochfeld 1979, Fleischer 1986, Mason 1986), may contribute to parasitism differences between Field Sparrows and Indigo Buntings. Nonforest Indigo Buntings and Field Sparrows appear to have very similar nest sites, and I often found multiply parasitized Indigo Bunting nests within a few meters of active unparasitized Field Sparrow nests having similar heights.

Results of this study suggest that whereas nest microhabitat features such as concealment can partly explain parasitism, their importance may depend upon habitat and host species characteristics. A nest microhabitat variable, side concealment, explained parasitism frequency for Indigo Buntings from both habitats combined and for moderately-parasitized nonforest Indigo Buntings, but did not explain parasitism for heavily-parasitized forest buntings. For forest-nesting Indigo Buntings, nest microhabitat features appear to be overridden by habitat type. Although Field Sparrow nests are better concealed than Indigo Buntings, they appear to possess characteristics unrelated to nest microhabitat that make them less vulnerable to parasitism than Indigo Buntings. These results suggest that researchers also should consider factors such as cowbird abundance (Hoover and Brittingham 1993, Robinson et al. 1995), cowbird habitat preference (Zimmerman 1983, Hahn and Hatfield 1995), or host species characteristics (Gochfeld 1979, Mason 1986), when addressing the relationship of nest site and microhabitat features to cowbird parasitism.

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