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VARIATION IN LOCAL-SCALE EDGE EFFECTS: MECHANISMS AND LANDSCAPE CONTEXT

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Abstract. Ecological processes near habitat edges often differ from processes away from edges. Yet, the generality of "edge effects" has been hotly debated because results vary tremendously. To understand the factors responsible for this variation, we described nest predation and cowbird distribution patterns in forest edge and forest core habitats on 36 randomly selected plots in three states in the midwestern United States. We tested four hypotheses that may explain the variation and mechanisms responsible for edge effects among the 36 plots: (1) the landscape context, (2) the local predator community, (3) the local bird (host–prey) community, and (4) the nest site microhabitat structure. We used artificial nests baited with quail and clay eggs to determine nest predation patterns and predators and used point count surveys to determine cowbird and host abundance in forest edge and forest core habitats.

Raccoons, opossums, canids, and birds accounted for most predation of artificial nests. Neither local host abundance nor mean nest concealment of artificial nests significantly influenced nest predation rates in habitat edge or in habitat core. Nest predation was significantly greater in highly fragmented landscapes than in unfragmented landscapes and was significantly higher in edge habitats than in core habitats. However, detection of edge effects varied, depending upon landscape type. Higher predation rates in edge habitats were detected in highly and moderately fragmented landscapes, but not in unfragmented landscapes. Both mammalian and avian predator groups contributed to higher predation rates along edges in highly and moderately fragmented landscapes.

Cowbird abundance was significantly related to host abundance, but the effect of hosts varied depending upon habitat type. In edge habitats, cowbird abundance was negatively associated with host abundance in all three landscapes studied. By contrast, cowbird abundance was positively associated with host abundance in core habitats. Once the effects of host abundance were removed, cowbird abundance in core habitat was greater in highly fragmented landscapes than in moderately and unfragmented landscapes, but did not differ between the latter two. In edge habitat, cowbird abundance did not differ between landscapes, but abundance in edges tended to be highest in the highly fragmented landscape and lowest in the unfragmented landscape. Cowbird abundance did not vary between edge and core habitat in any of the landscapes studied.

We suggest that the first approximation to predicting the impact of agricultural or permanently managed edges on forest songbird reproductive success is to assess habitat characteristics at the landscape scale. Given geographic location, local factors such as host abundance and predator composition should be assessed.

Key words: Brown-headed Cowbirds; edge effects; forest songbirds; habitat landscapes and fragmentation; host–Cowbird relationships; Molothrus ater; *nest predation; predator community.*

INTRODUCTION

Ecological processes near habitat edges often differ from processes away from edges, and the generality of "edge effects" has been hotly debated (e.g., Reese and Ratti 1988, Paton 1994). For forest-nesting migratory birds, the presence of forest edge, often a sharp boundary between a forest and surrounding pasture, cropland, or residential area, may represent a hostile environment because of increased nest predation and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*, Askins 1995). Negative correlations exist between the amount of habitat edge at the landscape scale and the proportion of nests that are parasitized or lost to predation (Robinson et al. 1995), and parasitism and predation directly affect the viability of local populations for some forest nesting species (Robinson 1992, Porneluzi et al. 1993, Donovan et al. 1995*b*). Yet, forest edges per se might not create this hostile nesting environment. Studies that specifically test for edge-re-

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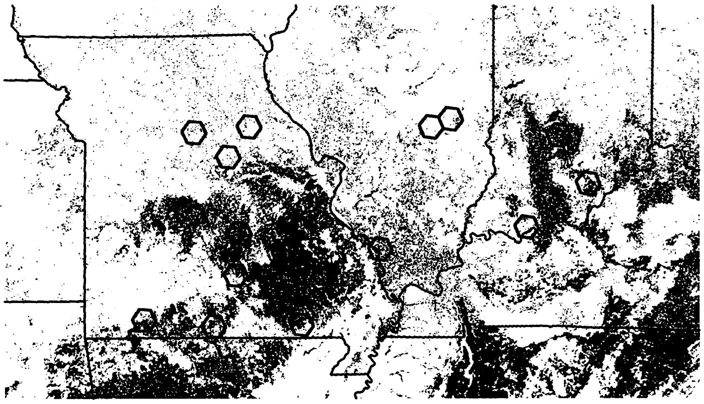

FIG. 1. Location of study region and 18 study hexagons located in highly fragmented, moderately fragmented, and unfragmented landscapes.

lated increases in nest predation and parasitism show varying results (reviewed in Paton 1994). In some studies, nest predation and cowbird parasitism levels are significantly higher near edges; other studies demonstrate that levels of nest predation and parasitism are similar in edge and in core habitats. Documenting the existence (or lack thereof) of edge effects should no longer be the focus of ecological and conservation debates for birds. Rather, understanding the conditions that lead to edge effects should be pursued.

We tested four hypotheses that might explain this variation in edge effects in nest predation patterns: (1) forest composition at the landscape scale, i.e., does the proportion of forest in the surrounding landscape affect predation levels and whether edge effects exist (Yahner 1988, Martin 1992)?; (2) local-scale host–prey abundance, i.e., are nest predation levels higher near edges because of an increased abundance of potential food sources (nests) for predators near edges (Gates and Gysel 1978)?; (3) local-scale predator community, i.e., is a dominant nest predator or nest predator community responsible for edge effects due to their foraging behavior (Andren and Angelstam 1988, Nour et al. 1993, Yosef 1994)?; and (4) local-scale nest-microsite concealment, i.e., are nests near edges less concealed by vegetation than are core nests, leading to increased predation there (Ambuel and Temple 1983, Martin and Roper 1988)?

For Brown-headed Cowbird distribution, we tested whether distribution in edge and core habitats depend upon (1) landscape habitat composition, i.e., does the proportion of forest in the surrounding landscape impact cowbird abundance and the distribution of cowbirds in edge and core habitat (Donovan et al., *in press*); and (2) local-scale host abundance, i.e., do edge effects vary depending upon the local abundance of potential hosts for cowbirds to parasitize (Robinson et al., *in press*, Thompson et al., *in press*)?

Our objectives were to document nest predation and cowbird distribution patterns in forest edge and forest core habitat on 36 forest plots in the Midwestern United States; and to test the hypotheses previously described to explain the observed variation in edge effects among the 36 plots.

STUDY AREA AND METHODS

Experimental design

We used a completely randomized split-plot experimental design to document cowbird and nest predation patterns in 18 locations within a defined region in Illinois, Indiana, and Missouri (Fig. 1). These locations (replicates) varied in the amount of forest cover at the landscape scale: (1) highly fragmented landscapes (<15% forest cover, $n = 6$ replicate locations); (2) moderately fragmented landscapes (45–55% forest cover, $n = 6$); and (3) unfragmented landscapes (>90% forest cover, $n = 6$; Fig. 1). Data were collected on two plots in each study location ($N = 36$ plots). In each plot, cowbird distribution and nest predation patterns were determined in two habitat types, forest edge and forest core. We used a split-plot analysis because more than one measurement was made on each plot (edge and core habitats were both measured). The main effects in our model were landscape (three levels of forest cover at the landscape scale) and habitat (edge vs. core habitat). We also measured host abundance, nest predator community composition, and nest-site microhabitat characteristics (nest concealment) on study plots within each location to determine the mechanisms that best explain why predation and cowbird distribution patterns vary.

Study region and study plot selection

We defined our study region to minimize geographic differences in migratory bird breeding phenology while simultaneously encompassing a broad range of landscape configurations, nest predator community structures, and cowbird abundance. The study region was entirely within the Ozark Broadleaf Forest Ecoregion in the United States (McNab and Avers 1994), and consisted of oak–hickory forest and mixed hardwood forest. Dominant tree species within the oak–hickory forest included white, black, scarlet, and northern red oak; and dominant tree species within the mixed hardwood forest included yellow poplar, white oak, northern red oak, sugar maple, and beech (Braun 1950, Eyre 1980).

We used a Geographic Information System (GIS) (MicroImages, Incorporated, Lincoln, Nebraska) to randomly select study locations within our study region. We derived a forest cover map with a 1-km resolution and Lambert's azimuthal equal area projection from the Forest Maps of the United States 1993 Resource Planning Applications Program (USDA Southern Forest Experiment Station advanced high-resolution radiometry data). We overlaid the forest cover map with a grid of ~300 hexagons (18 km per side, 864 km^2 area) in a random fashion. We obtained forest cover statistics for each hexagon and identified hexagons with <15%, 45–55%, or >90% forest cover. These landscape classes are the main effect of landscape in our split-plot analyses. Our research was confined to public lands, so we eliminated all hexagons that did not contain public land from the pool of potential study locations. We randomly selected six hexagon locations from each landscape category (Fig. 1). Hexagons were rejected if suitable study plots within the hexagon could not be located or if they abutted a previously selected hexagon. The sole exception to this sampling scheme occurred in central Illinois, where two adjacent hexagons were sampled due to limited public lands. The random selection of hexagons and the size/distribution of hexagons were thought to ensure independence of cowbird and predator communities among the locations we studied; most predator and cowbird home ranges do not exceed this scale (Thompson 1994). Hexagon locations were considered replicates in split-plot analyses; thus, $n = 6$ replicate hexagon locations per forest landscape category. Total sample size was $N = 18$.

Within each hexagon, we established two study plots ($N = 36$ study plots). Study plots were mature forests with ample core habitats (forest habitat >60 yr of age and >250 m from any habitat edge) that were adjoined by agricultural fields (row crop, hay, pasture), early successional old fields, or by managed (mowed, burned) wildlife openings that exceeded 300 m in width. We identified potential plot locations within each selected hexagon. For most hexagons, only a few locations met our criteria for plot establishment. If more than two potential plot locations were identified in a hexagon, we randomly selected two plots for study. In all hexagons, the two plots were geographically separated by >5 km.

In each study plot, five sampling points, >200 m apart, were established in both forest-edge habitat and forest-core habitat. Edge sampling points were located 50 m from the edge, and core sampling points were located >250 m from any type of edge or major disturbance. These habitat classes are the main effect of habitat in our split-plot analyses. In nine plots, only nine points could be physically established, but most plots consisted of 10 sampling points. In total, 350 points were sampled: 115–119 points in each landscape, 171 points in forest-edge habitat, and 179 points in forest-core habitat.

We measured four habitat characteristics on each point in each plot. We recorded the species and diameter of trees >3 cm diameter at 1.3 m above ground (diameter at breast height, i.e., dbh) that were selected with a two-factor metric prism. We estimated canopy closure by averaging four spherical densiometer readings taken at each point, and estimated the percentage of live, woody, and herbaceous ground covers <1.3 m tall within a 2-m radius circle centered on the point. We calculated mean tree diameter, mean basal area, mean canopy closure, and mean ground cover for each landscape × habitat combination.

Point count protocol

We used 10-min point counts to survey cowbird and host abundance at each sampling point in each plot (Ralph et al. 1995). Surveys began after migratory bird territories were established and ended before most nests had fledged (12 May–17 June 1995). Counts began 15 min after sunrise and continued until all 10 points on a plot were sampled (~2.5–3 h after sunrise). We recorded bird observations within 50 m of the point. Although this limited the total number of bird detections, use of a fixed-radius sampling protocol ensured that both forest edge and core habitats were equally sampled, and that cowbirds were utilizing the habitats we sampled. Four trained observers conducted surveys. Each plot was surveyed by two different observers, and all observers surveyed approximately half of the study plots. To minimize observer effects across landscapes and habitats, all observers surveyed an equal portion of landscape and habitat types. For each point, we determined the maximum number of observations for each species across the two surveys, and used this number to compute the mean detections ($n = 5$) of cowbirds and hosts in each treatment in each plot (F. Thompson, *personal communication*).

We surveyed male and female cowbirds (based on call type, Darley 1968) and all potential cowbird hosts. Use of surveys to assess potential parasitism pressure on songbirds is justified because cowbird abundance is highly correlated with parasitism levels within our study area (Thompson et al., *in press*). Surveyed hosts were predominantly singing males, and included those species that breed during the time cowbirds actively lay eggs and also receive cowbird eggs in >10% of the nests (based on nests located within the study region [Robinson et al. 1995 and references therein]), and on parasitism rates from the literature (Friedman and Kiff 1985). Possible errors in host detection may have occurred because hosts vary widely in their detectability, and because females of some species may also sing (e.g., Northern Cardinal, *Cardinalis cardinalis*). However, because the study plots within our study region were randomly selected and contained a similar complement of host species, errors in host detectability should have been distributed randomly across landscapes and habitats.

Artificial nest protocol

In each study plot, we used artificial nests to determine nest predation rates in edge and core habitat, and documented the nest predator and nest-site microhabitat associated with each artificial nest. Although artificial nests may not reflect daily survival rates of real nests (Willebrand and Marcstrom 1988, Reitsma et al. 1990), they can be used to document generalized nest predation patterns (Paton 1994). We established 15 nests in each treatment (core and edge), so 30 nests were established in each plot ($N = 1080$ nests). Nest positions were randomly established within 50 m of the forest edge for the edge treatment, and within a 50-m wide transect in the forest core for the core treatment. To reduce the probability that a small number of predators were responsible for all predation events (Laurance and Yensen 1991), we positioned all nests no less than 50 m from other nests in the treatment.

Artificial nests were commercial canary wicker baskets (10.5 cm in diameter × 5.5 cm deep) that were placed on the ground and partially concealed with leaf and grass litter to simulate a generic ground nesting warbler (Wilcove 1985). We wore latex gloves when handling nests and eggs to reduce human scent. Although human scent can influence predation rates on artificial nests (Whelan et al. 1994), all nests were established in the same manner, so any biases were distributed equally across landscapes and habitats. We baited each nest with one Northern Bobwhite (*Colinus virginiana*) egg and one artificial (clay) egg. Use of clay eggs allowed better assessment of predators, including small predators that may be physically incapable of depredating quail eggs (Haskell 1995). Clay eggs were formed from Sculpie brand modeling compound (Polyform Products, Incorporated, Shiller Park, Illinois) and mimicked quail eggs in shape and color. We checked and scored each nest as depredated or not depredated after five full nights of exposure. We considered a nest as depredated when either the clay or quail egg showed evidence of predation. We collected the clay eggs and identified nest predators by examining tooth or beak impressions made in the clay (Møller 1987, 1989, Haskell 1995; P. Porneluzi, *personal communication*).

To test the nest microsite concealment hypothesis, we measured concealment of each artificial nest with a card containing 25 (3.5 cm × 3.5 cm) colored squares arranged in a five-by-five checkerboard fashion. We placed the card at the nest location, examined the card at a distance of 1 m perpendicular to the card, and counted the number of squares that were <50% obstructed by vegetation. We obtained five concealment measurements at each nest location, one measurement in each of the four cardinal directions parallel to the ground and one measurement from the top of the nest. Scores ranged from 0–25 unobstructed squares, and we calculated the mean of all five scores to obtain a single nest-concealment score for each artificial nest.

Data analyses

General analyses.—We calculated mean cowbird abundance and nest predation rates (number of depredated nests divided by 15) for each habitat in each plot ($N = 72$). We assessed the normality of these and other variables by examining stem-and-leaf plots and normal probability plots of residuals (SAS/STAT 1990). We used Bartlett's test and examined residual patterns to assess homogeneity of variance. Nest predation rates were transformed using standard arcsine square-root transformations to stabilize variances and normalize data. Mean host abundance and mean nest concealment met standard criteria for analysis of variance. Mean cowbird abundance data, however, were not normally distributed and had unequal variances, and transformations did not remedy these violations. Therefore, we ranked cowbird abundance and ranked host abundance across all plots to assess cowbird distribution across landscapes and habitats (Conover and Iman 1981, Potvin and Roff 1993). We used a completely randomized split-plot analysis to examine how mean ranked cowbird abundance and nest predation rates were distributed across habitat types (edge or core) and landscapes, and tested potential interactions between the two main effects (i.e., tested the landscape hypothesis). In each analysis, replicate hexagon locations ($n = 6$) within forest landscape categories were used as the error term to test the main effect of landscape, and replicate hexagons within landscapes × habitat were used as the error term to test the main effect of habitat and the interaction between habitat and landscapes. In all analyses, we examined post hoc comparisons of means among the landscapes and treatments (least squares means procedure, SAS/STAT 1990) and adjusted the significance level to maintain an experiment-wise Type I error rate of 0.05.

Covariate analyses.—To assess cowbird abundance in different landscapes and different habitats, we used the general analysis described above but included mean ranked host abundance as a covariate. Similarly, we assessed transformed nest predation rates, but included both mean host abundance and mean nest concealment as covariates. The use of covariates provided a method to test the effect of the covariate on the response variable (cowbird abundance and predation rates), and to adjust means after the effects of the covariate were removed. For example, if cowbirds cue into hosts, use of hosts as a covariate allowed determination of the response of cowbirds to hosts, and also allowed determination of the effects of landscape and habitat once the effect of hosts was removed. For both cowbird and

TABLE 1. Results of split-plot analysis of variance for host abundance, nest concealment, nest predation rate (adjusted and unadjusted for host abundance), avian predation, mammalian predation, and cowbird abundance.

Dependent variable	Hex:Landscape MS, df	Hex:Landscape × Habitat MS, df	Landscape MS, df (*P*)	Habitat MS, df (*P*)	Landscape × Habitat MS, df (*P*)
Host abundance	9.61, 15	0.82, 15	6.20, 2 (0.54)	0.17, 1 (0.66)	0.77, 2 (0.41)
Ranked host abundance	1214.6, 15	125.2, 15	872.5, 2 (0.50)	5.55, 1 (0.84)	143.2, 2 (0.34)
Nest concealment	18.80, 15	4.74, 15	48.19, 2 (0.11)	119.23, 1 (0.0002)	7.78, 2 (0.23)
Nest predation (no covariates)	0.88, 15	0.036, 15	0.48, 2 (0.016)	0.31, 1 (0.011)	0.18, 2 (0.021)
Nest predation (host covariate)	0.087, 15	0.045, 15	0.25, 2 (0.10)	0.33, 1 (0.016)	0.19, 2 (0.034)
Mammalian predation	0.093, 15	0.037, 15	0.21, 2 (0.14)	0.13, 1 (0.085)	0.16, 2 (0.032)
Avian predation	0.022, 15	0.018, 15	0.049, 2 (0.14)	0.12, 1 (0.020)	0.020, 2 (0.35)
Ranked cowbird abundance	716.1, 15	126.1, 15	4590.5, 2 (0.0097)	382.7, 1 (0.10)	482.7, 2 (0.045)

Note: MS, df, and *P* are mean squares, degrees of freedom, and significance level. Main effects were landscape type (highly, moderately, and unfragmented landscapes) and habitat type (edge vs. core). In each analysis, replicate hexagons within forest landscape categories (hex:landscapes) were used as the error term to test the main effect of landscape, and replicate hexagons within landscapes × habitat (hex:landscape × habitat) were used as the error term to test the main effect of habitat and the interaction between habitat and landscapes. Cowbird analyses are based on ranked abundances and are unadjusted for host abundance, a significant covariate.

nest predation analyses, we performed two statistical tests to determine whether covariance analysis was appropriate. First, because the covariates should not be influenced by the landscapes or habitats in any way, we used the split-plot model to determine how each covariate was distributed to allow clear interpretation of results (Neter et al. 1990). Second, we tested whether slopes of each covariate were parallel across all main effects, a requirement of covariate analysis (Neter et al. 1990). If the covariate interacted with any main effect, we analyzed data separately depending on the nature of the covariate × main effect interaction. For all models, we refer to these tests as "full model" tests. In the final (reduced) models, we included the covariate if the covariate itself was significant and met the requirements of covariate analysis, and excluded the covariate if it was not significant (Neter et al. 1990). The results of these analyses indicated the relationship between the covariate and the dependent variables, and indicated the relationship between the dependent variable and the main effects once the effect of the covariate was removed.

Predator identification.—To test whether particular nest predators accounted for the variation in edge effects among the 36 study plots, we described the predator community for each landscape and habitat type. We used a Fisher's Exact Test for each predator to test for differences in predation patterns among landscapes and among habitats. Because the number of predation observations for each species was small, we also grouped nest predators into avian and mammalian predator guilds. We tested whether the variation in predation patterns differed among the two guilds by analyzing predation rates using the split-plot analysis previously described for each predator guild separately. Covariates were not used in these tests.

RESULTS

Habitat characteristics of study plots

Our stringent plot criteria partially ensured that all plots were similar in habitat structure. Although the plots varied in tree species composition, the mean number of stems per hectare, mean basal area, and mean canopy closure did not differ among the landscape and habitat combinations (one-way ANOVA, $P = 0.59$, 0.24, and 0.73, respectively). Mean ground cover and dbh varied among the landscape and habitat combinations ($P = 0.0001$ for each), but neither varied systematically among landscapes and habitats; both variables were thought to have little influence on predation levels or on cowbird abundance.

General covariate relationships in landscapes and habitats

Host abundance did not vary among landscapes or habitats, nor was there an interaction between landscapes and habitats (Table 1 and Fig. 2). Nest concealment did not differ among landscapes, but was significantly greater in edge habitats than in core habitats. This pattern held for all landscapes (Table 1). Thus, to clearly evaluate the influence of nest concealment on predation patterns, we evaluated edge and core habitats separately.

Nest predation patterns

We were unable to relocate 16 of the 1080 nests established among the different landscapes and habitats, and omitted these nests from our analyses. Of the 1064 relocated nests, 344 quail eggs and 326 clay eggs showed signs of predation, and 367 nests were scored as depredated. Twenty-three of the 36 plots showed higher predation rates in edge habitats than in core habitats.

In the full model with covariates, nest concealment did not influence predation levels on artificial nests ($F = 2.06$, df = 1, $P = 0.16$), so the regression slopes between the nest concealment and predation rate were not significantly different from zero (Fig. 3). This pattern held when examining core and edge habitats separately ($F = 0.00$, df = 1, $P = 0.98$; and $F = 0.15$, df

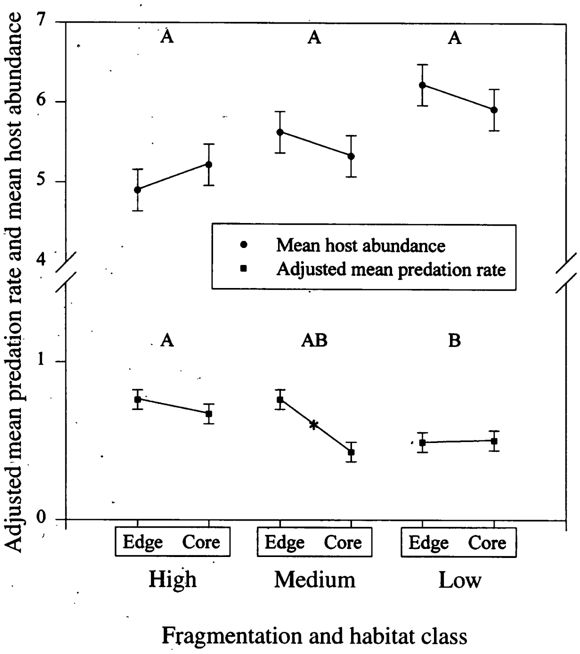

FIG. 2. Mean host abundance and predation rates in edge and core habitats in highly fragmented (high), moderately fragmented (medium), and unfragmented landscapes (low). Fragmentation classes with the same letter were not significantly different. Within landscapes, habitat means separated by an asterisk were significantly different.

= 1, $P = 0.70$ in core and edge habitats, respectively). Additionally, this pattern held across all landscape types (concealment × habitat × landscape interaction $F = 0.44$, df = 2, $P = 0.65$; Fig. 3). Therefore, we rejected the hypothesis that increased predation along edges is driven by nest site microhabitat features.

Host abundance, however, was a significant covariate in explaining nest predation patterns ($F = 5.71$, df = 1, $P = 0.025$; Fig. 3). Contrary to our predictions, nest predation increased as host abundance decreased in both edge and core habitats (Fig. 3). This pattern held for all landscape types (host abundance × habitat × landscape interaction $F = 1.56$, df = 2, $P = 0.23$). Therefore, we rejected the hypothesis that increased nest predation rates along edges are due to increased host abundance along edges. To ensure that predation means were properly adjusted for host abundance, we used a reduced model that included hosts as a covariate but excluded nest concealment as a covariate. This reduced model allowed us to test the landscape hypothesis, i.e., test for differences in predation rates among landscapes and habitats and their interaction once the effect of host abundance was removed.

The reduced split-plot model on nest predation rates was significant (Table 1). Nest predation patterns differed among landscapes and among habitats. Nest predation levels were higher in habitat edges than in habitat cores, but this pattern interacted with landscape (Table 1 and Fig. 2), indicating that edge effects varied depending upon landscape type. We examined five post hoc mean comparisons of predation rates: we tested for differences in predation levels among landscapes and between edge and core habitats separately for each landscape. Predation rates did not differ between highly and moderately fragmented landscapes ($P = 0.21$, Fig. 2), but tended to be higher in highly fragmented landscapes than in unfragmented landscapes ($P = 0.035$). In highly fragmented landscapes where nest predation levels were high, nest predation levels were slightly but not significantly higher in edge habitats than in core habitats ($P = 0.31$). In moderately fragmented land-

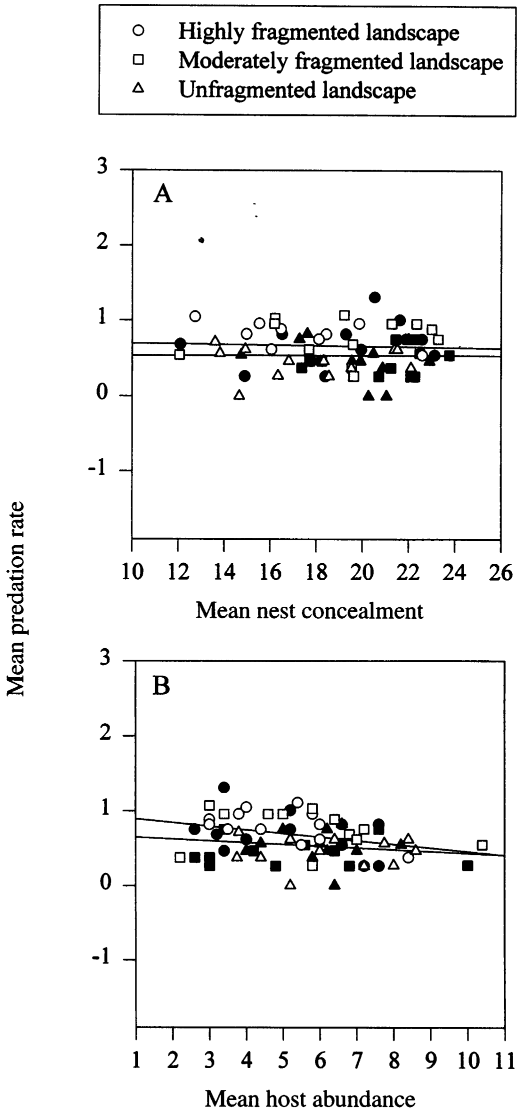

FIG. 3. (A) Relationship between mean nest predation rate and average nest concealment (number of unobstructed squares) of artificial nests in edge (open symbols, upper regression line) and core (filled symbols, lower regression line) habitats. (B) Mean nest predation rate and mean host abundance in edge (open symbols, upper regression line) and core habitats (filled symbols, lower regression line).

TABLE 2. Number (percentage) of clay eggs depredated by each nest predator in each landscape and habitat type, based on 1066 possible predations by each predator. Eggs depredated by more than one predator were scored as a predation attempt by all contributing predators.

Predator	Number predated, total (%)	Landscape				Habitat		
		High	Moderate	Low	P	Edge	Core	P
Bird	35 (10.1)	18 (5.2)	11 (3.2)	6 (1.7)	0.049	22 (6.3)	13 (3.7)	0.126
Canid	36 (10.3)	16 (4.2)	8 (2.3)	12 (3.4)	0.252	15 (4.3)	21 (6.0)	0.397
Chipmunk	14 (4.0)	7 (2.0)	3 (0.9)	4 (1.1)	0.418	9 (2.6)	5 (1.4)	0.298
Coyote	5 (1.4)	3 (0.9)	1 (0.3)	1 (0.3)	0.545	4 (1.1)	1 (0.3)	0.217
Fox	4 (1.1)	3 (0.9)	0 (0.0)	1 (0.3)	0.183	3 (0.9)	1 (0.3)	0.373
Opposum	41 (11.8)	13 (3.7)	13 (3.7)	15 (4.3)	0.902	26 (7.5)	15 (4.3)	0.082
Raccoon	91 (26.1)	36 (10.3)	36 (10.3)	19 (5.5)	0.028	43 (12.4)	48 (13.8)	0.661
Rodent	14 (4.0)	6 (1.7)	5 (1.4)	3 (0.9)	0.671	10 (2.9)	4 (1.1)	0.116
Skunk	8 (2.3)	2 (0.6)	2 (0.6)	4 (1.1)	0.613	3 (0.9)	5 (1.4)	0.726
Squirrel	4 (1.1)	1 (0.3)	1 (0.3)	2 (0.6)	0.702	3 (0.9)	1 (0.3)	0.373
Unknown mammal	21 (6.0)	7 (2.0)	12 (3.4)	2 (0.6)	0.021	13 (3.7)	8 (2.3)	0.281
Unknown predator	3 (0.9)	2 (0.6)	1 (0.3)	0 (0.0)	0.665	2 (0.6)	1 (0.3)	0.624
Missing	72 (20.7)	46 (13.2)	15 (4.3)	11 (3.2)	0.001	48 (13.8)	24 (6.9)	0.001
Total	348 (100)	160 (46)	108 (31)	80 (23)		201 (58)	147 (42)	

Note: P indicates significance value of Fisher's exact test for differences among landscapes and among habitats.

scapes where predation was moderate, predation levels were significantly higher in edge habitats than in core habitats (P = 0.0017). In unfragmented landscapes where nest predation levels were low, predation was slightly but not significantly higher in core habitats than in edge habitats (P = 0.85, Fig. 2). These results support the hypothesis that the percentage of forest cover at the landscape scale influences predation levels and the existence of edge effects.

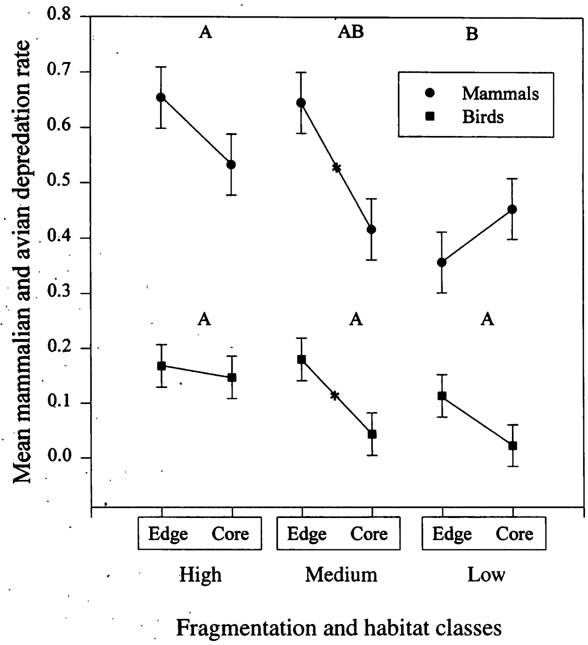

FIG. 4. Mean mammalian and avian predation rates in edge and core habitats in highly fragmented, moderately fragmented, and unfragmented landscapes. Fragmentation classes with the same letter were not significantly different. Within landscapes, habitat means separated by an asterisk were significantly different.

Predator identification

Of the 1064 nests, 326 clay eggs (30.6%) showed signs of predation (Table 2). Seventy-two of the depredated clay eggs were carried away by the nest predator, making identification impossible. Twenty-two eggs showed signs of predation by more than one predator species. Twenty-one predations were executed by unknown mammalian predators, and three predation cases defied identification of any sort (Table 2). Other unknown predators were classified in generic categories such as canid or rodent.

Raccoons, opossums, unknown canids, and birds accounted for most of the predation events (26.1, 11.8, 10.3, and 10.1%, respectively). Bird and raccoon predation patterns varied among landscapes, but did not differ between edge and core habitats (Table 2). The proportion of clay eggs that were removed by the predator was highest in highly fragmented landscapes and along edges (Table 2); unfortunately this removal of clay eggs prohibited the evaluation of edge effects on a predator-by-predator basis.

The split-plot model for predation by mammals as a group was not significant. However, predation patterns varied depending upon landscape and habitat type (Table 1). Predation by mammals tended to be higher in highly fragmented landscapes than in unfragmented landscapes (P = 0.054, Fig. 4), but rates in moderately fragmented landscapes were not significantly different than in either highly or unfragmented landscapes (P = 0.52 and P = 0.17, respectively). Increased predation rates along edges were detected but depended on landscape type (Table 1). Predation rates did not differ between habitats in either highly fragmented or unfragmented landscapes (P = 0.14 and 0.24, respectively), but were greater in habitat edges than habitat cores in moderately fragmented landscapes (P = 0.0102, Fig. 4).

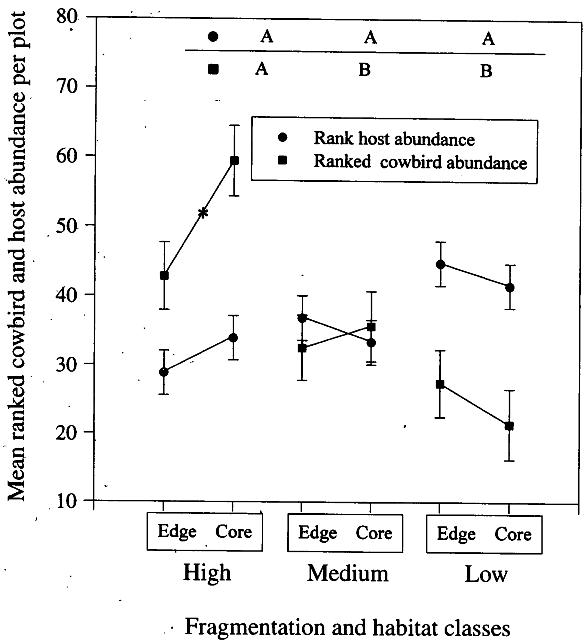

FIG. 5. Mean ranked cowbird abundance and mean ranked host abundance in edge and core habitats in highly fragmented, moderately fragmented, and unfragmented landscapes. Adjusted mean ranked cowbird abundance shows nearly identical pattern. Fragmentation classes with the same letter were not significantly different. Within landscapes, habitat means separated by an asterisk were significantly different.

Few nests were depredated by birds. Avian predation patterns did not differ among landscapes (Table 1), but differed between edge and core habitats (Table 1); the frequency of predation was higher in edge than in core locations. This pattern was consistent (Fig. 4).

Based on these results, the local-scale predator community hypothesis was weakly supported. Both mammals and birds contributed to edge effects. Mammalian predation along edges appeared to be driven by landscape type, but analyses on a predator-by-predator basis did not indicate that a single predator species was responsible for most predation events along edges. Avian predation patterns, however, indicated increased predation levels along edges in all landscape types.

Cowbird abundance

The simple model of ranked cowbird abundance (without hosts as a covariate) was highly significant (Table 1). Variation among hexagons within a landscape accounted for much of the variation, indicating that local factors significantly influenced cowbird distribution. Landscape factors also significantly influenced cowbird distribution: cowbird abundance was significantly greater in highly fragmented landscapes than in moderately fragmented ($P = 0.035$) and unfragmented landscapes ($P = 0.0031$), but abundance in moderately and unfragmented landscapes did not differ ($P = 0.25$; Fig. 5). We did not detect increased cowbird abundance along edges (Table 1; Fig. 5). Cowbird abundance was significantly greater in core habitats than in edge habitats in highly fragmented landscapes ($P = 0.0064$); no differences were detected in moderately fragmented landscapes ($P = 0.52$). Only in unfragmented landscapes did cowbird abundance tend to be greater along edges, but this difference was not significant ($P = 0.62$; Fig. 5).

Host abundance was a significant covariate, but the influence of hosts on cowbird abundance depended upon habitat type (host × habitat interaction, $P = 0.016$). Cowbird abundance appeared to be positively related to host abundance in core habitats, but not in edge habitats (Fig. 6). Once the effect of host abundance was removed, cowbird distribution patterns in edge and core habitats in different landscapes were nearly identical to the pattern previously described (Fig. 5).

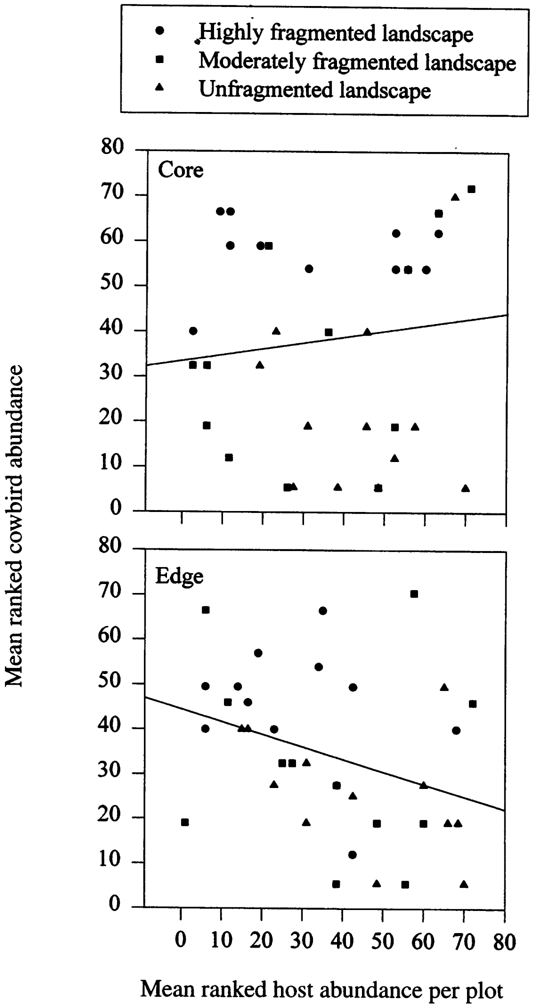

FIG. 6. Relationship between mean ranked cowbird abundance and mean ranked host abundance in core habitats (top) and edge habitats (bottom) in highly fragmented, moderately fragmented, and unfragmented landscapes.

Based on these results, we rejected the hypothesis that edge effects vary with local-scale host abundance. Additionally, increased cowbird abundance along edges was not demonstrated in our study.

DISCUSSION

Edge effects

Our results suggest that, even in the absence of data on local host abundance or nest predator composition, predation patterns and cowbird distribution in habitat edges and cores can be explained by examining habitat features at the landscape scale. Thus, the effect of a permanent agricultural or managed edge is not the same in all landscape situations. Edge effects depend, at least in part, on the landscape context, indicating that results obtained from locally conducted studies should be evaluated in light of landscape-scale forest cover.

Edge effects in nest predation patterns were detected in highly and moderately fragmented landscapes, and both mammals and birds contributed to increased predation along edges in our study area. Because mammals accounted for most predation events, as a guild they influenced predation patterns in our analyses more than birds. An important caveat regarding this result is that birds tend to depredate off-ground nests more frequently than do mammals (Yahner and Scott 1988); P. Porneluzi, *personal communication*). Given the limitations of our experimental design, mammalian predation was significant, although we were not able to clearly evaluate predation on a predator-by-predator basis. A more useful approach to understanding predator response to edges would be to focus on the nest-searching behavior of individual predator species in a variety of landscapes, and assess predator abundance and predator perception of the landscape on a species-by-species basis (Lima and Zollner 1996; W. Dijak, *personal communication*).

We did not document edge effects in cowbird distribution in our study region. Cowbird mobility is one reason why edge effects in distribution were not apparent: cowbird home ranges encompass feeding habitats in open grassy areas, breeding habitats in woodlands, and a wide range of roosting habitats; and typically range from 564–1124 ha in the midwest (Thompson 1994, Thompson and Dijak, *in press*). In the mornings, cowbirds move to breeding habitats to search for host nests, and although it has been suggested that cowbirds use edges or open areas to locate host nests, we found no difference between edge and core habitats based on censuses conducted during peak cowbird egg laying. Because of their mobility, cowbirds may have the leisure of selecting high-quality hosts in both edge and core habitats in landscapes that provide ample breeding and feeding areas. The only trend in edge effects was detected in unfragmented landscapes, possibly because cowbird feeding opportunities in such landscapes are limited and there may be energetic costs to penetrating deep into forest core in such landscapes; or because cowbird numbers are low there, and ample hosts exist close to the edges (Donovan et al., *in press*).

Our results demonstrate that cowbird abundance was negatively associated with host abundance in edge habitats but positively associated with host abundance in core habitats. We offer two hypotheses regarding this pattern. First, the host community may have differed between edge and core habitats, and cowbirds may actually assess the quality of host community in terms of cowbird fitness. For example, if the edge host community consisted of hosts with defenses against brood parasitism, cowbirds may forego edge hosts and key into naive core hosts that readily raise cowbirds and thereby enhance cowbirds fitness. Second, local cowbird density combined with landscape features may influence the relationship between host and cowbird abundance. In core habitats, for example, cowbird–host relationships were strongest in moderately fragmented habitats where both feeding and breeding opportunities abound. In highly fragmented and contiguous landscapes, however, this relationship was not as strong, perhaps because cowbirds may be limited by breeding or feeding resources in those landscapes, respectively. Where cowbird densities are high, hosts may be saturated with parasites and host–cowbird relationships may be weak. Direct observations of parasitized nests in different landscapes with varying cowbird abundance are needed to test these hypotheses.

Landscape effects

Our experimental results strongly support the hypothesis that landscape-scale habitat patterns significantly influence overall nest predation patterns and cowbird abundance. Field studies corroborate this, and show that the distribution of cowbirds is best explained when landscape habitat patterns are considered (Coker and Capen 1995, Donovan et al., *in press*). Likewise, daily nest survival and the level of parasitism on real nests are significantly correlated with habitat patterns at the landscape scale (Robinson et al. 1995, Thompson et al., *in press*).

Landscape considerations seem logical for cowbirds because they utilize different habitats for feeding and breeding activities in the midwestern United States (Thompson 1994). The probability of detecting a cowbird depends not only on the presence of hosts, but also on the presence of a nearby feeding area. Both types of habitats need to be assessed simultaneously. For this reason, the distribution of species that utilize more than one habitat in their daily activities may be better explained by landscape patterns than the distribution of species that utilize only one type of habitat. In predominantly forested landscapes, cowbird numbers may be limited by sufficient feeding habitats, rather by than hosts. For example, in a heavily forested landscape in Vermont (94% forest cover), cowbird distribution at one patch was best explained by examining the area of the forest patch, the distance to the closest opening (potential feeding area), and the number of livestock areas (known feeding areas) within 7 km of the patch (Coker and Capen 1995). By contrast, in severely fragmented landscapes (<1% forest cover) cowbirds may be limited by host abundance and also by the poor reproductive success of hosts in fledging cowbirds (Donovan et al. *in press*). Thus, abundances may peak in landscapes that offer ample feeding and breeding opportunities.

Nest predators as a group vary tremendously in habitat use, and assessment of landscape patterns alone may not fully explain nest predation patterns in different areas. For example, levels of daily nest survival are not as tightly correlated with landscape features as parasitism levels are (Robinson et al. 1995), indicating that different predator species are affected by landscape patterns differently. Raccoons, crows, and opossums reach their highest densities in highly fragmented landscapes (Andren 1992; W. Dijak, *personal communication*), potentially because their distributions are associated with developed and agricultural habits that are interspersed with forest habitat. Other predators may be equally abundant in forests that vary in their landscape composition. Similarly, some predators may focus nest-searching activities along edges (Gates and Gysel 1978, Andren and Angelstam 1988, Yosef 1994), while others are equally abundant in both forest edges and forest cores. Although predators may be specific to a habitat or landscape type, the effect of a predation act on a songbird nest is the same regardless of the predator—it results in a reduced number of fledglings. However, predicting the effect of a particular predator species may be difficult because predator communities vary from habitat to habitat (Picman and Schriml 1994), and one set of nest predators may replace another set of predators in a different landscape or habitat.

Conservation implications

Although landscape habitat features explained a significant amount of variation in cowbird distribution and nest predation patterns, the high variation in nest predation rates, cowbird abundance, and host abundance within replicate hexagons in a landscape should not be ignored. This high variation within landscapes indicates that, in addition to landscape considerations, local-scale processes can strongly influence cowbird distribution and nest predation patterns. One potentially important local effect that we did not measure was the type of nonforest land-use in each landscape. For instance, variation in the quality of non-forest feeding habitats in the landscape could have contributed to variation in cowbird abundance within landscapes. Cowbird abundance at a local scale also may be influenced by density-dependent habitat selection and searching behavior. Similarly, composition of nonforest habitats could affect predator abundances, and within a given landscape, different types of nonforest habitat or disturbances can influence parasitism and predation levels (P. D. Doran, D. R. Whitehead, and D. E. Winslow, *unpublished manuscript*). Therefore, the composition of the entire landscape mosaic should be analyzed to predict the impacts of edges on songbirds.

We suggest that the first approximation to predicting the impact of agricultural or managed edges on forest songbird reproductive success is to assess habitat characteristics at the landscape scale. Cursory examination of the landscape context of studies reviewed by Paton (1994) reinforce our conclusions (T. M. Donovan, *personal communication*; M. J. Hartley and M. L. Hunter, Jr., *personal communication*). Our results also support the notion that ecological processes must be viewed at multiple scales for accurate interpretation of the mechanisms and their effects (e.g., Wiens et al. 1993, Thompson et al., *in press*). Because local-scale processes like edge effects may be driven by habitat patterns at larger spatial scales, we reiterate the view that conservation plans for long-term persistence of many bird species should utilize a top-down regional approach where coarse-grain objectives are developed at a regional or landscape scale and local-scale decisions are made in light of the regional or landscape context (Probst and Crow 1991, Freemark et al. 1995, Petit et al. 1995).

Finally, while we determined under what local and landscape conditions edge effects might occur, we did not assess the potential impact of edge effects on songbird populations. Edges may or may not have a detrimental effect on overall population size, depending upon the proportion of the population attempting to breed in lower quality edge habitats and edge-dominated landscapes (Temple and Cary 1988, Thompson 1993, Donovan et al. 1995*a*). Mechanisms that influence this proportion are presently unknown.

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