EVALUATION OF SPATIAL MODELS TO PREDICT VULNERABILITY OF FOREST BIRDS TO BROOD PARASITISM BY COWBIRDS

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Abstract. We constructed alternative spatial models at two scales to predict Brown-headed Cowbird (*Molothrus ater*) parasitism rates from land cover maps. The local-scale models tested competing hypotheses about the relationship between cowbird parasitism and distance of host nests from a forest edge (forest–nonforest boundary). The landscape models tested competing hypotheses about how landscape features (e.g., forests, agricultural fields) interact to determine rates of cowbird parasitism. The models incorporate spatial neighborhoods with a radius of 2.5 km in their formulation, reflecting the scale of the majority of cowbird commuting activity. Field data on parasitism by cowbirds (parasitism rate and number of cowbird eggs per nest) were collected at 28 sites in the Driftless Area Ecoregion of Wisconsin, Minnesota, and Iowa and were compared to the predictions of the alternative models. At the local scale, there was a significant positive relationship between cowbird parasitism and mean distance of nest sites from the forest edge. At the landscape scale, the best fitting models were the forest-dependent and forest-fragmentation-dependent models, in which more heavily forested and less fragmented landscapes had higher parasitism rates. However, much of the explanatory power of these models results from the inclusion of the local-scale relationship in these models. We found lower rates of cowbird parasitism than did most Midwestern studies, and we identified landscape patterns of cowbird parasitism that are opposite to those reported in several other studies of Midwestern songbirds. We caution that cowbird parasitism patterns can be unpredictable, depending upon ecoregional location and the spatial extent, and that our models should be tested in other ecoregions before they are applied there. Our study confirms that cowbird biology has a strong spatial component, and that improved spatial models applied at multiple spatial scales will be required to predict the effects of landscape and forest management on cowbird parasitism of forest birds.

Key words: brood parasitism; Brown-headed Cowbirds; forest birds; forest edges; fragmentation; Molothrus ater; neotropical migratory songbirds; risk; scale; spatial models.

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite that can reduce the reproductive success of many species of neotropical migratory songbirds (Mayfield 1977, Brittingham and Temple 1983, Robinson et al. 1995*b*, Thompson et al. 2000). Prior to the 1800s, cowbirds were limited primarily to open grasslands and plains of central North America, but expanded eastward as forests were cleared for settlement (Mayfield 1965). As they expanded their range, they came in contact with host species that exhibit low levels of behavioral defenses against brood parasitism. This has resulted in high levels of cowbird reproduction and a reduction in host reproductive success (Robinson et al. 1995*a*, Hosoi and Rothstein 2000).

Cowbird numbers appear to be affected by the quantity, quality, and spatial arrangement of feeding and breeding habitat (Robinson et al. 1995*b*, Tewksbury et al. 1998). Breeding activities (nest searching and egg laying) and feeding can be separated spatially and temporally because cowbirds do not need to care for young or defend nests. Cowbirds usually feed in shortgrass habitats or with grazing animals (Mayfield 1965, Dufty 1982, Rothstein et al. 1986, Morris and Thompson 1998). They breed in a wide variety of habitats, including forests containing hosts with little ability to resist parasitism. In Midwestern landscapes, cowbirds may commute up to 5 km between feeding and breeding habitats (Thompson 1994), suggesting that even concentrated feeding areas may provide access to large areas of breeding habitat (Rothstein et al. 1984). Furthermore, it has been suggested that cowbirds may select habitats with high host densities (Gates and Gysel 1978, Rothstein et al. 1986, Gates and Griffen 1991, Donovan et al. 1997, Thompson et al. 2000), which may, in turn, be related to landscape characteristics such as the interspersion of habitats and edge (Thompson et al. 2000).

Increased understanding of landscape factors that determine the parasitism rates on host species inflicted

by cowbirds is very important for the conservation of host species (Robinson et al. 1995a). Models capable of predicting the spatial distribution of cowbird parasitism activity relative to land uses and forest management activity are needed to understand the potential consequences of management and development alternatives. The construction of these models is difficult because of the large spatial extent of the factors that determine parasitism, the logistics of collecting data on parasitism rates across large regions, and the complex interactions that probably mediate cowbird parasitism activities. One approach is to construct alternative models based on competing hypotheses of the factors regulating parasitism rates. Empirical data can then be compared with the predictions of these models to eliminate models with poor explanatory ability.

The factors that determine the impacts of cowbird populations on host species are not completely understood, and these factors may differ between predominantly forested landscapes and those dominated by agriculture (Robinson et al. 1995b, Hochachka et al. 1999, Thompson et al. 2000). Some factors are likely to operate at a landscape scale, whereas others may influence cowbird breeding activity at a local scale. Landscape-scale factors include abundance and configuration of feeding habitat (Brittingham and Temple 1983, Donovan et al. 2000), abundance of forested breeding habitat (Robinson et al. 1995b), and degree of forest fragmentation (Askins 1995, Donovan et al. 1995). Local-scale factors include distance from edge, edge configuration, host density, and the presence of perching sites (Barber and Martin 1997, Donovan et al. 1997, Thompson et al. 2000). Variation in cowbird abundance at large regional scales is correlated with parasitism (Hoover and Brittingham 1993, Smith and Myers-Smith 1998), but we ignored this variable because our study was conducted within one region.

Our objective in this study was to evaluate how the relationships among these factors determine cowbird parasitism rates in landscapes of the upper Midwest. We wished to examine a local-scale factor (distance from forest edge) and several landscape-scale factors (amount of feeding, forested, and forest edge habitat, and forest fragmentation). Our approach was to construct alternative models of how these factors interact to determine cowbird parasitism activity, and then to compare the predictions of these models to empirical data as a means to better understand the importance of each factor.

Alternative local-scale models

A factor long thought to influence parasitism rates on a local scale is the distance of nests from the forest edge. Several studies have found a negative relationship, in which parasitism rates are higher near forest edges than they are deeper into the forest (Brittingham and Temple 1983, Yahner and Scott 1988, Evans and Gates 1997). However, others have documented no relationship (Donovan et al. 1997) or a positive rela-

tionship, with parasitism being higher in forest interior habitat (Hahn and Hatfield 1995).

Alternative landscape-scale models

It is clear that cowbirds are not abundant in areas beyond commuting distance from feeding habitat (usually livestock agriculture or shortgrass) (Rothstein et al. 1984, Thompson 1994, Robinson et al. 1995b, Curson et al. 2000). However, it is not clear how cowbirds respond to changes in the abundance and distribution of feeding habitats and forested breeding habitats (Thompson et al. 2000) when these habitats are within commuting distance. We propose alternative models of cowbird response to the spatial distribution of these habitats across a landscape. (1) Local cowbird abundance may be determined primarily by the availability of feeding habitat within commuting distance (food-dependent hypothesis), and parasitism rates would be a function of the size of the local cowbird population that can be supported by available food resources (Morris and Thompson 1998). This hypothesis assumes that host densities are relatively homogeneous and that the configuration of breeding habitat does not affect parasitism rates. This hypothesis would most likely be true in landscapes where feeding habitat is sparse, and the location of breeding activity would be related to the proximity of feeding habitat (e.g., Winslow et al. 2000). (2) Alternatively, local cowbird parasitism rates may be determined primarily by the abundance of forest in the surrounding landscape (forest-dependent hypothesis). Such a relationship has been documented using coarse land cover data (1-km cells), and assumes long commuting distances ≥ 10 km (Donovan et al. 1997, Hochachka et al. 1999). (3) Cowbird abundance may be determined primarily by the spatial configuration of breeding (forest) habitat (fragmentation-dependent hypothesis). It is well known that cowbirds are not found in large, contiguous forests (Holmes et al. 1992, Donovan et al. 1995, Evans and Gates 1997), and that parasitism rates are related to fragmentation on a regional scale (300–900 km^2) (Robinson et al. 1995b). Such a relationship is not known at the landscape scale (>20 km^2). The density of potential hosts may be related to the abundance of forest edge produced by the dissection (convoluted edges) of forested habitat (Donovan et al. 1997, Thompson et al. 2000). (4) Feeding habitat and breeding habitat may interact to determine parasitism rates. The amount and quality of feeding habitat may determine the size of the local cowbird population, and the individuals of that population may disperse among the available hosts living in the breeding habitat. If host densities were highest in edge habitats, as predicted by the ecological trap hypothesis (Gates and Gysel 1978), then parasitism rates would be related to the ratio of feeding habitat to edge habitat (edges-dispersed hypothesis). (5) Conversely, it may be possible that food supply and edge abundance interact synergistically such that parasitism rates are related to the product (multiplied)
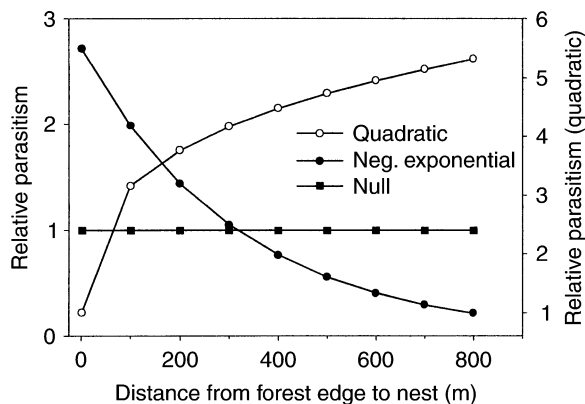
Fig. 1.   Functions used to represent the competing local-scale hypotheses predicting the rate of Brown-headed Cowbird (*Molothrus ater*) parasitism as a function of the distance of nests from a forest edge.

of feeding habitat and edge habitat (edges-facilitated hypothesis).

METHODS

The models tested in this study are extensions of the model described in Gustafson and Crow (1994). Their purpose is to predict the relative vulnerability of neotropical migrant forest birds to cowbird brood parasitism for each forested cell on a GIS raster grid. The models require a land cover map delineating forest, row crop agriculture, and grassy habitats.

Alternative local-scale models

We developed three local-scale models that represent competing hypotheses about the relationship between parasitism rate (v) and distance from edge (d, in meters) at any given location (i): null hypothesis of no relationship; negative exponential model; and positive quadratic model. The negative exponential function $v_i = 10^{-0.0014d_i}$ was developed by Gustafson and Crow (1994) from the data of Brittingham and Temple (1983). We developed a positive quadratic function, $v_i = d_i^{1/4}$, to approximately mirror the negative exponential function as a competing model (Hahn and Hatfield 1995). The forms of these functions are shown in Fig. 1. The null model was tested by regressing parasitism rate and mean distance from the edge of the study sites and testing the null hypothesis that the slope was equal to zero. If the null was rejected, we would then select between the two competing distance-to-edge models by regressing v_i against the parasitism rate on the study sites, selecting a model based on the sign of the slope and the F statistic.

Alternative landscape-scale models

We constructed five spatial models that represent the assumptions of the competing landscape-scale models. These models also incorporated the local-scale distance-to-edge function deemed best supported by em-

pirical evidence. We used the models to generate predictions of relative cowbird parasitism rates for 28 sites in Wisconsin, Minnesota, and Iowa, representing a range of forest fragmentation and intensity of agricultural land use typical of the Driftless Area Ecoregion of the Midwest. Field data on rates of parasitism by cowbirds were collected at each site and were compared to the predictions of the models using regression analysis to assess the predictive ability of the models.

The alternative models differed in their assumptions about how cowbird parasitism rates are impacted by spatial variation in the abundance and configuration of feeding habitat and forest habitat across the landscape. We chose the scale of analysis for the landscape-level models by assuming that the response of cowbirds to landscape features occurs at a scale related to the distance that cowbirds commonly commute between feeding habitats and breeding habitats. Although maximum commuting distances may reach ≥7 km (Rothstein et al. 1984, Curson et al. 2000), average commuting distances are usually much less (Robinson et al. 1993, Thompson 1994, Hanksi et al. 1996, Gates and Evans 1998). Landscape characteristics were generally better correlated with parasitism rates when calculated within a 2.5 km radius of our study sites than when calculated at smaller (1.5-km) or larger (5.0-km) scales. We used an analysis window with a radius of 2.5 km around each site in this study. We will detail the other assumptions made for each model.

We generated areal estimates of feeding habitat, forest fragmentation, and forest edges within commuting distance of each study site (2.5 km) using ERDAS Imagine GIS software. Cowbirds in the Midwest appear to prefer grassy habitats, even when their availability is low (Thompson and Dijak 2000). Thompson (1994) observed ~80% of feeding activity by radio-marked cowbirds in shortgrass (livestock-grazed or mowed) habitats, 10% in tallgrass and old-field habitats, and 10% in row crops. We assumed that these ratios reflect the value of these feeding habitats for cowbirds because his study sites were relatively close to ours. Based on Thompson's (1994) findings, for each site i, a weighted sum of feeding habitat pixels (f_i) within the window was tabulated for each grid cell within the analysis window, where the weights represent the relative value of each land cover as feeding habitat for cowbirds (Table 1):

$$f_i = \left[\sum w(l_j) \right] \Big/ J \quad \forall j$$

where j is used to index the J cells within 2.5 km of site i, and $w(l_j)$ is the weight assigned to the land cover l at cell j. The value of f for each site is an estimate of the relative capacity of the surrounding landscape (within 2.5 km of the site) to feed cowbirds.

We calculated the percentage of forest (p) within 2.5 km of each site by calculating the percentage of forested cells within the analysis window. To quantify forest fragmentation within commuting distance of each site, we used the GISfrag index (Ripple et al.

TABLE 1. Recoding scheme used to produce the land cover map categories used in the competing cowbird models.

Original class†	Recoded class‡	Feeding habitat weight
URBAN HIGH	URBAN	0
URBAN LOW	GRASS	8
AG ROW CROP	AGRICULTURE	1
AG FORAGE CROP	GRASS	8
AG CRANBERRY BOG	AGRICULTURE	1
GRASSLAND	GRASS	8
GRASS COOL	GRASS	8
GRASS WARM	AGRICULTURE	1
GRASS OLD FIELD	AGRICULTURE	1
FOREST CONIFER	FOREST	0
FOREST DECIDUOUS	FOREST	0
FOREST MIXED	FOREST	0
WATER	WATER	0
WET MEADOW	WET MEADOW	0
WET SHRUB	WET MEADOW	0
WET FOREST	FOREST	0

† The original classes were those in the satellite image classifications produced by the GAP program of the USGS (Scott et al. 1993).

‡ The recoded classes were used in the land cover maps used as input for the competing spatial models.

1991). This index works equally well for dissected (convoluted) and insular (disconnected) fragmentation patterns (Gustafson 1998). GISfrag is calculated from a map showing the distance of each forested cell from the nearest forest edge, produced using a proximity (search) function in the GIS. The value of each cell represents the distance (d) of that cell (in pixels) from a forest edge. We calculated the GISfrag index (g) for each site i by calculating the mean value of d for all cells within 2.5 km of site i:

$$g_i = \left(\sum d_j \right) \big/ J \quad \forall j.$$

GISfrag is low when the forest within 2.5 km is highly dissected (most cells have low values because they are close to an edge), and the value of GISfrag increases as fragmentation decreases.

We also quantified the amount of forest edge (e) within commuting distance of each site i by counting the number of cells in the distance-to-edge map that were next to an edge ($d = 1$):

$$e_i = \sum d_j \quad \forall d_j = 1.$$

The alternative models predicting relative vulnerability to cowbird parasitism (v) were formulated from these spatially derived variables and the best-fit distance-from-edge function (de). We did not attempt to standardize the values of v among models (which vary widely in magnitude); in our analyses, we assumed that they should vary linearly with parasitism rates. The model formulations are as follows: food-dependent, $v_i = f_i \times$ de; forest-dependent, $v_i = p_i \times$ de; fragmentation-dependent, $v_i = g_i \times$ de; edges-dispersed, $v_i = (f_i/e)_i \times$ de; and edges-facilitated, $v_i = (f_i \times e_i) \cdot$ de.

Study sites

We compared the models using data collected in the Driftless Area Ecoregion of western Wisconsin, south-

eastern Minnesota, and northeastern Iowa, USA (Fig. 2). The landforms in this area are characterized by maturely dissected, upland plateaus with steep bedrock ridges up to 150 m in height, descending to river drainages that ultimately flow to the Mississippi River (Bailey et al. 1994, McNab and Avers 1994). Prior to European settlement, the ecoregion was covered by an oak savanna complex of mixed grasslands with forests in areas protected from fire (steep, north-facing slopes of silver maple [*Acer saccharum*] and basswood [*Tilia americana*] and riverine forests of elm [*Ulmus* spp.], ash [*Fraxinus* spp.], and cottonwood [*Populus deltoides*] [Curtis 1959, Cahayla-Wynne and Glen-Lewin 1978]. The historical oak savanna forests, under fire suppression and modern agricultural practices, have succeeded to closed-canopy oak–hickory forests of

1 Great Lakes Plain   4 Till Plains
2 Driftless Area   5 Dissected Till Plains
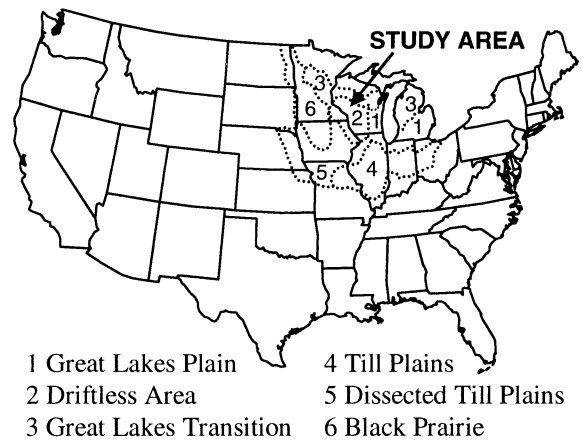3 Great Lakes Transition   6 Black Prairie

FIG. 2. Location of the study area. Dotted lines delineate ecoregions (BBS physiographic strata). The Driftless Area ecoregion in the Midwest, where the 28 study sites are located, is labeled as 2.

small to medium size within a matrix of row and forage crops. As a result of these processes, there are more closed-canopy forests in the ecoregion now than prior to European settlement. The complex topography and erosive soils support a less intensive agriculture than in many parts of the Midwest, with agriculture occupying 30–40% of the landscape. We monitored 1888 nests of forest-breeding birds at 28 sites to estimate rates of cowbird brood parasitism. The sites were embedded in landscapes that ranged from 12% to 56% forested and 2% to 38% agriculture (calculated from the GAP land cover maps using 10 km radius buffers around each study site; M. Knutson, M. Friberg, G. Niemi, and W. Newton, *unpublished manuscript*). A land cover map of the study area was derived from LANDSAT Thematic Mapper classifications produced by the USGS Gap Analysis Program (30-m cell size; Scott et al. 1993). The Minnesota and Wisconsin portions of the map were produced using a common image-processing protocol (Lillesand et al. 1998). The Iowa classification method is described on the Iowa GAP web site.[7] Each classification was converted to a common set of land cover classes, and the three maps were combined and filtered using a clump-and-sieve algorithm to reduce classification errors. The algorithm converted patches <4 pixels in size (any shape) to the cover class of the nearest neighboring pixel, producing an effective minimum mapping unit of 3600 m². Because our analysis involved large spatial neighborhoods, we reduced processing time by aggregating to a 60-m cell size using a majority aggregation rule, and combined classes (Table 1, Fig. 3).

Empirical test data collection

We monitored 20 of the plots each year from 1996 to 1998. The remaining eight plots were monitored only in 1997 (M. Knutson, M. Friberg, G. Niemi, and W. Newton, *unpublished manuscript*). Plot sizes ranged from 9 to 59 ha, averaging 31 ha. All plots were located on state or federal forested land free of cattle grazing. Data collection followed standard nest-monitoring protocols. Nest searches were conducted between 0500 and 1100 during May, June, and July of each year. Songbird nests were found and rechecked every ~4 d until fledging. Mirrors or video cameras extending to 8 m above the ground were used to check nest contents. For each nest, we recorded the species, nesting stage, evidence of nest fate, and the number of cowbird eggs or chicks. The location of each nest was recorded using a PLGR+96 (Rockwell International Corporation, Cedar Rapids, Iowa, USA) GPS (Global Positioning System).

Analysis

Because we were interested in species that were negatively impacted by parasitism, we excluded from our analysis species that were inappropriate hosts (e.g.,

most cavity nesters) or were cowbird egg rejecters tending to remove cowbird eggs from their nests (Friedmann and Kiff 1985). We calculated cowbird parasitism rates and the average number of cowbird eggs per nest in three ''distance-from-edge'' categories (0–300 m, 300–600 m, >600 m) for each plot. Because some plots did not have any nests >300 m from edge, this resulted in 38 estimates of distance-related parasitism rates that could be compared to model predictions. We transformed parasitism rates using an arcsine transformation and transformed the counts of number of eggs per nest using a square-root transformation (Sokal and Rohlf 1969). These values were averaged for plots that were monitored in multiple years.

After testing the competing local-scale models as just described, we substituted the surviving distance-to edge-function for de in the equations of the landscape-scale models, and calculated predictions for each study site using each model. We compared cowbird parasitism activity to the predictions of the models for each site. Because the nests on each site were scattered over a map area of 10–15 cells, we used the average predicted vulnerability value of those cells on which nests were located. We plotted the transformed parasitism rates and number of cowbird eggs per nest against the model predictions for each of the alternative cowbird models. We fit a least squares linear model to these plots and tested the hypothesis that the slope was equal to zero.

For heuristic purposes, we mapped the predictions of each model across the study area. The pixel values of these maps represent the relative vulnerability (v) of forest birds to cowbird parasitism. They were generated by applying the model equation at each forested cell (i) in the satellite classification map of the study area, using the spatial modeling capabilities of ERDAS Imagine NT.

RESULTS

Cowbird parasitism rates averaged 8% for all species ($N = 1888$) and 14% for those species that accept cowbird eggs ($N = 1167$; Table 2). Parasitism rates of acceptor species ranged from 4.5% to 34% among the 28 sites. There was a significant, positive linear relationship between the mean distance of sites from the forest edge and the parasitism rate ($F = 17.1$, $P > F = 0.0002$, df $= 1, 36$) and cowbird eggs per nest ($F = 19.02$, $P > F = 0.0001$, df $= 1, 36$), so the null hypothesis of no relationship was rejected (Fig. 4). The negative exponential function was also discarded because the empirical trend was significantly positive. The quadratic distance-from-edge function provided a better fit between the parasitism rate and the distance of the nest from the forest edge ($F = 21.0$, $P < 0.0001$, df $= 1, 36$) than did a linear function, and it was substituted for de in the equations for the landscape-scale models.

Parasitism rate

The only landscape-scale model without significant explanatory power ($\alpha < 0.05$) was the edges-dispersed
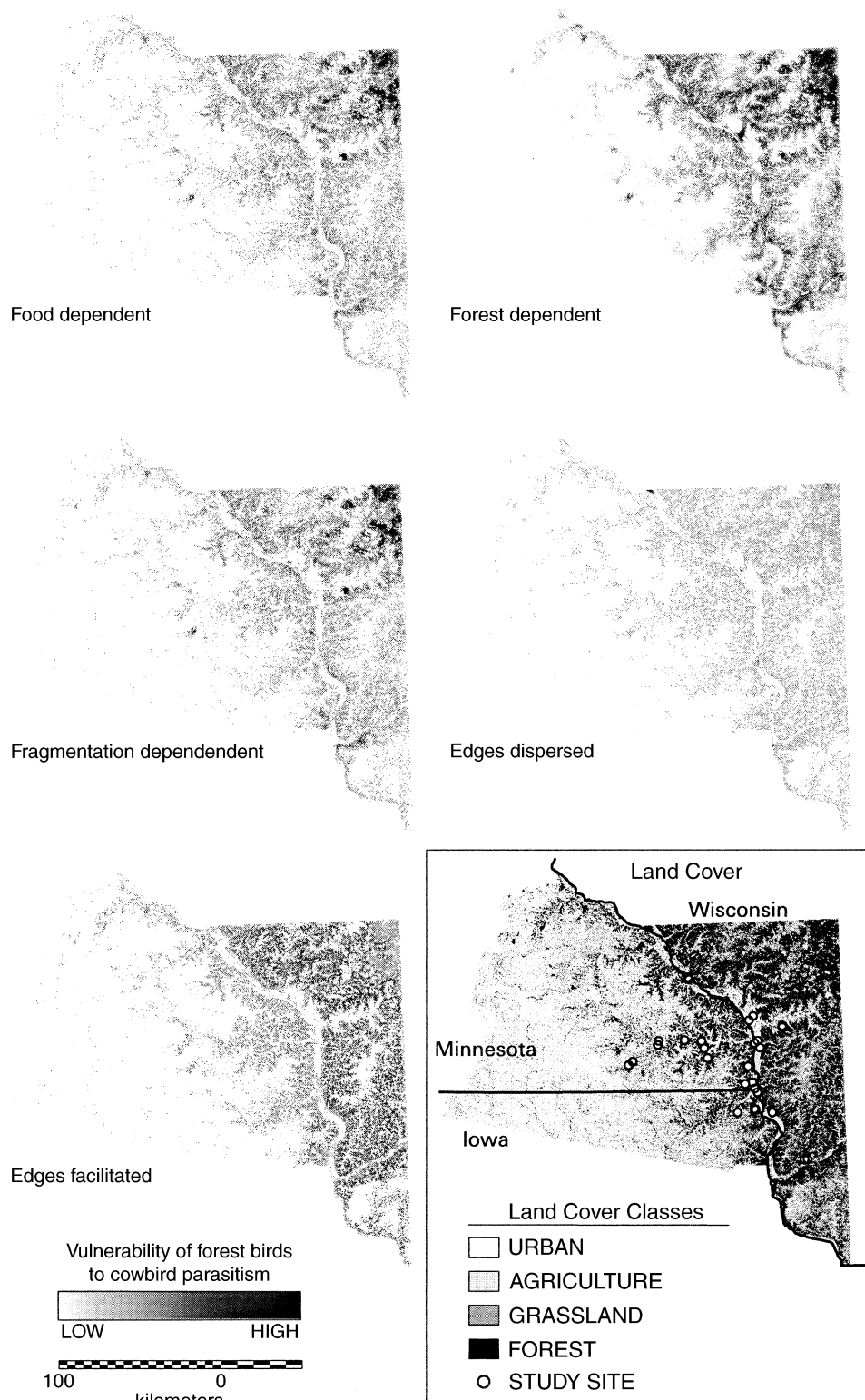
FIG. 3. Spatial realization of the predictions of the competing models across the study area. The maps were produced by calculating the equations for each model for each forested cell on the land cover map.

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TABLE 2. Summary of host species nest data (sample size and percentage parasitized by Brown-headed Cowbirds) used in the analyses.

Species†	Scientific name	No. nests	Nests parasitized (%)
Wood Duck[I]	*Aix sponsa*	1	
Hooded Merganser[I]	*Lophodytes cucullatus*	1	
Cooper's Hawk[I]	*Accipiter cooperii*	2	
Ruffed Grouse[I]	*Bonasa umbellus*	2	
Wild Turkey[I]	*Meleagris gallopavo*	17	
Mourning Dove[I]	*Zenaida macroura*	2	
Black-billed Cuckoo[I]	*Coccyzus erythrophthalmus*	2	
Yellow-billed Cuckoo[I]	*Coccyzus americanus*	3	
Whip-poor-will[I]	*Caprimulgus vociferus*	3	
Ruby-throated Hummingbird[I]	*Archilochus colubris*	41	
Red-headed Woodpecker[I]	*Melanerpes erythrocephalus*	6	
Red-bellied Woodpecker[I]	*Melanerpes carolinus*	24	
Yellow-bellied Sapsucker[I]	*Sphyrapicus varius*	44	
Downy Woodpecker[I]	*Picoides pubescens*	41	
Hairy Woodpecker[I]	*Picoides villosus*	24	
Northern Flicker[I]	*Colaptes auratus*	5	
Pileated Woodpecker[I]	*Dryocopus pileatus*	2	
Eastern Wood-Pewee[A]	*Contopus virens*	132	2.27
Acadian Flycatcher[A]	*Empidonax virescens*	12	16.67
Willow Flycatcher[A]	*Empidonax traillii*	1	
Eastern Phoebe[A]	*Sayornis phoebe*	2	
Great Crested Flycatcher[I]	*Myiarchus crinitus*	22	
Eastern Kingbird[R]	*Tyrannus tyrannus*	6	
Tree Swallow[I]	*Tachycineta bicolor*	12	
Blue Jay[R]	*Cyanocitta cristata*	27	
Black-capped Chickadee[I]	*Poecile atricapilla*	42	
White-breasted Nuthatch[I]	*Sitta carolinensis*	11	
Brown Creeper[I]	*Certhia americana*	7	
House Wren[I]	*Troglodytes aedon*	23	
Blue-gray Gnatcatcher[A]	*Polioptila caerulea*	126	3.17
Eastern Bluebird[I]	*Sialia sialis*	1	
Veery[A]	*Catharus fuscescens*	5	20
Wood Thrush[A]	*Hylocichla mustelina*	36	52.78
American Robin[R]	*Turdus migratorius*	154	
Gray Catbird[R]	*Dumetella carolinensis*	78	2.56
Brown Thrasher[R]	*Toxostoma rufum*	8	
Cedar Waxwing[R]	*Bombycilla cedrorum*	9	
Yellow-throated Vireo[A]	*Vireo flavifrons*	8	
Warbling Vireo[A]	*Vireo gilvus*	42	2.38
Red-eyed Vireo[A]	*Vireo olivaceus*	41	34.14
Blue-winged Warbler[A]	*Vermivora pinus*	7	28.57
Yellow Warbler[A]	*Dendroica petechia*	54	11.11
Cerulean Warbler[A]	*Dendroica cerulea*	2	
American Redstart[A]	*Setophaga ruticilla*	305	16.39
Prothonotary Warbler[A]	*Protonotaria citrea*	139	19.42
Ovenbird[A]	*Seiurus aurocapillus*	27	44.44
Kentucky Warbler[A]	*Oporornis formosus*	1	
Common Yellowthroat[A]	*Geothlypis trichas*	2	
Scarlet Tanager[A]	*Piranga olivacea*	65	7.69
Northern Cardinal[A]	*Cardinalis cardinalis*	36	2.78
Rose-breasted Grosbeak[A]	*Pheucticus ludovicianus*	101	3.96
Indigo Bunting[A]	*Passerina cyanea*	30	56.67
Eastern Towhee[A]	*Pipilo erythrophthalmus*	8	12.5
Chipping Sparrow[A]	*Spizella passerina*	7	14.28
Field Sparrow[A]	*Spizella pusilla*	8	
Song Sparrow[A]	*Melospiza melodia*	17	17.65
Red-winged Blackbird[A]	*Agelaius phoeniceus*	20	10
Common Grackle[I]	*Quiscalus quiscula*	10	10
Baltimore Oriole[R]	*Icterus galbula*	24	

† Letters following species indicate their status: A, cowbird egg acceptor species; R, cowbird egg rejecter species; and I, species inappropriate as cowbird host.

model ($F = 0.39$, $P > F = 0.54$, df = 1, 36; Fig. 5). The abundance of edge habitat was not correlated with the parasitism rate ($r = 0.15$, $P > r = 0.45$; not shown). The best models (highest R^2) were the forest-dependent and forest-fragmentation-dependent models, in which more heavily forested and less fragmented landscapes had higher parasitism rates. However, much of the explanatory power of these models results from the inclu-
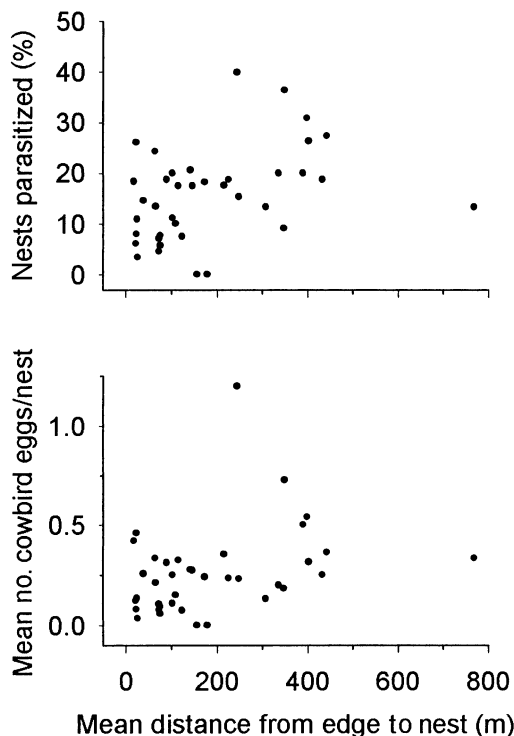
FIG. 4. Relationship between levels of cowbird parasitism and mean distance of nests from the forest edge. Nests on each of the 28 study sites were assigned to three distance-from-edge categories, and the mean distance of all nests in a category at each site was calculated and plotted on the *x*-axis. Values on the *y*-axes were calculated from nests in each distance category at each site.

sion of the distance-to-edge function. When it was omitted, the food-dependent model also became insignificant, ($F = 0.79$, $P > F = 0.38$), and R^2 dropped for all of the models except the edges-dispersed model (Fig. 6).

Cowbird eggs per nest

Similar results were obtained when parasitism was measured as the average number of cowbirds eggs found in host nests (Fig. 7). The edges-dispersed model was not significant, and the best models were the forest-dependent and fragmentation-dependent models. When the distance-to-edge function was omitted from these models, only the fragmentation-dependent model remained significant (Fig. 8). Some of the reduction in model fit when the distance-to-edge function was omitted may be attributed to an apparent outlier (3.5 standard deviations from the mean) found on one of the study sites.

Each model produced a different spatial distribution of vulnerability values across the Driftless Area ecoregion (Fig. 3). The variability within each map resulted from the spatial distribution of feeding and forested habitats. The differences between the maps were produced by differences in how the model equations integrated the landscape-scale distributions of feeding habitat and forest configuration.

DISCUSSION

Cowbird parasitism rates in our study were well below those reported in several other studies in the midwestern United States (Hoover and Brittingham 1993, Robinson et al. 1995*a*, 1995*b*, 1999). Robinson (1999) reported that ∼70% of cowbird acceptor species had parasitism rates exceeding 40% in Illinois. Brittingham and Temple report parasitism rates of 38–92% for the Baraboo Hills of Wisconsin, USA, a site within the Driftless Area ecoregion. However, our overall parasitism rates are comparable with the 7–12% parasitism of Acadian Flycatcher nests found at the Kettle Moraine State Forest in Wisconsin, a site within the Wisconsin prairie–forest ecotone, near the edge of the Driftless Area ecoregion. Although parasitism rates are low, Table 3 shows that cowbird abundances are not unusually low in the Driftless Area. In fact, cowbird abundances are higher in the Driftless Area than in the Till Plains (central Illinois and central Indiana, USA), where the effects of cowbird parasitism on host species are severe (Robinson 1992), but lower than in ecoregions located just west of the Driftless Area (Table 3).

Evaluation of alternative hypotheses using spatial models

The models that we tested were designed to predict the spatial variation in cowbird parasitism of forest birds at the landscape scale from readily available land cover data. Each model represents an alternative hypothesis about how cowbirds respond to landscape composition and spatial pattern. The models make interacting assumptions that confound the interpretation of our results, such as our assumptions about the relative importance of land cover as feeding habitat for cowbirds, and cowbird commuting distance.

Our results strongly suggest that distance from edge is important at the local scale, with parasitism impacts being highest away from the edge. These results are counter to those found by Brittingham and Temple (1983) in similar landscapes in Wisconsin. Some investigators have suggested that host density may be related to habitat edges (e.g., Thompson et al. 2000). Our results suggest that host densities may be lower in edge habitats and higher in larger patches of forest in the Driftless Area ecoregion. At the larger landscape scale, our study suggests that the abundance of edge habitat is not relevant for predicting cowbird parasitism. Both models that incorporated edge abundance generally performed worse than did models without edges as a factor.

The strong, positive relationship between the amount of forest and cowbird parasitism is also counter to that in many studies examining this relationship across a broader area (e.g., Robinson et al. 1995*b*, Donovan et al. 1997, Hochachka et al. 1999). However, these studies used forest coverage calculated from classifications of AVHRR images depicting *dominant* land cover on a large cell (1.1-km resolution), providing estimates of
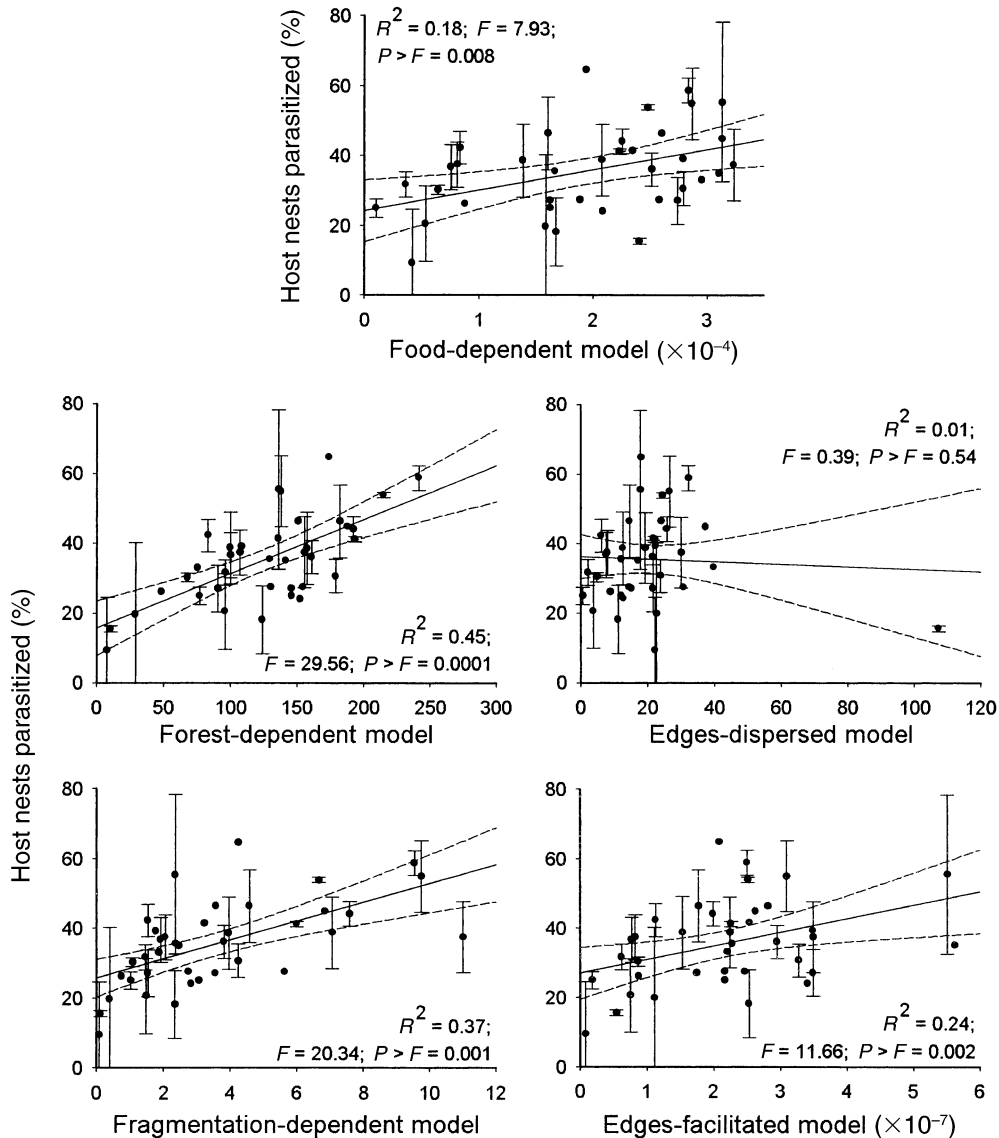
FIG. 5. Relationship between the mean (across-years) percentage of host nests parasitized by cowbirds and model predictions. These models include the quadratic distance-to-edge function. The x-axes show unitless, relative values. Percentage values on the y-axes were transformed using an arcsine transformation, and error bars show the standard error of the mean. Points without error bars represent plots measured in only a single year. For all F tests, df = 1, 36. (Note that the scale numbers for the x-axis in the top plot and the bottom right plot have been multiplied by 10^{-4} and 10^{-7}, respectively, for the purposes of presentation.)

forest coverage that may have high uncertainty. Furthermore, the relationship between forest coverage and parasitism found in the Midwest by Hochachka et al. (1999) was not significant. Similarly, the finding of higher parasitism activity in less fragmented forests is counter to some findings (Robinson et al. 1995b, Donovan et al. 1997), although in agreement with others (Hahn and Hatfield 1995). There are also scale differences among those studies. For example, Donovan et al. (1997) used percentage of forest within 864-km^2 hexagons on a 1-km grid cell map as a surrogate for fragmentation. Robinson et al. (1995b) used 314-km^2

circles to calculate patch size and forest interior on a 1:250 000 scale map. By such measures, all of our landscapes would be considered highly or moderately fragmented. Our measure of fragmentation (GISfrag) was calculated at a much smaller scale (20-km^2 circles on a 60-m grid cell map).

Our finding of higher parasitism in more forested landscapes is probably related to the relatively fragmented nature of these landscapes. Because forests are relatively rare throughout our study area (12–56%; see Fig. 3), cowbirds may be attracted to local areas of relatively contiguous forests. Our results are in agree-
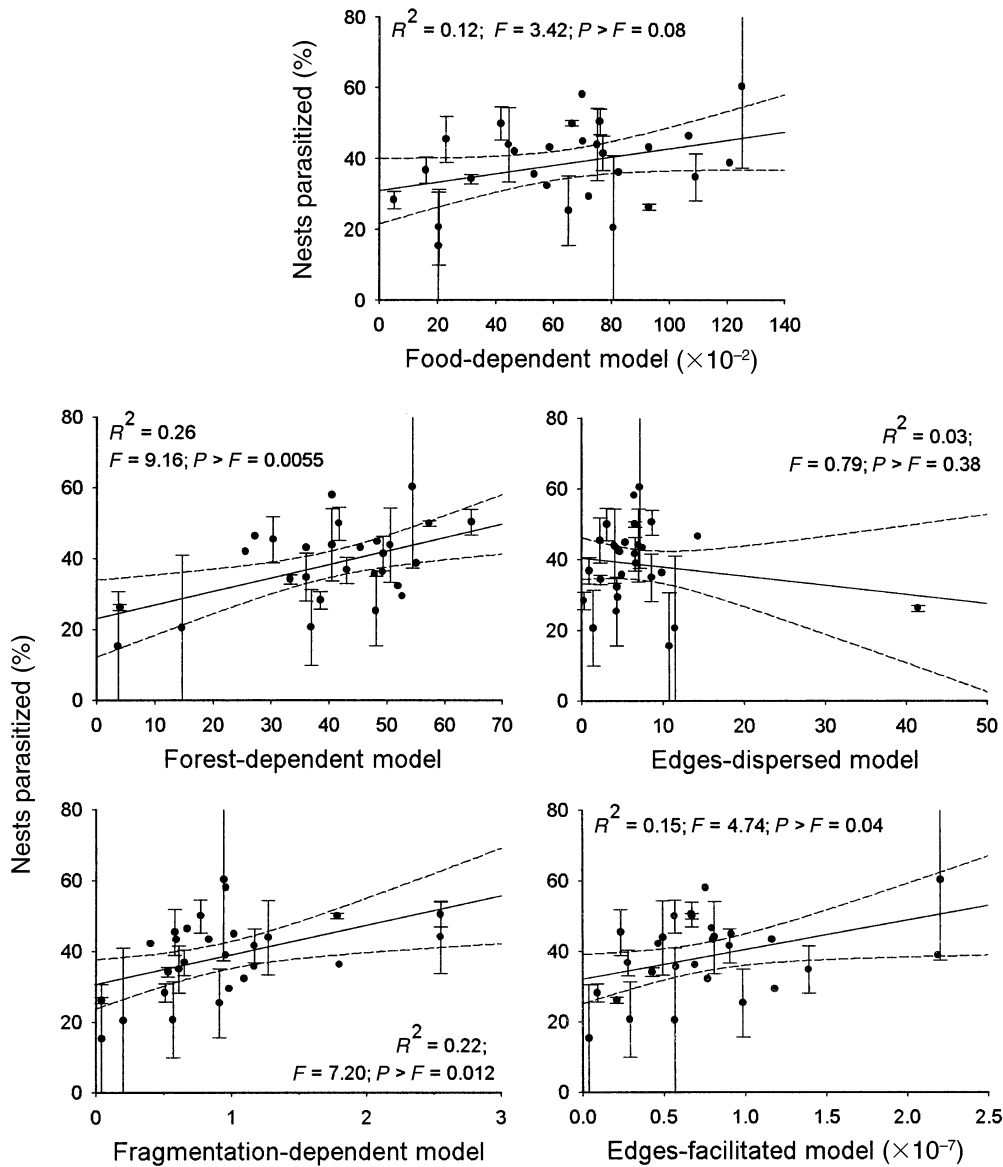
FIG. 6. Relationship between the mean (across-years) percentage of host nests parasitized by cowbirds and model predictions. These models do not include the distance-to-edge function. The x-axes show unitless, relative values. Percentage values on the y-axes were transformed using an arcsine transformation, and error bars show the standard error of the mean. Points without error bars represent plots measured in only a single year. For all F tests, df = 1, 36. (Note that the scale numbers for the x-axis in the top plot and the bottom right plot have been multiplied by 10^{-2} and 10^{-7}, respectively, for the purposes of presentation.)

ment with those from a study of cowbirds in a New York, USA landscape (55% forest), which found higher parasitism rates in the interior of large forests than in the edge-associated bird community, even though our overall parasitism rates were lower. In heavily forested landscapes (>80% forested), parasitism rates are consistently low because cowbird feeding areas are rare (Robinson et al. 1995b, Hanski et al. 1996). Cowbird parasitism levels and the importance of the parasitism edge effect vary with the regional level of fragmentation (Robinson et al. 1995a). This suggests that our

results apply primarily over the range of forest proportion that we studied, and perhaps only within the Driftless Area ecoregion. Our models should be tested in other ecoregions before they are applied there.

Caveats

We used a smaller scale of analysis (2.5 km radius) than did other related studies (10 km and 50 km radius; Robinson et al. 1995b, Donovan et al. 1997, Hochachka et al. 1999). We reasoned that using a scale of analysis determined by a common commuting distance rather
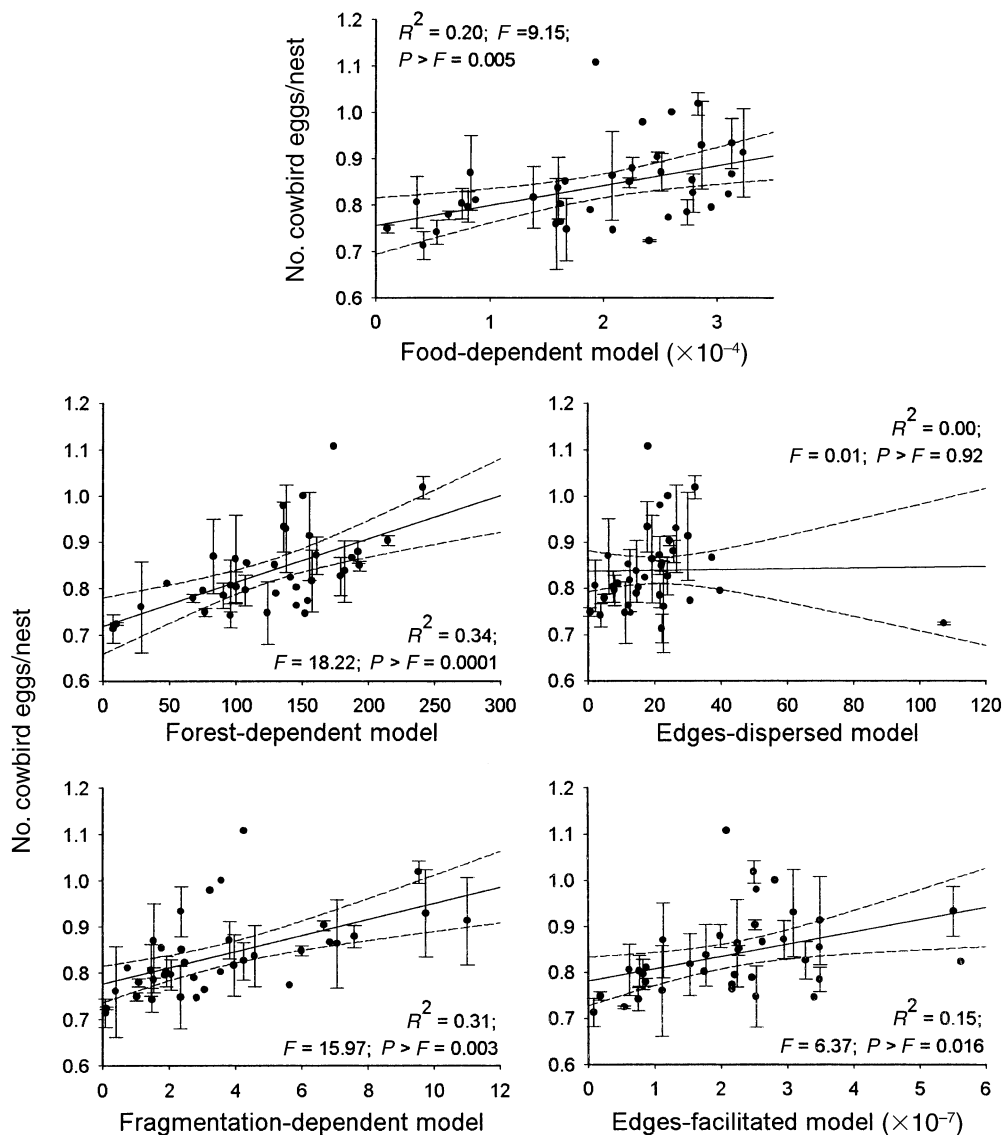
FIG. 7. Relationship between the mean number (across years) of cowbird eggs per nest and model predictions. These models include the quadratic distance-to-edge function. The x-axes show unitless, relative values. Numbers of eggs were transformed using a square-root transformation, and error bars show the standard error of the mean. Points without error bars represent plots measured in only a single year. For all F tests, df = 1, 36. (Note that the scale numbers for the x-axis in the top plot and the bottom right plot have been multiplied by 10^{-4} and 10^{-7}, respectively, for purposes of presentation.)

than the maximum (and therefore rare) distance would provide better predictive ability. Although we do not suggest that we have found the best scale for these analyses, our models have better predictive ability than similar models used in the midwestern United States that employ coarser land cover data (e.g., Hochachka et al. 1999).

Eight of our sites were sampled in only one year. The error observed in the sites sampled for three years suggests that year-to-year variability is substantial (Figs. 4–6). Because these single-year data are distributed across the range of model predictions, we believe that they do not bias the significance tests of the mod-

els. When sites with only one year of data were omitted from the tests of the models, the relative significance of the models remained the same except for two instances in which the fragmentation-dependent model became slightly more significant than the forest-dependent model (i.e., predicting the number of cowbird eggs per nest with the distance-to-edge function, and predicting the parasitism rate without the distance-to-edge function).

Although several of our models have predictive power, a substantial amount of unexplained variation remains. Host density is likely to be an important factor (Evans and Gates 1997, Tewksbury et al. 1998) even
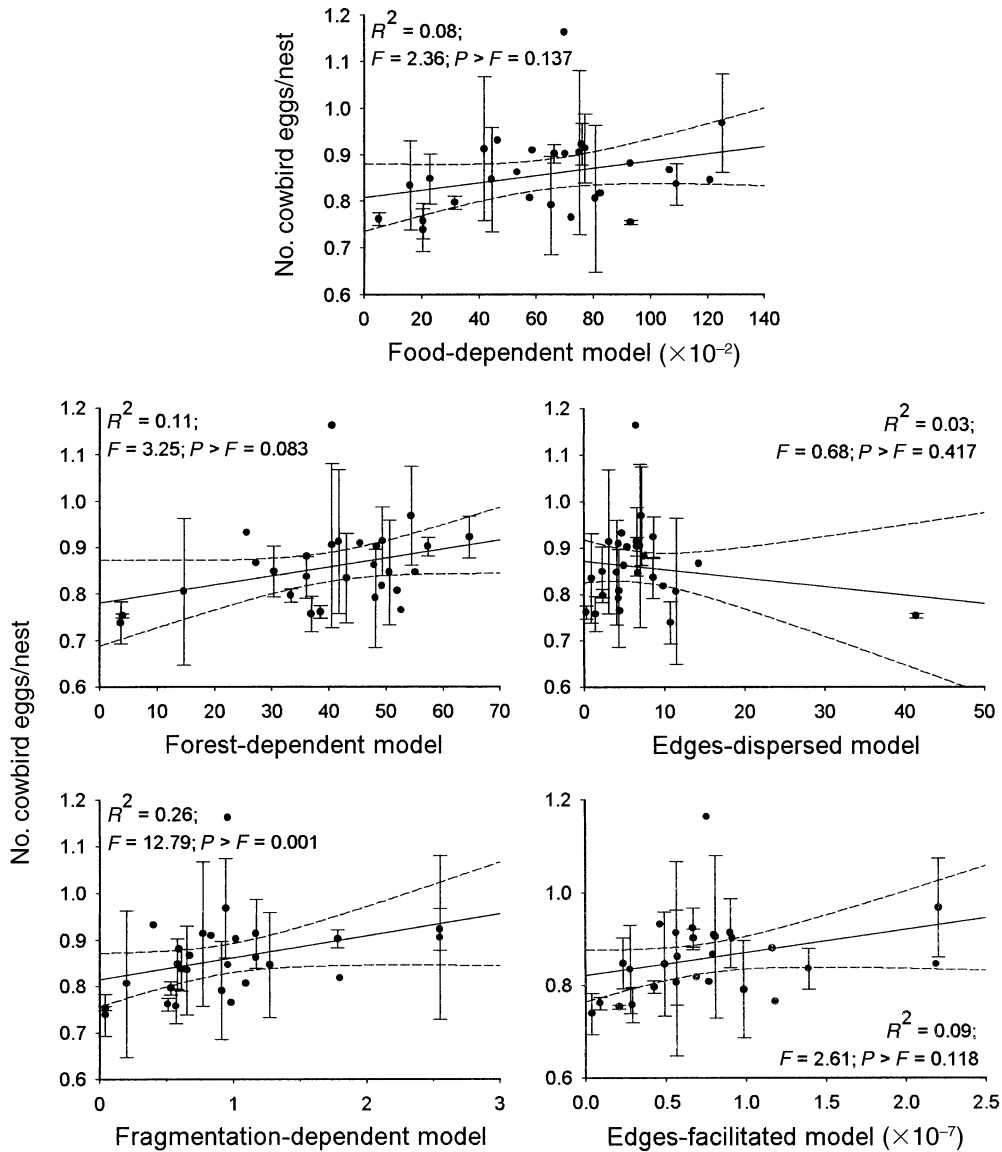
FIG. 8. Relationship between and the mean number (across years) of cowbird eggs per nest and model predictions. These models do not include the distance-to-edge function. The x-axes show unitless, relative values. Numbers of eggs were transformed using a square-root transformation, and error bars show the standard error of the mean. Points without error bars represent plots measured in only a single year. For all F tests, df = 1, 36. (Note that the scale numbers for the x-axis in the top plot and the bottom right plot have been multiplied by 10^{-2} and 10^{-7}, respectively, for purposes of presentation.)

TABLE 3. Brown-headed Cowbird population trends and relative abundance (number of birds per route) during the period 1996–1999 for several Upper Midwestern ecoregions, calculated from the USGS Breeding Bird Survey online database (Sauer et al. 1999).

Ecoregion (BBS physiographic strata)	Geographic location†	Trend (change/yr, %)	Mean no. birds/route
Great Lakes Plain	1	−1.0	13.93
Driftless Area	2	−2.3	23.69
Great Lakes Transition	3	−2.4	15.52
Till Plains	4	1.0	11.95
Dissected Till Plains	5	0.6	29.16
Black Prairie	6	−0.3	31.30

† Numbers refer to ecoregions (BBS physiographic strata) as shown in Fig. 2.

though forest edges may not be related to host density. Some studies suggest that host density is related to fragmentation in the Midwest (Donovan et al. 1997). This may help to explain the strength of the fragmentation-dependent model. Food supply that is not represented in satellite image classifications (e.g., feedlots, bird feeders) may also explain some of the variation; including such food sources could provide better predictive models in the future. Cowbird parasitism activity may be highly variable, both among years (this study) and within a single season (Norris 1947).

Implications

We believe that there are several possible explanations for our results that are related to the biological needs of cowbirds, the hosts, and the interactions with predators of bird nests. Firstly, Brown-headed Cowbirds require suitable hosts and suitable densities of these hosts to successfully parasitize broods. Because most of the hosts are forest passerines (Brittingham and Temple 1983), cowbirds are indirectly affected by the same factors that affect the distribution and abundance of host densities. In landscapes such as those studied here, fragmentation by agricultural and urban land uses results in higher edge density and reduced patch sizes, which have been documented to reduce the incidence and population size of many passerines (Robbins et al. 1989). If host populations are reduced near edges or in smaller forest patches, then cowbirds should be less successful in parasitizing those hosts.

Secondly, several studies have documented higher predation rates on passerine bird species nesting near edges (Wilcove et al. 1986, Paton 1994). Even though higher parasitism rates by cowbirds have been documented near edges (Brittingham and Temple 1983), higher predation rates may partly offset cowbird reproductive success near edges because both the host species and cowbirds are preyed upon. Hanski et al. (1996) reported relatively low cowbird parasitism rates of 9.6% ($N = 311$), but only 1.7% of host nests yielded any cowbird fledglings because predation rates exceeded 50%. Yet, Knutson et al. (M. Knutson, M. Friberg, G. Niemi, and W. Newton, *unpublished manuscript*) observed that nest success in our study area was highest for bird species nesting near the edge (0–74 m) in comparison with those nesting further from the forest edge. Because nest predation is the most common factor causing nest failure (Ricklefs 1969, Martin 1993), the nest predator assemblage and their affinities for various habitats within the landscape may have a large impact on the nesting success of the songbirds (and cowbird young) living in or near those habitats.

The patterns observed in our study could be explained if cowbird foraging areas were of higher quality near the larger forest patches, and if host densities were higher and predation rates were lower in the forest interior. Testing this hypothesis will be difficult, however, because (1) quantifying the extent and distribution of cowbird foraging areas will require detailed landscape analyses; (2) determining host densities will require extensive field sampling; (3) finding nests is a demanding and expensive task; and (4) assessing the distribution and abundance of the many nest predators in the landscape is a massive assignment.

We agree with the hypothesis that, in regions dominated by forests, cowbird parasitism is low because cowbird populations are limited by food availability. Conversely, in regions where forests are rare, cowbird abundance is limited by host availability. In intermediately fragmented landscapes (such as the one we studied); where forests occupy ~30–50% of the landscape, cowbirds may also be limited by host availability. Our results suggest that the expected reproductive gain for cowbirds in these intermediately fragmented landscapes may be higher in more contiguous forests because forest-interior birds tend to have fewer cowbird defenses, yet cowbird foraging areas are within commuting distance of forest-interior habitats (Thompson 1994).

The variability of cowbird parasitism rates is important to consider when developing ecoregional bird conservation plans. Lacking specific nesting success information from a particular site, land managers may incorrectly assume that only large, contiguous forests have value. Our data demonstrate that cowbird parasitism rates can be relatively low even in moderately fragmented landscapes in the Midwest.

Summary

Spatial models such as those presented here can be used to investigate hypotheses about the relationship between landscape pattern and ecological response. We found that landscape composition (abundance of feeding and breeding habitat) and the configuration (fragmentation) of forest habitat were important in our study sites. The abundance of edge habitat and the interaction of edges with feeding habitat appeared to be unrelated to cowbird parasitism. We found a clear, positive relationship between the distance of nests from the forest edge and rates of cowbird parasitism. However, precise prediction of local cowbird activity requires detailed local information. Our study supports the idea that cowbird biology has a strong spatial component, and that improved spatial models applied at multiple spatial scales will be required to provide the capability to predict the effects of landscape and forest management on cowbird parasitism of forest birds.

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