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Title page photograph of a flock of juvenile Brown-headed Cowbirds by Stephen I. Rothstein.

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Abstract

The distribution of Brown-headed Cowbirds should reflect the distribution of their feeding (agricultural or grassy areas) and breeding (host) resources. Because an increase in one resource (e.g., agricultural areas) is often at the expense of the second resource (forest hosts), relationships between cowbird abundance, forest area, and number of hosts may reflect this trade-off. We studied cowbird distribution and abundance in the extensively forested Missouri Ozarks and in fragmented central Missouri. Cowbirds were more abundant on fragments than on unfragmented Ozark study areas, even though hosts were more abundant in the Ozarks. In the Ozarks, there was no relationship between cowbird and host abundance, possibly because cowbirds there were limited more by feeding habitat than by hosts. In contrast, cowbird abundance on fragments was positively related to host abundance, possibly because cowbirds there were limited more by hosts than by food.

Although cowbirds frequently occur in fragmented landscapes, their reproductive success ultimately depends on the ability of hosts to fledge cowbirds successfully. We examined the nesting success of cowbirds in habitats of varying sizes and shapes. The number of cowbird eggs per nest increased as forest size decreased, but daily survival of cowbirds in host nests increased as forest size increased. Thus, a second type of trade-off occurred in that more eggs were laid per nest in fragments where fledging success was relatively low, and fewer eggs were laid per nest in unfragmented forests where fledging success was relatively high.

We examined habitat characteristics at varying spatial scales (1-, 3-, 5-, and 10-km radius circles) to determine what habitat scale best explains cowbird distribution and abundance. Abundance was most strongly related to percentage of forest cover and forest perimeter-to-area ratio at the 3–5-km radius scale. These results suggest that in addition to local-scale factors, Brown-headed Cowbirds may be regulated by habitat characteristics at the landscape scale and that any future cowbird population control should incorporate land management at spatial scales of more than 3 km.

Introduction

A species' distribution and abundance often reflects the distribution of its resources (Brown 1984). For Brown-headed Cowbirds, food resources are distributed in open grassy or agricultural areas whereas breeding resources (hosts) are often distributed in forested areas (Rothstein et al. 1984, Thompson 1994; Thompson and Dijak, Chapter 10, this volume). The probability that a cowbird occurs in a forest therefore depends at least partly on the probability that a feeding area is nearby. As areas become more forested, cowbird breeding opportunities may increase but feeding opportunities may decline. Conversely, as forest habitat is converted to agricultural habitat, feeding opportunities may increase but breeding opportunities may decrease because cowbirds parasitize grassland and shrubland hosts less frequently than forest hosts (Robinson et al., Chapter 33, this volume). The occurrence of cowbirds within landscapes that vary in the amount of forest and agricultural areas may reflect this apparent trade-off between breeding and feeding resources.

A second type of trade-off is also expected to occur within landscapes of varying forest cover. Cowbird production ultimately depends on the nesting success of host species (Lowther 1993). Cowbird hosts on small, fragmented forests often experience higher nest predation than hosts on large, unfragmented forests (Wilcove 1985, Askins et al. 1990, Robinson 1992, Donovan et al. 1995, Robinson et al. 1995). In fragmented landscapes, the distribution of breeding and feeding resources may be optimal for cowbirds, but these landscapes are also suitable for many nest predators (Dijak 1996, Donovan et al. 1997). Thus, cowbirds that lay their eggs in nests within a highly fragmented landscape may experience low nesting success if host nests are frequently depredated. Such fragments may constitute cowbird population sinks, where reproduction does not compensate for adult mortality (Pulliam 1988). In contrast, cowbirds in large, unfragmented forests may be food limited, but depredation in large forest tracts is low, and cowbirds that lay eggs there may be more successful than cowbirds in fragmented forests.

Our goal was to document cowbird distribution and compare cowbird reproductive success in landscapes that vary in the amount of forest and nonforest cover. Our objectives were to (1) compare cowbird abundance in fragmented central Missouri forests with that in the extensively forested Ozark region, (2) determine if cowbird abundance is related to the number of hosts (breeding resources) in fragmented and unfragmented habitats, (3) compare the number of cowbirds per host nest and the nesting success of cowbirds in forests of varying size, and (4) examine the relationship between cowbird abundance and the distribution of forested (breeding) and nonforested (feeding) areas at several landscape scales.

Methods

Cowbird Distribution and Abundance

We studied Brown-headed Cowbird distribution and parasitism on seventeen study plots within seven forest tracts of varying size and shape in Missouri from 1991 to 1993 (Table 30.1). A total of nine fragmented study plots were situated in the highly fragmented central Missouri landscape, and eight study plots were situated within the heavily forested Ozarks in southeastern Missouri (Figure 30.1). In 1991, nine fragmented plots and six contiguous forest plots were studied. In 1992, two additional plots were added within contiguous forest, and one fragmented plot was dropped from the study. Study plots were approximately 22 ha. Forest tracts containing study plots ranged from 7.4 to 18,258 km^2 (Table 30.1). Plots were located within mature oak-hickory forest and appeared to be homogeneous in forest structure (Wenny et al. 1993). The nonforested portion of these landscapes was predominantly cool-season pasture.

We gridded each study plot in 150-m intervals. Grids were established by randomly selecting a point within the forest and situating a grid around that point. Fifteen points along grid intersections were designated "counting points." All counting points were located more than 70 m from an ecotonal edge between forest and nonforest habitat.

Within each plot, we surveyed abundances of Brown-headed Cowbirds and potential hosts by 10-min point counts (Verner 1988) at the 15 counting points. Each point was counted four times during the breeding season. Three to four different observers conducted counts each year according to a protocol described in detail in Donovan et al. (1997) that minimized effects of observer variability (Verner and Milne 1989). Counts began after most territories were established (after 5 May) and ended by mid-June when most nests had fledged young.

In each 10-min count, bird detections were recorded within 50-m and 70-m fixed-radius circles, as well as total (unlimited distance) detections. The mean number of detections in each distance class was computed for each plot in each year. Mean detections at a plot were based on 15 counting points that were censused 4 times within a season ($N = 60$ counts). We selected the appropriate distance class (50 m, 70 m, or unlimited distance) for analysis based on univariate F-tests. In this chapter, we used the unlimited distance class in all analyses because it yielded the highest F-value in discriminating Brown-headed Cowbirds on fragments and contiguous forests (Bradley and Schumann 1957). However, results were similar for the 50-m and 70-m distance classes.

Female cowbirds were differentiated from males based on rattle or chatter calls (Darley 1968). Because female cowbirds are responsible for parasitism and its consequences for host species, we present point-count results for female cowbird detections alone and for all cowbird (male and female) detections. Caution must be used in interpreting female detections based solely on rattle calls because the social context in which these calls are given and how they influence detectability are poorly understood (Lowther 1993; Rothstein et al., Chapter 7, this volume).

We compared cowbird abundance on fragmented ($N = 9$ plots) and contiguous forests ($N = 8$ plots) using a repeated measures analysis of variance, with landscape (fragmented or contiguous) as a main effect and year as a repeated effect. Replicate plots within a landscape were used as the error term.

Relationship of Host Abundance and Cowbird Abundance

Host abundance was surveyed in the same manner as for Brown-headed Cowbirds, and records consisted predominantly of singing males. We identified hosts as those species that bred during the time Brown-headed Cowbirds were censused and received Brown-headed Cowbird eggs in over 10% of their nests (based on nests located within the study plots and parasitism rates in the literature). Possible errors in host detection may have occurred because hosts vary in their detectability and because females of some species may sing (e.g., Northern Cardinal, *Cardinalis cardinalis*). We summed the number of potential hosts at a given plot in a year over all host species, and used all observations of hosts to compute mean host abundance for each plot.

We compared host abundance on fragmented ($N = 9$ plots) and contiguous forests ($N = 8$ plots) using a repeated measures analysis of variance, with landscape (fragmented or contiguous) as a main effect and year as a repeated effect. Plots within a landscape were used as the error term.

Simple linear regressions were used to determine the relationship between cowbird abundance and host abundance

Table 30.1. Description of the Seven Forest Tracts Containing 17 Study Plots

Forest	Plots[a]	Sites[b]	Type[c]	Area (km²)	Perimeter (km)	Perimeter-to-Area Ratio	Forest Area[d] r = 1 km	Forest Area[d] r = 3 km	Forest Area[d] r = 5 km	Forest Area[d] r = 10 km
Ashland	2	1	frag	40.6	142.5	3.5	2.5	18.9	41.4	132.3
Bennitt	1	1	frag	20.2	51.9	2.6	3.1	17.8	41.4	114.9
County J	2	1	frag	7.9	37.1	4.7	1.4	7.7	22.4	72.7
Fulton	1	1	frag	7.4	32.7	4.4	2.3	6.3	15.0	63.2
Hungry Mother	1	1	frag	24.9	82.2	3.3	2.5	16.8	37.1	103.1
Whetstone	2	1	frag	39.0	150.8	3.9	2.6	14.0	28.6	105.9
Ozarks	8	4	cont	18,258.0	16,842.9	0.9	3.1	27.3	75.7	289.4

[a] Number of study plots situated within a particular forest tract.

[b] Number of sites within a forest tract.

[c] Forest types are fragmented plots (frag) within central Missouri or contiguous plots (cont) within the Ozarks region.

[d] Areas are in square kilometers.

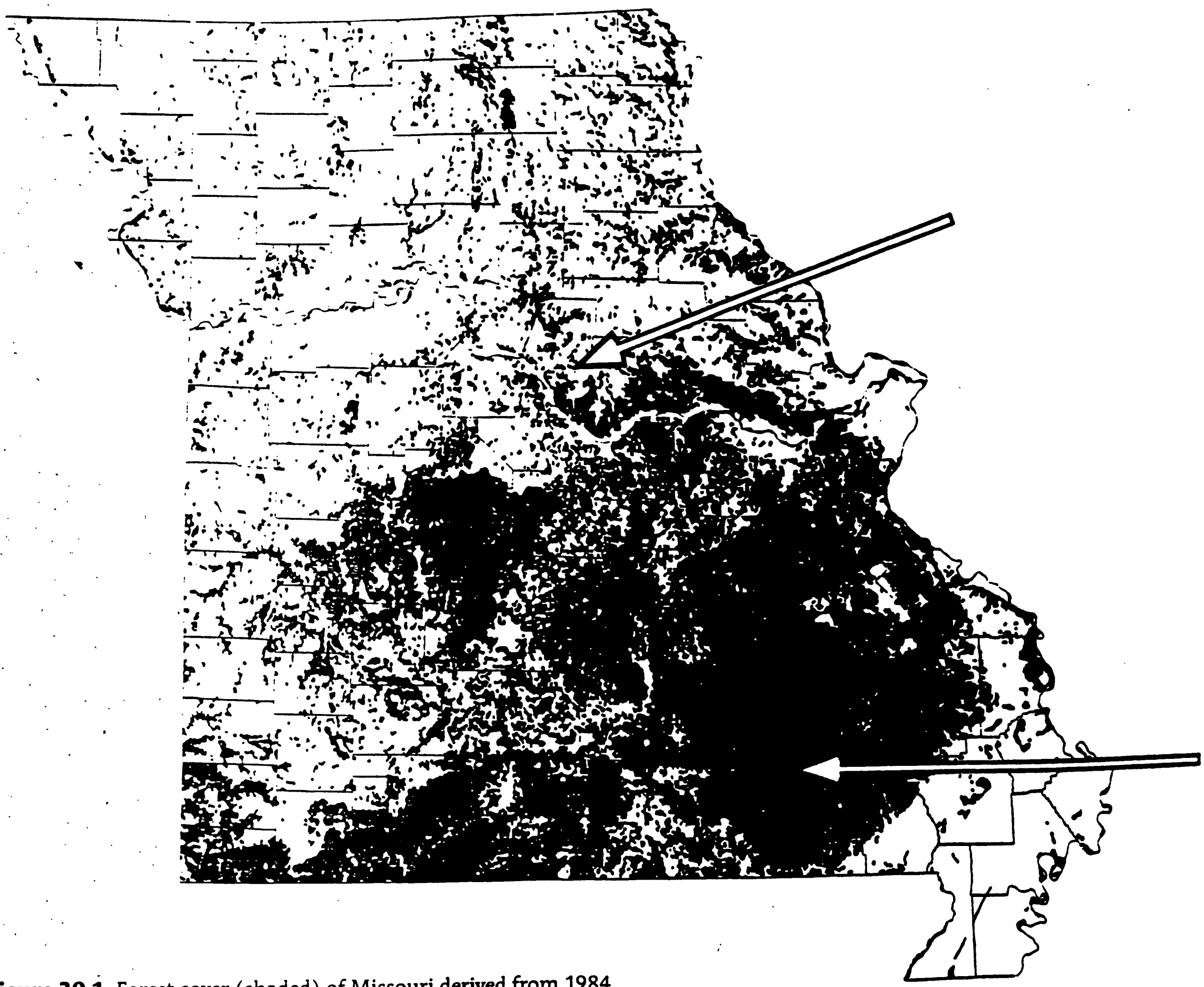

Figure 30.1. Forest cover (shaded) of Missouri derived from 1984 Transverse Mercator scenes showing general locations of study plots within fragmented central Missouri ($N = 9$ study plots) and unfragmented Ozarks in southeastern Missouri ($N = 8$ study plots).

at the plot level for each landscape. In these analyses, cowbird and host abundance at a plot were considered separately for each year because abundance of each varied between years (thus, $N = 17$ for the fragmented landscape, $N = 14$ for the contiguous landscape). Separate analyses were used because host abundance differed between the two landscapes examined.

Reproductive Success of Cowbirds in Landscapes of Varying Forest Cover

Nests that contained cowbird eggs were located in 1991–1993 on four forest tracts of varying size and were monitored every three to five days. These forest tracts included the Ashland, Hungry Mother, and Bennitt fragments and the unfragmented Ozarks (Table 30.1). For each parasitized nest, we recorded the number of cowbird eggs, chicks, and fledglings. We determined the mean number of cowbirds per nest in each forest, and used Spearman's rank correlation to determine if there was an association between the number of cowbird eggs per nest and log forest area.

We calculated daily survival of cowbirds on a per-egg basis (Mayfield 1975) and used those estimates to determine the probability that a cowbird egg would survive to fledging (nesting success). In multiply parasitized nests, these estimates may be upwardly biased because cowbirds may remove conspecific eggs. Because the incidence of multiple parasitism is related to forest size (see below), we considered this potential bias as unimportant because it would bias *against* showing an effect of forest size on cowbird nesting success. We calculated survival days across host species within a site to determine cowbird daily survival for each forest. This approach was necessary because sample sizes of parasitized nests on a per-host basis were limited. However, all hosts were forest-interior species and have similar responses to parasitism. In addition, the composition of parasitized hosts was fairly consistent among the four forests we studied for this analysis, with the large Wood Thrush being the most frequently parasitized host in three of the four plots (Table 30.2). Nevertheless, caution should be used in interpreting cowbird survival data from a combination of host nests, because hosts vary in their ability to fledge cowbird young; future studies should include effects of host quality. We used Spearman's rank correlation to determine if there was an association between cowbird daily nest survival and log forest area.

Landscape Patterns and Cowbird Abundance at Selected Spatial Scales

Because cowbird distribution may represent a trade-off between feeding and breeding resources, we examined landscape characteristics at different spatial scales to determine the habitat scale that best explains cowbird distribution. We used an existing forest-cover GIS database developed by the Missouri Department of Conservation and the Geographic Resources Center at the University of Missouri–Columbia (Giessmann et al. 1986) to compute landscape statistics at 1-, 3-, 5-, and 10-km radius spatial scales. The distribution of forestland in Missouri was determined from sixteen Landsat Satellite Thematic Mapper photographic images obtained during the 1984 growing season (Giessmann et al. 1986). Areas of more than 2 ha with at least 10% canopy cover were considered forested habitat and were digitized using an analytical mapping system. Files were incorporated into a GIS, and Map Overlay Statistical System (MOSS) was used to manage digitized data to produce forest area estimates and maps.

We located all seventeen study plots within the GIS database. Some fragmented study plots were situated within the same forest polygon; all plots within the heavily forested Ozarks were situated within the same forest polygon (Table 30.1). For fragments, we averaged cowbird detections among plots that were located within the same forest polygon for analyses. As a result, six forest tracts were evaluated in the fragmented landscape. Although all eight contiguous plots were located within the unfragmented Ozarks, these plots were spatially located as four paired plots that were separated by more than 5 km, and thus the four pairs were considered as independent. We averaged cowbird detections of paired plots for analyses ($N = 4$). For clarity, these ten forests ($N = 6$ fragments and 4 contiguous) will be called sites; sites consisted of 1–2 study plots (Table 30.1).

We calculated the percentage of forest cover and perimeter-to-area ratio within 1-, 3-, 5-, and 10-km radius circles on each site (Figure 30.2 and Table 30.1). We evaluated the relationship between cowbird abundance at a site ($N = 10$) and percentage of forest cover and perimeter-to-area ratios at these scales. This scale of evaluation is appropriate because female cowbirds move up to 10 km between feeding and breeding areas within a breeding season in this region (Thompson 1994; Thompson and Dijak, Chapter 10, this volume).

We used simple, univariate regression models to determine if linear relationships existed between cowbird abundance, cowbird survival, and percentage of forest cover and perimeter-to-area ratio across sites at the 1–10-km radius scales. We examined the adjusted r^2 for each model to determine the scale (1-, 3-, 5-, or 10-km radius circles) at which the linear relationship was strongest.

Results

Cowbird Distribution and Abundance

Brown-headed Cowbirds occurred much more frequently on fragmented central Missouri plots than on extensively forested Ozark plots (Table 30.3). Results were similar for analyses based solely on female cowbird detections (Table 30.3). Additionally, cowbirds increased between 1991 and 1992 (repeated measures analysis of variance main effect of year, able 30.2. Numbers of Parasitized Nests Located for Each Host Species in Each Forest

orest	ACFL	BAWW	INBU	KEWA	NOCA	OVEN	REVI	WEWA	WOTH	Total
Ashland	1 (1)	0 (0)	1 (1)	4 (5)	1 (3)	2 (6)	0 (0)	2 (4)	11 (31)	22 (51)
Bennitt	1 (1)	0 (0)	0 (0)	1 (3)	1 (1)	0 (0)	0 (0)	3 (6)	2 (6)	8 (17)
Hungry Mother	1 (1)	0 (0)	0 (0)	0 (0)	1 (2)	1 (2)	1 (3)	4 (10)	9 (24)	17 (42)
Ozarks	3 (3)	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)	3 (3)	2 (2)	1 (1)	11 (11)

Note: Total number of cowbird eggs or young detected in parasitized nests of each host species is shown in parentheses. Abbreviations: ACFL, Acadian Flycatcher. BAWW, Black-and-white Warbler. INBU, Indigo Bunting. KEWA, Kentucky Warbler. NOCA, Northern Cardinal. OVEN, Ovenbird. REVI, Red-eyed Vireo. WEWA, Worm-eating Warbler. WOTH, Wood Thrush.

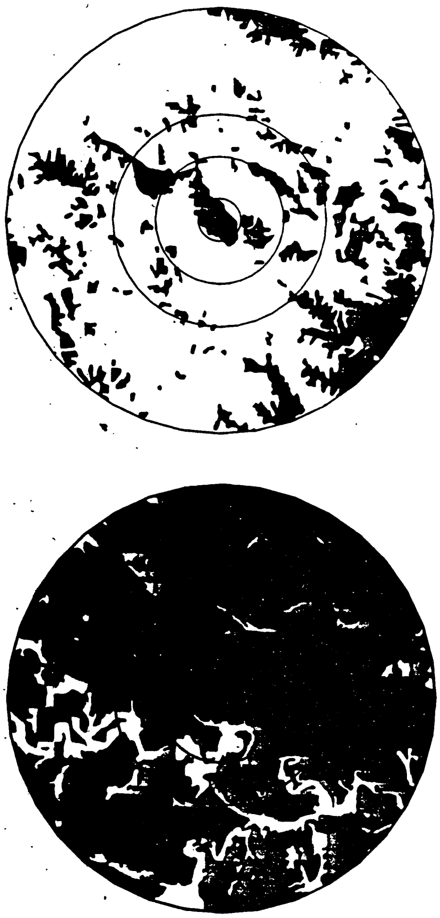

Figure 30.2. Images of a fragmented central Missouri study site (top) and a contiguous forest southeastern Missouri study site (bottom) showing the forest cover (shaded) within 1-, 3-, 5-, and 10-km radius circles.

$F = 18.00$, $P = .001$), and this increase was greater on fragments than in contiguous forests (landscape x year interaction, $F = 15.98$, $P = .002$).

Relationship of Host Abundance and Cowbird Abundance

Although cowbirds were more abundant on fragments, hosts were more abundant in unfragmented habitat (Table 30.3). Cowbird abundance at a plot was related to the abundance of potential hosts at a plot, but this relationship depended on the forest landscape in question. On fragmented study plots, cowbirds (males and females combined) were positively related to the number of hosts (Figure 30.3). This trend was not significant when examining female cowbirds alone ($F = 2.70$, $P = .12$, $r^2 = 0.153$). In contrast, cowbird (males and females combined) and host abundances were not related in unfragmented Ozark plots ($F = 3.11$, $P = .10$, $r^2 = 0.21$).

Reproductive Success of Cowbirds in Landscapes of Varying Forest Cover

We analyzed the incidence of multiple parasitism and nest survival on four forests of varying size. In the Ozarks, parasitism was almost nonexistent; of more than 500 host nests located in the Ozarks, only 11 nests (six host species) were parasitized (Faaborg and Clawson unpubl. data). On the three fragments, 47 total nests (eight host species) containing 110 cowbird eggs or young were located (Table 30.2). All nests in the Ozarks were singly parasitized, whereas most nests in fragments were multiply parasitized (mean = 2.55 cowbird eggs/parasitized nest, SD = 1.35; Wilcoxon two-sample test, $Z = -3.76$, $P = .000$). Of the eight host species on fragments, nests of six hosts were multiply parasitized. In the three fragments studied, parasitized Wood Thrush nests contained the majority (> 50%) of the cowbird eggs located. Figure 30.4 shows that the number of cowbird eggs per parasitized nest increased as forest size decreased (Spearman's rank correlation, $r_s = -1.00$, $P = .000$). In contrast, cowbird nesting success (the probability that a cowbird egg would survive to fledging) increased as forest size increased ($r_s = 1.00$, $P = .000$).

Table 30.3. Repeated Measures ANOVA at a Study Plot Showing Main Effect of Landscape

	Fragments			Contiguous			
Detections	Mean	SD	*N*	Mean	SD	*N*	*P*
Mean BHCO[a]	0.95	0.32	17	0.27	0.12	14	.000
Mean female[b]	0.20	0.12	17	0.04	0.02	14	.000
Mean host	5.66	1.32	17	6.88	0.78	14	.004

[a] Female and male cowbird observations.

[b] Female cowbird observations only.

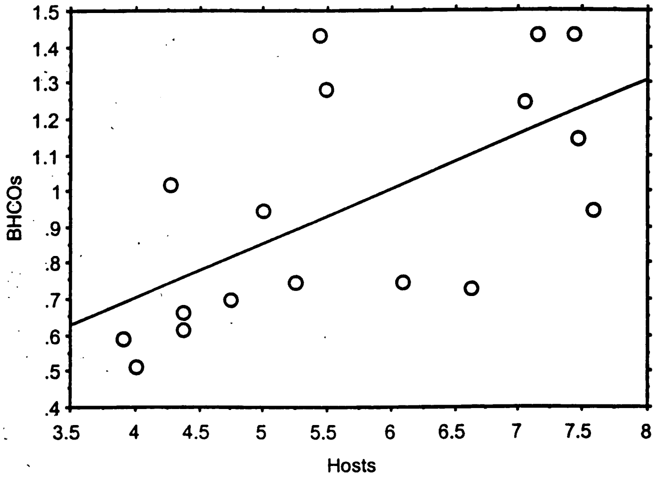

Figure 30.3. Relationship between cowbirds (male and female) and hosts on fragmented study plots in central Missouri. Cowbird abundance = 0.15 (number of hosts) + 0.096; $F = 9.59$, $P = .007$, $r^2 = 0.39$. Because cowbird abundance varied with years, the relationship of cowbirds to hosts was calculated separately for each year ($N = 9$ plots in 1991 and 8 plots in 1992).

Landscape Patterns and Cowbird Abundance at Selected Spatial Scales

Cowbird abundance (male and female) was not related to forest area at the 1-km scale ($P = .073$) but was negatively related to forest area at the 3-, 5-, and 10-km scales ($P = .002$, .001, and .000, respectively), as shown in Table 30.4. The variation in cowbird abundance was best explained by the variation in percentage of forest cover at the 10-km scale (adj. $r^2 = 0.854$). The abundance of female cowbirds was negatively related to percentage of forest cover at all spatial scales analyzed (Table 30.4). The variation in female cowbirds was best explained by variation in percentage of forest cover at the 3-km and 5-km scales (adj. $r^2 = 0.93$ for both scales).

Cowbird abundance was also related to the perimeter-to-area ratio of the landscape in question (Table 30.4). The variation in cowbird abundance was positively related to the variation in perimeter-to-area ratio at the 3-, 5-, and 10-km scales ($P = .009$, .002, and .001, respectively) but not at the 1-km scale ($P = .117$). Female cowbirds showed a similar pattern but were significantly related to perimeter-to-area ratios at all scales examined. As with forest area, the relationship between cowbird abundance and habitat edge was best explained at spatial scales greater than 3 km (Table 30.4).

Host abundance was positively related to percentage of orest cover and negatively related to perimeter-to-area ratio t the 3-, 5-, and 10-km scales ($P = .04, .03, .04$, and $P = .03$, 03, .04, respectively), as shown in Table 30.4. Host abunlance was not related to percentage of cover or perimeter-to-rea ratio at the 1-km scale ($P = .08$ and .18, respectively).

Discussion

Cowbird Distribution and Abundance

Cowbirds evolved in open grasslands where their breeding and feeding resources overlapped spatially (Lowther 1993), but presettlement populations were potentially limited because many sympatric hosts evolved strategies against parasitism (Briskie et al. 1992). In the past 200 years, however, cowbirds have benefited tremendously by the clearing of forests for agricultural purposes (Brittingham and Temple 1983). These changes in landscape have increased feeding resources (agriculture) and introduced new breeding resources (naive hosts) that were previously inaccessible to cowbirds.

Telemetry studies in Missouri and New York have shown that although feeding and breeding resources can overlap spatially, cowbirds often move considerable distances between breeding and feeding areas (Thompson 1994; Hahn and Hatfield, Chapter 13, this volume). In Missouri, female cowbirds tend to breed in host-rich forests in the early morning and move to open grassy or agricultural areas to feed later in the day (Thompson 1994). In the Ozarks, feeding areas are limited and there may be costs (energetic, behavioral) in moving longer distances to sites with abundant hosts. In contrast, mixed forest and agricultural landscapes in central Missouri possess both breeding and feeding resources for cowbirds; the distribution of these two resources in fragmented landscapes may be more favorable for cowbirds than in heavily forested landscapes.

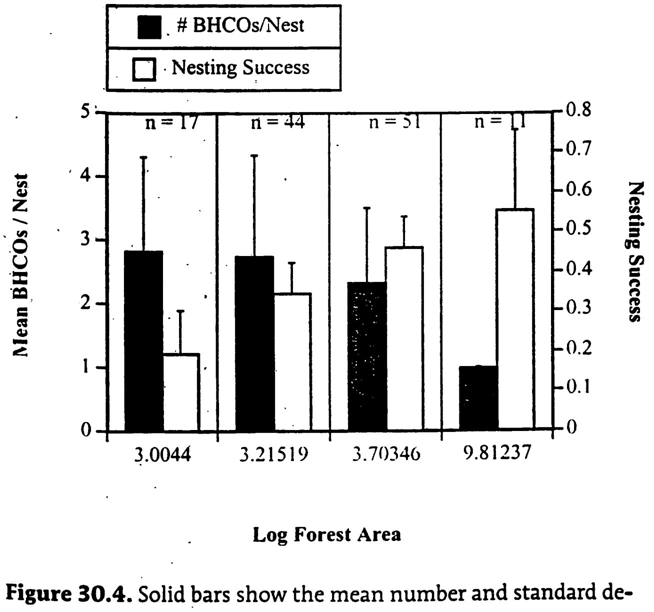

Figure 30.4. Solid bars show the mean number and standard deviation of cowbird eggs per parasitized nest in forests of different areas; stippled bars show nesting success ± SE of cowbirds in forests of different areas.

At some point, however, severely fragmented forests within agricultural landscapes may lack sufficient hosts. There may be costs in traveling between breeding and feeding areas in such landscapes. The fragmented landscape in central Missouri averaged approximately 32% forest cover at the 10-km scale (8% core habitat, Donovan et al. 1995). Thus, the fragmented landscape we studied was perhaps too forested to show an effect of host limitation. We suggest that future studies focus on determining the distribution of cowbirds across an even broader spectrum of forest-field landscapes.

Trade-offs in Host Abundance, Cowbird Abundance, and Reproductive Success

Although cowbirds breed in a wide variety of habitats, several studies suggest that cowbirds select habitats with high host densities (Rothstein et al. 1986, Verner and Ritter 1983; Thompson et al., Chapter 32, this volume). However, this relationship may depend on whether feeding resources are nearby. In our study, cowbird abundance was not related to host abundance in large unfragmented forests, despite an abundance of breeding opportunities, possibly because cowbirds were limited more by feeding resources than by host resources. Our study plots were situated well within forest core habitat, buffered from cowbird feeding habitats. In heavily forested landscapes such as the Ozarks, positive associations between host and cowbird abundance may be evident in portions of the forest that are located near agricultural openings.

In many forest habitats throughout the United States, the total number of forest hosts and host densities decrease as forest area decreases (Askins et al. 1990, Wenny et al. 1993), creating an interplay of trade-offs between forest size, host abundance, and cowbird abundance in fragmented landscapes. In our study, as forest size decreased, hosts were less common but cowbirds increased. As forest size increased, host abundance increased but cowbird numbers decreased. Additionally, host nests in fragments were often multiply parasitized and had low nesting success, whereas host nests in the Ozarks were singly parasitized and had higher nesting success.

We suggest that habitat distribution patterns in fragmented landscapes contribute to the incidence of multiple parasitism by increasing the number of female cowbirds that seek limited host resources. We do not believe that increased incidence of multiple parasitism in fragments is a sampling artifact due to differences in host susceptibility to parasitism. First, although we combined host species to examine

Table 30.4. Univariate regressions of Cowbird and Host Abundance against Percentage of Forest Cover and Perimeter-to-Area Ratios at Selected Spatial Scales

Dependent Variable	Independent Variable	Scale	Slope	Adj. r^2	P
BHCO abundance	% forest cover	1 km	−1.503	0.266	.073
		3 km	−1.059	0.670	.002
		5 km	−1.106	0.773	.001
		10 km	−1.463	0.854	.000
	Perimeter/area ratio	1 km	+0.154	0.189	.117
		3 km	+0.126	0.547	.009
		5 km	+0.127	0.685	.002
		10 km	+0.129	0.773	.001
Female BHCO abundance	% forest cover	1 km	−0.534	0.678	.002
		3 km	−0.303	0.939	.000
		5 km	−0.296	0.933	.000
		10 km	−0.366	0.850	.000
	Perimeter/area ratio	1 km	+0.053	0.480	.016
		3 km	+0.039	0.900	.000
		5 km	+0.036	0.905	.000
		10 km	+0.033	0.839	.000
Host abundance	% forest cover	1 km	+3.899	0.258	.077
		3 km	+2.148	0.351	.042
		5 km	+2.170	0.378	.034
		10 km	+2.033	0.357	.042
	Perimeter/area ratio	1 km	−0.353	0.117	.177
		3 km	−0.288	0.383	.033
		5 km	−0.273	0.415	.026
		10 km	−0.251	0.370	.037

Note: N = 10 sites.

multiple parasitism and nest survival in forests of varying size, the composition of host nest samples was similar on all fragments, with cowbird eggs being laid primarily in Wood Thrush nests. Second, Wood Thrush nests show the least variation in predation rates in relation to forest size compared to other hosts (Robinson et al. 1995, Chapter 33, this volume). Third, the relationship between multiple parasitism and forest size is the same even when analyzed on a per-species basis (Thompson et al., Chapter 32, this volume). Thus, multiple parasitism appeared to increase as forest size decreased, even though cowbird nesting success was lower there.

Although we have suggested that landscape habitat patterns contribute to multiple parasitism and high predation rates in fragmented landscapes, alternative explanations should be evaluated. An alternative to the landscape hypothesis is that the number of parasites in a nest may influence nesting success more than forest area per se. In our study areas, however, nesting success of cowbirds in singly versus multiply parasitized nests did not differ (Donovan unpubl. data; also see Trine, Chapter 15, this volume). Thus, we suggest that landscape features influence the trade-off between cowbird occurrence, host occurrence, and cowbird nesting success. A clear understanding of such trade-offs requires studying host and cowbird distribution, cowbird philopatry, and cowbird nesting success across many landscapes that vary in their distribution of cowbird breeding and feeding areas. Additionally, comparisons of annual and lifetime fitness of females that parasitize hosts on fragments with females that parasitize hosts on larger forest tracts would be illuminating.

Management Implications

Cowbird Abundance and Habitat Features at Selected Spatial Scales

Our analyses suggest that cowbird occurrence is best explained by forest cover and perimeter-to-area ratio at spatial scales greater than 3 km. Many studies of the distribution of cowbirds have focused on local-scale factors such as distance to edge, vegetation characteristics, size and shape of the study plot, etc. (Robinson et al. 1993). Although local habitat characteristics may influence cowbird distribution (Uyehara and Whitfield, Chapter 24, this volume), we emphasize that cowbird populations may also be regulated by landscape-scale habitat patterns. For female cowbirds, relationships between cowbird distribution and forest cover were the strongest when habitat characteristics were examined 3–5 km from the study site. For all cowbirds, these relationships gained strength as scale increased (Table 30.4). These results suggest that in managing cowbird numbers, habitat characteristics should be evaluated beyond the local scale (Robinson et al., Chapter 33, and Thompson et al., Chapter 32, this volume).

Strong biological reasons may underlie the patterns we detected. Telemetry studies of female cowbirds in fragmented central Missouri revealed that cowbirds move on average 1–2 km between breeding and feeding areas (range 0.03–7.34 km; Thompson 1994; Thompson and Dijak, Chapter 10, this volume). In these movements, suitable feeding and breeding habitat is apparently bypassed. Because cowbirds can move great distances to optimize their resource use, managing for forest area or perimeter-to-area ratios at scales of less than 3 km may have little impact on cowbird distribution if the surrounding landscape provides optimal cowbird feeding and breeding resources.

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