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# USE OF DIFFERENT HABITATS BY BREEDING BROWN-HEADED COWBIRDS IN FRAGMENTED MIDWESTERN LANDSCAPES

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*Abstract.* We compared levels of brood parasitization and relative abundance of Brown-headed Cowbirds (*Molothrus ater*) in forests, savannas, shrublands, and grasslands in seven regions of Illinois, 1985–1997. Our primary objective was to determine if cowbirds avoid habitats in which rates of nest predation or abundances of unsuitable hosts are high. Bird communities differed significantly among vegetation types in the proportion of species with defenses against cowbirds (rejecter species that abandon or eject cowbird eggs, aggressive nest defense) and in overall nest predation rates. The relative abundance of cowbirds and the community-wide levels of parasitization were lowest in grasslands, which also had significantly higher nest predation rates than the other three vegetation types. Parasitization levels were highest in forests, but community-wide levels of parasitization in forests and savannas did not differ significantly when rejecter species were eliminated from the analysis. The relative abundance of cowbirds was highest in savannas, even though savannas had a significantly higher proportion of species that reject cowbird eggs than forests. Forests and shrublands did not differ significantly in cowbird abundance, in spite of significantly higher proportions of rejecters in shrubland bird communities. We found little evidence that cowbirds avoided habitats with higher nest predation rates within regions; cowbirds avoided grasslands even in regions with low nest predation rates on grasslands birds. These results suggest that cowbird habitat selection is not necessarily fine-tuned to the quality of available hosts in this landscape. Managers can reduce community-wide parasitization in this landscape by restoring grasslands, which are used less by cowbirds, and savannas, which contain a high proportion of species with defenses against parasitization. Future research directions should focus on habitat-specific breeding success of cowbirds, new studies of host defenses, and the behavioral mechanisms underlying habitat and host selection in cowbirds.

*Key Words:* Brown-headed Cowbird, forest, grasslands, Illinois, *Molothrus ater,* savanna, shrubland, rejecters, use of plant communities.

The Brown-headed Cowbird (*Molothrus ater*) breeds in a wide range of habitats throughout North America (Robinson et al. 1995b). Because cowbirds can breed and forage in different areas, they are much less restricted in their habitat requirements than most birds. This uncoupling of feeding and breeding also gives cowbirds an opportunity to choose habitats based solely on the availability of hosts as long as foraging sites are available nearby (within 7 km; Rothstein et al. 1984, Robinson et al. 1995b). Although cowbirds are extremely generalized in their use of hosts, which may make fine-grained assessment of habitat unlikely, they are also known to revisit nests they have parasitized (Arcese et al. 1996), which gives them an opportunity to assess their own breeding success in an area.

Relatively little is known, however, about cowbird preferences, if any, for particular habitats for breeding (reviewed in Robinson et al. 1995b). Hahn and Hatfield (1995) reported that cowbirds preferred to search for host nests in forest rather than more open, shrubby vegetation types. Similarly, Strausberger and Ashley (1997) and Robinson et al. (in press) reported generally higher levels of parasitization in forest than in shrubland/edge and grasslands in Illinois where all plant communities are within the cowbirds' daily commuting range. None of these studies, however, compared the relative abundance of cowbirds and suitable hosts (species that do not reject cowbird eggs or abandon parasitized nests) among the different vegetation types. If cowbirds occur in proportion to the availability of suitable hosts, then use of vegetation types may reflect different proportions of suitable hosts. If, on the other hand, cowbirds do not avoid vegetation types with fewer suitable hosts, then differences in community-wide levels of parasitization among vegetation types may simply reflect the proportion of species that reject cowbird eggs and hence have low frequencies of parasitization (Strausberger and Ashley 1997). To distinguish among these possibilities, we need data on the ratio of cowbird abundance to host abundance in different vegetation types.

The issue of habitat use by cowbirds has important management implications. Restoring plant communities that cowbirds avoid may be a high conservation priority in chronically fragmented landscapes in which nearly all areas are accessible to cowbirds. Restoration of plant communities that contain high proportions of unsuitable hosts may also be effective. If cowbirds do not avoid vegetation types with high proportions of rejecters or in which nest predation rates are high, then such vegetation types may act as population sinks (Pulliam 1988) and

TABLE 1. STUDY AREAS BROKEN DOWN BY REGION IN ILLINOIS

| Region (years of study) | Location | Plant communities included (number of sites) |
|---|---|---|
| Driftless Area (1992–1994, 1997) | Extreme northwestern Illinois in Jo Daviess and Carroll counties | Grassland (1), shrubland (3), forest (6) |
| Prairie Parklands (1995–1997) (Joliet Arsenal/ Midewin National Tall-grass Prairie) | Northeastern Illinois in Will County | Grassland (3), shrubland (2) |
| Rock River Valley (1994–1997) | Northcentral Illinois in Lee and Ogle counties | Grassland (1), shrubland (2), forest (3) |
| Illinois River Valley (1994–1996) | Central Illinois in Tazewell, Peoria, and Mason counties | Savannah (3), forest (3) |
| Illinois Ozarks (1989–1997) | Southern Illinois in Union, Alexander, and Jackson counties | Shrubland (2), forest (4) |
| Cache River (1993–1997) | Southern Illinois in Johnson and Pulaski counties | Grassland (1), shrubland (3), forest (8) |
| East-central Illinois (1985–1997) | Champaign, Piatt, Vermillion, Moultrie, and Shelby counties) | Shrubland (2), forest (4) |

ecological traps (Gates and Gysel 1978) for cowbirds, as argued by Donovan et al. (in press).

In this paper, we explored habitat use by Brown-headed Cowbirds in a landscape where all possible study areas were equally accessible to cowbirds (i.e., all were within 7 km of extensive cowbird feeding habitat; Thompson 1994, Thompson et al. in press). We documented composition of host communities in each vegetation type, relative abundance of cowbirds, and levels of parasitization for forests, savannas (including open woodlands), shrublands, and grasslands. We used these data to test the following hypotheses for differences among vegetation types in parasitization levels (Strausberger and Ashley 1997, Robinson et al. in press). (1) Cowbirds prefer forests (Hahn, and Hatfield 1995). If true, we predicted that both community-wide parasitization levels and the ratio of cowbird abundance to host abundance should be significantly lower in more open vegetation types (e.g., shrublands, savannas, and grasslands) than in forests. (2) Cowbirds avoid some habitats because they have a higher proportion of rejecters (i.e., species that eject cowbird eggs or abandon parasitized nests). If cowbirds behave adaptively, then we predicted that cowbirds would avoid vegetation types with more rejecters or that cowbird:host ratios would reflect the availability of suitable hosts rather than all potential hosts (including rejecters). Alternatively, if cowbirds do not avoid these habitats, then lower parasitization levels in some vegetation types may simply reflect high proportions of rejecters. To test this hypothesis, we also compared parasitization levels of species that do not reject cowbird eggs. (3) Cowbirds avoid habitats that have a higher proportion of species that mob cowbirds, which prevents cowbirds from parasitizing other species in the community as well (Robertson and Norman 1976, Clark and Robertson 1979, Neudorf and Sealy 1992). We predicted that vegetation types with lower parasitization levels would also have a significantly higher proportion of mobbers. (4) Cowbirds avoid habitats with chronically higher levels of nest predation. If cowbirds do not avoid habitats with high predation rates, then they may be susceptible to ecological traps (i.e., they may prefer population sinks). (5) Differences in vegetation structure among vegetation types may account for varying parasitization levels. We cannot test this hypothesis directly because it is not clear which habitats should be easiest for cowbirds to search for nests. For this reason, we discuss this hypothesis, but did not make or test any predictions derived from it.

## STUDY AREAS AND METHODS

Study areas were located throughout Illinois (Table 1); we only included sites in an agricultural landscape matrix in which all sites were surrounded by row crops where cowbirds feed in Illinois (Thompson 1994), and we excluded sites in urban areas such as Chicago. We divided our sites into seven regions (Table 1), each of which contained at least two vegetation types for which we have data. Grasslands included a diverse array of management types, including native and non-native vegetation, burned and unburned sites, and grazed and ungrazed sites. Shrublands included regenerating clearcuts, old fields at varying stages of succession, areas in which shrubs had invaded grassland plant communities (e.g., unburned areas and willow thickets in wet areas), and shrubby borders of forest tracts and forest streams. Savannas included oak (*Quercus*)-dominated forests on dry, sandy soils and on ridgetops. All savanna sites had been burned to retain canopy openness. Forests included both upland and floodplain sites and were all dominated by various species of oaks and hickories (*Carya*). We excluded forests dominated by non-native trees such as pines (*Pinus*) and black locusts (*Robinia pseudoacacia*). Landscapes within a 10-km radius around study sites (Robinson et al. 1995a) varied among regions from mostly (>70%) row crops (Prairie Parklands, Illinois River Valley, Rock River, Cache River, East-central Illinois) to roughly 50% forested (Illinois Ozarks).

Within each study site, we censused birds and searched for and monitored the progress of nests following protocols used previously in the Midwest (Robinson 1992, Robinson et al. 1995a, Brawn and Robinson 1996). Censuses were conducted from 15 May to 5 July (southernmost sites), 25 May to 5 July (central sites), and 1 June to10 July (northernmost sites). Censuses were conducted only by experienced observers carefully trained in point count methods (Hutto et al. 1986) from 05:40–11:00 CST on days with little wind and no rain. Censuses usually ended by 10:00 except for occasional days when singing activity (number of detections per point) did not drop until later in the morning. Depending upon the plot, census points were either arranged in a grid at 150–300 m intervals (small plots), or along transects (large study areas) at 150–300 m intervals. Observers stopped at each census point and began counting birds immediately. For each bird heard or seen, we estimated its distance from the census point, noted whether it was heard or observed, and noted its compass direction. Birds heard or seen flying overhead were not recorded. Censuses lasted 5 minutes. Any birds flushed from near the census point as the observer approached were counted as having been recorded during the census under the assumption that they would likely have remained at the point had they not been scared away by the observer. Special care was taken to avoid double-counting birds either at the same point or at consecutive points by carefully noting compass directions to verify countersinging (two or more individuals singing at the same time) and possible movements. For species in which both sexes vocalize (e.g., Northern Cardinal *Cardinalis cardinalis,* Acadian Flycatcher *Empidonax virescens,* Eastern Wood-Pewee *Contopus virens*), we recorded songs versus calls separately (Acadian Flycatcher) and tried to distinguish between pairs by not double-registering birds that were singing close to each other. This method is somewhat subjective, but was often facilitated in cardinals by extensive interactions between the sexes (calling, alarm behavior, feeding fledglings) that often made it possible to see both sexes of a pair.

For forests, shrublands, and savannas, we used all birds heard within a 70-m radius (Robinson et al. in press). We only used data from sites at which at least 15 point counts were conducted (either 15 separate points or replicates of a smaller number of points for smaller tracts). For grasslands, we used a 100-m radius to accommodate the much greater visibility and reduced obstruction to sounds in this very open environment. Special care was made in grasslands to record singing males separately to reduce overestimates of species in which females often perched conspicuously (e.g., meadowlarks *Sturnella* spp., Red-winged Blackbird *Agelaius phoeniceus*).

To compare relative abundance of cowbirds and hosts, we used the cowbird:host ratio of Robinson et al. (in press). To calculate this ratio, we summed up all cowbird registrations per point within a 70-m radius using only cowbirds giving the distinctive "rattle" vocalization, which is given mainly by females (over 99% of the time; S.K. Robinson, unpubl. data). We used only female registrations because many vocalizing males appeared not to be mated and therefore posed no threat to hosts. We then summarized all records of potential host species recorded within 70 m of census points. The ratio of female cowbirds:hosts within 70 m of census points was then calculated and used as an index of the relative abundance of cowbirds. For forests, the cowbird:host ratio appears to be a good predictor of parasitization levels (Robinson et al. in press). This ratio, however, has never been used in more open vegetation types in which many potential hosts have effective defenses against parasitization. For this reason, we calculated two ratios, one for all potential hosts (open-cup nesters, mass less than 70g to exclude large species that are rarely parasitized, such as Blue Jay *Cyanocitta cristata,* Common Grackle *Quiscalus quiscula,* and Mourning Dove *Zenaida macroura*; Strausberger and Ashley 1997) and another for hosts that lack strong defenses against parasitization. For this latter ratio, which we refer to as the cowbird:suitable host ratio, we excluded unsuitable hosts, which include species that eject cowbird eggs (Eastern Kingbird *Tyrannus tyrannus,* Gray Catbird *Dumetella carolinensis,* Brown Thrasher *Toxostoma rufum,* American Robin *Turdus migratorius,* Warbling Vireo *Vireo gilvus,* Western Meadowlark *Sturnella magna* [B.D. Peer, unpubl. data], and Baltimore Oriole *Icterus galbula*), species that often abandon parasitized nests (Bell's Vireo *Vireo* *bellii,* Yellow Warbler *Dendroica petechia,* Prairie Warbler *D. bicolor,* Chipping Sparrow *Spizella passerina,* and Field Sparrow *S. pusilla*), and species that aggressively mob cowbirds (Eastern Wood-Pewee, Eastern Kingbird, Willow Flycatcher *Empidonax traillii,* and Red-winged Blackbird). All of these species are at least occasionally parasitized in Illinois (e.g., Strausberger and Ashley 1997). But, if cowbirds generally avoid these unsuitable hosts, then the cowbird:suitable host ratio may be a better index of relative abundance of cowbirds. If, on the other hand, cowbirds do not discriminate among suitable and unsuitable hosts, then the index derived from all potential cowbird hosts (suitable and unsuitable hosts that build open-cup nests) may be a better index of habitat suitability. Information on host defenses was obtained from multiple sources, including Friedmann (1929, 1963), Berger (1951), Mumford (1952), Barlow (1962), Rothstein (1975 a,b), Slack (1976), Friedmann et al. (1977), Robertson and Norman (1977), Scott (1977), Nolan (1978), Friedmann and Kiff (1985), Graham (1988), Freeman et al. (1990), Hill and Sealy (1994), Neudorf and Sealy (1992), Sealy (1996), and Burhans (in press).

All sites in Table 1 were subjected to at least one field season of intensive nest searching and monitoring. Nest searching began in late April and continued until late July-early September. In this paper, we only used nests that were built from 20 April to15 July, the main period of cowbird egg laying in Illinois (S.K. Robinson, unpubl. data). Nest contents were checked every 3 days until young fledged, eggs or young were depredated, or the nest abandoned. We used the Mayfield (1975) index to estimate daily predation rates for the incubation and nestling periods combined. For each species, we used all nests over all years from a region to obtain composite nest parasitization levels (percentage of nests parasitized only) and daily predation rates (percentage of nest contents eaten by predators per day).

Our methods may overestimate predation rates if we are attracting predators to some nests and may underestimate nest predation events that occur late in the nestling phase. We tried to reduce these biases by placing flagging tape at least 5 m from nests and checking nests from as far away as possible, especially in plant communities with dense ground-level vegetation (e.g., unburned and ungrazed grasslands, shrubby old fields). It seems inevitable, however, that our activities made some nests more conspicuous to some predators and that this potential bias is different among vegetation types (e.g., visually hunting predators may have an easier time watching nest monitoring crews in open plant communities). For this reason, inter-habitat comparisons of nest predation rates must be interpreted with caution. To reduce possible underestimates of predation rates late in the nest cycle, we made a concerted effort to find families or look for nearby renesting attempts in the area around nests that were found empty late in the nestling phase.

### STATISTICAL ANALYSIS

For each species, we derived a region-specific nest predation rate and frequency of parasitization for each habitat for up to seven regions. We arbitrarily included only species for which we had at least 10 nests within a region to reduce potential artifacts of small sample sizes. To compare state-wide levels of nest predation and cowbird parasitization, we combined data from all seven regions to generate frequency distributions of parasitization levels and daily nest predation rates for each vegetation type. Therefore, the combined nests of a species in a given region was the unit of replication for this analysis. We chose this method because we think it better represents state-wide parasitization levels because widespread species present in a habitat throughout the state are weighed more heavily than rare, or geographically restricted species that may not represent a significant potential resource to cowbirds. We also compared and explored habitat-specific nest predation rates and levels of parasitization among vegetation types within each region. We compared the frequency distributions of predation and parasitization rates among plant communities (overall or within regions) with exact Kruskal-Wallis tests (Mehta and Patel 1995). Exact tests (based on permutation procedures) are free from assumptions about the asymptotic properties of test statistics that may be violated with small samples. We compared vegetation types on a pairwise basis and adjusted our judgement of significance based on the Bonferoni inequality and a 0.05 nominal alpha level.

To compare relative abundance of cowbirds among vegetation types, we calculated site-specific cowbird:host ratios. Sites that were less than 5 km apart were combined. Sites that were greater than 5 km apart were treated as separate samples to increase sample sizes of vegetation types that are only present in a few regions (Table 1). We log transformed the cowbird:host ratios and performed one-way analyses of variance (ANOVA) to compare vegetation types. Homogeneity of variances were evaluated with Levene's test; in case where heteroscedasticity was detected, we derived Welch F-statistics where degrees of freedom are approximated. Post-hoc differences were carried out with pairwise t-tests using Bonferonni-adjusted signifi-

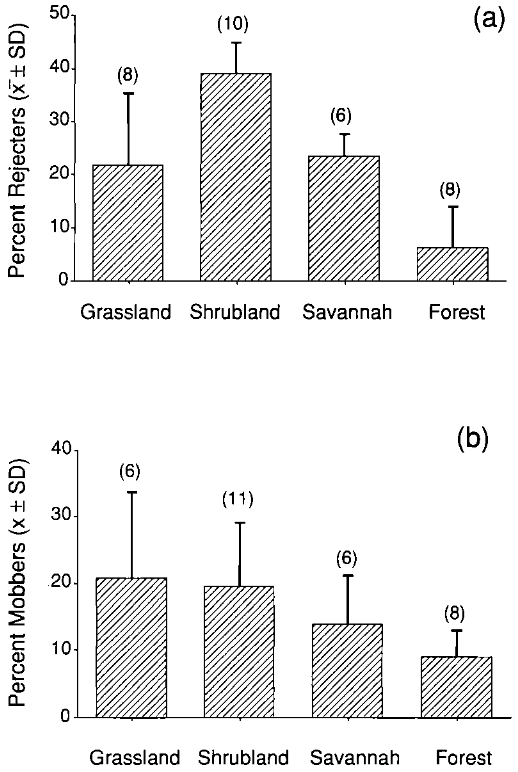

FIGURE 1. Percentage of rejecters (a) and species that mob cowbirds (b) in different vegetation types detected in census samples from sites located at least 50 km apart in Illinois. (N) = number of sites censused.

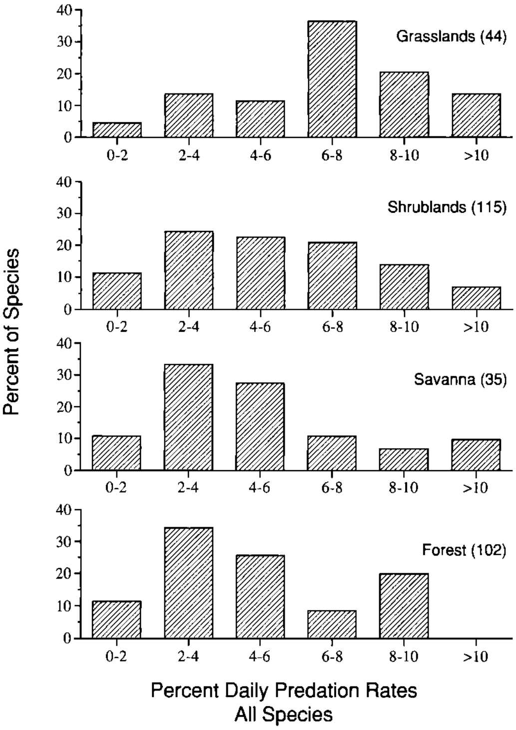

FIGURE 2. Distribution of daily nest predation rates in different vegetation types calculated using the Mayfield (1975) index. Data from all seven regions in Table 1 are pooled for this analysis.

cance levels. Other habitat traits such as percentage composition were compared with one-way ANOVA on arcsine-transformed data. We used the same census data to calculate proportions of the total number of potential hosts detected within 70 m of census points that reject cowbird eggs or mob nest predators.

## RESULTS

### HOST COMMUNITY COMPOSITION

#### *Proportion of rejecters*

The proportion of known rejecter species (those that abandon parasitized nests or eject cowbird eggs) varied significantly ($F_{3,14} = 38.02$, $P < 0.001$) among vegetation types (Fig. 1a). In shrublands, an average of 40% of the hosts detected during point counts were rejecters compared with 23–26% in grasslands ($P < 0.01$) and savannas ($P < 0.05$) and 6% in forests ($P < 0.01$). In forests, only the American Robin was a rejecter, and it only nested in 3 of the 8 forest sites. We know relatively little, however, about egg rejection by such grassland cowbird hosts as the Bobolink (*Dolichonyx oryzivorus*), which is rarely parasitized, and the Eastern Meadowlark (*Sturnella neglecta*), which at least occasionally ejects cowbird eggs (B.D. Peer, unpubl. data).

#### *Proportion of mobbers*

Plant communities varied significantly in the proportion of mobbers ($F_{3,27} = 2.97$, $P = 0.044$). Forests generally had a lower proportion of individuals that mob cowbirds, but we detected no specific pairwise among plant communities differences (Fig. 1b); the Eastern Wood-Pewee is the only forest species that attacks cowbirds regularly (S.K. Robinson, pers. obs.). Grassland and shrublands have the highest proportion of mobbers, mainly as a result of high populations of Red-winged Blackbirds. Red-wings, however, were absent or very rare in three of the six grasslands censused.

#### *Comparative nest predation rates*

Community-wide levels of nest predation generally varied significantly between vegetation types (Fig. 2). Nest predation rates were

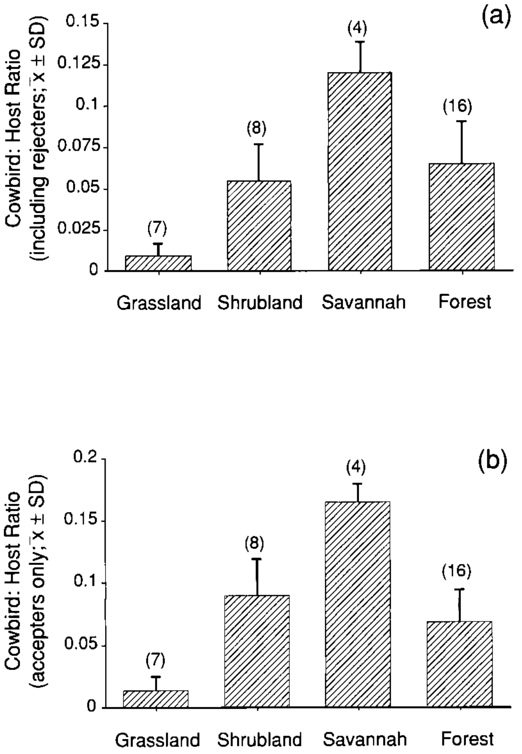

FIGURE 3. Ratio of female cowbirds to hosts (a) including hosts that eject cowbird eggs and abandon parasitized nests and (b) including hosts that usually accept cowbird eggs detected within 70-m radii of census points in sites separated by at least 50 km.

higher in grasslands than in shrublands (K = 8.35, P = 0.004), savannas (K = 13.35, P < 0.001), and forests (K = 14.67, P < 0.001). None of the other vegetation types differed significantly (shrub vs. savanna K = 1.253, P = 0.263; shrub vs. forest: K = 2.01, P = 0.151; savanna vs. forest: K = 0.025, P = 0.878).

### Cowbird Use of Different Habitats

Cowbird:host ratios differed significantly among vegetation types whether all hosts were included (Fig. 3a; $F_{3,31} = 20.53$, $P < 0.001$; all pairwise comparisons differed at $P < 0.01$ except for shrublands and forests) or only suitable hosts were included (Fig. 4; $F_{3,31} = 29.53$, $P < 0.001$; all pairwise comparisons different at $P < 0.01$ except for shrublands and forests). Grasslands consistently had the lowest relative abundances of cowbirds and savannas had the highest abundances. Shrublands and forests did not differ significantly in the relative abundance of cowbirds.

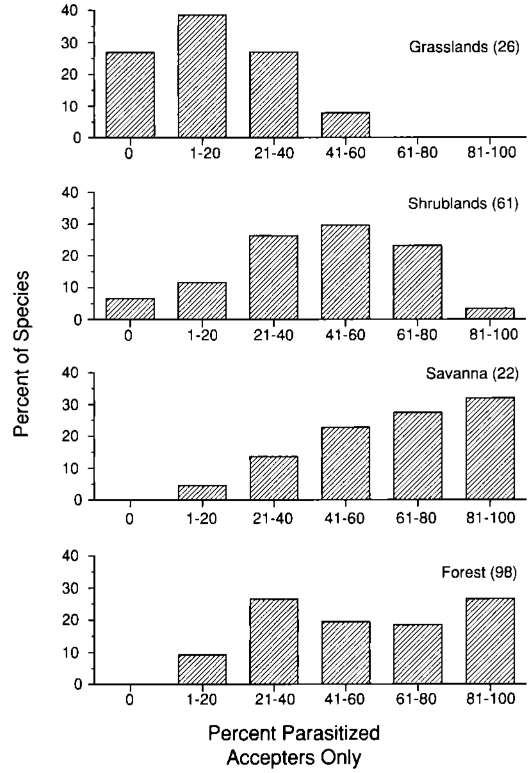

FIGURE 4. Distribution of parasitization levels of all cowbird hosts that accept cowbird eggs. Data from all seven regions in Table 1 are pooled for this analysis.

### Levels of Parasitization in Each Vegetation Type

Levels of cowbird parasitization were lower in grasslands than in all other vegetation types regardless of whether rejecters were included (Fig. 5; Kruskal Wallis tests, grassland vs. shrublands, K = 3.46, P = 0.06; grasslands vs. forests, K = 68.78, P < 0.01,; grassland vs. savannas K = 11.97, P < 0.001) or excluded (Fig. 4; Kruskal Wallis tests, grasslands vs. shrublands, K = 22.4, P < 0.001, grasslands vs. savannas, K = 27.8, P < 0.001; grasslands vs. forests, K = 38.14, P < 0.001). Community-wide levels of parasitization were significantly higher in shrubland and savannas than in forests (Fig. 5; shrubland vs. forest, K = 59.33, P < 0.001; savannas vs. forests, K = 5.046, P = 0.022; savanna vs. shrubland, K = 6.955, P = 0.006). Savannas and forests, however, did not differ significantly from forests when rejecters were excluded from the analysis (Fig. 4, K = 1.714, P = 0.193). Shrublands had relatively fewer heavily parasitized species (80–100% par-

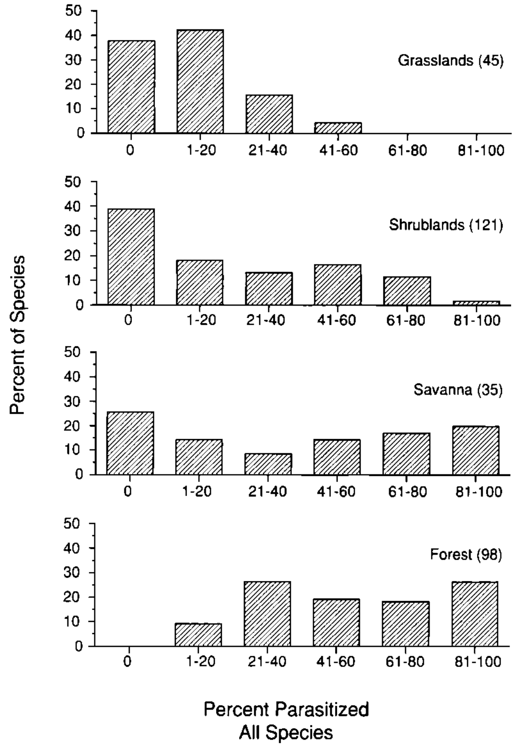

FIGURE 5. Distribution of parasitization levels experienced by all potential host species nesting in different vegetation types in Illinois. Data from all seven regions in Table 1 are pooled for this analysis.

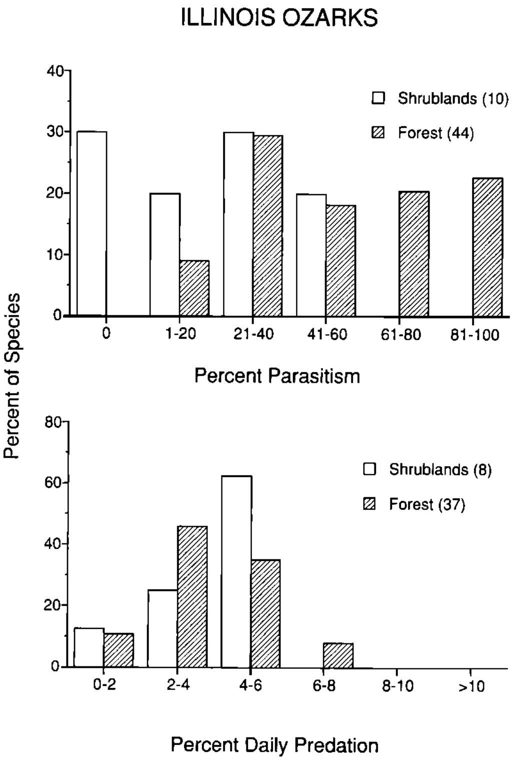

FIGURE 6. Habitat-specific distribution of levels of cowbird parasitization and daily nest predation rates within the Illinois Ozark region of extreme southwestern Illinois.

asitization levels) than forests (K = 7.44, P = 0.006) and savannas (K = 10.45, P < 0.001).

## PARASITIZATION VS. NEST PREDATION

To determine if cowbirds were less abundant in areas with high nest predation rates, we compared levels of parasitization and nest predation within regions where we had data from more than one habitat (Figs. 6–9). In the Cache River (Fig. 6), levels of nest predation were significantly higher in shrublands (K = 6.47, P < 0.001) in which parasitization levels were low, although not significantly lower than forest (K = 3.61, P = 0.062). In the Illinois Ozarks, however, parasitization levels were significantly lower in shrublands (Fig. 7; K = 10.54, P < 0.001), but levels of nest predation did not differ between forests and shrublands (K = 0.28, P = 0.597). In the Rock River area (Fig. 8), parasitization levels were significantly lower in grasslands than in forest (K = 8.656, P = 0.002) and were lower in shrublands than in forest (K = 5.618, P = 0.166), but levels of nest predation did not differ significantly among plant communities. Similarly, in the Driftless Area (Fig. 9), parasitization levels were significantly lower in grasslands than in forest (K = 14.31, P < 0.001) and lower in shrubland than in forest (K = 10.49, P < 0.001), but nest predation rates did not differ significantly among any of the vegetation types.

## DISCUSSION

We found pronounced differences among different vegetation types in parasitization levels, but there was little to suggest that these differences represented adaptive habitat selection by cowbirds. Cowbirds consistently were less abundant in grasslands (see also Strausberger and Ashley 1997, Robinson et al. in press), even in one area in which nest predation rates were lower in grasslands than in adjacent forests. Cowbirds were not less abundant in savannas and shrublands even though these vegetation types typically contained high proportions of rejecters and mobbers and even though nest predation rates were often higher in shrublands than in forests. The differences in community-wide levels of parasitization in shrublands, savannas, and

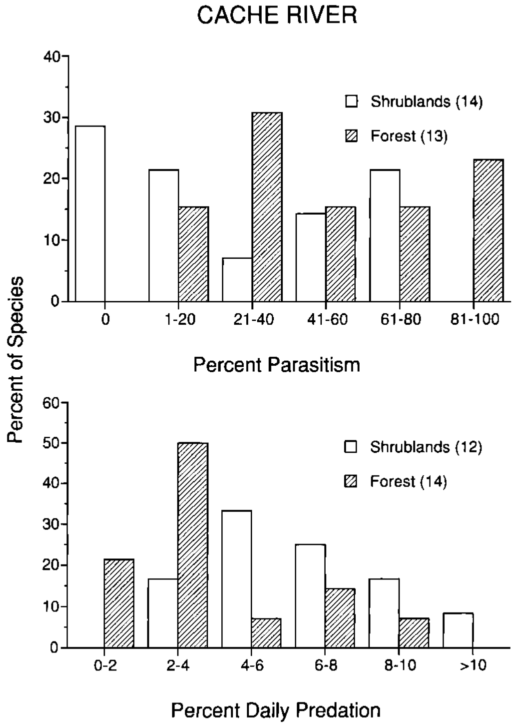

FIGURE 7. Habitat-specific distribution of levels of cowbird parasitization and daily nest predation rates within the Cache River region of extreme southcentral Illinois.

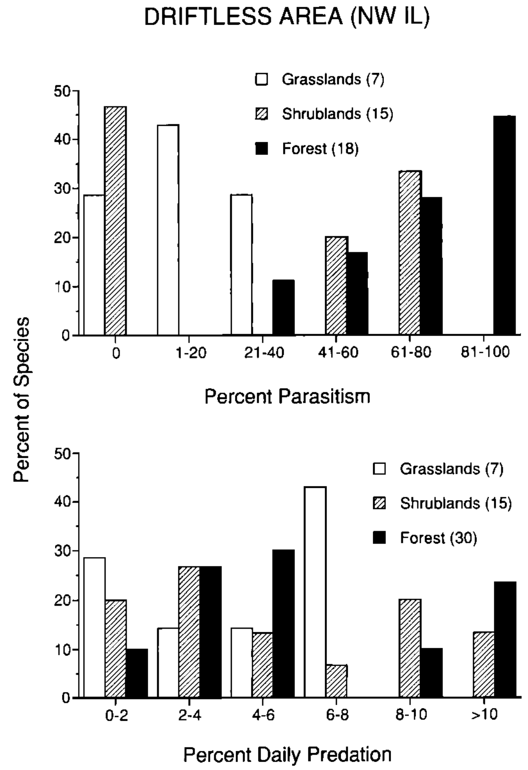

FIGURE 8. Habitat-specific distribution of levels of cowbird parasitization and daily nest predation rates in the Driftless region of far northwestern Illinois.

grasslands (Fig. 5) were much less apparent when rejecters were excluded from the analysis (Fig. 4). Prime cowbird hosts gain little or no protection from parasitization by nesting in communities with a high proportion of rejecters. Cowbirds were most abundant in savannas even though the proportion of suitable hosts was generally lower than in closed-canopy forests.

We did not find strong support for any of the predictions we tested. Based on cowbird:host ratios, cowbirds were not disproportionately abundant in forests (hypothesis 1) in this landscape, as found by Hahn and Hatfield (1995). The relative abundance of cowbirds was highest in savannas, intermediate in shrublands and forests, and consistently lowest in grasslands. The apparent avoidance of grasslands is interesting given that this is the habitat in which cowbirds historically were most abundant (Mayfield 1965). Although a detailed analysis of landscape composition around each site is beyond the scope of this paper, we have no evidence that cattle pastures were more prevalent near savannas. Several of our grassland sites were being actively grazed during our study.

We also found no evidence that cowbirds were less abundant in vegetation types with high proportions of rejecters (hypothesis 2) and mobbing species (hypothesis 3). Cowbirds were most abundant in savannas, which had intermediate abundances of rejecters and mobbers; similarly, they were just as abundant in shrublands as they were in forests even though shrublands had much higher proportions of mobbers and rejecters. We know relatively little about the defensive behavior of many grassland hosts. Recent experiments in the Driftless Area showed that Western Meadowlarks usually eject cowbird eggs and Eastern Meadowlarks eject about half of the eggs from experimentally parasitized nests (B. D. Peer, unpubl. data). If comparable defenses are also found in such rarely parasitized species as the Bobolink, then we may be underestimating the extent to which grassland birds have evolved resistance to parasitization. The mobbing activities of Red-winged Blackbirds may deter cowbirds from some grasslands, but many grasslands with no red-wings were also avoided by cowbirds (J. L. Herkert, unpubl. data).

Evidence that cowbirds avoided vegetation

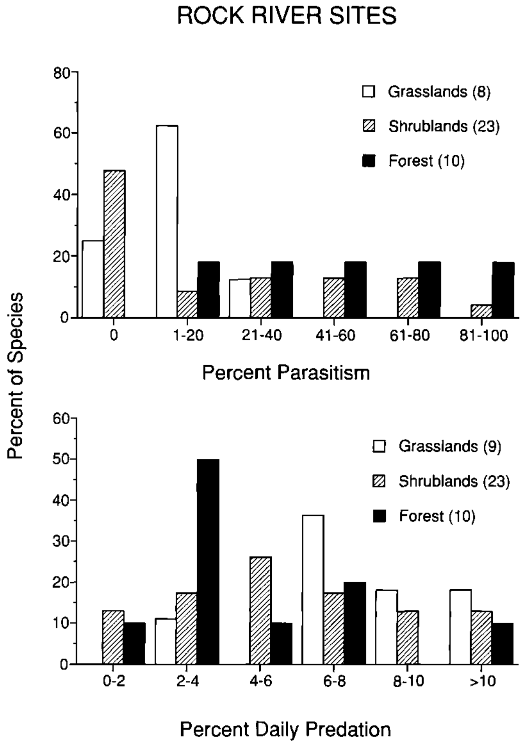

FIGURE 9. Habitat-specific distribution of levels of cowbird parasitization and daily nest predation rates in the Rock River region of northcentral Illinois.

types with higher nest predation rates (hypothesis 4) was mixed. Data from one of the four sites for which we have enough data to compare nest predation rates among vegetation types (Figs. 6–9) showed reduced parasitization levels in a habitat with higher nest predation rates (Fig. 8). Data from the other regions, however, showed strong differences in parasitization levels, but not predation rates (Figs. 7–9). In another site in a suburban landscape of northeastern Illinois, Strausberger and Ashley (1997) found high levels of cowbird parasitization in a shrubby area in which nest predation rates were generally over 85%. They concluded that nest predation rates may be too unpredictable to provide reliable cues to habitat selection or host selection within vegetation types.

Although we did not test the hypothesis that vegetation structure affects habitat selection (hypothesis 5), there are some indications that vegetation structure is important. Grasslands may be extremely difficult for cowbirds to search because of a lack of perches, the difficulty of detecting nests in dense grass, and the cryptic behavior of hosts near their nests (Zimmerman 1983). Parasitization levels tend to be higher near woody vegetation in grasslands, but even near such potential cowbird perches, parasitization levels were still less than 20% for nearly all species (J.L. Herkert and S.K. Robinson, unpubl. data). The other three plant communities generally have many potential perches and no vegetative layer as dense as grass in unburned tallgrass prairie. The marked preference for savannas may reflect a preference for this vegetation type, which usually occurs at the transition of grasslands and forests. Historically, savannas and shrubby streamside vegetation may have often been the closest source of both host nests and suitable perches for searching.

## CONSERVATION IMPLICATIONS

The apparent avoidance of grasslands by cowbirds and the comparatively high proportion of species with effective defenses against cowbirds in more open vegetation types suggest that the best approach to reducing cowbird parasitization in chronically fragmented landscapes may be to maintain and restore grasslands, shrublands, and savannas. Cowbirds appear not to be a significant problem for most grassland birds and many of the cowbird's most frequent hosts are much less abundant in savannas than in forests (J. D. Brawn, unpubl. data). Similarly, shrublands contain few prime cowbird hosts and many species with effective defenses, or long breeding seasons that extend well beyond the period of cowbird breeding activity (S. K. Robinson and J. D. Brawn, unpubl. data). Regional landscape composition may influence the effectiveness of favoring one habitat over another. Tallgrass prairie bird communities in Kansas, for example, have extremely high levels of parasitization (Elliott 1978), as do shrubland bird communities in at least one suburban area in Illinois (Strausberger and Ashley 1997). For this reason, restoring more open plant communities may not always reduce parasitization. In the less-fragmented sections of Illinois, parasitization levels can be reduced for some species by increasing the proportion of forest interior (Morse and Robinson, in press). In most of the agricultural Midwest, however, it is unlikely that forest tracts will ever be large enough to provide a complete refuge from cowbirds.

Restoring more open plant communities may also negatively affect cowbird populations if heavily used habitats such as savannas and shrublands are population sinks for cowbirds, whereas forests are not. In this scenario, shrublands and savannas may be ecological traps because they attract cowbirds, but fail to provide conditions for successful nesting. Before we can assess this possibility, however, we need additional studies of habitat-specific breeding productivity of cowbirds and to determine whether or not cowbirds avoid unsuitable hosts and plant communities in which nest predation rates are high. The cowbird's well-documented habit of revisiting parasitized nests (Arcese et al. 1996) may enable them to assess host-specific nesting success and modify subsequent choice of hosts and even breeding habitat. We found no evidence for such fine-grained assessment of habitat quality by cowbirds, but perhaps this reflects the saturation of all vegetation types and hosts within communities in Illinois (see below).

## FUTURE RESEARCH QUESTIONS

1. Are cowbirds more selective of habitats in regions where they are less abundant? In the agricultural Midwest cowbirds are very common and, it is possible that habitats are saturated. In regions where cowbirds are less abundant, preference for forests may be more evident because cowbirds seek those plant communities first. In the scenario, we might expect forests to fill up initially and other, less productive plant communities to be used secondarily. A reduction in cowbird populations might lead to disproportionate reduction in intensity of parasitization in savannas and shrublands. The reduced abundance of cowbirds in the northeastern U.S. compared with the Midwest (Hoover and Brittingham 1993) might explain why cowbirds avoided shrublands in Hahn and Hatfield's (1995) study area. In addition, we might expect cowbirds to be more selective of hosts within plant communities, although Weatherhead (1989) and Strausberger and Ashley (1997) found little evidence of adaptive avoidance of poor hosts in shrubland plant communities.

2. To what extent do cowbirds contribute to nest predation rates? Scott and McKinney (1994) and Arcese et al. (1996) found evidence that cowbirds may depredate unparasitized nests to increase future availability of nests to parasitize. We have little evidence of higher nest predation rates in vegetation types with high abundance of cowbirds. Savannas, for example, had similar nest predation rates to forests even though cowbirds were most abundant in savannas. Evaluating this hypothesis would require cowbird removal experiments.

3. Do cowbirds avoid unsuitable hosts or are low parasitization levels in nests of rejecters simply caused by hosts removing eggs before they are counted by observers? The Gray Catbird, an ejector species, is parasitized in some plant communities in northeastern Illinois (Strausberger and Ashley 1997; J. D. Brawn, unpubl. data), indicating that cowbirds may not always avoid this species (see also Scott 1977, Slack 1996).

4. Are there additional species with previously undescribed defenses against parasitization and are these species more likely to be found in more open vegetation types? Low parasitization levels of species such as Bobolinks (Strausberger and Ashley 1997), Northern Cardinals (Scott and Lemon 1996) and Yellow-breasted Chats (*Icteria virens*) (Thompson and Nolan 1973), may result from partial defenses against cowbirds. Recent experimental manipulations of grassland birds in Illinois revealed surprisingly high frequencies of egg ejection in two species of meadowlark (B. D. Peer, unpubl. data). Additional experiments will help identify the true proportion of suitable hosts in different vegetation types and will also shed light on Mayfield's still uncorroborated hypothesis (Robertson and Norman 1976, 1977, Rothstein and Robinson 1994) that birds of open plant communities, which presumably have a longer coevolutionary history with cowbirds, are more resistant to cowbirds. Similarly, multi-species defensive aggregations (Clark and Robertson 1979) might be more prevalent than suspected.

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