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Community-wide patterns of parasitism of a host “generalist” brood-parasitic cowbird

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Abstract The brown-headed cowbird (*Molothrus ater*) is a generalist obligate brood parasite. Despite intensive study and growing concern over the negative impact of cowbird parasitism on populations of many hosts, very little is known about the factors influencing community-wide patterns of cowbird parasitism. Using systematic nest searches, nest parasitism was studied over two breeding seasons at a study site in northeastern Illinois encompassing grassland, forest-edge, and forest habitat, supporting a diverse avian community. Parasitism was observed for 18 out of 34 altricial bird species found nesting at the study site. A total of 299 cowbird eggs and nestlings were found in 191 of a total of 593 nests. Analyses revealed several ecological and behavioral factors associated with frequency of parasitism and the resulting distribution of cowbird eggs. Much higher frequencies of parasitism were found in edge and forest habitats than in grassland. Within the edge habitat, open nests were parasitized significantly more often than cavity nests. Among open nests in the edge habitat, the two largest species were never parasitized. Host behavior, particularly egg-ejection behavior, was associated with a reduced observed frequency of parasitism, but at least three species known to eject cowbird eggs were sometimes parasitized. For six common hosts capable of rearing cowbirds, we found no correlation between level of parasitism and host nest-survivorship, suggesting that fine-grained assessments of host quality by female cowbirds do not influence patterns of parasitism among acceptable host species, or that differences in host quality are not great and/or predictable enough for such fine-grained assessments. Our results suggest that when a variety of possible nests are available, the level of parasitism on a particular species is a balance between

a cowbird's preference for a particular species and the effectiveness of host species' defenses. A conceptual model was developed that incorporates the observed correlation of cowbird eggs or nestlings with habitat, nest-type, host species' body mass, and host behavioral defenses. Additional community-wide studies of cowbird parasitism will test if this model is applicable to other avian communities.

Key words Brown-headed cowbird · *Molothrus ater* · Brood parasitism · Host choice

Introduction

The brown-headed cowbird (*Molothrus ater*, hereafter cowbird) parasitizes over 220 bird species (Friedmann and Kiff 1985). Female cowbirds may lay 40 or more eggs annually in the nests of other species (Scott and Ankney 1983). Some hosts have been found to have 80–100% of their nests parasitized and parasitism can reduce the survival of host nestlings (Payne 1977). Parasitism may therefore act as a strong force in the evolution of host-parasite relationships, and selection for host defenses against parasitism will occur. In response, selection on cowbirds to elude host defenses may result in a coevolutionary arms race.

It is not known what determines patterns of parasitism when the nests of multiple species are available. Factors affecting patterns of parasitism may include host availability, cowbird densities, and effectiveness of host defenses against parasites (McGeen and McGeen 1968; Rothstein et al. 1984). Species differ in their quality as cowbird hosts, varying in response to cowbird egg, nestling diet, nest survivorship, and nestling feeding mechanisms (Mason 1986; Wiley 1988). To maximize reproductive success, cowbirds may selectively parasitize hosts with the highest probability of rearing cowbird young while avoiding inadequate or low-quality hosts (Friedmann 1963; Rothstein 1976; Payne 1977; Fleischer 1985). A closely related species, the shiny cowbird

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(*M. bonariensis*) shows a preference for at least one host species (Post and Wiley 1977). Alternatively, cowbirds may parasitize all available species in proportion to their abundances. This strategy would be adaptive if assessment of host quality is imperfect, resulting in cowbirds bypassing some high-quality host species (Rothstein 1975).

Some species accept most cowbird eggs laid in their nests ("acceptors") while other species have effective behaviors such as egg ejection, nest desertion, or egg burial that reduce parasitism ("rejectors"; Rothstein 1975). Although it is difficult to obtain accurate measures of parasitism for rejector species (nests must be monitored prior to egg ejection), the role of rejectors at the community level will depend upon the host choice practices of female cowbirds. If cowbirds do not avoid nests of rejector species, rejectors may serve as sinks for cowbird eggs. Different potential host species may reduce parasitism through aggressive nest defense (Robertson and Norman 1976; Neudorf and Sealy 1992). The evolution of effective anti-parasite defenses may be related to historical interactions and recent range expansion of the cowbird. Originally restricted to the Great Plains, habitat alterations within historic times have enabled the cowbird to increase and expand its range to include all 48 lower states. "Naive" host populations, only recently sympatric with cowbirds, may be particularly vulnerable to parasitism, possibly because anti-parasite behavioral adaptations have not yet evolved or become common (Mayfield 1965; but see Rothstein 1975).

Because the cowbird is a host generalist, it is unlikely to be subject to conventional density-dependent processes generally thought to regulate host-specific parasite associations (May and Robinson 1985). The population density of the cowbird is not likely to track the density of any single host species when cowbirds are reared by more than one species. As a result, declines of particular host populations may occur without a significant reduction in cowbird population size. Any species that is preferred as a host is potentially at risk of population decline, while those already rare or limited in distribution may face the most immediate threat of extinction. Presently, brown-headed cowbird parasitism threatens at least five bird species with extinction and is implicated in the decline of many others (Rothstein and Robinson 1994).

Information regarding host choice, host defense, and the resulting community-wide patterns of cowbird parasitism will help clarify the dynamics of host-parasite coevolution and identify characteristics which make a species susceptible to parasitism. Previous community parasitism studies have limited utility for identifying factors affecting the distribution of cowbird eggs in the total avian community for reasons including: (1) limited species diversity or nest sample sizes (McGeen and McGeen 1968; Scott 1977; Elliott 1978; Folkers 1982); (2) parasitism data originating from different locations (Robertson and Norman 1976, 1977); and (3) lack of

data on all potential hosts in the community (Norris 1947; Hahn and Hatfield 1995). Here we report a community-wide study of cowbird egg distribution at a single location with many potential host species. Our goal was to identify the factors affecting the distribution of cowbird eggs in the avian community. We collected data over two breeding seasons using systematic daily searches for all bird nests. The study site included grassland, forest-edge, and forest habitats. The data we collected on parasitism levels were used to identify ecological or behavioral (either host or parasite) factors correlated with observed patterns of parasitism. Specifically, we tested whether parasitism levels were associated with habitat, nest type, host size, host quality (estimated from nest survival rate), host abundance or host behaviors such as egg-ejection.

Methods

Systematic searches for all bird nests at the 78-ha study site at the Morton Arboretum (DuPage County) were undertaken during the 1994 and 1995 cowbird breeding seasons. Cowbirds are historically native to this area (Mayfield 1965). The study site was mixed habitat, with approximately 8 ha forested, 10 ha grassland, and the remaining 60 ha forest-edge habitat (open areas of lawn and water interspersed with trees and shrubs). Information on all nests, both parasitized and unparasitized, including the number of cowbird eggs/nestlings in each, was recorded. Parasitism frequency is equal to the proportion of nests parasitized. Only those nests available for parasitism (i.e., nests in the egg-laying stage) during the course of the cowbird laying season were included (Scott 1977). To prevent sampling biased towards species with nests that are easier to find, we increased our search efforts for species whose nests are more difficult to find. Nests of edge-nesting species were principally found by actively searching edge areas. Nests of typically grassland nesting species and other ground nesters were located through active searching and by two individuals dragging a rope between one another to flush nesting birds as described by Higgins et al. (1970). In the forest habitat, we tried to find all nests regardless of height, although previous studies have found that cowbirds prefer to parasitize nests located on or near the ground (Hahn and Hatfield 1995). Nests high in the trees were principally found by cuing in on vocalizations and nesting activities, as were some nests in other habitats. Our study site was predominately edge and grassland so there were relatively few birds nesting high in trees.

All cowbird eggs and nestlings were removed from parasitized nests at the time of discovery for use in a separate genetic study and replaced with plaster of Paris eggs painted to resemble cowbird eggs as described by Rothstein (1975). Evidence suggests that egg replacement does not influence the parasitic behavior of cowbirds because the frequencies of parasitism were similar for both nests in which cowbird eggs were replaced in the egg-laying stage (when parasitism generally occurs) and the incubation stage (where little parasitism generally occurs; Hann 1941). All nests, both parasitized and unparasitized, were monitored until nestlings fledged or nest failure occurred. Nests found in the egg-laying stage were monitored daily. Nests found in more advanced stages were monitored at approximately 3-day intervals.

Our data presented both opportunities and challenges for analyses. A major strength of the data is that for nearly all comparisons (e.g., habitat, nest-type, host size), there were a large number of nests with multiple species well represented (Appendix). This allowed us to identify characteristics shared by nests that were correlated with parasitism frequency more clearly than with samples restricted to individual species. Another strength of the data is that they are expansive and encompass numerous factors that have

been previously suggested to influence cowbird parasitism, such as habitat-type, nest-type, host size, and behavioral responses of the host to parasitism. However, the independent variables of interest cannot be fully crossed, limiting options of analyses.

For statistical power, we used individual nests rather than species as data points. A potential criticism of this approach, that one over-represented species might account for significant patterns, was circumvented because no comparison was excessively biased by a single species (Appendix). Several characteristics such as nesting habitat, nest-type and host body mass were correlated with frequency of parasitism and offered a logical hierarchy for organizing the analyses and allowed for the development of our conceptual model (Fig. 1). Fisher exact tests (for 2 × 2) and chi-square tests of independence (for larger matrices) were used to detect differences in parasitism frequencies between nest assemblages grouped by shared characteristic. For example, nests were first categorized by habitat and a chi-square test used to identify differences in parasitism frequencies among nests in different habitats. Analyses proceeded hierarchically beginning with habitat-type. To avoid confounding characteristics affecting parasitism levels, only nest assemblages having intermediate frequencies of parasitism were retained for further analyses at the next level of the hierarchy. For example, in the first level of our hierarchy, nests found in the forest and grassland were eliminated from further analyses because they en-

countered total and no parasitism, respectively, leaving the edge-nesting species for further analyses because they experienced intermediate levels of parasitism. We recognize that extensive collinearity of variables is likely. Species effects, for example, will be pronounced, with individual species having characteristic nesting habitat, body mass, and behavior and should be considered when assigning effects to the factors tested at each level, such as habitat, nest-type, and so on.

Following habitat analysis, a Fisher exact test was used to determine if there was a relationship between nest-type (open or cavity) and frequency of parasitism, using only the data from the edge habitat (where all cavity nests were found). Next, using only data from species with open nests in the edge habitat, a Fisher exact test was used to test for a relationship between species' mass (≥100 g and < 100 g) and frequency of parasitism. Values for host body mass were obtained from Dunning (1993). Next, we used a Fisher exact test to look for a relationship between the distribution of cowbird eggs found in nests and the typical behavioral response of hosts to cowbird eggs (e.g., the classification of a species as either a cowbird egg acceptor or rejector).

Of the species remaining for analyses (relatively small birds, edge-nesting with open-type nests that accept cowbird eggs), seven had sample sizes ≥15 nests. A chi-square test was used to determine if frequencies of parasitism varied significantly among these seven species. For six species, data were gathered in 1995 to determine whether one measure of "host-quality," nest survivorship, was correlated with the level of cowbird parasitism. Although we did not directly measure host-quality by the relative success of each species in raising cowbirds, all six of these species are known to accept cowbird eggs, have diets favorable for nestling cowbirds and have feeding mechanisms adequate for the rearing of cowbirds to the point of fledging (Friedmann 1963). Therefore, nest survivorship is a potentially important measure of host-quality. To correct for biases imposed by nests found in advanced stages, we used the method of Mayfield (1975) for calculating the nesting success rate for the egg-laying through fledging periods. Because we were interested in the quality of a species as a cowbird host, average cowbird incubation and nestling time lengths, eleven and ten days, respectively, were used (Payne 1977; Woodward 1983). Two days were used for the host egg-laying period prior to the onset of incubation, for a total of 23 days from the egg-laying through the fledging period. Therefore, survivorship values are equal to the probability that a nest will survive 23 days, the minimum time estimated to fledge at least one cowbird. We used a chi-square test and a Kruskal-Wallis test to determine if either the frequency or the intensity of parasitism (mean number of cowbird eggs per nest) varied among these six common host species. Using a Spearman rank test, we looked for a correlation between parasitism frequency and both nest survivorship and number of nests found for each of the six common host species.

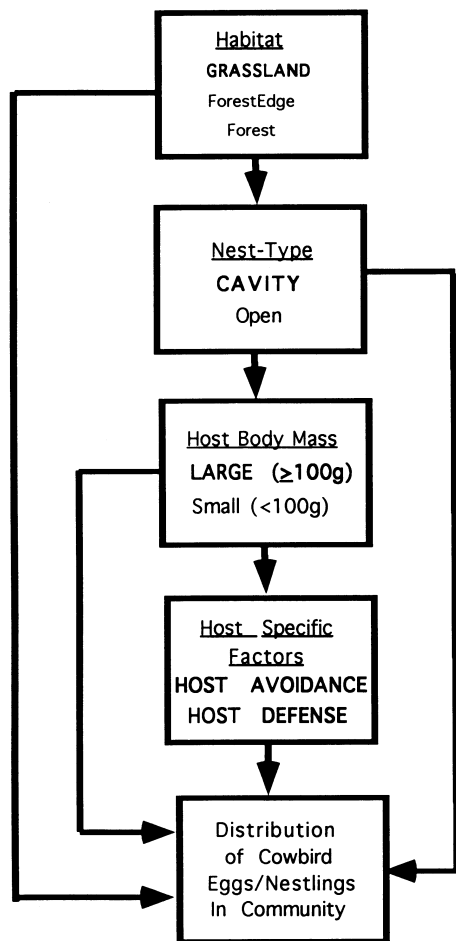


Fig. 1 Conceptual model proposed to explain the distribution of cowbird eggs and nestlings during the 1994 and 1995 breeding seasons at the Morton Arboretum site. At each level, hosts that fall into the categories shown in *upper case letters* were observed to have a significantly lower frequency of parasitism. All species that do not belong in one of the categories in upper case letters had a high frequency of parasitism

Results

A total of 593 nests of 34 altricial bird species were found at the study site (Appendix). A total of 299 cowbird eggs or nestlings were found in 191 nests of 18 species. Of these 299 cowbird eggs or nestlings, 254 (86%) were found in the nests of six species (northern cardinal, red-winged blackbird, indigo bunting, song sparrow, field sparrow and chipping sparrow). The remaining 45 cowbird eggs or nestlings were found in the nests of 12 other host species. Among the six most commonly parasitized hosts, parasitism frequencies ranged from 40% for chipping sparrows to 83% for indigo buntings. Parasitism of five less abundant species (orchard oriole, eastern towhee, red-eyed vireo, wood thrush and rose-breasted grosbeak) was 100%. The

cowbird breeding seasons extended for 12 weeks in both years: from 2 May to 17 July in 1994 and from 28 April (beginning of week 1, Fig. 2) to 18 July in 1995, as in-

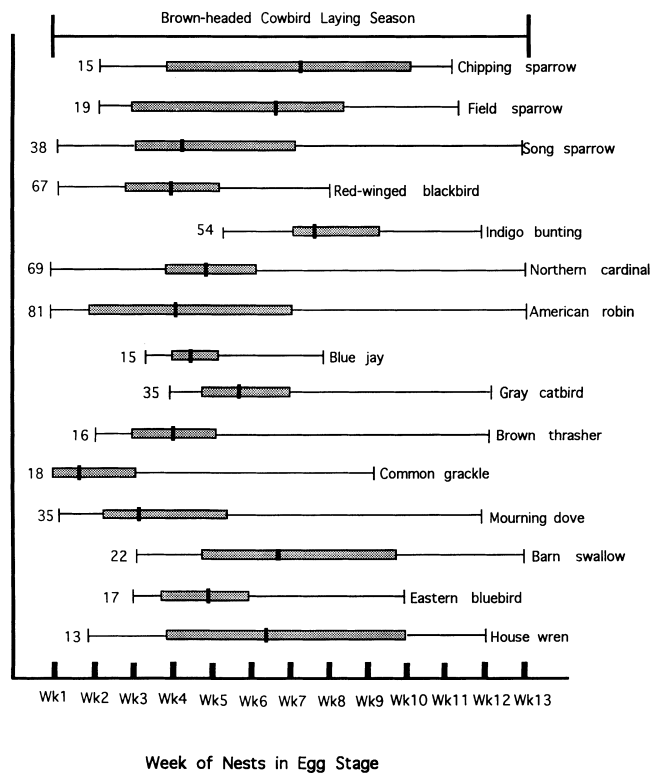


Fig. 2 Availability of nests during the 1994 and 1995 cowbird breeding seasons at the Morton Arboretum, northeastern Illinois. The cowbird breeding season extended for 12 weeks in each year, from 2 May to 17 July in 1994 and from 28 April (beginning of week 1) to 18 July in 1995, as indicated by finding fresh cowbird eggs in host nests. Only species with ≥ 15 nests are included. Availability was determined by finding nests in the egg stage or by estimating the age of nestlings based on development, then back-dating. Horizontal lines represent the range of nests in the egg stage, vertical lines represent the median date of nests in the egg-stage, and the shaded box represents the range of 25% of the nests on either side of the median. The start and end of the cowbird egg-laying season is indicated at the top. The number to the left of the bar for each species indicates the number of nests

dicated by finding fresh cowbird eggs in host nests. Data for each host species in each year are given in the Appendix. The data for the two years were combined because the composition of the breeding community and levels of parasitism were similar in each year.

Of the 34 nesting species at the study site, 27 are typically found nesting in the edge habitat, four are grassland nesters, and three are forest nesters (Appendix). No cowbird eggs or nestlings were found in 22 nests of four grassland species (bobolink, eastern meadowlark, grasshopper sparrow and dickcissel), while all nine nests of the three forest species were parasitized. Of the edge-nesting species, levels of detectable parasitism varied widely. The average intensity was 1.57 cowbird eggs per parasitized nest and the average frequency of parasitism was 32% for all nests combined. The effect of habitat-type on frequency of parasitism is significant (Table 1, $\chi^2 = 29.4$, $df = 2$, $P < 0.001$).

Using data from the edge-nesting species, we compared those with open nests to those that nested in cavities (black-capped chickadee, tree swallow, eastern bluebird, and house wren). Only one incidence of cowbird parasitism was recorded in 41 cavity nests (an eastern bluebird nest). The effect of nest type on frequency of parasitism is significant (Table 2, Fisher exact test $P < 0.001$).

We compared parasitism frequency and species body mass and found that 53 nests of two large species (≥ 100 g) with open-type nests in edge habitat were never parasitized while 39% of nests of smaller species (< 100 g) were parasitized; the difference is significant (Table 3, Fisher exact test $P < 0.001$).

The nests of smaller edge species (< 100 g) with open nests were divided into two categories using the classification suggested by Rothstein (1975), those of species that reject most of the cowbird eggs laid in their nests (8 species), and those that accept most cowbird eggs (13 species, Appendix). Of the eight rejector species, five (blue jays, eastern kingbirds, cedar waxwings, warbling vireos, and American robins) were never found to be parasitized, suggesting that they were either avoided or 100% effective in

Table 1 Observed parasitism level in different habitats

Habitat	Host nests			Cowbird eggs or nestlings	
	No. nests	No. parasitized	% Parasitized	No.	Avg. no. per parasitized nest
Forest-edge	562	182	32	286	1.57
Forest	9	9	100	13	1.44
Grassland	22	0	0	0	0
Total	593	191	32	299	1.57

Table 2 Observed parasitism levels of different nest types

Nest-type	Host nests			Cowbird eggs or nestlings	
	No. nests ^a	No. parasitized	% Parasitized	No.	Avg. no. per parasitized nest
Open	521	181	35	285	1.58
Cavity	41	1	2	1	1

^a All nests found in the forest-edge habitat

cowbird egg ejection (Sealy 1996). The nests of three rejector species were found to be parasitized at low to moderate levels; 13% (2 of 16) for brown thrashers, 11% (4 of 35) for gray catbirds, and 25% (2 of 8) for Baltimore orioles. Cowbird eggs in these nests were in advanced stages of incubation confirming that rejector species are indeed parasitized and egg ejection by these species is not always an immediate or absolute response. Frequencies of parasitism observed for these three species are minimal, since additional cowbird eggs were likely ejected before nest monitoring. As expected, significantly fewer nests of rejector species were found parasitized compared to acceptors (Table 4, Fisher exact test $P < 0.001$).

Parasitism frequency varied significantly among the remaining species ($n = 7$) with nest sample sizes ≥ 15 ($\chi^2 = 37.0$, $df = 6$, $P < 0.001$). Notably, the barn swallow was never observed to be parasitized, and was therefore not considered further. Nests of remaining species (northern cardinal, red-winged blackbird, indigo bunting, song sparrow, field sparrow and chipping sparrow) were parasitized 40–83% of the time (Table 5); differences were marginally significant ($\chi^2 = 10.9$,

$df = 5$, $P = 0.052$). Intensity of parasitism among these six species ranged from 1.3 to 1.7 cowbird eggs or nestlings per parasitized nest, however, these differences were not significant ($K = 7.77$, $df = 5$, $P = 0.17$). In 1995 nest survivorship for these six host species ranged from 3 to 11% of nests surviving. No correlation was found between nest survivorship and either the frequency ($r_s = 0.32$, $n = 6$, $P > 0.05$) or intensity of parasitism ($r_s = 0.10$, $n = 6$, $P > 0.05$). No correlation was found between the number of nests found of each of the six species and frequency ($r_s = 0.37$, $n = 6$, $P > 0.05$) or intensity of parasitism ($r_s = 0.49$, $n = 6$, $P > 0.05$).

Discussion

Our data set represents one of the most extensive community-wide studies of cowbird parasitism for a diverse avian fauna. The study site was selected for a number of reasons, primarily its variety of habitats and the number of nesting species. A large number of host nests allowed factors associated with parasitism to be tested in a hierarchical fashion. Parasitism frequencies were highly

Table 3 Observed parasitism level of hosts with different body masses

Body mass ^a	Host nests ^b			Cowbird eggs or nestlings	
	No. nests	No. parasitized	% Parasitized	No.	Avg. no. per parasitized nest
≥ 100 g	53	0	0	0	0
< 100 g	468	181	39	285	1.58

^a Based on data from Dunning (1993)

^b Only open-type nests found in the forest-edge habitat used

Table 4 Distribution of cowbird eggs in the nests of species that typically accept or reject them

Response to parasitic egg ^a	Host nests ^b			Cowbird eggs or nestlings	
	No. nests	No. parasitized	% Parasitized	No.	Avg. no. per parasitized nest
Accept	305	173	57	272	1.57
Reject	163	8	5	13	1.63

^a Classification from Rothstein (1975); Sealy (1996)

^b All nests were open-type from host species with an average body mass of < 100 g (Dunning 1993) found nesting in forest-edge habitat

Table 5 Species-specific parasitism levels of hosts^a with varying nest survival rates

Species	Nest survival rate ^b	% Nests parasitized (n)	Parasitism intensity ^c
Song sparrow	0.11 (9 losses/99.5 nest-days)	66 (38)	1.7
Red-winged blackbird	0.11 (20 losses/220.0 nest-days)	42 (67)	1.3
Indigo bunting	0.09 (21 losses/215.0 nest-days)	83 (54)	1.7
Field sparrow	0.06 (8 losses/69.5 nest-days)	53 (19)	1.3
Northern cardinal	0.03 (36 losses/248.0 nest-days)	65 (69)	1.7
Chipping sparrow	0.03 (8 losses/56.5 nest-days)	40 (15)	1.3

^a All hosts had open-type nests in the edge habitat, and had mean body masses < 100 g (Dunning 1993) and accept cowbird eggs (Rothstein 1975)

^b Probability a nest will survive 23 days

^c Average number of cowbird eggs/nestlings per parasitized nest

variable among the available host species and several ecological and behavioral factors were found to be associated with the pattern of observed cowbird parasitism while other hypothesized relationships were not validated.

Habitat effects

A significant relationship existed between type of habitat and level of parasitism, with nests in grassland remaining free of parasitism, 100% of nests in forest being parasitized and nests in the edge varying in their level of parasitism. Since the grassland species nesting here (bobolinks, eastern meadowlarks, grasshopper sparrows, and dickcisse) are not known to practice egg ejection, they must either possess other effective anti-parasitic defenses or be avoided by female cowbirds (Rothstein 1975). The ground-nesting habit of grassland species at the study site probably does not account for their absence of parasitism. At our study site, 36 of 38 song sparrow nests (an edge-nesting species) were built directly on the ground and incurred a high frequency of parasitism. Elliott (1978) found that eastern meadowlarks, grasshopper sparrows and dickcissels were all heavily parasitized at a study site in Kansas and bobolinks have reported to be parasitized elsewhere (Friedmann 1963). The differences found in our study relative to these other studies raises the possibility that female cowbirds adjust their parasitic behavior depending upon the availability of alternative host, with cowbirds preferring to parasitize species with the least effective defense behaviors. This would result in changing parasitism patterns in different host communities. In our study, nests in the grassland may have been avoided if nesting species were more effective at defense compared to species nesting in other habitats. Alternatively, cowbirds may avoid grassland species if they nest at lower densities compared to other habitats. Studies have indicated that cowbirds appear to prefer breeding habitats with high host densities (Verner and Ritter 1983; Rothstein et al. 1986). Although we did not quantify nest density, species in the grassland appeared to nest at much lower densities compared to species in other habitats.

Nest type

Protection from cowbird parasitism appears to be offered by nesting in cavities. Only one cowbird egg was found in 41 cavity-type nests, although all four cavity-nesting species at our study site have previously been shown to accept cowbird eggs (Rothstein 1975). Other studies have also found low levels of parasitism for most cavity nesters (e.g., Friedmann 1963; but see Petit 1991). Thirty-five cavity nests were in nest boxes with the same sized entrance holes and the single incidence of parasitism occurred in one of these nest boxes, suggesting that

cowbirds could enter some cavities. We also released five female cowbirds into the nest boxes and determined that they could indeed pass through the entrance holes. Cowbirds may avoid cavity nests because they represent a risk. A cowbird may not know whether a nest owner is present until after entering the cavity at which time the cowbird may risk injury, egg damage, or nest desertion (Wiley 1988; Neudorf and Sealy 1994). This may be especially likely to occur because cowbirds generally parasitize nests prior to sunrise, making nests in cavities especially difficult to monitor (Scott 1991).

Body mass

The nests of the two largest species, the common grackle and mourning dove, were never parasitized even though they accept cowbird eggs (Rothstein 1975). These species are over 2.5 times larger than female cowbirds and also lay the largest eggs (see Dunning 1993). Others have found similarly low frequencies of parasitism for these species (reviewed in Friedmann 1963). The lack of parasitism may be explained by either effective host defense or avoidance by cowbirds. The large mass and aggressive nature of the common grackle may discourage parasitism, as may its habit of nesting in colonies which may increase the effectiveness of nest defense (Friedmann 1963; Wiley and Wiley 1980). Alternatively, cowbirds may actively avoid the nests of larger species because such species are poor hosts. Cowbird eggs may not receive sufficient contact with the brood patch when incubated with larger host eggs. Further, the host's nestlings may be larger at hatching, preventing a cowbird from successfully competing for food. The mourning dove's specialized feeding mechanism may also make it a poor host. Food exchange between adult and nestling mourning doves requires special structural and behavioral adaptations which likely prevent mourning doves from raising cowbirds to independence (Friedmann 1963; Wiley 1988). A complete absence of parasitism on 53 nests of these two species suggests cowbirds are avoiding them.

Species-specific factors

Parasitism of rejector species confirms that female cowbirds do not completely avoid laying in the nests of all rejector species and suggests other cowbird eggs were likely ejected before nest monitoring. Rejector species may thus be acting as an important sink for cowbird eggs, indirectly reducing parasitism levels of acceptor species. Because cowbirds typically remove host eggs prior to parasitism, even rejector species are likely to suffer from parasitism through egg loss (Zimmerman 1983; Robinson et al. 1995; but see Weatherhead 1989). Parasitism of rejector species has been observed in other cowbird studies (Rothstein 1976; Friedmann et al. 1977; Scott 1977).

With the exception of the barn swallow and the American goldfinch, the remaining 13 species (those that nest in the edge, weigh <100 g, have open-type nests, and accept cowbird eggs) were heavily parasitized. Only one goldfinch nest was found during the cowbird breeding seasons and it did not contain a cowbird egg. The reason barn swallows were not parasitized remains unclear. Cowbirds may avoid barn swallows because they feed their fledglings in mid-air, perhaps to train them to catch flying insects (Friedmann 1929). Fledgling cowbirds may be unable to learn this behavior. Wiley (1988) found that species with unusual adult-to-chick feeding mechanisms were never parasitized by the shiny cowbird in Puerto Rico. Similarly, tree swallows have been shown to be inappropriate hosts for cowbirds (Mills 1988).

All remaining 11 species were parasitized at levels $\geq 33\%$; however, only 6 of these species were abundant enough for statistical analyses. The probability of nest survival from egg laying to fledging for these species ranged from 3 to 11% and nest losses were largely due to predation. For these six species, there was no significant correlation between nest survivorship and level of parasitism. This suggests that cowbirds are not making fine-grained assessments of host quality among acceptable hosts, or that these differences in quality are not large enough or predictable enough for fine-grained assessments (Friedmann 1963). A lack of correlation between number of nests found for a species and either frequency or intensity of parasitism suggests cowbirds are not forming search images for the most abundant hosts.

The wide variation in parasitism frequencies among these six common host species (40–83%), along with a lack of correlation with host quality, indicates that other factors may affect parasitism frequencies. One possibility is aggressive nest defense. Many host species have been shown to recognize and respond with aggression towards cowbird models placed at their nest (e.g., Robertson and Norman 1976; Smith et al. 1984; Neudorf and Sealy 1992). For example, at our study site red-winged blackbirds had a relatively low frequency of parasitism compared to the other acceptable hosts species and those nesting in more open edge habitat, or in groups, experienced especially low levels of parasitism, suggesting that red-winged blackbirds have behavioral defenses that reduce parasitism.

Factors similar to those that we found to be correlated with brown-headed cowbird parasitism patterns at our study site in Illinois have been identified as important in communities parasitized by shiny cowbirds in Puerto Rico. For example, Wiley (1985) suggested that shiny cowbirds in Puerto Rico do not parasitize hosts in proportion to their abundances and that parasitism levels may vary with habitat. An additional study by Wiley (1988) found evidence that shiny cowbirds prefer high-quality hosts with open-type nests and similarly sized eggs, although the latter result may have been a spurious correlation. Although we found no evidence for

fine-grained host preference, we did find evidence that cowbirds avoid species that are likely to be poor hosts due to their large size and/or specialized feeding mechanisms.

Model

The factors identified as influencing patterns of cowbird parasitism at our study site were used to develop a conceptual model (Fig. 1) which arranges the factors in a hierarchical fashion. Arrows indicate possible direct and indirect factors which led to the observed pattern of cowbird egg distribution. At the top is habitat; nests located in grassland habitat were not parasitized. The effect of habitat may be direct (i.e., cowbirds avoid grassland) or indirect (i.e., species nesting in grassland have effective antiparasitic behaviors). At the next level we place nest type, with cavity nests (which are only found in edge and forest habitats) nearly unparasitized. Again, the effect could be direct (i.e., cowbirds cannot enter holes) or indirect (acting through avoidance behaviors of female cowbirds). Because we have evidence that cowbirds can pass through the nest box holes at the Morton Arboretum, the latter explanation is favored. We then compared parasitism frequency with host body mass and suggest that a lack of parasitism of host species that are substantially larger than cowbirds (common grackles and mourning doves) may be the result of cowbird avoidance rather than effectiveness of nest defense. The final factors affecting parasitism levels are species-specific and may be the direct result of cowbirds' avoidance of certain species and/or the effective host defenses. Our model may only be applicable to systems where there are diverse habitats and numerous potential host species. Additional community-wide studies of cowbird parasitism will test if this model is applicable to other avian communities.

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Appendix Data on species found nesting at the study site during the 1994 and 1995 cowbird breeding seasons

Species	1994		1995		Total		Nest Type
	Parasitized (n)	Total (n)	Parasitized (n)	Total (n)	Parasitized (n)	Total (n)	
Forest-edge habitat							
House wren (<i>Troglodytes aedon</i>)	0	4	0	9	0	13	Cavity
Eastern Bluebird (<i>Sialia sialis</i>)	1	7	0	10	1	17	Cavity
Tree Swallow (<i>Tachycineta bicolor</i>)	0	3	0	3	0	6	Cavity
Black-capped chickadee (<i>Parus atricapillus</i>)	0	2	0	3	0	5	Cavity
Northern cardinal (<i>Cardinalis cardinalis</i>)	12	23	33	46	45	69	Open
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	10	26	18	41	28	67	Open
Indigo bunting (<i>Passerina cyanea</i>)	17	19	28	35	45	54	Open
Song sparrow (<i>Melospiza melodia</i>)	10	18	15	20	25	38	Open
Field sparrow (<i>Spizella pusilla</i>)	4	5	6	14	10	19	Open
Chipping sparrow (<i>Spizella passerina</i>)	3	4	3	11	6	15	Open
House finch (<i>Carpodacus mexicanus</i>)	0	0	4	6	4	6	Open
Yellow warbler (<i>Dendroica petechia</i>)	3	4	0	1	3	5	Open
Orchard oriole (<i>Icterus spurius</i>)	1	1	3	3	4	4	Open
Common yellowthroat (<i>Geothlypis trichas</i>)	1	2	0	1	1	3	Open
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	0	0	2	2	2	2	Open
American goldfinch (<i>Carduelis tristis</i>)	0	1	0	0	0	1	Open
Barn swallow (<i>Hirundo rustica</i>)	0	9	0	13	0	22	Open
Mourning dove (<i>Zenaidura macroura</i>) ^a	0	15	0	20	0	35	Open
Common grackle (<i>Quiscalus quiscula</i>) ^a	0	8	0	10	0	18	Open
Warbling vireo (<i>Vireo gilvus</i>) ^b	0	1	0	0	0	1	Open
Brown thrasher (<i>Toxostoma rufum</i>) ^c	0	5	2	11	2	16	Open
Gray catbird (<i>Dumetella carolinensis</i>) ^c	0	10	4	25	4	35	Open
Baltimore oriole (<i>Icterus galbula</i>) ^c	0	1	2	7	2	8	Open
Blue jay (<i>Cyanocitta cristata</i>) ^c	0	7	0	8	0	15	Open
Eastern kingbird (<i>Tyrannus tyrannus</i>) ^c	0	2	0	2	0	4	Open
Cedar waxwing (<i>Bombycilla cedrorum</i>) ^c	0	2	0	1	0	3	Open
American robin (<i>Turdus migratorius</i>) ^c	0	30	0	51	0	81	Open
Grassland habitat							
Bobolink (<i>Dolichonyx oryzivorus</i>)	0	2	0	5	0	7	Open
Eastern meadowlark (<i>Sturnella magna</i>)	0	1	0	5	0	6	Open
Grasshopper sparrow (<i>Ammodramus saviannarum</i>)	0	1	0	4	0	5	Open
Dickcissel (<i>Spiza americana</i>)	0	4	0	0	0	4	Open
Forest habitat							
Red-eyed vireo (<i>Vireo olivaceus</i>)	0	0	6	6	6	6	Open
Wood thrush (<i>Hylocichla mustelina</i>)	2	2	0	0	2	2	Open
Rose-breasted grosbeak (<i>Pheucticus ludovicianus</i>)	1	1	0	0	1	1	Open

^a Body mass ≥ 100 g (Dunning 1993)^b Rejector species (Sealy 1996)^c Rejector species (Rothstein 1975)

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